Guenther Witzany *Editor*

Biocommunication of Animals

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Dedicated to Karl von Frisch (1886–1982)
Nobel laureate (Decoding the Language
of the Bees)

Preface

Many biologists are not very familiar with current definitions of 'language' and 'communication' in contrast to linguistics, communication science, pragmatic action theory, and sociological theories. If we speak about (i) the three categories of signs (index, icon and symbol); (ii) the three complementary non-reducible levels of semiotic rules' syntax, pragmatics and semantics; and (iii) communication as rule-governed sign-mediated interactions, it can easily be seen that all these categories are nearly unknown in biology, especially in molecular biology, cell biology, genetics and related disciplines.

Communication is defined as the sign-mediated interaction between at least two living agents, which share a repertoire of signs (which represents a kind of natural language) that are combined (according to syntactic rules) in varying contexts (according to pragmatic rules) to transport content (according to semantic rules).

We will see that biocommunication of animals integrates the biology of rather different species with their communicative competencies, and gives a more coherent explanation and description of the full range of animal capabilities than would be possible by mechanistic or even reductionist approaches.

May 2013

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Chapter 1
Why Biocommunication of Animals?

Guenther Witzany

Abstract Current knowledge indicates communicative interactions within and between organisms in all domains, i.e. bacteria, protozoa, animals, fungi and plants as essential. Communicative interactions are necessary within organisms – intraorganismic – to coordinate cell-cell interactions, similar to tissues and organs especially in complex bodies. Interorganismic communication we find in all signal mediated interactions between species and related species (species-specific). If species communicate with non-members or in the case of symbiotic interactions we term them transorganismic communication. Throughout all kingdoms of life we do not find any coordination and organization that does not depend on communication. In contrast to biocommunication of bacteria, fungi, plants and viruses communicative interactions between animals show signs that depend on vocal and visible expression patterns. This means although also animals depend in most cases on volatile substances such as pheromones to identify group identity of self and non-self a variety of signs transport meaning via tactile behavior, vocal sounds and visual gestures. This opens a variety of combinatory possibilities and broaden the communicative competencies and its complexity exponentially in comparism to biocommunication of bacteria, fungi and plants.

1 Introduction: On the Road to the Biocommunication Concept

When we consider the biocommunication of animals, we first must become familiar with the current terms of communication (and with the signalling system, what we would term language or code, which is used to communicate).

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If we speak about language and communication we usually think of humans that talk to each other and communicate to organize common goals and to coordinate common behaviour. But since Karl von Frisch received nobel prize for detection and investigation of bee languages and dialects we noticed that even non-human social animals might communicate to reach complex behavioural patterns. Nearly the same time nobel laureate Manfred Eigen insisted in that if we speak about the genetic code we speak about a real language not just as a metaphor (Witzany 1995). Concerning these fundamental insights I developed the biocommunicative approach which investigates both, communication (1) and language (2) as universal requirements for life. The first investigation on this was published in 1993 (Witzany 1993) followed by an english translation version in 2000 (Witzany 2000). Especially the results in virology and the role of viruses in evolution and developmental processes exemplified a variety of the proposed pre-assumptions therein (Witzany 2009; Villarreal and Witzany 2010). This was outlined first as a program in 2010 (Witzany 2010) concerning bees, corals, plants, fungi, bacteria, viruses und subviral RNAs. Several more detailed exemplifications followed in a series of books I edited between 2011 and 2012 with leading researchers in their field (Witzany 2011a, 2012; Witzany and Baluska 2012a).

2 The Benefit of the Biocommunication Method

The advantage of a methodical adaptation of communication and linguistic terminology is that it provides appropriate tools for differentiation at specific levels, which is otherwise difficult to describe in non-reductive terms by pure physiology. The result of this is that language like structures and communication processes occur at the simplest levels of nature. Language and communication are not the evolutionary inventions of humans, nor are they anthropomorphic adaptations to describe nonhuman entities. It is an empirical fact that all coordination and organisation within and between cells, tissues, organs and organisms needs signs, i.e. molecules that serve as signals or symbols in messages, or serve as vital indicators of environmental conditions. Because no natural code can encode itself, in the way that no natural language can speak itself, these signs must be sensed and interpreted in the correct way by biological agents, i.e. there must be subjects of sign production and sign interpretation. The consequence of this is that sensing, as well as interpretation, may fail. This can result in inappropriate behaviour, or even be of fatal consequence, for cells, tissues, organs, and organisms.

3 The Machine Metaphor for Living Organisms Is Outdated

The method of analysing any part of a machine in detail to get a picture of the whole functional blueprint, which can then be used to reproduce or manipulate it, or to produce an even more perfect example, taking artificial genetic engineering as an example, is still useful if we are dealing with machines. In contrast communication between cells, cellular components, tissues, organs and organisms is far from being a procedure that can be reduced to mechanistic input/output or cause/reaction descriptions. It is evident that communication processes between living organisms include a variety of non-mechanistic circumstances and competences that must be fulfilled in parallel if communicative acts are to have successful consequences, for example, to innovate common coordination to adapt to new environmental conditions. Machines cannot create new programs out of a functional blueprint, which is in contrast to the abilities of living organisms that are able to communicate between each other. The universal Turing machine and the self-reproducing machines of von Neumann still remain at the conceptual stage. However, no single self-reproducing machine had ever been observed within the last 80 years. There are good reasons for this, because it is, in principle, impossible that an artificial machine could reproduce itself (Witzany and Baluska 2012b; Baluska and Witzany 2013). In contrast to the artificial machines which cannot reproduce themselves, the living cells and organisms can reproduce itself and – additionally, generate an abundance of behavioral motifs for which no algorithm can be constructed, such as de novo generation of coherent nucleotide sequences.

4 Communication and Language in Living Nature

Coherent with current knowledge about natural communication processes communication is defined as the sign-mediated interaction between at least two living agents, which share a repertoire of signs (which represents a kind of natural language) that are combined (according to syntactic rules) in varying contexts (according to pragmatic rules) to transport content (according to semantic rules). This means monological concepts such as the sender – receiver narrative cannot explain the emergence of commonly shared meanings.

Contrary to former concepts the importance of this result is that these three levels of semiotic rules (semeion = sign) are complementary parts of any natural language or code. If one level is missing, according to Charles Morris, we cannot seriously speak of language or signal mediated communication. Therefore, the most recent definition of communication is: sign-mediated and rule-governed interactions, i.e. interactions that depend on a shared repertoire of signs and rules (Witzany 2010). However, these features are lacking in abiotic interactions; no semiotic rules are necessary if water freezes to ice.

Additionally, we know that mathematical and mechanistic theories of language are less helpful in investigating natural language and real-life communication processes, because such theories cannot explain typical features of communication between living entities, which are not formal (i.e. for which no algorithm is available), such as (i) the *de novo* generation of coherent, sentences or sequences or (ii) different and even contradictory meanings of identical syntactic sequences/sentences. This means that no natural language or code speaks, or codes, itself but requires living agents that are competent in such languages or codes (Witzany 2011b).

In the biology of the twentieth century, the physiology of all manner of cells, tissues, organs and organisms, was the mainstream direction of biological research and experiments. In the 1970s, an increasing use of "communication" as a metaphor also arose in biology. During the last decade of the twentieth century, interest in communication (no longer being used as a metaphor) within, and between, organisms overtook that of the purely physiological understanding of organisms. This was due to concrete communication processes designating varying contexts in real life circumstances. Cell-to-cell communication now dominates contemporary cell biology, including knowledge of a great variety of signalling pathways, serving for both organization and coordination of production, release, uptake, interpretation and processing of context-dependent "information" (content) within and between cells. Context dependency determines the crucial fact that, it is not the syntax (grammar) of a sequence of signs (information) which determines the meaning (semantics), but the context (pragmatics) in which the concrete use of the sequence occurs.

In parallel, the use of "language" as a metaphor has increased since the middle of the twentieth century with the improved knowledge of the genetic code. Most of the processes that evolve, constitute, conserve and rearrange the genetic storage medium (DNA), are terms that were originally used in linguistics. For example: nucleic acid language, genetic code, "code without commas" (F. Crick), coding, copying, translation, transcription, "genetic text" (F. Jacob), sequence homology, etc. Meanwhile, the linguistic approach also lost its metaphorical character, and the similarity between natural languages and codes, and the genetic storage medium of DNA have not only been accepted, but have been adapted in epigenetics, comparative genomics, bioinformatics, biolinguistics, biocommunication theory and biosemiotics.

5 Communicative and Linguistic Competencies, or: The Primacy of Pragmatics

Firstly, no single organism is able to communicate as an emerging property; it must be part of a community, society or swarm of organisms that share an identity and have a competence to sense whether others are part of this identity or not (self/non-self differentiation competence), even if this competence is solely shared genetically. To communicate it is necessary that organisms have assets that serve as signs, signals or symbols, such as chemical molecules, either produced directly by the organism, or as secondary metabolites, or even molecules in the surroundings, but which can be manipulated according to the organisms needs. In the case of animals, especially complex ones, visible and audible sign repertoires evolved.

Secondly, organisms must also share a competence to use these signs in a coherent manner, which means using these signs in a strict temporal and spatial context. In most cases it is not just one sign, but several, that are combined in a specific manner to transport messages or information. This represents a common feature of sign use in communication processes, and is termed the correct combination or syntax.

Thirdly, organisms are part of the natural habitat in which they live, together with similar organisms of the same or related species, but usually also with an abundance of unrelated organisms. This historically developed context exactly represents the natural history of the swarms or communities in the way that they have evolved certain abilities and are able to mount appropriate response behaviours to enable their survival. These competencies, which include sensing, monitoring, learning and memory, are preconditions for faster adaptation.

Finally, the signalling molecules, which serve as signs, transport messages with meanings (semantics). The informational (semantic) content which is transported, triggers certain response behaviours in the same, related, or even unrelated, organisms. Interestingly, the signal sequence or content does not necessarily depict a strict meaning, i.e. a function, but can vary according to different situational contexts. This means that identical signs can transport a variety of different messages according to different contextual needs. The different uses of identical signs, or sequences, enable the generation of dialects within the same species that can transport messages which are micro-ecosphere specific. This includes a very sensitive self/non-self recognition between slightly differently adapted populations of the same species in the same ecological habitat.

Although sign-mediated interactions (i.e. communication processes) are very reliable in most cases, they do not function mechanistically in a strict sense. Syntax (combination), pragmatics (context) and semantics (content) must function in parallel to ensure and optimize coordination, and thus survival of group members.

These three levels of semiotic rules (syntax, pragmatics and semantics) do not function mechanistically but can be varied, deleted, or, in certain circumstances, and in contrast to the capabilities of machines, generated *de novo*. Additionally, semiotic rules do not function by themselves but need semiotic subjects, i.e. living organisms that utilise such rules. If no living organism is present, semiotic rules, signs and communication are absent. Although highly conserved semiotic rules are modifiable, environmental circumstances, such as stress, can trigger adaptive responses. In such cases, signals may transport new messages which previously did not exist, broadening the communicative competences of organisms, i.e. broadening their evolutionary capabilities.

Natural communication assembles the full range of signal mediated interactions that are necessary in order to organise all evolutionary, and developmental coordination within, and between, cells, tissues, organs and organisms.

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Chapter 2
Signs of Communication in Chimpanzees

Mary Lee A. Jensvold, Lisa Wilding, and Savannah M. Schulze

Abstract Chimpanzees communicate with facial expressions, vocalizations, postures, and gestures. Vocalizations are of many types for both close and distance communication. Identity of individuals and groups is apparent in vocalizations. Vocalizations occur in specific contexts and there is evidence that some carry referential meaning. Gestures occur in a variety of modalities and chimpanzees vary the modality appropriately with the attentional state of the partner. Communities of chimpanzees have specific repertoires of gestures and the same gesture among communities varies in form. In cross-fostering research chimpanzees acquired American Sign Language. One young chimpanzee acquired signs from his mother and other signing chimpanzees. In a remote videotaping procedure the chimpanzees signed to each other using a variety of signs in a variety of contexts. Other studies have examined chimpanzee communication using artificial languages. Chimpanzee communication shows flexibility as partners navigate through interactions and gestures are acquired through social learning.

1 Introduction

Chimpanzees are in the order of primates. Organisms in this order tend to be social, live in groups and have parallel adaptations in physiology and behavior to facilitate communication. This includes hairless faces with many muscles and high visual acuity. Chimpanzees communicate using vocalizations, facial expressions, postures, and gestures (Goodall 1986). They live in groups of 20–100's of individuals with fluid

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subgroupings. Community members have complex and long lasting relationships characterized by close communication such as during grooming bouts, as well as long distance communication between members at separate locations.

2 Facial Expressions

Like humans, chimpanzees possess a variety of facial expressions that contribute to the overall meaning or message (Parr 2004). Humans and chimpanzees share similar facial anatomy and similarities between the two species in emotional expression occur indicating that facial expressions are an important avenue for chimpanzee communication. Using a ChimpFACS coding system researchers found more than 250 facial expressions in chimpanzees. (Burrows et al. 2006; Parr et al. 2007). Chimpanzee facial expressions are tied closely to vocalizations but can be produced both in their absence and in combination with them.

3 Postures

Chimpanzees use a variety of postures, which communicate information about the signaler (Goodall 1986; McCarthy et al. 2012). For example a bipedal posture occurs in a highly aroused chimpanzee. It is often accompanied by pilo erect hair, also a sign of high arousal. A submissive chimpanzee displays a crouching posture. Chimpanzees present body parts to other chimpanzees to solicit grooming. The presents also are postures.

4 Vocalizations

Acoustic communication is closely adapted to environmental conditions and the function of the signal. Low-frequency vocalizations are required in dense vegetation and other sounds must be able to travel over long distances. Chimpanzee vocalizations are no exception.

Vocalizations are necessary for long distance communication. Geographic ranges of chimpanzee communities can cover large distances such as 25 km^2 (Lehmann and Boesch 2002) so members may be separate and traveling alone. Although, as social beings chimpanzees often travel together in subgroups. Vocalizations are a way to maintain contact with community members over long distances and they also occur in behavioral contexts with close proximity, such as play and grooming. A calm chimpanzee is very quiet, yet in times of emotional arousal a chimpanzee can be quite loud. Overall chimpanzees spend proportionally much of their time in silence, unlike a bird.

Chimpanzees produce many types of vocalizations which include pant hoots, screams, barks, grunts, pants, whimpers, squeaks, cough grunts, and laughter and mouth sounds (see Goodall 1986; Slocombe and Zuberbühler 2010 for review). Some vocalizations are loud reaching all community members while others are quiet and only reach members in the subgroup.

Pant grunts are a series of submissive noisy grunts joined together by voiced inhaled elements (Crockford and Boesch 2005; Goodall 1986). A subordinate when approaching or approached by a higher-ranking individual produces pant grunts. Pant grunts help to maintain friendly relations between members of the community. Greetings between friendly individuals will result in a soft pant grunt; however, if the subordinate is apprehensive, the pant grunt is louder matching the level of apprehension.

The hoo is a distinctive part of a whimpering sequence (Crockford and Boesch 2005). Produced by both infant and mother when physical contact needs to be re-established, the chimpanzee repeats the hoo several times. An adult also produces a hoo vocalization, often with pouted lips, when begging for food or grooming. If this vocalization occurs in rapid succession, rising and falling in pitch, it grades into a whimper (Goodall 1986).

The whimper, most commonly occurs in infants, reflects distress and need; however, whimpering can also occur in subordinate, older individuals when refused food by a higher-ranking individual. Whimpers can grade into screams (Crockford and Boesch 2005; Goodall 1986; Slocombe and Zuberbühler 2010).

In response to threats subordinates will produce a short, shrill squeak (Crockford and Boesch 2005). As fear increases, squeaks can grade into screams, which again grade back to squeaks when the subordinate becomes less agitated (Goodall 1986).

Chimpanzee laughter is a soft, repetitive, breathy, guttural sound of low intensity produced through repetitive sequences of air being drawn into the lungs and then exhaled (Ruch and Ekman 2001). Laughing occurs more often in infants and juveniles and results most frequently during tickling encounters, but also in other physical contact play, such as wrestling or play biting (Vettin and Todt 2005; Slocombe and Zuberbühler 2010).

Panting consists of rapid, shallow breathing, and occurs during greeting, groom, and feeding excitement. Typically, an open mouth presses against the body or face of the partner. Copulation pants can be mistaken for laughing; however, a sound spectrograph analysis reveals that not only are copulation pants more rapid, but it lacks the voiced inhalation phase of laughter (Goodall 1986; Slocombe and Zuberbühler 2010).

Chimpanzees produce a variety of grunt vocalizations. Community members use soft grunts when traveling or foraging together. The extended grunt occurs during rest sessions. The nest grunt is produced when an individual is looking for a suitable nest area, making a nest, or settling down for the night. Soft food grunts occur during the first minutes of feeding on a highly desired food item (Goodall 1986; Slocombe and Zuberbühler 2010).

The huu vocalization is an alarm call and occurs in situations of surprise, slight anxiety, or puzzlement. Small snakes and unknown sources of sounds can elicit the huu vocalization, even when the chimpanzee is alone (Slocombe and Zuberbühler 2010). Sounding much like the hoo vocalization, the huu does not have the characteristic pouting lips (Goodall 1986).

Chimpanzees make loud sounds that are audible over long distances. Of these pant hoots are the most studied. Chimpanzees pant hoot most often in the morning and overall pant hoots increase with a rise in the numbers of males per party, and high ranking males call more often than low-ranking males (Wilson et al. 2007). Pant hoots occur when arriving at a new food source, when two parties meet, during travel, after returning from patrolling the territorial boundaries, during social excitement, spontaneously during feeding, and at night during nesting (Slocombe and Zuberbühler 2010).

High pitched, loud screams, emitted most often in a series occur when an individual is highly stressed, fearful, frustrated, or excited (Crockford and Boesch 2005; Goodall 1986). Screams travel long distances and may serve to solicit help from other members of the community to troubled individual. Screams occur in three subtypes: victim scream, tantrum scream, and copulation scream. The victim scream, produced when the caller is attacked, is harsh and prolonged and is accompanied by the sounds of the actual beating (i.e., hitting and stamping sounds). Infants rejected during weaning or adults indecisive if they should retaliate after an attack, emit a tantrum scream. Females emit a copulation scream during mating, which consists of a clear, high pitched sound of variable length (Goodall 1986).

Barks, usually produced in long sequences, are loud and sharp, varying in pitch. Waa barks are loud and are produced by participants or observers of agonistic encounters. After an attack, the victim's screams will change to waa barks, if he receives support from allies. A soft bark or cough threat is a grunt made with a slightly open mouth by a high ranked individual to a low ranked individual, serving as a mild warning to not approach or to prevent an unwanted action (Goodall 1986). Alarm calls, consisting of a long drawn-out wraa occur when a chimpanzee encounters a potential dangerous animal or abnormal behavior in a community member. Wraa serves as a distant call, alerting other members of danger, and also to intimidate the dangerous intruder (Goodall 1986).

When approaching a desirable food source or feeding, large parties of chimpanzees emit pant hoots, barks, grunts, and a loud, high pitched sound called the loud aaa (Crockford and Boesch 2005; Goodall 1986). The loud aaa occurs only in the context of feeding and most commonly by males.

5 Other Sounds

Chimpanzees produce other sounds that are not vocalizations since there is no voicing. Captive chimpanzees produce unique sounds such as bronx cheers, lipsmacks, and pants in interactions with humans (Hopkins et al. 2007; Bodamer and Gardner 2002). Free-living males drum tree buttresses, which is audible up to 1 km and is often accompanied by pant hoots. Chimpanzees will use this when traveling in large mixed-sex parties. In the Tai Forest, Ivory Coast drumming indicates differences in travel direction and resting periods (Boesch 1991). Differences in patterning of drumming occur between communities of chimpanzees (Arcadia et al. 2004) and between individuals within a community (Arcadia et al. 1998).

6 Individual and Community Differences

Vocalizations provide information about the vocalizer and community. Individual identity is apparent to listeners and appears in spectrograph analysis (Marler and Hobbett 1975). In a captive experiments chimpanzees recognized other individuals by hearing pant hoots (Kojima et al. 2003). In the field arrival pant hoots contain information about the status of the signaler in the hierarchy (Clark and Wrangham 1993). Screams indicate whether the signaler is the victim or aggressor in a conflict (Slocombe and Zuberbühler 2005a). In a playback experiment researchers (Herbinger et al. 2009) played recordings of pant hoots from chimpanzees in the neighboring community, a distant community from 70 km away, and community members. The listening chimpanzees pant hooted in response to the pant hoots of neighbors, but screamed in response to pant hoots of strange chimpanzees. They responded the least to pant hoots of community members.

Members of a free-living community have pant hoots more like each other than those of neighboring communities and this difference is not explained by genetic similarities (Crockford et al. 2004). This is supported by a captive finding in which there were differences between the pant hoots of two groups (Marshall et al. 1999). These findings suggest that communities of chimpanzees have vocal dialects (Slocombe and Zuberbühler 2010).

7 Meaning in Vocalization

Do vocalizations portray the signaler's internal state or information about external events? Seyfarth and Cheney (2003 for review) developed a playback method in which they played recordings of alarm calls, which are acoustically distinct, to vervet monkeys. Monkeys gave specific responses to specific types of calls. For example when monkeys heard the eagle alarm call they looked up and ran for cover. When monkeys heard the snake alarm call they stood bipedally and looked around. These experiments provided strong evidence that vervet monkey alarm calls contained referential information; they contained information about the specific type of predator. The playback technique now has been used with numerous species, including chimpanzees (Slocombe and Zuberbühler 2005b).

Some chimpanzee vocalizations show acoustical variation and occur in specific situations. Pant hoots provide information about the quantity of food. Additionally pant hoots vary depending up the chimpanzees' activities such as arrival at a food source versus traveling (Notman and Rendall 2005). Barks vary as a function of the context; hunting snakes versus the presence of a snake. When chimpanzees combined these barks with other behaviors, their specificity increased (Crockford and Boesch 2003). Although these two studies found acoustical differences, they do not include the playback component that confirms if listeners perceive the differences in vocalization and use the information within them to gain information from the environment.

In playback experiments with captive chimpanzees (Slocombe and Zuberbühler 2005b), vocalizations carried information about food value. Highly valued foods were ones that the chimpanzees preferred. Also vocalizations carried information about food type; they were specific and consistent to bread and bananas. In another experiment, one chimpanzee used vocalizations to gain information about the location of food.

8 Gestures

Gestures are “discrete, non-locomotor limb and head movements, regardless of the receptive sensory modality (sight, sound, touch) that occurred when [chimpanzees] were in proximity and engaged in social interaction immediately before, after, or during the movements” (Tanner and Byrne 1999, p. 216). Some researchers include intentionality in definitions of gestures. Intentionality includes checking the partner. For example the signaler must look at the recipient or wait for a response from the recipient (Hobaiter and Byrne 2011; Pika and Mitani 2006). Gestures occur in one or more of three communicative modalities: visual, auditory, and tactile (Goodall 1986). Thus some gestures make sounds such as a handclap, some are silent such as an arm wave, and some involve contact between two individuals such as a tap.

Tomasello et al. (1994) created a comprehensive ethogram of captive chimpanzee gestures. They recorded 259 occurrences of gestures in captive juvenile chimpanzees. Two gesture combinations occurred in 90 instances and three gesture combinations occurred in 11 instances. Hobaiter and Byrne (2011) reported that a free-living group of chimpanzees in Budongo, Uganda used 4,397 instances of gestures in 120 h of video footage. There were 66 distinct gesture types which occurred in a broad range of behavioral contexts.

Gestures are used from an early age and develop over time into a reliable communication system in chimpanzees and other ape species as well. Social gestures such as begging are present in infant chimpanzees between the ages of 9 and 12½ months. Following the use of the begging gestures infants begin to use other gestures to initiate tickling or grooming sessions (Plooij 1984). The grooming handclasp is a gesture used in grooming interactions. It appears at about 4 years of age with mothers molding the gestures. As juveniles develop they begin to use the gesture with other members of the community (Nakamura and Nishida 2013). This shows evidence for social learning of gestures.

If gestures are learned through social processes, there should be differences between the gestural repertoire of various communities. In a seminal study researchers working at nine different long-term chimpanzee field sites collaborated and developed a list of 65 behavior patterns (Whiten et al. 1999). The behaviors were classified in terms of their local frequency of occurrence. There were 39 behaviors including gestures that the researchers determined were cultural variants since they were absent in some communities and customary or habitual in others. It included gestures such as leaf clipping, rain dance, knuckle knock, and grooming hand-clasp.

The grooming hand-clasp gesture is when grooming partners hold each others' hand and groom with the other hand. The hand-clasp occurs customarily in some communities of chimpanzees such as Kalinzu and Kibale in Uganda, and Lope in Gabon and is absent or rarely seen in others (Nakamura 2002). There are differences in the use of the hand-clasp among chimpanzees in western Tanzania. The Kasoge chimpanzees use this gesture however it is absent in the nearby Gombe chimpanzees (McGrew and Tutin 1978). In Gombe grooming partners instead grasp an overhead branch. Among the communities within Mahale there is variation in form of the hand-clasp. The M group uses a form in which partners' palms face each other. The K group uses this palm-to-palm form in addition to a non-palm-to-palm form, which involves support at the wrist (McGrew et al. 2001). Chimpanzees at Chimpfunshi, an African sanctuary, used varying forms of the hand-clasp which were specific to their group. Of the four groups, two never used the hand-clasp, and one used palm-to-palm (Van Leeuwen et al. 2012). De Waal and Seres (1997) reported the propagation of the hand-clasp as new social custom in a group of 20 captive chimpanzees. The gesture originated from a single female individual and she initiated the use of the hand-clasp mostly with immediate adult kin spreading it to other individuals. This body of evidence strongly suggests that gestures are socially transmitted.

During interactions, for communication to be successful partners must make adjustments to each other or the audience. Free-living chimpanzees attenuate vocalizations in response to the audience. For example chimpanzees pant grunt in greeting and individuals only produce it in interactions with higher ranking individuals. Females produced more pant grunts to other individuals when the alpha male was absent (Laporte and Zuberbühler 2010). Free-living chimpanzees were more likely to emit an alarm call in the presence of others who were unaware of the predator than those who were aware (Crockford et al. 2012). Females were less likely to produce a copulation call in the presence of a higher ranking female (Townsend and Zuberbühler 2009). During attacks victims changed the acoustic structure of screams based on the ranking of bystanders in relation to the aggressor (Slocombe and Zuberbühler 2007). This variation in vocalizations in relation to the composition of the audience shows flexibility in the production of sounds. Although, chimpanzees show vast more flexibility in the use of gestures.

Several experiments show that captive chimpanzees adjust sounds and gestures depending upon the state of the partner. In captive settings chimpanzees used mouth sounds such as bronx cheers or produced noise such as cage banging or handclap when human caregivers had their back turned. Then chimpanzees made gestures (Hostetter et al. 2001; Leavens et al. 2004) such as points or signs of ASL (Bodamer and Gardner 2002) when caregivers turned to face them. In interactions with conspecifics chimpanzees were less likely to use a visual gesture if the partner was inattentive. When partners failed to respond, a chimpanzee was more likely to persist with a subsequent gesture (McCarthy et al. 2012; Liebel et al. 2004; Roberts et al. 2012a).

Like vocalizations, gestures themselves carry referential meaning. Roberts et al. (2012b) found that within the same group of chimpanzees reported above, individuals were able to understand the meaning of gestures even when they were not associated with a context. Recipient's responses depended upon the particular gesture even when it occurred outside of its usual context. These findings are supported by sign language studies with chimpanzees in which chimpanzees acquired human gestures of American Sign Language (ASL).

Ethologists use the procedure called cross-fostering to study the interaction between environmental and genetic factors by having parents of one species rear the young of a different species. Primate cross-fostering projects date to the 1930s, when Kellog and Kellog (Kellog 1968) raised the infant chimpanzee Gua for a period of 9 months with their son. In the 1950s, Hayes and Hayes (Hayes and Nissen 1971) cross-fostered the chimpanzee Viki while attempting to teach her to talk. After 4 years she was able to say four words, "mama", "papa", "cup", and "up". This research demonstrated that chimpanzees cannot speak, leading to the search for other means of testing the language and other cognitive abilities of apes.

Gardner and Gardner (Gardner et al. 1989) cross-fostered the infant chimpanzee Washoe and immersed her in ASL. In teaching ASL to Washoe, caregivers imitated human parents teaching human children in human homes. For example, they called attention to objects, expanded on fragmentary utterances, and molded Washoe's hands into the shape of new signs. In a second project, the Gardners' cross-fostered four more chimpanzees, Moja, Pili, Tatu, and Dar. All of these cross-fosterlings acquired and used signs in ways that paralleled human children. The size of their vocabularies, appropriate use of sentence constituents, number of utterances, proportion of phrases, and inflection all grew robustly throughout the 5-year cross-fostering process.

In 1979 at the University of Oklahoma Washoe adopted a 10-month-old chimpanzee son, Loulis. Human signing was restricted in Loulis' presence to test whether he would learn ASL from other chimpanzees rather than from humans. Loulis began to sign in 1 week, and at 73 months of age had a vocabulary of 51 signs (Fouts et al. 1989). As adults Washoe, Loulis, Dar, Tatu and Moja signed to each other and to themselves (Bodamer et al. 1994). They initiated conversations (Bodamer and Gardner 2002) and maintained topics with humans. When human interlocutors feigned a misunderstanding, the chimpanzees adjusted their responses appropriately (Jensvold and Gardner 2000; Leitten et al. 2012). The chimpanzees' patterns of conversation with human caregivers resemble patterns of conversation found in similar studies of human children.

In August 1983 during a 15-day period video cameras remotely recorded the chimpanzees with no humans present. Every day during the study period the video

Table 2.1 Frequency of Chimpanzee-to-Chimpanzee signed interactions

	Initiator						
		Washoe	Moja	Tatu	Dar	Loulis	Total
Receiver	Washoe	–	7	21	8	12	48
	Moja	1	–	0	2	3	6
	Tatu	0	0	–	6	12	18
	Dar	0	1	1	–	27	29
	Loulis	0	7	28	53	–	88
	Total	1	15	50	69	54	

cameras were recorded for two 20-min periods between the hours of 9:00 a.m. and 5:00 p.m. Forty-five recording periods were scheduled so that each hour of the day was sampled randomly without replacement either five or six times. Loulis initiated 451 interactions, both signed and non-signed, with the other chimpanzees. Forty percent (181) of those interactions were directed to his male peer, Dar. Loulis used 206 signs in his interactions and 114 of those were directed toward Dar (Fouts 1994).

For each signed utterance on the videotapes the observer recorded the context, the initiator of the sign, the recipient of the sign, the sign gloss and the description of its form, and the number of times signs occurred within the utterance. From this record we now report the other chimpanzee-to-chimpanzee signs on the videotapes. Washoe, Moja, Tatu and Dar initiated 134 chimpanzee to chimpanzee interactions. Table 2.1 shows the frequency that each chimpanzee initiated a signed interaction. The data for Loulis is from Fouts et al. (1989, Table 9.2). The chimpanzee initiated 188 signed interactions. The total for receivers is 189 because Dar directed one interaction to both Loulis and Tatu. Loulis initiated the most interactions and Washoe initiated the least. Dar received the most interactions and Moja received the least. Dar and Loulis were the most frequent dyad with 167 signed interactions and Loulis and Tatu were the second most frequent dyad with 76 signed interactions. Most of the interactions occurred in the Affinitive Social (33 %) and Play (38 %) contexts.

Table 2.2 shows the variety of signs that were used by Washoe, Moja, Tatu, Dar and Loulis. The data for Loulis is from Fouts (1994, Table 3). The chimpanzees used 36 different signs and there were 369 chimpanzee to chimpanzee signs on the videotapes. The chimpanzees also combined signs. For example on 7/31/83 at 14:11:30 Dar hung above Loulis and signed to him FRIEND MORE CHASE MORE. Loulis then played with Dar.

Cianelli and Fouts (1998) found that the chimpanzees often used emphatically signed ASL signs during high arousal interactions such as fights and active play. For example, after separating Dar and Loulis during a fight and with all the chimpanzees still screaming, Washoe signed COME HUG to Loulis. He signed NO and continued to move away from her. The signs were recorded as emphatic because they were large. Emphasis occurs by making signs larger or faster just as emphasis in speech is loud or more rapid speech. These results indicate that the chimpanzees' signing is very robust indeed and is a regular part of interactions.

Table 2.2 Signs used in Chimpanzee-to-Chimpanzee interactions

Sign	Frequency
Ball	2
Blanket	1
Brush	3
Can‘t	1
Catch	2
Chase	5
Clean	1
Come	29
Dar	3
Drink	7
Eat	1
Food	9
Friend	1
Gimme	3
Go	1
Good	14
Groom	11
Gum	3
Hat	1
Hug	3
Hurry	155
Me/Mine	17
More	10
Out	5
Peekaboo	5
Person	3
Pretty	1
Shoe	3
Tatu	3
That	4
Tickle	42
Time	2
Toothbrush	1
Want	4
Washoe	5
You	8

Terrace et al. (1979) claimed to have replicated the Gardners’ cross-fostering project with a chimpanzee named Nim. The young chimpanzee spent 6 h each day in a classroom while a string of teachers drilled him with questions and demands for signing. If he wanted something, the teachers withheld it until he named it. Terrace found that Nim made few spontaneous utterances and often interrupted his teachers. This procedure differed greatly from the Gardners’ cross-fostering project, in which the young chimpanzees were treated like human children. Terrace’s failure to create a comparable environment for language acquisition led to Nim’s failures. Later studies showed Nim made more spontaneous utterances and interrupted less in a conversational setting than in a drill setting (O’Sullivan and Yeager 1989).

9 Artificial Communication

In the 1970s the Gardners' research sparked research using artificial systems to examine grammatical skills in chimpanzees. Premack used plastic tokens which varied in shape and color to represent words. The chimpanzee Sarah learned rules for their order and used them to answer simple questions about attributes of objects (Premack and Premack 1983). Rumbaugh tested a chimpanzee's grammatical ability using Yerkish, a system of individual symbols (known as lexigrams) each representing a word, and rules for their ordering. Lana used lexigrams to generate sentences to ask for goods and services. Later Savage-Rumbaugh attempted to train a bonobo, Matata, to use lexigrams. While Matata failed to use the lexigrams, her infant son, Kanzi, who was present during training, did use them (Hillix and Rumbaugh 2004). Devoid of face-to-face interaction, these artificial systems reveal little about conversational behavior, but they do demonstrate apes' capacities to use syntax.

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Chapter 3
African and Asian Elephant Vocal Communication: A Cross-Species Comparison

Angela S. Stoeger and Shermin de Silva

Abstract Although living in substantially different habitats, African (*Loxodonta* sp.) and Asian (*Elephas maximus*) elephants are extremely social and intra-specific communication is therefore highly developed in these species. In particular, elephants are very vocal and acoustic signals play an integral part within the society of African and Asian elephants. In this chapter, we provide a cross-species comparison of the African savannah elephant (L. africana) and Asian elephant vocal communication systems, discussing the acoustic structure of various call types, examples of vocal imitation and sound production mechanisms. We aim to explore what the similarities and differences in the communication system of the two species could reveal about call functions, and the ecological conditions that have shaped these communication systems. In light of this, we suggest future comparative investigations of African and Asian elephants that may provide deeper insights into the evolutionary and cognitive bases of the complex signalling mechanisms.

1 Introduction

The African (*Loxodonta africana* and *Loxodonta cyclotis*) and the Asian (*Elephas maximus*) elephants, comprise the last survivors of the Elephantidae, a once numerous sub-group of the order Proboscidea (Shoshani 1998). Most recent research results

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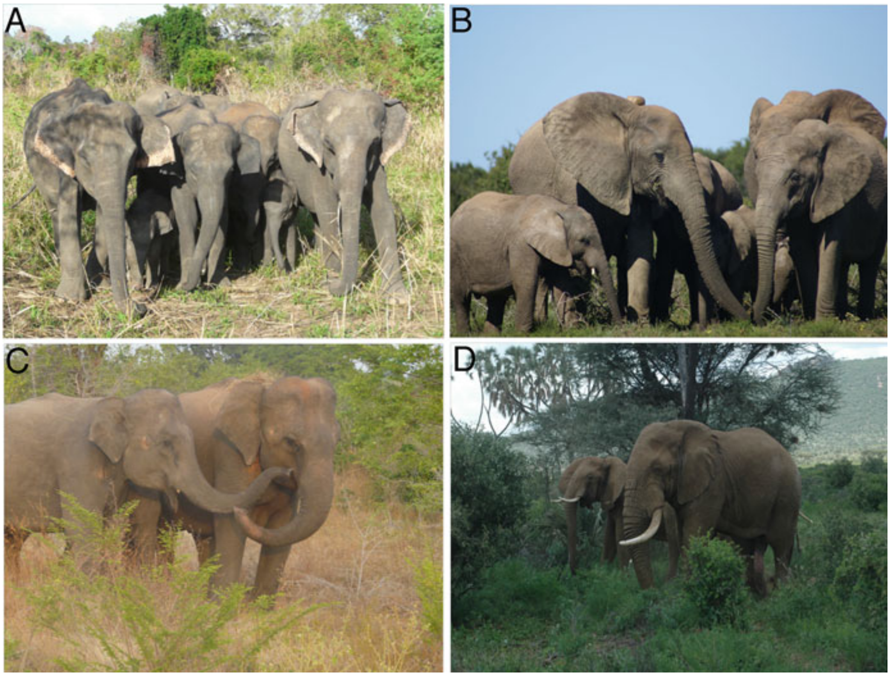

Fig. 3.1 Asian and African savannah elephants. Family group of *Elephas maximus* (**a**) and *Loxodonta africana* (**b**). Figure (**c** and **d**) show social interactions in elephants which are often accompanied by vocalizations: (**c**) shows two Asian elephants touching and smelling each other with their trunks, a behavior often accompanied by soft growls or rumbles, and (**d**) shows a female African elephant (*in the back*) uttering a rumble in response to the bull next to her

using mitochondrial DNA suggest that the ancestors of African elephants diverged from the lineage leading to mammoths and Asian elephants ~6–8 million years ago (Krause et al. 2006; Rogaev et al. 2006; Rohland et al. 2007). Although they live in substantially different habitats today, the representatives of each elephant species are all very social (de Silva and Wittemyer 2012; Douglas-Hamilton 1972; Fishlock and Lee 2013; Moss 1983; Turkalo 2001) and intra-specific communication is therefore highly developed (Fig. 3.1). Elephants make use of defined and versatile visual, tactile, olfactory, seismic and acoustic cues to communicate with their conspecifics. In particular, elephants are highly vocal, and acoustic signals play an integral part within the society of African and Asian elephants.

Despite early descriptions of acoustic signals produced by the Asian elephant (McKay 1973; Payne et al. 1986) to a large extent research on elephant vocal communication has been conducted on the African savannah elephant (for a detailed review see Soltis 2010). In this chapter we offer a cross-species comparison of African savannah and Asian elephant vocal communication based on existing literature and personal research experiences, discussing sound production, acoustic structure, and behavioral contexts. Rather than providing a comprehensive review, our aim is to explore what the similarities and differences could reveal about call functions, and the ecological conditions that have shaped these communication systems. Because terminology across species and authors is not always consistent, we discuss only general classes of signals that are acoustically well-supported, and attempt to disambiguate whenever possible. We further discuss the examples of vocal mimicry common to both elephant species, providing strong evidence for the capability of vocal learning. We exclude infant and juvenile vocalizations because their acoustic features cannot be always directly classified in categories similar to those of adult vocalizations and often vary in function (Stoeger-Horwath et al. 2007; Herler and Stoeger 2012). While modification of infant vocalizations with age may take place simply due to physical changes, the discovery that elephants are capable of vocal learning begs the question of whether vocal learning may in fact be developmentally critical in the acquisition of an adult repertoire. Focusing on adult vocalizations, we conclude with some reflections on why these signals may have evolved within their particular contexts and suggest future comparative investigations of African and Asian elephants that may provide deeper insights into the ecological, evolutionary, and cognitive bases of the complex signaling mechanisms.

2 Vocalization Types and Contexts

Elephant acoustic signals can be broadly classified along two general dimensions: frequency range, and the presence/absence of harmonics (periodicity). High frequency harmonic signals include *trumpets*, *squeals* and *squeaks* (cf. chirps: McKay 1973; Poole et al. 2005; Nair et al. 2009) while low frequency signals include *growls* and *rumbles* (Berg 1983; McKay 1973; Payne et al. 1986; Poole et al. 1988). By definition, these are periodic sounds, although the harmonic structure of trumpets and squeaks is coarse. In contrast variants of *barks* and *roars* tend to be predominantly a-periodic or chaotic sounds, though they may contain tonal regions at onset or toward the latter half. Several graded variants of these broad call types or combinations of multiple call types also occur, such as *roar-rumbles* (de Silva 2010; Poole 2011). A-typical sounds that do not resemble any of these general categories also appear, but more infrequently. Here we present the broad categories and contexts, for which contextual observations and acoustic attributes are sufficiently well-supported, summarized in Table 3.1.

2.1 Growls and Rumbles

Growls and rumbles constitute the lowest frequency vocalizations produced by elephants, for which the fundamental frequency is typically infrasonic (<20 Hz). The term *growl* was used to describe low-frequency vocalizations in both African and Asian elephants (Berg 1983; McKay 1973), however the term has fallen out of use

Table 3.1 The broad categories and contexts for which contextual observations and acoustic attributes are sufficiently well-supported

Signal	*L. africana*	*E. maximus*
Growl/nasal rumble	X[2, 12]	X[1,10]
Rumble variants	X[2,4,6,7,8]	X[1,3,9,10]
Bark	X[2,]	X[10]
Roar	X[2,4,6]	X[1,9,10]
Long roar/bellow/scream	X[4]	X[1,10]
Combinations of bark/roar/long roar and rumble/growl	X[11]	X[10]
Squeak/chirp		X[1,9,10]
Squeal/chirp		X[10]
Trumpet	X[2,6]	X[1,9,10]
Nasal trumpet (play trumpet?)	X[11]	
Musth chirp-rumble		X[10]

[1] McKay (1973) – n.b. ‘long roar’ and ‘roar’ are not distinguished
[2] Berg (1983)
[3] Payne et al. (1986)
[4] Poole et al. (1988)
[5] Langbauer (2000)
[6] Leong et al. (2003)
[7] Soltis et al. (2005a, b)
[8] Wood et al. (2005)
[9] Nair et al. (2009) – n.b. ‘long roar’ and ‘roar’ are not distinguished
[10] de Silva (2010)
[11] Poole (2011)
[12] Stoeger et al. (2012a)

in more recent literature. Following Poole et al. (1988) low-frequency vocalizations in *Loxodonta* are generally termed *rumbles.* Because of these discrepancies, we discuss these classes of low frequency vocalizations separately for the two genera and then offer some interpretations.

2.1.1 Elephas

In Asian elephants, the terms *growl* (McKay 1973) and *rumble* (Payne et al. 1986) have both been used to describe low-frequency acoustic signals. Subsequently, de Silva (2010) distinguishes two call types on the basis of visual and acoustic cues. When growling, the only visual cue the vocalizer exhibits is depressed cheeks; the mouth is nearly closed and the posture is generally very still. Rumbles are accompanied by more obvious visual cues such as an open mouth, and sometimes up-tilted head. Growls tend to have lower and flatter fundamental frequency contours than rumbles, while lacking any energy above 500 Hz (de Silva 2010). Growls produced by Asian elephants generally sound softer to human ears than rumbles (McKay 1973, de Silva personal observations), thus the audible calls described by Payne et al. (1986) as ‘low soft rumbles’ might correspond to those termed growls by McKay & de Silva. Growls have been documented in wild populations of elephants in southern Sri Lanka (de Silva 2010; McKay 1973). Other populations of *E. maximus* also produce growls (e.g. peninsular Malaysia and Borneo, de Silva personal observations), thus it is likely to be a widespread call type.

Growls constitute over 60 % of the recordings made in southern Sri Lanka and are individually distinctive (de Silva 2010). Adult males produce these vocalizations rarely. Growls are produced in numerous behavioral contexts, including social encounters, movement and alarm. Where occurring in conjunction with threat displays and disturbance, growls usually follow the initial display and appear to be targeted at conspecifics rather than at the source of disturbance. Growls are therefore likely to be multi-functional socially-oriented vocalizations.

Rumbles occur in contexts similar to growls (de Silva 2010; Nair et al. 2009). They tend to be accompanied by more animated behavior, such as rapidly flapping ears and widened eyes, which suggest a greater degree of arousal. While Nair et al. (2009) do not explicitly distinguish rumbles from growls, de Silva (2010) found that the former occur less frequently than the latter. In both the Indian and Sri Lankan populations, the majority of rumbles occur in non-aggressive social situations, while the second most frequent contexts are disturbance and movement (de Silva 2010; Nair et al. 2009). Again, females are far more likely to produce these vocalizations than males.

2.1.2 Loxodonta

Rumbles (Berg 1983; Poole et al. 1988) are by far the most studied vocalizations of African elephants and have been associated with numerous social behaviors (Leighty et al. 2008a, b; Poole 2011; Soltis et al. 2005a). Structurally distinct forms have been linked with reproductive and emotional states in female African elephants (Leong et al. 2003; Poole 1989; Soltis et al. 2005b, 2011). Males may use these acoustic cues to find estrous females and also produce their own rumble variants during the male reproductive condition of *musth* to advertise themselves to females as well as potential rivals (Poole 1989, 1999). Three types of rumbles were also found to be associated with the general behavioral states of feeding, resting, socialization and agitation (Wood et al. 2005). Recently rumble variants have been shown to function as alarm calls, elicited by the sound of bees (King et al. 2010).

There is further evidence that rumbles are used to coordinate the movement and spacing of social groups, helping affiliated individuals find one another as well as triggering defensive or exploratory behavior among those that are unaffiliated (Leighty et al. 2008a, b; McComb et al. 2000). Given that rumbles are both individually distinctive and recognized by elephants as such (Soltis et al. 2005b; McComb et al. 2000), together with the assertion that rumbles can potentially travel very long distances due to their low frequency (Garstang 2004), there has been a lot of attention on the role of these signals in coordinating group movement over long ranges.

2.1.3 Comparing the Low Frequency Signals of Elephas and Loxodonta

Rumble and growl variants in both species are used in short-, as well as in long-distance communication. While single calls occurring in the context of departures have frequently been termed 'Let's go' rumbles (Langbauer 2000; Nair et al. 2009) it is not apparent that there is an acoustically distinct rumble type that signals departure as opposed to other cues such as the posture and rank of the vocalizer, and concurrent behavior by herself and her associates. But antiphonal calling exchanges among multiple individuals have been associated with concerted movement (O'Connell-Rodwell et al. 2012). Although some authors distinguish multiple types of rumbles based on context (Langbauer 2000; Poole 2011) the consensus appears to be that rumble variants acoustically grade into one another (Soltis 2010).

Whereas low-frequency signals can potentially travel great distances in open environments under suitable ambient conditions (Garstang 2004), in the relatively dense environments that Asian elephants typically occupy the utility of these signals is likely in their ability to pass around objects such as trees and undergrowth. These considerations are discussed further in sections that follow.

3 Barks, Roars and Longroars

Barks, roars and longroars are chaotic broadband signals that generally lack a clear harmonic structure and the categories differ only by their duration (de Silva 2010). Males and females of both genera produce these vocalizations, however, longroars have only been distinguished from roars in Asian elephants (Berg 1983; de Silva 2010; Leong et al. 2003; Nair et al. 2009; Poole 2011). Barks and roars occur in the context of aggression or distress (de Silva 2010; Nair et al. 2009; Poole 2011). Barks tend to be given by the aggressor while roars seem to be given by those experiencing discomfort (de Silva 2010). In adult Asian elephants bark-rumble combinations also occur in the context of coordinating movement and appear to elicit more immediate responses from group members than rumbles in isolation (de Silva, personal observation). Thus they may signal greater urgency, however this has not been experimentally tested. In both genera, roars and/or long roars occur in situations of elevated (mainly negative) excitement, such as mating, distress, or as contact calls when individuals are separated.

Distress vocalizations in general (in primates, in elephants and other mammalian species) are thought to function to recruit aid and assistance from kin, who, in the worst case, might be out of sight. While the individuality in roars or barks of adult elephants has not been investigated, since low-frequency vocalizations are individually distinctive, the combination of roars/barks with rumbles might enhance the information about individuality and enable the recruitment of kin to support the calling individual (Stoeger et al. 2011). The fact that both species regularly combine high arousal calls with low-frequency vocalizations needs further investigation concerning the functional relevance of these interesting combinative signals.

4 Trumpets

Trumpets are the characteristic vocalization associated with elephants. Both genera produce these vocalizations, which like roars, tend to occur under conditions of heightened excitement or distress. Trumpets are also produced in agonistic or defensive interactions, such as when charging or retreating. Although both genera share these acoustically similar signals, they may differ in functionality. *E. maximus* tends to produce roars and longroars more often than trumpets when excited whereas *L. africana* produce trumpets more often (de Silva, personal observation). In addition, *L. africana* produces a sound that has been termed '*nasal trumpet*' accompaning play or mild disturbance (Poole 2011). Though it appears to be unvoiced, it is a vibratory rather than smooth exhalation of air "like a very large man blowing his nose" (Poole 2011). We note however that regular trumpets also seem to be nasally emitted, together with voiced components (Stoeger, unpublished data).

5 Squeaks, Squeals and Chirps

Squeaks (de Silva 2010) or chirp*s* (McKay 1973; Poole et al. 2005; Nair et al. 2009) and squeals are produced only by *E. maximus*. Squeaks/chirps are short high-frequency bursts that usually occur as a rapid sequence. The fundamental frequency contour of individual sounds is often 'u' shaped but can be highly variable and can at times lack clear structure. Squeals/chirps have the more typical rise-fall frequency contour of most other vocalizations and are of longer duration than squeaks. They are piercing and tonal.

Squeaks generally occur in the context of disturbance or play (in which mock alarm is feigned). Unlike roars or longroars, in which the vocalizer is experiencing distress or physical discomfort, squeaks and squeals may signal alarm. They are given when confronting a potential threat such as humans or canid predators. It is common for these calls to be given together with other vocalizations such as trumpets or rumbles, which recruit other individuals. They are also uttered when the caller is behaving submissively, such as when retreating from a threat or backing away. Sub-adult and adult females also sometimes squeak in the presence of a musth male while reversing into him, and in this context they appear to signal ambivalence and excitement rather than alarm.

6 Male Vocalizations Associated with Musth (Musth Chirp-Rumble and Musth Rumble)

In southern Sri Lanka, bulls in musth were occasionally observed producing a short, repetitive vocalization, which was termed the *'musth chirp-rumble'* (de Silva 2010). The call resembles a short inhalation (0.25 s, 250 Hz), followed by a longer low frequency exhalation (0.75 s, 60 Hz). Although the second segment was powerful enough to be audible even to humans over an indeterminate distance while the caller was out of view, it was often absent altogether. These rare vocalizations occurred either during prolonged contests between musth males, or while consorting with an estrous female. Though acoustically different from the 'musth-rumble' of *L. africana* males (Poole et al. 1988), which is a rumble variant, they may serve a similar function in advertising male reproductive state in addition to chemical signals found in the urine and temporal secretions. They may also be analogous to the 'wa-hoo' contest vocalizations of chacma baboons (Kitchen et al. 2003), and rutting calls produced by ungulates, that are honest signals of body size and condition.

7 Other Acoustic Signals and Displays

Both genera produce loud 'whoosh' exhalations from the trunk as threat displays, which are called 'snort' in African elephants. Snorts are short and sharp, broadband sounds produced by blowing air through the trunk. Snorts seem to be purposeful, in contrast to the 'blows' that appear to be made for the purpose of cleaning the nasal passages (Poole 2011). Snorts in African elephants are often produced during intense social excitement or to alert other group members. *E. maximus* in addition bounces the trunk on the ground (c.f. 'boom' McKay 1973 or 'trunk-bounce' de Silva 2010). These are not vocalizations, strictly speaking, though they are distinctively loud acoustic displays. A few further vocalizations described for both species by various authors are either rare or pose the difficulty that terminology, acoustic features and production contexts are not possible to compare across taxa. These include the 'rev', 'croak' and 'chuff' of *L. africana* (Leong et al. 2003) and the 'chirp-rumble' and 'croak-rumble' of *E. maximus* (de Silva 2010), therefore, these vocalizations will not be discussed further here.

8 Vocal Learning in Elephants

Vocal learning ability (a crucial component of human speech) has evolved independently in several distantly related taxa, typically to allow the learning and cultural transmission of complex, conspecific calls (Fitch 2000; Janik and Slater 1997). Elephants seem to be among the few mammalian species that can modify their vocalizations in response to auditory experience, based on published instances of vocal imitation in captive African and Asian elephants.

In 1982, Wemmer and Mishra already documented an interesting case of observational learning of an unusual whistling sound production method in an Asian elephant. This female elephant acquired this method from another one (who originally invented this whistling production) with which it was associated closely during its youth (Wemmer and Mishra 1982). This unusual whistling sound was produced by pressing and blowing with the tip of the trunk against the lower lip.

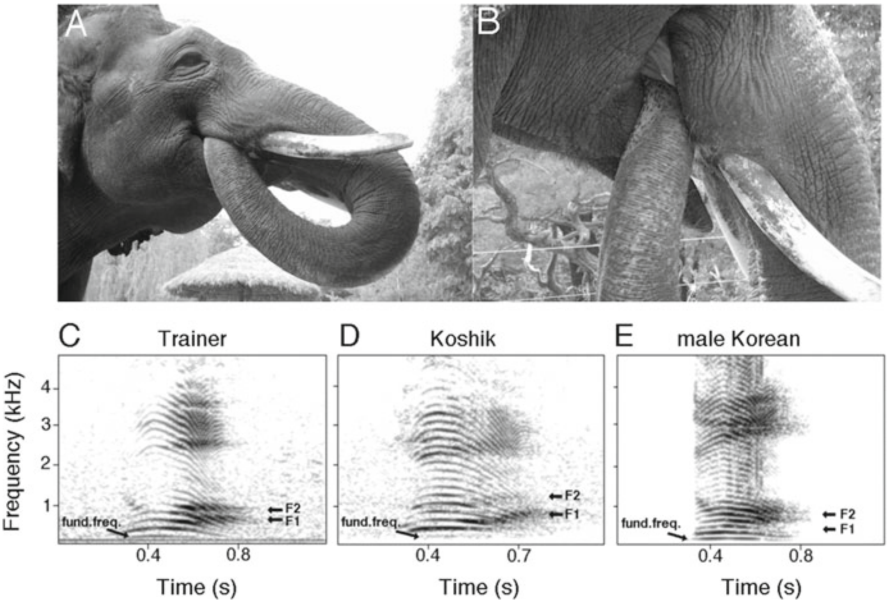

Fig. 3.2 Koshik's imitation of human speech. (**a**, **b**) Koshik's posture during speech imitation and spectrograms exemplifying the speech utterance 'nuo' (meaning 'lay down') of the trainer (**c**), the elephant's (Koshik) imitation (**d**) and a 40-year-old male Korean speaker (**e**) with no experience of Koshik's Korean output

Stoeger et al. (2012b) documented a male Asian elephant that imitates human speech in Korean. That animal, named Koshik, was captive-born in 1990 and translocated to the Everland Zoo in 1993, where two female Asian elephants accompanied him until he was 5 years old. From 1995 to 2002, Koshik was the only elephant in Everland. He was trained to physically obey several commands and was exposed to human speech intensively by his trainers, veterinarians, guides, and tourists. He eventually acquired the ability to reproduce human formants and fundamental frequencies with such precision that native Korean speakers could readily understand and transcribe the imitations as corresponding to several words. To create these accurate imitations of speech formant frequencies, Koshik places his trunk inside his mouth, modulating the shape of the vocal tract during controlled phonation (Fig. 3.2).

Poole et al. (2005) documented two cases of vocal imitation in African elephants: a 10-year-old female elephant accurately imitating the sounds of trucks, and a 23-year-old male African elephant that imitated the high-pitched chirping sounds typically produced by Asian elephants, though not by African elephants (this elephant, named Calimero spent 18 years with two female Asian elephants in a zoo).

The accomplishments of all these individuals were perhaps most surprising because they were seemingly spontaneous and self-taught. The determining factors for speech imitation in Koshik may be social deprivation from conspecifics during an important period of bonding and development when humans were the only available social contacts. Likewise, the African male elephant Calimero, who, as a juvenile, was the only African elephant among Asian elephants for a long period of time, or the Asian female elephant imitating the whistling sound of her companion. However, mimicking sounds in captive elephants might also be driven by boredom and other unnatural keeping conditions.

Whether vocal learning constitutes a byproduct of human enculturation and socially abnormal upbringing or whether it plays a crucial role in the natural lives of elephants needs to be investigated. In seals, baleen whales, and many passerine species, which vocalize or sing to attract mates and/or defend territories, vocal learning might help generate more complex songs or calls and thus increase reproductive success via sexual selection (Fitch 2000; Janik and Slater 1997; Marler 1970; Brainard and Doupe 2002; Jarvis 2004; Payne and Payne 1985). In elephants of both species, little is known about the functional relevance of male calls, which are produced more frequently during musth periods (Poole 1987; de Silva 2010). The males Koshik and Calimero, however, produced imitations throughout the year, independent of their musth. This would indicate that vocal learning is not necessarily associated with sexual selection in elephants.

Another hypothesis is that learned vocalizations function as an indicator of group membership (Janik and Slater 1997; Fitch 2000). Facilitating vocal recognition by heightening the similarity of vocalizations seems particularly important for animals living in social systems characterized by within-group cooperation and social interactions (including competition) between groups (Fitch 2000; Tyack 2003). Such systems are characteristic of many vocal learners including African and Asian elephants (Wittemeyer et al. 2005; de Silva et al. 2011). The finding that an African elephant matched calls of Asian elephants with whom he grew up, as well as the social circumstances under which Koshik's speech imitations developed, follow a pattern commonly seen in species capable of vocal learning in which calls converge as the animals form social bonds (Tyack 2003, 2008). On rare occasions, this takes place across species.

9 Sound Production Mechanisms of Low-Frequency Vocalizations

To date, the physiological mechanisms of elephant vocal production have been largely neglected. Nonetheless, the vocal characteristics accessible to receivers are determined by individual and species-specific mechanisms of sound production (Tayler and Reby 2010). This interaction between voice production, acoustic output and function requires understanding elephant sound production mechanisms when investigating their communication system. Here we discuss only low-frequency communication, which has been studied to a greater extent.

The low-frequency rumble, the most common African elephant sound, is a frequency-modulated, harmonically rich vocalization. It was commonly speculated that rumbles are produced in the larynx (e.g. Langbauer 2000), either by neurally controlled muscle twitching (AMC: active muscle contraction as in cat purring) or by flow-induced self-sustained vibrations of the vocal folds (MEAD: myoelastic-aerodynamic mode as in human speech and song) (Garstang 2004; Shoshani 1998, 2013). Applying direct high-speed video observations of an excised African elephant larynx (an 18-year-old female elephant that died due to natural causes), Herbst et al. (2012) demonstrated flow-induced, self-sustained vocal fold vibration in the absence of any neural signals. The observed fundamental frequencies in the excised larynx experiments (averaging 16.38 Hz) match well with fundamental frequencies documented in rumbles recorded from live adult female African elephants (e.g. Soltis 2010). Although those results cannot eliminate the possibility of an active muscle contraction mechanism in a living elephant, this study demonstrates that there is no need for such a twitching mechanism to produce loud and intensive low-frequency vocalizations.

Rumbles and growls in Asian elephants are quite similar in fundamental frequency and overall structure to rumbles of African elephants (Payne et al. 1986; Nair et al. 2009; de Silva 2010). Our knowledge about Asian elephant vocal tract anatomy is, however, very limited apart from a few descriptions of the basic laryngeal structures (Miall 1878). Nonetheless, considering the similar acoustic properties of African and Asian elephant rumbling vocalizations, one might assume that Asian elephants rely on the same myoelastic-aerodynamic production mechanism as suggested for African elephants. The elephant larynx most likely constitutes a vibrating system similar to that known in humans and other mammals. This indicates that flow-induced vocal fold vibration offers a physiologically and evolutionarily efficient means to produce the low-frequency vocalizations used so intensively in elephant vocal communication. This clearly warrants future comparative experiments in the manner of Herbst et al. (2012) with an Asian elephant larynx, combined with detailed comparative investigation of the elephant vocal tract anatomy.

Sound waves generated by vocal fold vibration in the larynx pass through the vocal tract, which contains air in the pharyngeal, oral, and nasal cavities, amplifying certain frequencies termed formant frequencies (or formants). In addition to the sound source, information about the supra-laryngeal vocal tract is required in order to understand and interpret the spectral characteristics of the acoustic output accessible to the receivers. Formant frequency values are generally determined by the length and shape of the vocal tract; long vocal tracts do produce lower and more closely spaced formants. As in most mammals, elephants emit vocalizations orally or nasally. The elephant's nasal vocal tract, however, is strongly elongated in relation to the oral path (considering that the un-extended trunk length of an adult female African elephant is about 1.7–1.8 m (Sikes 1971)).

Using an acoustic camera array to visualize sound emission, Stoeger et al. (2012a) recently demonstrated a physiological basis for distinguishing two forms of rumbles in the African species, those emitted nasally or orally (Fig. 3.3). Nasal and oral rumbles varied considerably in their acoustic structure. In particular, the mean frequency spacing of the first two formants predicted the estimated lengths of the two vocal paths (Fig. 3.3). This corresponded to a vocal tract length of about 2 m for

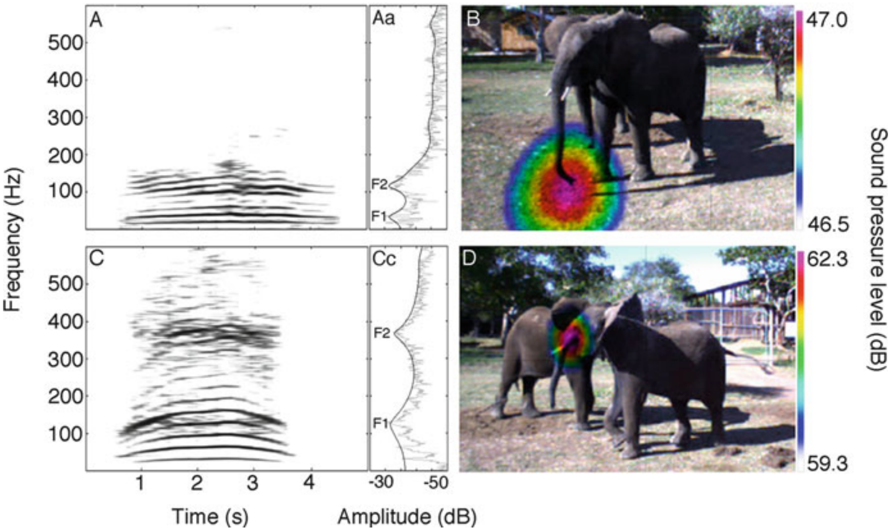

Fig. 3.3 Orally and nasally emitted rumble by a sub-adult female African elephant. Spectrogram and power spectra of a nasal (**a**) and oral (**c**) rumble revealing the differences in formant structure. (**b**) and (**d**) give the corresponding sound visualizations (For details on the methodology, see Stoeger et al. 2012a) for a nasal and oral rumble

nasal rumbles and about 0.7 m for oral rumbles in the investigated elephants (the study animals were younger than 17 years old and not yet fully-grown). Thus, by using the nasal path, an elephant potentially lowers its formants by about threefold. Moreover, the investigated African elephants produced the two different rumble types in two distinct contexts. In the females, the nasal rumbles predominated during long-distance contact calling, whereas oral rumbles were mainly observed during close-distance social bonding (the two males in the above study solely produced nasal rumbles). Preliminary data of adult African elephants indicate that all age classes do produce oral rumbles in certain situations (Stoeger et al. 2012a).

Initial investigations on low-frequency vocalizations of a 40-year-old female Asian elephant, applying the acoustic camera array at a zoo in Upper Austria, revealed similar results as documented in the African species. Although it has been possible to visualize only rumbles that were emitted orally, acoustic data of vocalizations exhibiting formant values that reasonably predict the estimated lengths of the nasal vocal tract (indicating that these vocalization was maybe emitted nasally) were also collected (see Fig. 3.4). These first results indicate that low-frequency vocalizations of Asian elephants can be also both orally and nasally emitted. In fact, the example given in Fig. 3.4d, e correspond to those calls categorized by de Silva et al. (2010) as *growl* (with the fundamental frequency in the infrasonic range, but little or no energy above 500 Hz). This suggests that the two genera produce structurally similar vocalizations using analogous production mechanisms, despite differences in nomenclature among authors.

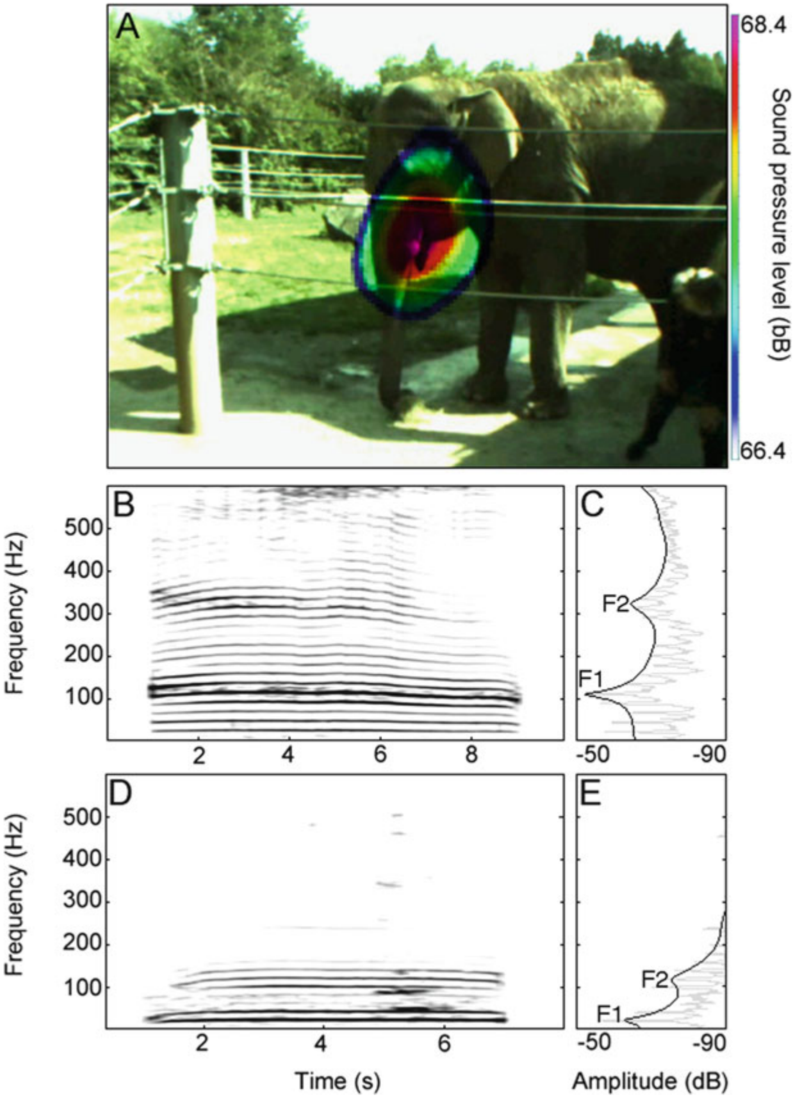

Fig. 3.4 Oral and nasal rumble emitted by a 40-year-old Asian female elephant. Sound visualization (**a**), the corresponding spectrogram (**b**) and the power spectra (**c**) of the oral rumble. (**d** and **e**) give the spectrogram and the power spectra of a rumble resembling the formant structure of a nasally emitted rumble

10 Ecological and Evolutionary Context

Whether elephants vary their vocal path systematically according to context or motivation and, by doing this, considerably vary the formant structure of their rumbles remains to be investigated in both species. Formants provide the acoustic basis for discriminating vowels in human speech, transferring important information (Petterson and Barney 1952; Lieberman and Blumstein 1988). The modulation of the first and the second formant also appears to play a role in referential calling in several nonhuman primates (*Papio hamadryas*: Andrew 1976, *Theropithecus gelada*: Richman 1976, *Ceropithecus aethiops*: Seyfarth and Cheney 1984, *Cercopithecus Diana*: Riede and Zuberbühler 2003). Previous studies on African elephants have also documented formant variation with context and arousal state (King et al. 2010; Soltis et al. 2009).

Apart from this, formants are reliable cues to body size in several mammals (Fitch 2000; Charlton et al. 2011; Harris et al. 2006; Reby and McComb 2003; Riede and Fitch 1999; Sanvito et al. 2007; Vannoni and McElligott 2008). This reflects the close relationship between the caller's overall body size, vocal tract lengths and the frequency spacing of the formants (Fitch 2006). Morphological adaptations to elongate the vocal tract in order to lower formants occur in several species. The size exaggeration hypothesis (Ohala 1984) was proposed to explain most of these observations (e.g. birds (Fitch 1999); red deer, *Cervus elaphus*, (Fitch and Reby 2001); big cats, *Panthera* sp. (Weissengruber et al. 2002); Goitred gazelles, *Gazella subgutturosa* (Volodin et al. 2011); koalas, *Phascolarctos cinereus* (Charlton et al. 2011); elephant seals, *Mirounga leonina* (Sanvito et al. 2007)). The low-frequency musth vocalizations of male elephants, as well as vocalizations produced during hierarchical interactions (also among females) may be under similar selective pressure.

An alternative explanation, though not mutually exclusive, is that lowering formants promotes long-distance call propagation (McComb et al. 2003). The low fundamental frequency could be a by-product of the large size of the elephant's vocal folds (10.4 cm in an adult female African elephant; Herbst et al. 2012) rather than a specially evolved mechanism for long-distance vocal communication. In contrast, the amplification of certain frequency regions by using the nasal vocal tract may have evolved due to selection pressures particularly relevant to social communication (McComb et al. 2003). During re-recordings of African elephant rumbling vocalizations in the Amboseli National Park, McComb et al. (2003) suggested that the most important frequency components for airborne long-distance communication of social identity in African elephants might be well above the infrasonic range. Their results showed that the harmonics centered around 115 Hz were more prominent and persistent. These harmonics (which highlighted the second formant) also decayed at a lower rate with increasing distance than frequency components below and above them. This frequency range also corresponds to the observed second formant of nasal rumbles in the study conducted by Stoeger et al. (2012a) (mean formant $2 \pm \mathrm{SD} = 128.76 \pm 32.57$ Hz). Harmonics in the 115-Hz area may experience less interference from wind noise than the fundamental frequency contour itself (McComb et al. 2003). This conclusion further corresponds with data on vocalizations collected in South Africa and Sri Lanka, where low-frequency components of rumbles recorded at a greater distance were often heavily masked by a low-frequency band of environmental noise (Stoeger and de Silva, unpublished data).

The hearing sensitivity of elephants has so far been investigated only in one 7-year-old female Asian elephant (Heffner and Heffner 1980, 1982). Those results showed that although this elephant was more sensitive to low frequencies than any other mammals (the lowest frequency of hearing was 17 Hz at 60 dB, which is nearly one octave below the comparable human threshold), the elephant was still considerably less sensitive to frequencies below 100 Hz than to those between 100 Hz and 5 kHz. One explanation is that elephants are better adapted for perceiving frequencies above 100 Hz than frequencies in the infrasonic range. More definitive conclusions will require further comparative experiments designed to test formant perception and the frequency ranges of best sensitivity in elephants of both species.

11 Conclusions & Future Directions

This chapter reveals similarities and discrepancies within the vocal communication system of African and Asian elephants. While there is clearly a need for more research on vocal communication in Asian elephants, as well as a shift from the emphasis on low-frequency vocalizations in African elephants, comparisons based on the existing literature offer some insights and directions of inquiry.

The adaptive significance of the extremely low formant frequencies of elephant rumbles remains largely unknown. Two interpretations are possible: the very low formants of nasally emitted elephant rumbles could reflect sexual selection pressures to sound larger (particularly relevant for males and during dominance interactions in females), or they could reflect natural selection pressures to maximize call propagation distances. Future studies on African and Asian elephants should investigate whether the formants in elephant rumbles consistently vary according to the size of the vocalizer (maybe also independent of the species), and also investigate the behavioral responses of male and female conspecifics to formant variations. Re-recording experiments could also reveal whether any size-related formant information persists over relevant distances in the various elephant habitats.

Further, comparative research on the physiological principles of elephant sound production is strongly warranted, investigating the production mechanism of prominent call types evident in all elephant species such as the trumpet. Trumpets seem to be emitted exclusively through the nasal passages (Stoeger, unpublished data), however, whether the sound originates through vocal fold vibration remains highly debated. Finally, the potential function of vocal learning within the natural communication system of *Elephas* and *Loxodonta* is a current topic that needs to be investigated.

There are species-specific differences in the vocal repertoire. The most remarkable is the high-pitched (repetitive) vocalizations (chirps or squeaks and squeals) of Asian elephants, which are completely missing in the African species. Whether African elephants might have lost these sounds after the split off from the lineage leading to the Asian elephants and the mammoths, or whether Asian elephants implemented those sounds recently remains a mystery. Yet, such discrepancies as well as similarities observed between elephant species can provide clues about morphological, behavioral or cognitive mechanisms that evolved to solve particular problems. Therefore, a stronger comparative focus might shed light on some of the most complex issues of elephant vocal communication.

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Chapter 4
The Information Content of Wolf (and Dog) Social Communication

Tamás Faragó, Simon Townsend, and Friederike Range

Abstract Wolves have a remarkably complex social system: they breed, hunt and keep large territories cooperatively. To maintain such an elaborate system, a similarly complex and sophisticated communication system would also be expected. Based on this, studying the vocal communication of wolves and comparing it with other canids of different levels of sociality can give an interesting insight to the relationship between social and communicative complexity and in the long run help to better understand the evolutionary origins of human language. Furthermore, the direct comparison of the wolf and dog vocal repertoire can provide intriguing details about the process of domestication.

In the following chapter we will describe the basic elements of the wolf and dog vocal repertoire, show their potential capability to convey information about the

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caller, its inner state and possibly the context of the vocalization. We will attempt to point out gaps in understanding regarding wolf and dog vocal communication, potential pitfalls in the current approaches and finally formulate possible directions for future research.

1 The Social System of the Wolf

Wolves are cooperative breeding canids living in family groups usually consisting of the breeding pair and their offspring from the previous 2–3 years (Mech 1970). In addition to cooperative raising of pups, wolves also defend their territories and are thought to hunt large game cooperatively. The pack's activity may be affected by hierarchical relationships within the family clan with an individual's position in the group's hierarchy strongly determining its priority of access to food (Van Hooff and Wensing 1987; Mech and Boitani 2010). Dominance relationships seem to differ between wild-living packs and wolves kept in captivity. In wild-living packs, juveniles usually demonstrate more submissive interactions with adults and therefore, older wolves effectively intimidate younger wolves. Littermates may squabble over food or during rough play, and pups are disciplined by older family members (Packard 2003). This model has been presented in two ways: first simply as separate linear hierarchies within each sex, influenced but not absolutely determined by age (Schenkel 1967; Zimen 1982) and second, as male dominance over females within each age class (Van Hooff and Wensing 1987; Zimen 1982)In captive packs, however, a linear hierarchy is more probable since individuals are added to the group sequentially and additions occur after each dominant-subordinate relationship has stabilized (Packard 2003). Moreover, wolves form close relationships with certain partners and, like non-human primates (see Aureli and De Waal (2000) for a review), engage in reconciliation and third-party post-conflict interactions (Cordoni and Palagi 2008; Palagi and Cordoni 2009). The latter has been considered to require 'cognitive empathy' and involves an understanding of third party interactions (Fraser et al. 2008). Further evidence for advanced cognitive skills comes from our own studies, showing that wolves follow the gaze of others (Range and Virányi 2011), use gaze cues as communicative tools to find hidden food (Virányi and Range submitted), easily learn from conspecifics (Range and Virányi, submitted) have specific numerical competence skills (Utrata et al. 2012) and have flexible control over their vocalisations (Mazzini et al. 2013).

In contrast to wolves, dogs – their domesticated relatives (Lindblad-Toh et al. 2005) – live in a human-dominated niche, which represents the dog's natural environment. Current evidence suggests an enhancing effect of domestication on the social skills of dogs in cooperative–communicative tasks involving humans (Hare and Tomasello 2005a; Miklósi et al. 2004). One of the more recent hypotheses, the 'emotional-reactivity hypothesis' suggests that selection on social-emotional systems could have provided an initial catalyst for wider social cognitive evolution in dogs and perhaps even in human evolution (Hare 2007; Hare et al. 2005; Hare and Tomasello 2005a, b). Indeed, dogs have some skills that wolves miss or develop later, even after extensive socialization by humans, and dogs show a better inhibitory control (e.g. following human pointing (Gácsi et al. 2009a; Virányi et al. 2008)). Due to their normally intensive socialization in the human environment (Scott and Fuller 1965), their individual experiences might further amplify these evolutionary changes as well as lead to additional adaptations to humans (Udell et al. 2009) (analogous to what is argued for the development of social cognition in children (Tomasello 1999)). However, despite the effects of domestication (Clutton-Brock 1995; Coppinger and Schneider 1995), mounting evidence suggests that the social organization of free-ranging dogs is modulated by the same ecological constraints that influence other wild canid social systems (Bonanni et al. 2010a, b, c; Cafazzo et al. 2010; Macdonald and Carr 1995; Pal et al. 1998a, b). Thus, although their morphology, physiology and behaviour have been partially modified during domestication (Clutton-Brock 1995; Coppinger and Schneider 1995), free-ranging dogs form stable social groups, characterized by conspecific cooperation and dominance as well as by affiliative interactions, including reconciliation and third-party post-conflict interactions (Bonanni et al. 2010a, c; Cafazzo et al. 2010; Cools et al. 2008).

As we can see, most aspects of wolf social life, such as its hierarchical structure, cooperation in hunting and defending territories, are complex and rich with variable levels of social interactions. One likely component to the success and maintenance of such an interactive social system is a diverse and rich communication system capable of conveying multiple information in a variety of modalities. Such a link between communication and sociality has previously been posited more generally for primates where increases in measures of social complexity (e.g. group size) map onto vocal complexity (repertoire size) (McComb and Semple 2005). In the following sections, we will investigate the vocal repertoire of wolves, to probe the extent of its complexity, particularly how different calls in the repertoire are capable of conveying variable information to conspecifics during interactions.

Studying natural behaviour and social communication of wolves is complicated due to the difficulties of data collection in the wild, and the artificial nature of captivity that can highly affect the outcome (as we saw above in the case of dominance hierarchies for example). Due to this we have only limited knowledge about wolf behaviour and their communicative system. Studying dogs however, provides a good opportunity to fill these cavities. Nevertheless, with this approach it is important to remain aware that although dogs and wolves are closely related, the process of domestication likely had a strong impact on and cause specific changes in behaviour. For example, with relying on food provided by humans (Axelsson et al. 2013), the selective pressure to be quiet (in order not to scare away game) was relaxed resulting in vocal exaggeration (Cohen and Fox 1976). Moreover, the directional selection of dogs to specialize for different tasks (like herding, hunting, guarding, weight pulling) could affect the behaviour of these animals via modifying their sensory and neurological capacities (Gácsi et al. 2009b) as well as their communicative abilities

(Feddersen-Petersen 2000). Bearing this in mind, in the following, where we have limited information about wolf communication and behaviour, we will discuss results from dog literature as a complement.

1.1 Possible Information Content of Vocalizations

In the acoustic domain information is encoded in the complex structure of sound waves produced during vocalizations. Measuring different acoustic parameters of these sounds and searching for associations with peculiarities of the caller or external events can provide insight into how these calls are used in communication (Bradbury and Vehrencamp 1998; Fitch and Hauser 2003). Application of the Source-Filter framework gives an excellent opportunity to better understand these mechanisms (Taylor and Reby 2010). In brief, this theory predicts that voice production is a two stage process in which the two functionally distinct parts of the vocal apparatus, the source and the filter, are involved (Fant 1960; Titze 1994). The source is essentially the larynx: the location of sound wave production. Here the specifically positioned vocal folds block the flow of air from the lungs and start to resonate, cyclically opening and closing. This interruption of airflow causes a pseudo-periodic pressure change in the exhaled air producing a sound wave (Truax 2001). This wave then forms the source signal, containing the fundamental frequency (the frequency of the cyclic opening and closing of the vocal folds), and its upper harmonics. The properties of the source signal is mainly determined by the stable (in short term) physical parameters (length, mass, form), the actively alterable by specific muscle movements (the tension of the vocal folds and the subglottal pressure) (Fitch and Hauser 2003). The former is mainly determined by the individual developmental processes, while the latter two are under the control of the nervous system.

During the oscillations of the two vocal folds irregularities, so called nonlinear events, can occur (Wilden et al. 1998). The occurrence of these events is unpredictable due to the complex oscillatory nature of the system, and these range from slight asynchrony of the vocal folds (subharmonics) to complete irregularity (deterministic chaos) (Fig. 4.1). Abrupt jumps can additionally occur in the fundamental frequency caused by the changes in the oscillatory state of the system. These elements will cause changes in the subjective harshness of the sound which can be identified via characteristic frequency structures (Fitch et al. 2002) and can be measured by the tonality of the source signals (Yumoto et al. 1982).

As this source signal passes through the upper respiratory tract (vocal tract) it is further modified. The air filling the vocal tract has specific resonant frequencies with which it can preferentially vibrate amplifying these frequency bands in the source signal, while attenuating others (Fant 1960). Thus it will act as a frequency band filter and the properties and position in the spectrum of the strengthened bands, the so called “formants”, depend acutely on the length and form of the vocal tract (Fitch 1999, 2000; Fitch and Reby 2001).

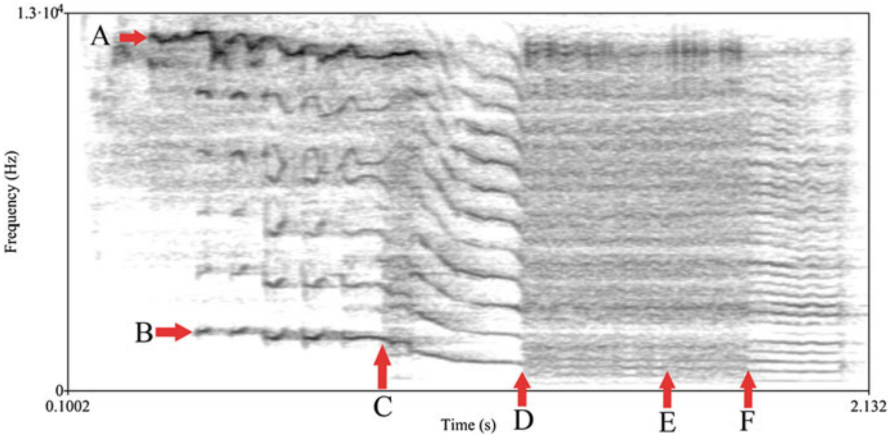

Fig. 4.1 Occurrences of nonlinear phenomena in a whine of a dog during separation from owner (Tamás Faragó's recording). *A*, Biphonation, a secondary fundamental frequency produced in the nasal tract of the dog. *B*, the main fundamental frequency with strong frequency modulation. *C*, Frequency jump with additional noise component. *D*, Noisy subharmonics. *E*, Deterministic chaos caused by the irregular resonances of the vocal folds. *F*, tonal subharmonics called frequency doubling caused by the asynchrony of the two vocal folds

All these frequency components of the signal and also its time parameters can carry information about the caller's physical, emotional, physiological state, identity and group membership (McComb and Reby 2009; Taylor and Reby 2010).

1.1.1 Cues of the Caller

For group living animals it can be essential to differentiate group members, both at the individual and the group level (Trivers 1971). As the elements of source are under the regulation of developmental and genetic factors, the properties of the source signal can subsequently provide identity cues (Taylor and Reby 2010). Besides using specialized calls that can function as signatures (Janik et al. 2006), the modulation of fundamental frequency (Owren et al. 1997), its noisiness (Fitch et al. 2002) and temporal features (Rendall et al. 1996) can serve as cues for recognition of identity.

As steroid hormone levels can additionally have an impact on both the development and the state of the vocal folds (Semple and McComb 2000), the structure of the fundamental frequency can further inform listeners regarding the quality (Charlton et al. 2012), age (Fischer et al. 2002) and dominance position (Fischer et al. 2004) and inner state of the signaller (Manteuffel et al. 2004).

In contrast, physical strength is more correlated with filter rooted cues. While the size and thickness of the vocal folds is not constrained by the body size, the length of the vocal tract is, which in turn mainly affects the dispersion of formant frequencies across the spectrum (Fitch and Hauser 2003). Thus formant dispersion can serve as a reliable indexical cue to size and indeed this has been observationally and empirically demonstrated across a range of species including red deer: (Reby and McComb 2003), bison: (Wyman et al. 2012), giant panda: (Charlton et al. 2009) and rhesus monkeys: (Fitch 1997).

1.1.2 Inner State

During social interactions, cues and signals of inner state can be especially important to predict the future behaviour of social partners (Ohala 1996). After studying and comparing calls of various mammalian and avian species Morton, (1977) formulated the Structural-Motivational rules. He found that following Darwin's antithesis principle, the structure of vocalizations differ specifically according to the inner state of the caller: aggressive, dominant vocalizations are elongated, broadband, noisy and low pitched, while fearful, submissive or playful calls are short, tonal and high pitched.

Furthermore, tonality and calling rate both can be associated with arousal in the nervous system, which can thus potentially signal the urgency of a vocalisation such as an alarm call (Blumstein and Armitage 1997; Townsend and Manser 2011) together with the closeness of a predator (Manser et al. 2002). The noisiness of the signals and the occurrence of nonlinearities is raised by the tension on vocal folds and the more forced exhales that can be caused by the higher level of arousal in the individual (Fitch et al. 2002). Due to the unpredictable nature of these chaotic events, they can play an attention grabbing role in alarm (Slaughter et al. 2013; Townsend and Manser 2011), distress (Chang and Thompson 2011) and also in sexual calls (Reby and Charlton 2011). However, in some species like yellow bellied marmots, alarm calls become more tonal and stable with the raise of stress measured by stress hormone levels (Blumstein and Chi 2011). These animals produce piercing calls in alarm, which probably a product of selection towards calls having immediate response from the listeners.

1.2 The Vocal Repertoire of Wolves and Dogs

The extent to which similar principles apply to the vocal communication system of wolves is based on only a handful of studies and these works almost exclusively focus on the information content of howls (Harrington 1986, 1987, 1989; Harrington and Mech 1979, 1983; Tooze et al. 1990). As exceptions, in the 1970s Cohen and Fox, and Tembrock published two thorough studies comparing vocalizations of canids (Cohen and Fox 1976; Tembrock 1976). In this work, researchers collected vocalizations from various captive canine species in numerous social contexts, and based on their spectrographic peculiarities differentiated call types, categorized and described their structure and postulated possible roles in social communication. Comparing the repertoires and use of calls in canids with different levels of sociality reveals a comparable pattern to that in primates (McComb and Semple 2005): with increasing social complexity, for example from solitary like manned wolves or pair living species as foxes to gregarious wolves and dogs, vocal complexity also increases with more and elaborate vocalisations in addition to a greater propensity for combinations and mixtures of calls (Cohen and Fox 1976; Fox and Cohen 1977). Besides these works only one study exists that provides a comprehensive description of the wolf vocal repertoire. Schassburger (1993) recorded, analysed and categorized a large amount of vocalizations from three captive wolf packs. Whilst pioneering, this work, similarly to the earlier comparative studies, is still based on listening and visual inspection of spectrographs and hence also subject to the arbitrary categorisation of humans. In light of this, together with the high variability of calls in wolves, the different authors' nomenclature and grouping can differ significantly causing confusion and making it problematic to categorize newly collected vocalizations.

2 Elements of the Repertoire

In the following part, we will give a summary of the main call types of the wolf vocal repertoire. During this we will follow mainly Schassburger's (1993) nomenclature with addition of grunts, groans and atonal calls from Cohen and Fox (1976). We attempt for the first time to unify the categorization used by different authors and, besides giving an acoustic description of these calls, we will show what information they are capable of conveying and what role they may play in the social life of wolves. We will also add and discuss dog calls too here with a nice outlook at the possible impact of domestication on the vocal behaviour. We will also try to identify hiatuses in the literature as a way to outline possible tracks for future research.

2.1 Tonal Calls

2.1.1 Whines

Whines are generally characterised as short, cyclic, high pitched and tonal vocalizations. Their fundamental frequency ranges between 400 and 2,000 Hz and their harmonic structure can be highly variable, often containing nonlinear phenomena such as biphonations, sidebands or subharmonics (Volodina et al. 2006). From the acoustic parameters alone, several different variants or subtypes of whines can be recognized (Fig. 4.2).

The *undulating whine* is an elongated variant that has a slightly variable fundamental frequency (Cohen and Fox 1976). Due to their cyclic frequency modulations, these calls might be considered as merged short whines. In comparison, *whimpers* are also elongated and contain a specific rise in frequency at the onset and fall in frequency at the offset, but otherwise have a stable fundamental frequency (Schassburger 1993; Tembrock 1976). Schassburger recognizes these whimpers as

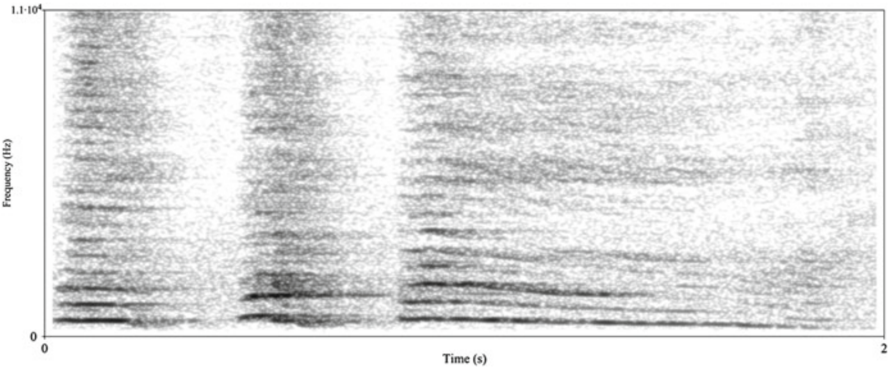

Fig. 4.2 Dog whine (Tamás Faragó's recording)

an independent call type based on the occurrence of noisy, broadband intervals but it is likely that these are just nonlinear subharmonics or chaotic events occurring during whine production. In a similar way *whistles* are also often characterised as distinct vocalizations (Robbins 2000). Whistles consist of secondary fundamental frequencies, which can occur as either biphonations accompanied by additional different calls or alone. These sounds are extremely high pitched (above 4 kHz) and tonal. While the exact mechanism underlying their production is unclear, is has been suggested that they are produced in the upper nasal tract (studied in dogs: Volodina et al. 2006).

Whines are produced in several different contexts, but primarily in stressful situations, such as during pack separation or conflict situations, which likely invoke negative inner states in the vocalising animals. However, whines may also be emitted during contact seeking behaviours or in combination with submissive behaviours. Their acoustic structure has the potential for conveying individually specific information (and hence acting as signature calls), although to date there is only one study supporting this notion. Goldman et al. (1995) found that a mother and a female helper emitted whines (referred to as squeaks in the publication) in the den when nursing the pups. Both individuals used these calls, but the whines had distinct fundamental frequencies potentially allowing for individual discrimination. When whines were emitted by various animals outside the den, the pups only approached if their mother produced the call suggesting that the wolf pups could use the information contained in the whines to discriminate their mother from other wolves. From the production perspective it is unclear whether the helper and the mother actively modified their whines in order to avoid spectral overlap or whether they used specific type of whines during nursing. As this was an observational study it is also unclear how pups might react if whines overlap with their mother's fundamental frequency, but originate from another individual.

The prominent nonlinear features of whines could also play a role in individual recognition since their occurrence can strongly depend on anatomical peculiarities (Fitch et al. 2002). Besides this, due to the fact that whines are used in separation

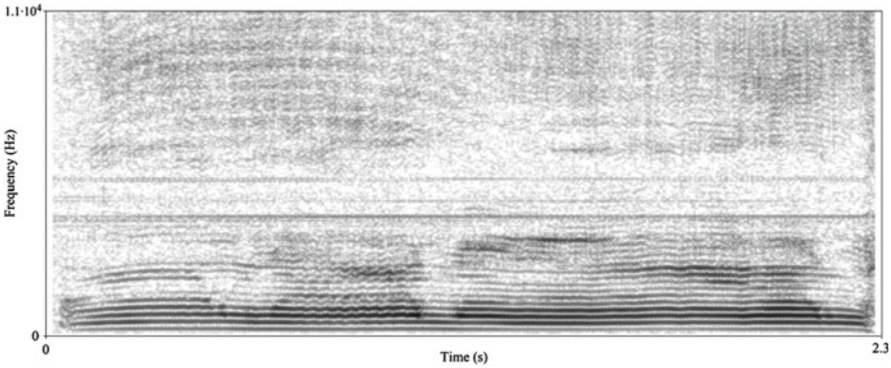

Fig. 4.3 Dog moan (Csaba Molnár's recording)

and contact seeking contexts, it could be posited that another important function of nonlinearities is to attract attention. Due to the unpredictable nature of nonlinear phenomena, bifurcations can prevent habituation to whines representing an effective tool to elicit the attention of social partners and ultimately avoid being ignored (Volodina et al. 2006).

2.2 Intermediate Calls

2.2.1 Moans

These vocalizations were first described in wolves by Schassburger. These calls are acoustically transitive forms between growls and whines. They are moderately long calls (0.1–1 s), with a low fundamental frequency (80–600 Hz), rapid frequency modulations and a varying level of tonality (probably due to frequent occurrence of nonlinear events) that differentiate these calls from whines. In contrast to growls, however, they have a higher fundamental frequency and are less noisy (Schassburger 1993) (Fig. 4.3).

These vocalizations have not yet been reported in natural settings (Passilongo et al. 2010), but they could play an important role in wolf communication. Schassburger reported that these calls are the product of ambivalent inner states of the individual such as a conflict between aggressive and fearful inner states. Accordingly, they can be found in almost every social context and are associated with ambivalent behaviours. Moans are also used in playful contexts and possibly serve as play signals to the partner, changing according to the role of the caller in play: the lead (controller) player emits moans closer to growls, while the controlled individual produces moans resembling whines. Moans also occur in domestic dogs during food begging contexts, although this easily can be a result of unintentional conditioning by the owner (as barks (Pongrácz et al. 2005), whines (Volodina et al. 2006) or growls (personal observation) can be used as begging signal in dogs).

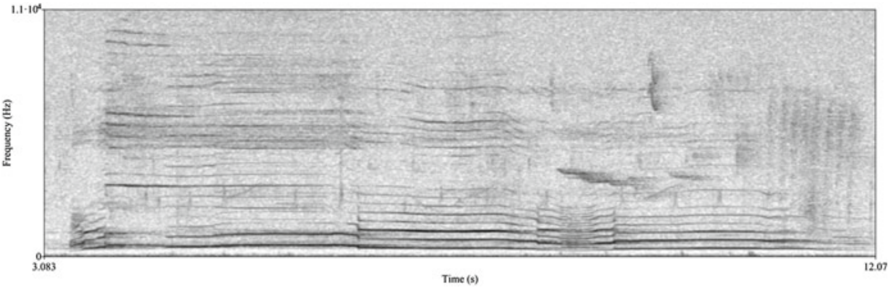

Fig. 4.4 Howl of a female wolf (Francesco Mazzini's recording)

2.2.2 Howls

Howls are probably the most prominent call of all wolf vocalizations. They are high amplitude, long range extended calls (1–10 s long) often with undulating fundamental frequencies varying between 150 and 2,000 Hz (Cohen and Fox 1976). Frequency alternations are stronger in the beginning and end, with occasional jumps in the middle (Tembrock 1976). Two main types of howls are differentiated: the "flat" and the more modulated "breaking" howls, although these categories possibly represent two extremes of variability (Palacios et al. 2007). The flat type is described by a stable fundamental frequency with a characteristic rise at the beginning, while the breaking howls have higher and more variable fundamental frequency characterized by abrupt changes, even pauses (Passilongo et al. 2010) (Fig. 4.4).

Wolves emit howls both alone and in choruses which can last for a few minutes, and are usually preceded by a single wolf howling and others joining in (Joslin 1967). The howls within these group choruses often become increasingly variable with time, and can be triggered by hearing other, unfamiliar wolves howling. Interestingly, wolf packs reply not just to conspecifics, but also to playbacks and humans imitating howls, which provides an excellent method to study these vocalizations (Harrington and Mech 1979).

The function howls serve can be considered at two communicative levels: inter- and intra-group communication. Howls are known to play a role in group cohesion, facilitating reassembly of members by providing individually distinctive information on location (Tooze et al. 1990). Due to their acoustic structure, howls can travel long distances without severe distortion and hence the information content remains reliably preserved. According to Nowak et al. (2006), the spontaneous howling activity of wolves peaks between July and October, during the season when pups were present. Most of the howls were recorded during dusk and they were emitted from the core area of the territory, and it seems that they mainly serve as long range contact maintenance between pack members (Nowak et al. 2006). Tooze et al. (1990) found that the fundamental frequency, particularly its variability, makes howls individually distinctive. Fundamental frequency also carries information about the maturation status of the individual: adults' howls have lower fundamental frequency than juveniles' howls (Harrington and Mech 1978), and unfamiliar packs seem to react only to howls from adult individuals (Harrington 1986). However, it still remains an open question whether wolves can use this information during communication and recognize or discriminate each other by howls.

Between groups, howls seem to play a role in territory defence, communicating location and advertisement of resource ownership (Harrington and Mech 1979). When humans mimic howls within the territory simulating a single stranger trespassing, the pack's reaction can range from silent avoidance to howling back and approaching the intruder, depending on multiple factors (Harrington and Mech 1979). For example, the breeding season and presence of young individuals can heighten the probability of howling and approach, either if the pack is around a fresh kill or assembly sites of the pack (rendezvous sites). Social status and pack size is also important, as larger packs and packs in the presence of the alpha individual respond more readily than smaller pack in the absence of the alpha (Harrington and Mech 1979). All these observations suggest the packs attempt to avoid any confrontation that can be costly or even lethal, unless they have to defend high value resources. In these cases, wolf packs often howl back revealing their position and try to search for and probably physically repel the intruder. In such situations, cues to physical strength and inner state represented in the howls could play a crucial role in preventing actual confrontations. Single howls can probably convey both types of information. On the one hand, howl length is associated with body size providing information about the resource holding potential of the individual (Harrington and Mech 1978), while tonality and frequency are both affected by the inner state of the wolves: the closer wolves approach an intruder, the lower the fundamental frequency and tonality of their howls (Harrington 1987). This acoustic change with inner state seems to closely follow Morton's structural motivational rules (Morton 1977). Interestingly, group howls seems to conceal the real size of the pack: for humans, the number of howling individuals is hard to estimate or measure by listening or analysing choruses. Probably the raising variability of the fundamental over the chorusing and the abrupt changes cause the so called "Beaue geste" effect providing an interesting example of potential information withholding (Harrington 1989). Recent findings also demonstrate that, whilst the number of individuals howling may be unclear, there can be recognizable group specific cues (mainly fundamental frequency and variance components and duration) in chorus howls (Zaccaroni et al. 2012). Such information likely facilitates the recognition of neighbouring packs, and extraction of up-to-date information regarding location.

2.2.3 Barks

The most prominent feature of barks are their short durations (0.2–0.6 s) and spectral shape that resembles a 'Christmas tree' formation due to the progressive lowering of energy in higher frequencies (Feddersen-Petersen 2000). Barks possess variable fundamental frequencies (150–900 Hz) and noisiness, and in structure they show a typical curved shape with fast raise and drop in frequency. Barks can be emitted as

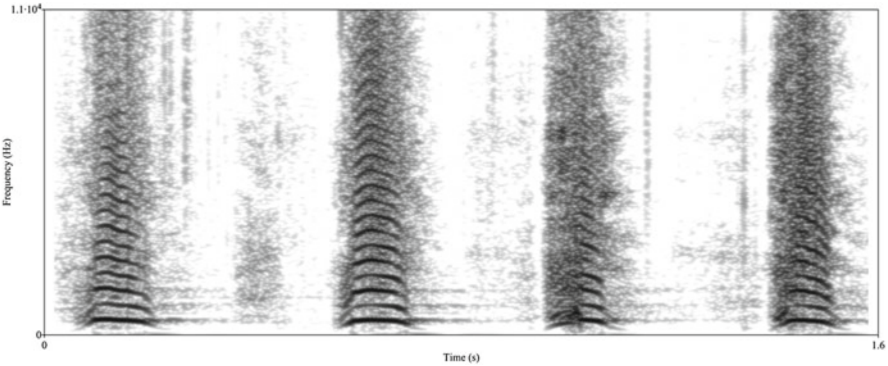

Fig. 4.5 Dog bark (Csaba Molnár's recording)

single calls or bouts. Several subtypes can be recognized, which are sometimes classified as different calls, but, as with the whines and howls previously described, we suggest that subtypes just represent extreme variants of barks. The most tonal barks with the highest frequency (above 400 Hz) are referred to as *yelps* (Cohen and Fox 1976; Schassburger 1993), which have been suggested to develop from whines by temporal shortening. At the other side of the range stands the *woof (or cough),* which has low fundamental frequency (90–120 Hz) and is noisy, produced by a short (0.1–0.15 s) burst of air emitted through closed or slightly open mouth and can be an intermittent form between barks and growls. Finally, real barks are noisy, loud bursts, with a medium fundamental frequency (150–170 Hz) falling between yelps and woofs (Fig. 4.5).

In wolves, barks and woofs are used primarily in threat contexts, such as territorial defence or dominance interactions, while yelps occur more in fearful situations and are used relatively infrequently (Schassburger 1993). This contrasts substantially with the vocal behaviour of dogs, which bark basically in any social context (Cohen and Fox 1976). This phenomenon has of course prompted many researchers to investigate this obvious discrepancy. Bleicher (1963) suggested that dog barks are just non-communicative bursts of excitement and Cohen and Fox (1976) argued that barks became hypertrophied during domestication due to the relaxation of selection pressure for silence. However, Cohen and Fox also emphasize that humans would prefer dogs during selection which provide information with their barks, but also suggest that selection towards high contextual specificity is unlikely. If the latter is true, barks should have gradually lost their communicative role (Coppinger and Feinstein 1991). Boitani and Ciucci (1995) findings show that feral dogs also use barks in similarly limited number of contexts as wolves supporting the relaxation hypothesis. By studying and comparing the acoustic structure of dog barks with other mammalian and bird vocalizations, Lord et al. (2009) raised the possibility that barks originally functioned as mobbing signals to threaten intruders and assemble pack members to protect their territory. They suggest that the hypertrophy of barks is due to the shrink of dogs' living area and the continuous disturbances in the human environment.

Another possible scenario is that during domestication barks were released from selective pressures and became more prominent. Later, due to the selective breeding by humans who preferred more communicative and understandable dogs, barks diversified to provide inner state information (Pongrácz et al. 2010) as well as contextual information (Tembrock 1976). This idea is supported by recent findings demonstrating that dog barks show specific contextual differences (Feddersen-Petersen 2000; Yin 2002; Yin and McCowan 2004). Moreover, it also appears that humans can categorize dog barks by their context surprisingly well and are able to assess their probable inner state (Pongrácz et al. 2005). For example, humans could discriminate dog barks recorded from situations when a stranger approached the household, before walks, when left alone or during play, irrespective of whether they owned a dog or not. Also they assigned aggressive inner state to barks recorded from agonistic contexts, happy inner states to playful contexts and fearful inner states to stressed contexts like separation from the owner. In a similar way to howls, barks conform to Morton's rules and humans apparently use their frequency, tonality and rhythm to recognize the dogs' inner states (Pongrácz et al. 2006). Further studies showed that dogs can also discriminate barks recorded from different contexts, and dogs can also differentiate between different barking individuals suggesting that these calls might convey specific identity information (Molnár et al. 2009). In spite of this, humans could not differentiate individual dogs by their barks, nor could owners recognize the bark of their own dog when confronted with barks of other individuals of the same breed (Molnár et al. 2006). Although there is a growing body of research on dog barks, it is important to highlight that only by directly comparing barking behaviour between dogs and wolves, and thorough acoustic analysis of barks from both species will it be possible to unpack why and how this interesting difference in their vocal behaviour emerged.

2.2.4 Grunt

Grunts are low frequency (85–200 Hz), short, harmonic or slightly noisy calls of wolf and dog pups (Cohen and Fox 1976) emitted during relief, comfort or pleasure. In dogs, they are also present in adulthood (Bleicher 1963). Our personal observations showed that they occur during scratching or petting by humans, especially in greeting situation, raising the possibility that this call is a paedomorphic relic, but further investigations would be necessary to support this hypothesis (Fig. 4.6).

2.2.5 Groan

Groans are spectrally and acoustically similar to moans. They have a relatively low or medium fundamental frequency (250–450 Hz) modulated periodically, with low level of spectral noise. These calls are emitted by dog pups and adults in acute distress, pain or sickness (Bleicher 1963), but mentioned by Cohen and Fox (1976) as general canid vocalization too.

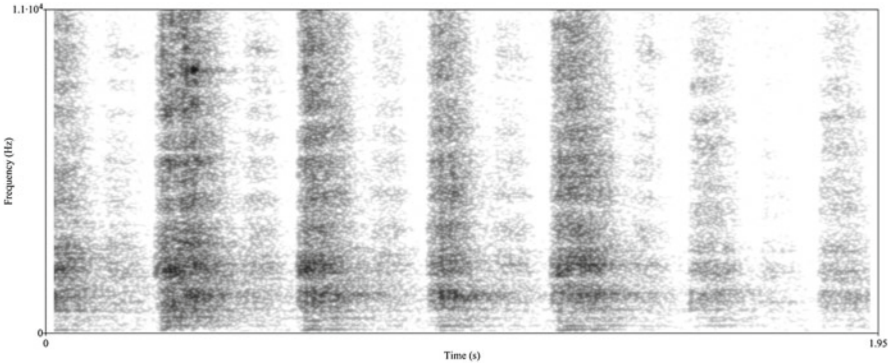

Fig. 4.6 Dog grunt (Tamás Faragó's recording)

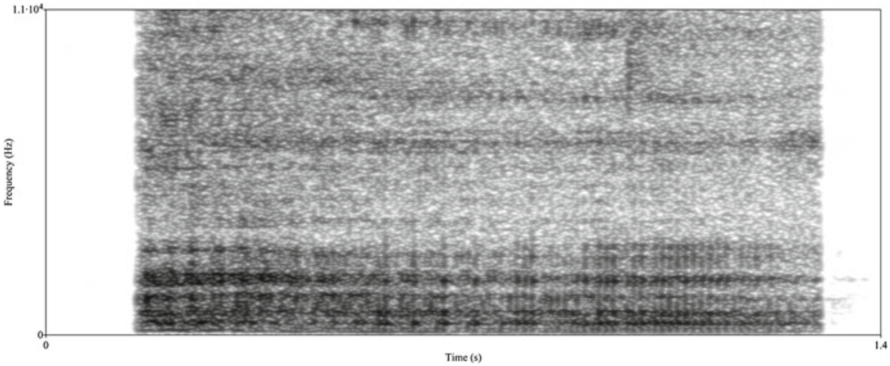

Fig. 4.7 Dog growl (Tamás Faragó's recording)

2.3 Noisy Calls

2.3.1 Growls

Growl vocalisations are generally elongated, broadband, low frequency (80–300 Hz) vocalizations with low frequency modulation and a high concentration of noise but still with a visible harmonic structure (Riede and Fitch 1999). Due to their low amplitude, growls are used only as short-range signals. On a behavioural level, two types are distinguished: the *snort*, which is the nasal form of the growl, emitted with closed mouth (Cohen and Fox 1976), and *snarl,* an intense version of growl with a low frequency (fundamental at 140–170 Hz) and a strong noise component (Tembrock 1976). This latter sound occurs with an opened mouth and is emitted with retracted lips and clearly visible, exposed canines. Growls in wolves and dogs can sometimes be shortened and repetitive becoming more similar to grunts and pants (Cohen and Fox 1976) (Fig. 4.7).

Growls are used by both species mainly in threatening and defensive contexts, such as expressing dominance, territoriality, protest, violation of personal space or protection of resources (Schassburger 1993), but also can appear during greeting (Cohen and Fox 1976) or social play (Feddersen-Petersen 2000). These playful growls (at least in dogs) are higher-pitched, short and pulsing in contrast to growls produced in threatening contexts, probably communicating playful inner state (Faragó et al. 2010b). This dichotomy between growls produced in playful and aggressive contexts is very similar to barks produced in different contexts. In line with this, humans are able to extract dogs' inner states from dog growl structure and they are able to recognize the context based on the acoustic properties (Faragó 2011). Moreover, in a playback study, Faragó et al. (2010b) found that dogs placed in a food competition context reacted with withdrawal only when the growls played back originated from a food guarding context. If they were exposed to playful growls or growls evoked by a threatening human, the dogs did not show retreat behaviour and took or ate the food suggesting that also dogs can extract contextual information from growls of other dogs. Interestingly, dogs' threatening and food guarding growls did not differ significantly in structure (although humans found threatening growls slightly less aggressive). Moreover, Kappe (1996) found that wolf pups modified their growls according to their inner state: during food defence, wolves growled longer with a higher peak frequency when they were hungry. This latter result is somewhat contradictory with what we might expect based on other vocalizations and Morton's motivational structural rules. Unfortunately, in this study detailed acoustic and behavioural analyses do not exist and thus it is possible that the raised peak frequency was due to changes in formant positions, while the fundamental frequency did not change or even lowered. This formant change can be easily caused by the difference in the opening of the mouth or the retraction of lips communicating a higher level of aggression.

As growls are used in agonistic contexts, it could be posited that they carry honest information about the physical strength of the individual. Indeed, the noisy and broadband acoustic structure of growls makes formants conspicuous, and their dispersion across the spectrum can act as indexical cue closely related with body size. In dogs, Riede and Fitch (1999) and Taylor et al. (2008) demonstrated formant cues to body size, and in the latter study particularly, it turned out that humans can reliably assess the size of the growling dog based on formant dispersion. Moreover, humans tend to rate growls as more aggressive if the dogs sound larger due to manipulation of formants (Taylor et al. 2010a). However, not only humans can use formant dispersion in growls as a source of size information. Faragó et al. (2010a) and Taylor et al. (2010a) both found in slightly different crossmodal matching experiments that dogs are able to assess the size of the growling dog via acoustic information alone. Furthermore, Faragó et al's results indicated that this works in a species specific way: the dogs were provided with two differently sized but otherwise identical dog pictures accompanied with agonistic, food guarding growls. The subjects showed a clear looking preference towards that dog picture which was matched in size to the growling dog. However, if the pictures showed geometric shapes or cats, this preference disappeared (Faragó et al. 2010a). Interestingly, if we played

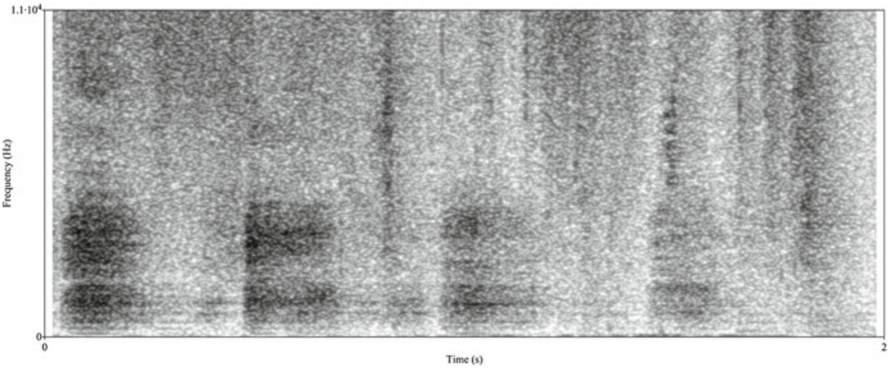

Fig. 4.8 Dog pant (Tamás Faragó's recording)

back dog growls recorded in a playful context, the dogs tended to look at the larger picture irrespective of the size of the dog emitting the growl (Bálint et al. 2013). This reaction is probably due to the fact that playful growls have lower formant dispersion making the source individual sound larger (Faragó et al. 2010b). We can assume that this potential exaggeration can be part of the playful communication together with the higher fundamental frequency and shortened duration.

These results together with the potential flexibility of the vocal apparatus of wolves and dogs (like retracting or protruding the lips, opening the mouth, positioning the tongue or pulling back the larynx (see for example Fitch and Reby (2001)), raise the possibility that canids are able to actively modify their vocalizations to influence their counterparts' behaviour, for example by making themselves sound larger during agonistic encounters or communicating playful intentions. In contrast to dog growls, we know little about growls in wolves and how dominance or social status can affect their growls. More work on wolf growls is imperative to better understand the function of growls generally and what role they play in establishing or maintaining social relationships.

2.4 Atonal Calls

These sounds are lacking any harmonic structure, and produced by turbulent flow of air, or mechanic noise.

2.4.1 Pant

Specific, noisy, forced in- and exhale, primarily associated with thermoregulation, but it occurs also during play soliciting and greeting contexts suggesting that they can also serve as communicative signals (Cohen and Fox 1976) (Fig. 4.8).

2.4.2 Tooth Snap

This sound is used in wolves, coyotes and dogs in play and agonistic contexts. The sound is generated by the fast closing and collision of the teeth, communicating high level of threat or excitement.

3 Conclusion

The wolf (and dog) vocal system represents an acoustically rich social communication system capable of conveying a diverse range of information. Elements of the repertoire can code both internal and external information, moreover, the ability of combining and mixing different calls raise the possibility of coding additional syntactical information as has been shown in several primate species (Arnold and Zuberbühler 2011; Candiotti et al. 2011). Besides investigating how information is coded in wolf vocalizations and how these calls are used in social contexts, the comparison with dog communication can provide important insights into how socialisation and domestication has and can influence communication (and cognitive) systems of animals. Studying how barks changed through domestication and artificial selection gaining a possible new function in dog-human communication, or how losing their ancestral social system de-emphasised howling in dogs ultimately may also help us to better understand the function of specific vocalisations from these animals and their communication systems. For such comprehensive studies however, it is indispensable to have a unified and objective classification of calls based on thorough measurements of numerous acoustic parameters and applying up-to-date multivariate statistical methods.

One explanation for the evolution of complex communication highlights social complexity as a major driving force (Dunbar 1998; McComb and Semple 2005). This hypothesis may also contribute towards our understanding regarding the emergence of language given that humans reside in the most complex social systems and also possess the most sophisticated communication system. Indeed, phylogenetic meta-analyses across the primate taxa support the predictions of the social and vocal complexity hypothesis. However, Fitch et al. (2010) emphasise, to understand the evolution of language and see what mechanisms were important in this process it is essential to compare a wide range of closely and distantly related species. Studying the link between vocal and social complexity in canids therefore provides a crucial comparative data point and from the comparative work of Cohen and Fox (1976) it seems that the communication system of canids also aligns with the social and vocal complexity hypothesis postulated by Semple and McComb (2005).

Several studies provide us with results regarding, how wolf howls are conveying individual or group specific information, although the perception side is far less investigated. Surprisingly, such basic questions such as whether or not wolves can differentiate or recognize others by their howls or other vocalizations are still not answered. To obtain a complete and holistic understanding of the wolf communication system, it would be necessary to rigorously and systematically test the functions of the calls empirically (e.g. with playback experiments, cross-modal designs) in controlled, semi-naturalistic conditions. The Wolf Science Center in Austria provides the opportunity to do such studies and not just with wolf, but also with dog packs raised and kept in the same way as the wolves.

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Chapter 5
Social Origin of Vocal Communication in Rodents

Stefan M. Brudzynski

Abstract The Chapter is focused on evolutionary origin of vocal communication in rodents, and particularly ultrasonic vocalization in rats. Several hypotheses are discussed, including mother-infant interaction and expression of emotional/motivational states as mechanisms initiating vocal communication. Other hypotheses or contributing factors to evolution of vocal signalling are also presented, as predator pressure and habitat type, size and complexity of the social group, and security motivation system. Rats developed several ultrasonic calls that are explained and categorized into five types: short and long 22 kHz calls, flat 50 kHz calls and frequency-modulated 50 kHz calls with or without trills. It is concluded that mammalian vocalizations serve as ethological transmitter, termed ethotransmitter, that is produced by specialized organ (larynx), selectively recognized and decoded by the brain of conspecifics, and capable of changing emotional state and behavior of the receivers.

Keywords Vocal communication • Ultrasonic vocalization • 22 kHz calls • 50 kHz calls • Rats • Rodents • Evolution of vocalization • Rat communication system • Ethotransmission

1 Introduction

Social communication in all vertebrates has a long phylogenetic history. Generation of acoustic signals and vocalizations is one of the oldest means of social communication in most vertebrates, from majority of fishes to mammals (Bass et al. 2008). It is important to emphasize that ancestral vocal communication is a trait found in

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relation to animal social behavior, thus, enhancement of communication between individuals of the same species is of particular evolutionary importance. Secondly, in spite of the fact that animals may communicate in many modalities (e.g., by movements, emission of acoustic, tactile, olfactory signals, or other means), visual and sound communication prevailed (Rosenthal and Ryan 2000). Although, visual communication may take many forms related to motion, pattern, colour, or light emission (bioluminescence), most researchers agree that acoustic communication has more advantages than the visual one (McFarland 1987). Vocal signals are not dependent on the daylight, they can be emitted from a far distance, or contrary to that, can be dissipated by vegetation in short rage communication or underground communication, they may not reveal location of the caller or have features facilitating its localization, and finally, they offer extremely rich possibilities of signal coding. Also, vocal signals may be easily perceived by members of one species but be undetectable to another (e.g., vocalizations with very low and very high sound frequencies).

This Chapter is focused on vocal communication in rodents, and predominantly in the rat species. Rodents have approximately 2,280 species, what represents 42 % of all mammalian species (Carleton and Musser 2005; Sales 2010), so they may be regarded as the most flourishing and biologically thriving mammalian group. They have relatively fast reproductive cycle (gestation period of 21 days and many generations per year), and managed to colonize most habitats on all continents, except Antarctica. This is particularly true for rats that have been regarded as the most successful mammalian species after humans. One of the factors contributing to this success is their well-organized social life (Nyby and Whitney 1978) and their well-developed vocal communication system (Brudzynski 2009).

2 Factors Contributing to Evolution of Rat Vocal Communication

As mentioned in the Introduction, vocal communication is the oldest and widespread interindividual signalling system in vertebrates. Embryological evidences provide support for this notion. Well-documented comparative evidence strongly suggests that vocalization is controlled by a highly conserved, homolog central pattern generating circuitry located in the caudal hindbrain. It originates from the last embryonic rhombomere (rh8, segment of the developing neural tube) and rostral spinal cord in all vocal vertebrates, and it represents a common ancestral compartment for vocal communication in vertebrates (Kelly and Bass 2010; Bass and Chagnaut 2012). Thus, emission and central regulation of vocalization had to appear very early in vertebrate evolution, and it was postulated to be based on evolution of the myelinated ventral vagal complex of the autonomic system (Porges 2001). The ventral vagal complex controls such behavioral patterns as eyelid opening, head turning, movements of facial muscles and mastication, middle-ear muscles, and laryngeal and pharyngeal muscles important for vocalization. Collectively, functions of this system are focused on control of sensory input from the environment and on social engagement, thus this system has been termed social engagement system (Porges 2001, 2003).

The following subsections provide hypotheses explaining the origin of vocal communication in rodents.

2.1 Mother-Infant Interaction

Vocal interaction of mothers with their infants was suggested as one of the initial evolutionary mechanisms stimulating development of mammalian vocal communication. Paul D. MacLean has suggested that there were three critical developments accompanying evolutionary emergence of early mammals: nursing, audiovocal communication with mother, and play (Maclean 1985). Infant vocalizations of numerous species, known as “crying” have been suggested as an universal occurrence in mammalian species and as a main component of vocal communication with mothers in all mammals (Newman 2007). The need for such evolutionary-preserved vocal communication with mother may be well explained in the rat species.

Rat infants are born as altricial pups. The term ‘altricial’ means that the newborns are incapable of independent life and their survival depends entirely on maternal help and nourishment. Rat pups are born naked, blind, deaf, and incapable of effectively moving around. Presence and activity of mothers is critical for pup feeding, digestion, cleaning, thermoregulation, hormonal communication, and pup immune function (Galler and Propert 1982; Gubernick and Alberts 1983; Moore and Chadwick-Diaz 1986; Pérez-Cano et al. 2012; Nagasawa et al. 2012). It is also critical that pups remain in the nest together with their siblings in a huddle. Huddling is important not only from the thermoregulatory reasons but it enables pups acquiring olfactory preferences and species-specific odors (Alberts 2007). An infant separated from the nest has no chances of survival. Pup vocalization, known as separation calls, isolation calls, or distress calls, in the case of a sudden isolation from the nest, is one of the mechanisms attracting mother’s attention and providing pup with maternal transport back to the nest and needed care (Hofer 1996; Zimmerberg et al. 2003; Wöhr and Schwarting 2008).

The isolation calls are usually emitted in large numbers and rats with higher emotionality traits emit significantly more calls than infants with low emotionality (Naito et al. 2000; Wöhr and Schwarting 2008). It is believed that this type of vocal communication could represent the starting point for continued development of vocalization and communication that would be paralleled by development of larynx (Hofer 2010). The vocalizations in a form of isolation calls would serve initially for communication with mother, and then they would be maintained, further developed, modified, and used for communication within the rat social group.

2.2 Expression of Emotional/Motivational State

Vocalizations emitted by altricial infants and stages of their vocal development might reveal details of phylogenetic development. The early infant-mother communication may serve as a "living fossil" and may have preserved stages of evolutionary development of communication. Results of experimental studies of rat infantile vocalizations (isolation calls or separation calls) suggested that in addition to their calling-for-help function, the isolation calls express infant emotional state (Hofer et al. 1999, 2002; Groenink et al. 2008; Hofer 2010). Pharmacological and genetic selection studies have further shown that pups that are separated from their mother are in a state of anxiety because anxiolytics (anti-anxiety pharmacological agents) can reduce that state and decrease number of vocalizations (Naito et al. 2000; Groenink et al. 2008). The magnitude of this state (or its urgency) is expressed in the number of emitted isolation calls per time unit (Naito et al. 2000), and possibly by increasing modulation of sound frequency in a fashion similar to ambulance siren, that intensifies with age (Brudzynski et al.1999). For example, it was found that pups having increased number of isolation calls at the postnatal day 10–12 by genetic selection had also decreased ability to recognize odors associated with their mothers (Harmon et al. 2008), thus could express intense anxiety.

These findings provide an insight into an early evolution of vocal communication of emotional states in rats. Natural selection has reinforced isolation calls as a means of increasing pups' survival, and at the same time, reinforced emotional communication. As indicated by Myron A. Hofer, this evolutionary process, involving pups and responding mothers that provided help to pups separated from the huddle, has increased both the trait of calling on the part of the pups, as well the trait of retrieving pups and being responsive and sensitive to infant cries on the part of the mothers (Hofer 2010). The fact that altricial rat pups are blind and deaf at birth (Schank and Alberts 2000) but still emit isolation calls, to which mothers respond, might indicate that evolution of emotional communication developed after, or with some delay after appearance of vocal signals serving primary survival.

Emotional communication would further develop in the adult social life. This can be observed in the ontogenetic development. After weaning, rats quickly develop adult type of vocalizations that can be divided into two large groups: the 22 kHz group of vocalizations expressing negative or aversive state, and the 50 kHz group of vocalizations expressing positive or appetitive state (Brudzynski 2007). Emission of vocalizations became inseparable from emotional expression. This may be demonstrated by selective breeding. Such a breeding in adolescence, which was based on the number of emitted ultrasonic vocalizations, can select different types of emotionality in adulthood (Burgdorf et al. 2008, 2009; Brudzynski et al. 2011).

2.3 Predator Pressure

The emission of vocalizations in adult rats signalling danger or potential danger was mostly observed in natural or semi-natural condition in response to close presence of a predator. Therefore, it has been hypothesized that evolution of ultrasonic communication in rats was initiated as an anti-predator defensive strategy, as a basic adaptation for survival (Blanchard and Blanchard 1989; Blanchard et al. 1991). Experiments performed by Robert J. Blanchard and his coworkers provided evidence that alarm calls emitted by a dominant rat in response to a predator (a cat) caused response of the entire rat colony that ran for hiding. This response included also those rats that have not encountered the cat directly (Blanchard and Blanchard, 1989; Blanchard et al. 1991). The calls emitted in this situation (the 22 kHz vocalizations) were termed alarm calls (Blanchard et al. 1991, 1992; Litvin et al. 2007). Emission of alarm calls would quickly inform other members of the colony about the presence of a predator and allow them to escape and hide without the need for a direct contact with predator. In the further process of evolution, rats would start using these calls also as an alarm signal related to any other danger or potential danger, or unpleasant stimulus, as it was shown for air-puff, footshock, aggressive opponent, or approach of an unfamiliar researcher (Thomas et al. 1983; Kaltwasser 1990; Brudzynski and Ociepa 1992; Tonoue et al. 1986; Brudzynski and Holland 2005). Other forms of rat ultrasonic vocalization would evolve later or concurrently to alarm calls.

This hypothesis is further supported by the fact that rodents have a large number of predators originating from almost all major groups of vertebrates and, thus, live under a significant predation pressure. Numerous species of reptiles, birds, and some mammals prey almost exclusively on rodents. Development of ultrasonic communication system has a highly adaptive value because many species of these predators (especially snakes and birds of prey) cannot hear ultrasounds (Sachs et al. 1978; Young 2003).

The fact that predation pressure can influence vocal communication is also supported by findings in primates. It was found in Diana monkeys that higher predation pressure increased complexity of acoustic communication (Stephan and Zuberbühler 2008).

2.4 Type of Predators and Habitat

Rodent species live in many habitats that vary in predation pressure. Such factors as the type of the habitat and presence of many predators using different hunting strategies were postulated to influence evolution of alarm vocalizations (Robinson 1981; Sherman 1985; Furrer and Manser 2009). Ground-dwelling sciurid rodents (as Belding's ground squirrels) living in open areas quickly run for hiding in response to any predator (Blumstein and Armitage 1997a), thus the argument was made that their evolution of alarm calls may not need to distinguish among predators but simply express different levels of urgency, depending on the proximity to the predator (Furrer and Manser 2009). On the other hand, rodents living in habitats rich in many predators that use different hunting strategies (from the air or from the ground), need information about the type of predator and this should be reflected in parameters of their alarm calls (Sherman 1985; Blumstein 1999; Furrer and Manser 2009).

Alarm vocalizations that unambiguously denote different predators are termed functionally referential calls (Blumstein 1999).

Functionally referential vocalizations may be emitted simultaneously with expression of emotional states. Such referential calls have been reported in many mammalian species (Manser 2001; Gifford et al. 2003; Slocombe, Zuberbühler 2005; Furrer and Manser 2009), however, it is believed that they do not work in the same way as word-like referential signals in humans because they are not universal and emitted only in specific contexts (Wheeler and Fischer 2012).

Rats live in a variety of habitats, although they are mostly borrowers. Rats are obligatory synantropic organisms, i.e., closely following humans and are not found far from human dwellings. Rats often use human proximity as a protection from other predators. Accordingly, it is difficult to fully compare them with other species living in the wild far from humans. Rats' alarm calls have not been found to be functionally referential, although, rats still have large variety of potential predators and use 22 kHz alarm vocalizations that have considerable acoustic variety allowing for additional coding (Brudzynski 2005; see Sect. 3.1, below). There are also reports from other rodent species (great gerbil) that their alarm calls have some variation of the calls dependent on the type of predator (Randall et al. 2005).

2.5 Size of the Social Group and Discrimination Among Individuals

Rats usually form small colonies of several individuals. However, depending on the environmental conditions, food and space availability, the size of the colony may reach hundreds of rats. Average size of a developed wild rat colony is between 100 and 200 individuals (Calhoun 1950; Würbel 2009). This is a large number of individuals for a mammalian species. It has been postulated that the increasing size of the social group may be a driving force for the development of vocal communication (Blumstein and Armitage 1997b; Pollard and Blumstein 2011). Increasing number of organisms within a social group would create a need to recognize individuals and remember past interactions with those individuals. Development of vocal communication could serve this purpose (Freeberg et al. 2012a). This process would lead to development of signature features in the individual vocalizations that would allow for individual recognition, both in the sense of discriminating other individuals, as well being discriminated by others (Pollard and Blumstein 2011).

Results of a recent study, comparing individual alarm calls of different species of sciurid rodents living in colonies of different sizes, concluded that the size of the social group (number of individuals) is linked with of the individuality of alarm vocalizations (Pollard and Blumstein 2011). Individuality was defined statistically as a condition, in which interindividual variation in the signal exceeds intraindividual variation. Species having larger number of individuals in their social groups, but not more complex organization of colonies, had more signature information in their alarm vocalizations (Pollard and Blumstein 2011, 2012). Such a driving force would have a purely social origin, that is, it would facilitate social recognition and interactions within the group, and perhaps improve social status. There is paucity of research on this topic in the rat species.

2.6 Security Motivation System

It has been suggested that a special motivational system has evolved, termed security motivation system, to cope with potential dangers, unpredictable risks, and uncertainty (Szechtman and Woody 2004; Hinds et al. 2010; Woody and Szechtman 2011). The security motivation would be geared toward recognizing indices of potential threats and engaging the organism in precautionary behavior. The security motivation system would drive animal preventive defensive behaviors, including vocalizations.

The defensive behavior has been classified as primary or secondary (Edmunds 1974). The primary defense decreases animal's changes of being detected by predator(s) (e.g., remain in hiding), while the secondary defense pertains to situations, in which the animal is already detected or found by the predator. The secondary defensive behaviors include immobility, avoidance, flight, or defensive threat and defensive attack. A common feature of all these primary and secondary defences is the fact that only one individual, the one demonstrating the behavior, can benefit from it. Development of vocal alarm system created a higher-order defensive behavior (Brudzynski and Holland 2005). Members of a social group do not need to be continuously screening environment for appearance of potential predator, but instead, they may largely relay on alarm calls being likely emitted by other members of the social group, who spotted the predator first (Brudzynski 2009).

The evolution of the security motivation system has added a new quality to this communication system. Rats, for example, do not need to wait until any member of the colony will detect or catch sight of a predator but they may try to predict presence of the predator based on some indirect observations. While classical alarm calls are emitted after detection of predator, vocal signals driven by the security motivation system would be emitted before any predator is spotted. These vocal signalling should be termed apprehensive vocalization and would be emitted for security reasons, i.e., just in case. The apprehensive vocalizations would be a next evolutionary step leading to communication about the future and probability of danger, and not only about the current events as in the case of alarm calls.

The apprehensive vocalizations inform the entire social group not about the actual presence of a predator but serve as a precautionary signalling of a potential danger. There are many indirect evidences that rats may use the 22 kHz calls in this manner in some situations in an analog way as rats emit anticipatory calls (Ma et al. 2010). Experimental rats are raised by friendly humans, are in frequent contacts with them, and spend their entire life in the cage environment. Even though, human caregivers provide protection, resources, and are always gentle with animals, rat may emit

22 kHz calls in response to close proximity of an unfamiliar person (Brudzynski and Ociepa 1992). These calls might be interpreted as apprehensive vocalizations because past experiences of these rats would not indicate any direct danger.

The drive from the security motivation system would promote development of larger social groups. This evolutionary mechanism might not be directly and causally related to the size of the social group itself but it may drive the size of the social group together with development of apprehensive vocalizations.

2.7 Complexity of the Social Group

Social complexity has been also suggested as a potential factor promoting and increasing vocal communication and communicative complexity, thus, social complexity was postulated as a driver of complex communication (Freeberg et al. 2012). Social complexity is defined as a social system, “in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time”. (ibid., p. 1787). Communicative complexity pertains to communication systems “that contain a large number of structurally and functionally distinct elements (…) or possess a high amount of bits of information (ibid., p. 1787).

Comparative study of alarm calls of ground-dwelling social sciurid rodents (ground squirrels, prairie dogs, and marmots) were chosen because these groups of rodents have wide range of social structures, as well substantially differ in acoustic structure of their alarm vocalizations (Pollard and Blumstein 2011, 2012). The results have shown that, although the size of the social group predicted alarm call individuality, social complexity predicted alarm call repertoire (number of distinct acoustic elements forming alarm calls) (Pollard and Blumstein 2012).

This finding was also confirmed in other mammals (McComb and Semple 2005) and it should also relate to rats. For example, social organization of rat and mouse colonies is different as to its complexity and vocal communication systems (Portfors 2007). Rat social organization is usually more closed, organized, and hierarchical with one dominant alpha male, as compared to mice having many overlapping local sub-populations (demes), each with a dominant male. Also, mouse social groups have higher population density and are less stable than those of rats (Nyby and Whitney 1978; Bronson 1979).

Although mice can emit many different types of ultrasonic vocalizations, particularly during reproductive behavior, their calls were not found to be clear indicators of positive and negative emotional states as it was found in the rat species, but they rather serve other social functions (Portfors 2007). Although, mice most probably do express their emotional states, their vocal communication system is not as clearly structured as that of rats. Finally, adult mice normally do not vocalize ultrasonically during agonistic (combative) or play situations but their ultrasonic calls are rather restricted to reproductive situations (Nyby 2010). Thus, it seems that rat social organization shows higher complexity and higher communicative complexity as compared to that in mice.

3 Ultrasonic Communication System of Adult Rats

Ultrasonic vocalization have been described in at least 50 species of rodents (Sales 2010), however vocal communication system of the rat have been studied and understood the best. Multitude of studies of rat ultrasonic calls, using behavioral, bioacoustics, physiological, and pharmacological methods, suggest that they have developed a communication system with distinguishable acoustic signals differing in semiotic content, that is demonstrating features of situation- or state-specific emission, as well as predictable behaviors in the receivers (Brudzynski 2005). Our understanding of communicative value of particular signals in this system is steadily increasing, and it may be summarized and explained in a form of dichotomous branching tree model (Fig. 5.1). Although, there is a considerable individual variation in parameters of vocalizations emitted by rats (Brudzynski and Holland 2005; Schwarting et al. 2007; Wöhr et al. 2008), that is also dependent on age, gender and gonadal hormone state (Haney and Miczek 1993; Basken et al. 2012), there are some basic elements distinguishing categories of vocalizations that are also recognized by rat receivers (Brudzynski and Chiu 1995; Burgdorf et al. 2008).

At each dichotomous branching point (numbers 1–5 in Fig. 5.1), the signals differ in acoustic features to such a degree that it allows the receivers for an unambiguous discrimination between the two signals. At the first point (1), rats need to make decision whether they will emit the audible squeak (or shrill) or an ultrasonic vocal signal. The audible vocalizations are emitted in close proximity to other individuals and are usually directed to predators (Litvin et al. 2007) or potential predators. They are also directed to other rats at very close distance or in direct contact with each other in urgent situations as during fight or perception of pain.

Emission of vocalization in the audible range of sound frequencies is risky because calls may be received by nearby predators and reveal position of the vocalizing animal. Therefore, rats usually emit the squeaks when they are already spotted by the predator, they do not have any obvious way of escape, and prepare themselves for an active defense (Litvin et al. 2007). In other situations, ultrasonic vocalizations are emitted. They are emitted from a distance and exclusively directed to members of their species, usually of the same social group. In Fig. 5.1, all categories of vocalization emitted in aversive situations are shown in a gray box on the left hand side (labeled AVERSIVE), while of categories emitted in appetitive situations are shown in gray box on the right hand side (labeled APPETITIVE). As mentioned previously and illustrated in Fig. 5.1, it seems that vocalizations signalling aversive states and dangerous situations evolved earlier, before the appetitive calls appeared.

3.1 Aversive Ultrasonic Vocalizations

At the dichotomous point two (point 2 in Fig. 5.1) when the rat is going to emit ultrasonic vocalization, the distinction between two categories of calls depends on the situation and the nature of the emotional state associated with this situation.

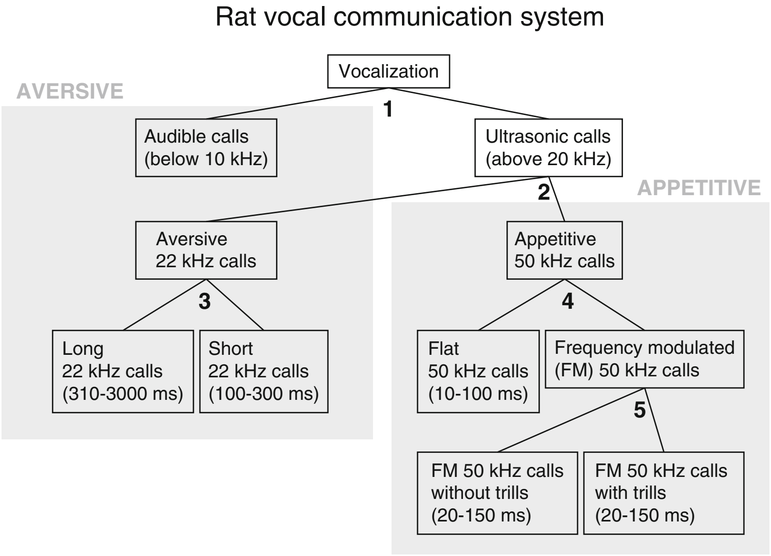

Fig. 5.1 Dichotomous branching tree model of rat vocal communication system. Five branching points are labeled with numbers *1–5*, leading to five distinct types of vocalizations described in the text. The distinction between audible or ultrasonic sound frequencies (in kHz) is based on human hearing. The range of durations of a single call for each type is given in ms. *Gray boxes* house two main groups of aversive or appetitive calls. Other details are explained in the text

The dangerous situations that threaten biological, physiological, or psychosocial integrity and stability will induce negative (aversive) emotional state in the animal and emission of alarm calls (Blanchard et al. 1991; Brudzynski and Holland 2005; Brudzynski 2007; Litvin et al. 2007; Burgdorf et al. 2008). All these calls are termed collectively ‘22 kHz’ vocalization category regardless of minor variations in frequency. Thus, this is a group of calls, not just calls with strictly 22 kHz frequency. The common features of these calls are their low sound frequency (within ultrasonic range), between 20 and 35 kHz, long call duration (300 – over 3,000 ms) and almost lack of frequency modulation, i.e., flat appearance on the sonographic record (Brudzynski and Holland 2005).

The 22 kHz calls appear in such situations as proximity of a predator (within the range allowing escape), physical danger or threat of a painful stimulus (e.g., foot-shock), unpredictable unpleasant stimulus (e.g., air-puff), defeat in aggressive contacts, or secession of physical contact after copulation (Barfield and Geyer 1975; Kaltwasser 1990, 1991; Blanchard et al. 1991, 1992; Brudzynski and Ociepa 1992; Brudzynski and Holland 2005).

The aversive 22 kHz calls may be further divided into two categories differing in the duration of single vocalizations (number 3 in the Fig. 5.1). The short calls may last from 20 ms to approximately 300 ms, while the long calls have duration from 310 ms to over 3,000 ms (Brudzynski et al. 1993). The longest 22 kHz call ever recorded had 3,940 ms (3.9 s, ibid.). Presently, it is not clear, what is the semiotic difference between these call categories, despite the fact that they may differ up to 150 times in duration. The long 22 kHz calls differ more than 10-times in duration within this category, so it may be suggested that the duration of the long 22 kHz signals expresses the urgency of the signal. However, if it is assumed that the increasing doses of pharmacological agent that can initiate 22 kHz calls (carbachol) represent increasing urgency, the results showed that the call duration decreased with the increasing dose of carbachol but the number of short 22 kHz calls increased (Brudzynski 1994). It is thus possible, that shorter 22 kHz calls, particularly emitted in large numbers might signal higher urgency. On the other hand, short calls (less than 300 ms) were also observed to be interdigitated with the long 22 kHz calls suggesting that they may play role in modifying the semiotic value of the long calls.

3.2 Appetitive Ultrasonic Vocalizations

The situations that increase safety and biological, physiological, or psychosocial stability will induce positive (appetitive) emotional states and emission of appetitive calls termed ‘50 kHz’ vocalizations (regardless of their frequency variation and modulation, number 4 in Fig. 5.1). The common features of the 50 kHz calls that distinguish them from 22 kHz calls are their high sound peak frequency, between 35 and 80 kHz, very short call duration (usually 20–150 ms), as well as significant frequency modulation of many of the calls (Brudzynski 2007, 2013; Burgdorf et al. 2008). Almost all acoustic parameters of 50 kHz vocalizations are not overlapping with parameters of 22 kHz vocalizations, thus allowing rats for an unambiguous distinction between positive and negative states of the caller (Brudzynski 2007).

The category of 50 kHz vocalizations can be further divided into the next two different types of 50 kHz calls with or without frequency modulation (point 4 in Fig. 5.1). The 50 kHz calls without frequency modulation are termed flat 50 kHz calls. Their frequency range is between 35 and 50 kHz, and their duration is between 10 and 100 ms, similar to other 50 kHz calls (Wöhr et al. 2008; Takahashi et al. 2010). The sound frequency, however, remains relatively unchanged over the duration of the call. On the other hand, the frequency modulated (FM) 50 kHz vocalizations range in frequency from approx. 40–80 kHz with call duration of 20–150 ms, and they have dramatically changing sound frequency within a single call (Burgdorf et al. 2008; Wright et al. 2010; Brudzynski et al. 2012). The frequency changes are usually abrupt in a form of steps or sine wave-resembling trills. Thus, the frequency modulation remains the distinguishing features between the flat and FM 50 kHz calls.

Although all types of 50 kHz calls are emitted in appetitive situations, the flat and FM 50 kHz calls are emitted in somewhat different circumstances. The FM 50 kHz vocalizations are emitted in rewarding and highly positively motivated situations, and intense affective states (Burgdorf et al. 2008, 2011; Burgdorf and Moskal 2010). The flat 50 kHz calls were interpreted as having social-coordinating function or serve as a contact call (Wöhr et al. 2008) and were also emitted during feeding behavior (Takahashi et al. 2010).

As illustrated in Fig. 5.1, the FM 50 kHz vocalizations may be further subdivided into two categories according to the nature of frequency modulation (point 5, Fig. 5.1). Frequency modulation may occur in a step form, a sudden jump in frequency up or down, or it can occur as a rapid non-step change in sound frequency. The other characteristic type of frequency modulation is the trill, a rapid fluctuation of sound frequency resembling a sing wave. The FM 50 kHz vocalization may have different forms, ranging from trills only, step-trill with one or more steps, to only steps and other frequency changes (Burgdorf et al. 2008; Wright et al. 2010). Trills seem to be emitted in the most emotionally charged situations, i.e., situations with the highest emotional arousal (Burgdorf et al. 2008). Since rats can distinguish vocalizations with frequency modulation from those non-modulated (ibid.), there is very likely that they can also distinguish trills from other forms of modulation. Therefore, the last two categories of FM 50 kHz calls are those with or without trills (point 5 in Fig. 5.1). Communication of states with the highest affective arousal would be associated with the trill-type FM 50 kHz calls. There is possibility of further division of FM vocalizations but this awaits further studies.

4 Vocalizations as Ethotransmitters

Vocalizations of rats play many biologically important communicative roles, as call for help, defense against predators, individual recognition, security of an individual, communicating with potential mates, and other roles. All those roles critically contribute to survival and well-being of an organism. From this reason, species-specific vocalizations acquired a higher biological importance than any other environmental stimuli. These signals not only convey information about emotional state from one organism to another but they are selectively recognized by recipients and are capable of quickly inducing a similar emotional state in the receivers (Kim et al. 2010; Parsana et al. 2012). It has been therefore postulated that mammalian vocalizations serve as ethological transmitters termed ethotransmitters (Brudzynski 2010, 2013). The ethotransmitters are produced by specialized organs (larynx), selectively recognized and decoded by the brain of conspecifics, and capable of changing the emotional state and behavior of the receivers (ibid.). Ethotransmitters form a specialized way of interindividual communication that guarantees faster and prearranged responding of organisms in vital situations and this is fully relevant to rat vocal communication. The mechanisms of these responses are not fully known but they might include activation of appropriate innate neural circuits and also be based on a rapid recruitment of the endocrine system (Remage-Healey and Bass 2006). In the instance of vocalization, the acoustic wave is the vehicle for communication but it is possible that other vehicles can serve for that purpose as well (e.g. in specialized chemical communication).

5 Conclusions

Vocal communication evolved very early in vertebrate evolution. There are several hypotheses explaining how and why audiovocal communication evolved in land animals, and particularly in rats. Most if not all of the hypotheses are mutually supplementing each other. Interaction between mother and infant, which is necessary for survival, and expresses emotional and motivational states, was mentioned as the most likely first evolutionary step. Predator pressure that includes the type of the predator, features of environment, and the security motivation, could critically contribute to development of adult vocal communication as a defensive measure. Finally, structure, complexity, and size of the social group could be the contributing mechanisms further facilitating development of vocal communication. Rats have developed a complex system of ultrasonic vocalization, which could be explained by a dichotomous branching tree model, which explains types of vocalizations having opposite or different semiotic values for the receivers at each branching point. The main dichotomous branches include audible versus ultrasonic calls, aversive 22 kHz calls versus appetitive 50 kHz calls, constant frequency calls versus frequency-modulated calls, and others. It is concluded that mammalian and rat ultrasonic vocalizations serve as ethotransmitters that provide a faster and prearranged way of communicating and responding in vital situations.

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Chapter 6
Why the Caged Mouse Sings: Studies of the Mouse Ultrasonic Song System and Vocal Behavior

Gustavo Arriaga

Abstract Laboratory rodents participate in a significant amount of communication using ultrasonic vocalizations (USVs), and two types of USVs have been studied extensively as measures of internal states: pup isolation calls; and adult USVs in aversive, rewarding or social conditions. Mouse (Mus musculus) USVs do not appear to signal affect but are used primarily during non-aggressive social encounters and may facilitate social interactions. The most well characterized adult mouse USVs are those produced by males when they detect the presence of a sexually mature female and after copulation. Although the general occurrence of these male mouse USVs has been known for decades, in depth analyses of their spectro-temporal and syntactic features and the supporting neural substrate have only recently begun. Nevertheless, the field of mouse ultrasonic vocal communication is advancing rapidly on multiple fronts: discoveries at the molecular level; initial descriptions of the neural systems for vocal production and control; characterization of mouse models of social communication disorders and neuropsychiatric dysfunction; and ethological perspectives on the social function of ultrasonic communication in mice. As the mechanisms of mouse USV production become better understood, it is becoming possible to employ mouse vocalizations for purposes of behavioral phenotyping in mouse models of various neurological disorders and investigating the basic mechanisms of neural control of social communication in mammals. This chapter will describe some of the recent findings related to mouse vocal communication, with an emphasis on adult ultrasounds, and discuss the current interpretations and potential opportunities for advances in the field.

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1 Introduction

Laboratory mice (*Mus musculus*) and rats (*Rattus norvegicus*) participate in a significant amount of communication using ultrasonic vocalizations (USVs) produced at frequencies ranging from 30–100 kHz (Constantini and D'Amato 2006; Portfors 2007). These vocalizations are by definition inaudible to humans, but they are well within the hearing range of the vocalizing animals. Traditionally, two types of USVs have been studied extensively in laboratory rodents as measures of internal states: pup isolation calls (Branchi et al. 2001; Brudzynski et al. 1999; D'Amato et al. 2005; Elwood and Keeling 1982; Hahn et al. 1987; Hofer and Shair 1992; Ise and Ohta 2009; Noirot 1972; Noirot and Pye 1969; Sales and Smith 1978; Wöhr et al. 2008a), and adult USVs in aversive or rewarding conditions (Brudzynski 2007, 2009; Burgdorf et al. 2007; Knutson et al. 2002; Wöhr et al. 2008b). Pup ultrasonic isolation calls are produced under conditions of cold or separation from the dam and are frequently used as an index of anxiety (Olivier et al. 1994). Reliable elicitation of isolation calls by quantifiable stimuli, and a well characterized developmental trajectory have made pup USVs a useful tool for testing the effects of anxiogenic or anxiolytic compounds (Dirks et al. 2002; Fish et al. 2000, 2004) and for phenotyping mouse models of neuropsychiatric disorders associated with deficits in vocal communication (Fischer and Hammerschmidt 2010; Scattoni et al. 2009). Similarly, the well-characterized 22 and 50 kHz calls of adult rats have been studied extensively as behavioral assays of negative and positive affective states, respectively (Brudzynski 2007, 2009; Burgdorf et al. 2007; Knutson et al. 2002). The predictive power of rat USV behavior with regard to affect is considered so reliable that emission rates of USV production are used as a selective breeding phenotype for generating strains as models of high anxiety and depression (Harmon et al. 2008). As the mechanisms of mouse USV production become better understood, it is becoming possible to employ mouse vocalizations in similar ways for purposes of behavioral phenotyping in mouse models of various neurological disorders and investigating the basic mechanisms of neural control of social communication in mammals.

Relative to rats, less is currently known about USV behavior in adult laboratory mice. Mouse USVs do not appear to signal affect but are used primarily during non-aggressive social encounters and may facilitate social interactions (Gourbal et al. 2004; Hammerschmidt et al. 2012a; Moles et al. 2007; Portfors 2007). The most well characterized adult mouse USVs are those produced by males when they detect the presence of a sexually mature female and after copulation (Constantini and D'Amato 2006; Gourbal et al. 2004; Guo and Holy 2007; Holy and Guo 2005; Musolf et al. 2010; Nyby 1983; Portfors 2007). Although the general occurrence of these male mouse USVs has been known for decades, in depth analyses of their spectro-temporal and syntactic features and the supporting neural substrate have only recently begun (Arriaga et al. 2012; Gourbal et al. 2004; Grimsley et al. 2011; Hoffmann et al. 2012; Holy and Guo 2005). Nevertheless, the field of mouse ultrasonic vocal communication is advancing rapidly on multiple fronts: discoveries at the molecular level; initial descriptions of the neural systems for vocal production and control; characterization of mouse models of social communication disorders and neuropsychiatric dysfunction; and ethological perspectives on the social function of ultrasonic communication in mice. Some of these findings are raising questions about the basic assumptions of the evolution and development of mammalian vocal systems, and new avenues for basic and clinical research are opening. This chapter will describe some of the recent findings related to mouse vocal communication, with an emphasis on adult ultrasounds, and discuss the current interpretations and potential opportunities for advances in the field.

2 Structure of Mouse Songs

Adult mouse USVs are typically composed of whistle-like notes produced at frequencies ranging from 35 to 100 kHz. Many species produce a diverse repertoire of vocalizations that can include calls, songs, laughs, and cries. Certainly, adult USVs are not the only vocalizations mice produce; therefore, it is important to address how they can be distinguished from other acoustic signals including pup USVs and adult calls.

2.1 Calls

Calls can be defined as continuous, distinct, and reproducible units of sound temporally isolated from other sound units by intervals of silence (Doupe and Kuhl 1999) and often contain multiple subunits called notes. Calls are used for communication in various species and may acquire semantic content with experience (Kaplan 2008; Marler and Slabbekoorn 2004; Seyfarth et al. 1980), may be emitted intentionally (Gyger et al. 1987; Karakashian et al. 1988), and may be produced in combinations that acquire semantic content independent of the content of the individual calls (Arnold and Zuberbühler 2008). In addition to semantic content, the spectral content of some calls can also be learned (Zann 1985, 1990).

Mice produce a variety of calls (Whitney and Nyby 1983). Some calls, like distress calls, are audible, and others, like courtship vocalizations, are purely ultrasonic. As the term ‘ultrasonic’ suggests, a broad call category can be easily distinguished simply because USVs are produced in a frequency range above the upper limit of human hearing. This frequency range-specific category can be broken down further by considering the vocalization-eliciting stimulus, social context of production, or the age of the vocalizing animal. The most commonly studied ultrasonic mouse calls are those produced when a pre-weaning pup is separated from the mother (Noirot 1972; Noirot and Pye 1969; Sales and Smith 1978). A nursing female mouse will respond reliably to pup isolation calls by locating the sound source and retrieving the pup to her nest (D’Amato et al. 2005; Noirot 1972;

Uematsu et al. 2007). Thus, the response of the animal receiving the acoustic signal may provide another useful feature for differentiating vocalizations produced in overlapping frequency ranges.

2.2 Syllables

Syllables are reproducible single acoustic units structurally similar to calls in that they can be made up of multiple notes. Although syllables are structurally similar to calls, they can be distinguished from calls by patterns of usage. Calls are typically produced in isolation or in short bursts and often obtain semantic content on their own, as previously described. Syllables, however, derive their classification from being included in a larger unit representing a longer series of rapidly produced vocalizations. A reproducible series of syllables with a relatively fixed order is labeled a 'motif'. By clustering units into motifs, an animal with a repertoire of only a few syllables can generate a wide variety of larger communication units. Thus, syllables can be void of specific meaning themselves, and they would not necessarily serve a communication function if produced in isolation. This distinction is not always entirely clear for units of sound that can serve a dual function. For example, the long call of male zebra finches can function alone as a contact call or be incorporated into a motif that is reproduced in song bouts (Zann 1990). In this case, the same acoustic signal could be labeled a call or a syllable depending on the context of production.

Adult mouse USVs feature reproducible sound units that can be grouped into general types by their spectral morphology. Most of these units are frequently produced in long sequences containing different types, and there is some evidence that motifs are present in these sequences (Holy and Guo 2005). The recurring units in adult male USVs are typically called 'syllables' because they are grouped into non-random series, rarely produced in isolation, and there is no evidence that they serve a communication function individually. Reliable and behaviorally meaningful syllable classification remains an active area of investigation that has not yet reached consensus. Various research groups have begun classifying notes based on some general morphological features of the ultrasonic whistles (Arriaga et al. 2012; Hammerschmidt et al. 2012b; Holy and Guo 2005; Scattoni et al. 2008a). The most obvious morphological distinction between syllable types may be the presence or absence of instantaneous 'pitch jumps' separating notes within a syllable. Therefore, the simplest syllable type doesn't contain any pitch jumps, but this category can be split into sub-types according to the pitch trajectory, syllable duration, or the presence of harmonics (Fischer and Hammerschmidt 2010; Grimsley et al. 2011; Kikusui et al. 2011; Scattoni et al. 2008a). For syllables containing pitch jumps, each jump marks the end of one note and the beginning of the next note. Two-note sequences can be easily identified by a single upward or downward pitch-jump. More complex syllables can be identified by the series of upward and downward pitch jumps occurring as the fundamental frequency varies between notes of higher and lower pitch. A combination of pitch jump sequences and frequency contours may be necessary to accurately capture the great variability of mouse vocal behavior.

2.3 Songs

A song is set of vocalizations, often elaborate, delivered periodically. Songs may be produced spontaneously or in response to an external stimulus such as the presence of a conspecific. Songs typically contain multiple syllable types, or categories of reproducible vocalizations distinct from other vocalizations comprising the song. The *sensu strictissimo* definition (Broughton 1963) can be applied to distinguish a series of syllables in a song from a succession of calls:

> ‘a sound of animal origin which is not both accidental and meaningless’
> containing,
> ‘a series of notes, generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time,’
> produced in,
> ‘a complete succession of periods or phrases’

Holy and Guo showed that courtship USVs from different males contain identifiable syllable types produced in regular temporal patterns that differed between individuals (Holy and Guo 2005). Their analysis of the spectro-temporal features of male courtship USVs demonstrated convincingly that these vocalizations satisfy all conditions required for classification as song. Visually, the song-like quality of male mouse courtship USVs can be appreciated in the spectrograms of long vocal sequences. Acoustically, when the pitch of courtship USVs is shifted to the audible spectrum they sound very similar to birdsong in both temporal and melodic structure. Importantly, the categorization of adult mouse USVs as songs does not imply that they are learned. There is a prevalent but erroneous assumption that songs are learned and calls are innate. As discussed in the following section, the relative contributions of innate and environmental factors on mouse vocal output have not been clearly resolved, and this is likely to be an area of vigorous research in the near future.

3 Ontogeny of Mouse Songs

Mouse ultrasounds were recently shown to change dramatically over development from pup isolation calls to more complex adult songs (Grimsley et al. 2011). All syllable types identified in adult songs are also produced by pups, although the relative proportions of the syllables in the repertoire vary across development. This suggests that a well-developed peripheral production mechanism is already present at a young age. Additionally, the complexity and higher-order structure of the vocal sequences is significantly greater in adults than in pups, which indicates developmental changes in central control mechanisms for ultrasonic production. These changes in syntactical complexity are accompanied by a refinement of the spectro-temporal parameters of each syllable type. In general, the distributions of syllable durations and peak frequencies become more normal and unimodal with a more positive kurtosis over the course of development. Adult syllables tend to be significantly shorter than similar pup calls. While most syllable types also showed a shift in the mean peak frequency, there was no clear trend for the direction (lower or higher pitch) in which the shift occurred in adults. These findings suggest that while robust vocal changes clearly occur during development, there is probably not a single peripheral mechanism, such as maturation of the vocal organ, that is responsible for all changes in syllable frequency.

If physical maturation is not driving vocal development, then what is? There is considerable debate about the role that auditory experience might play in USV development. The typical distress and isolation calls of pups are produced despite being unable to hear before postnatal day 10 and are generally considered to be innately specified (Ehret 1976; Romand and Ehret 1990). Because significant changes occur after the onset of hearing and adult USVs are significantly different spectro-temporally from pup calls (Grimsley et al. 2011), there has been interest in whether hearing plays a strong role in shaping adult USVs. Two studies have yielded negative results using deaf transgenic mouse strains, suggesting a non-existent or limited contribution from auditory experience (Hammerschmidt et al. 2012b). The first study published on this topic investigated mice with a knockout of the otoferlin gene on a mixed 129 ola/C57N background (Hammerschmidt et al. 2012b). The authors reported no difference in amplitude or acoustic features between the syllables of congenitally deaf and hearing-intact animals. However, the use of an uncommon and limited classification syllable scheme and failure to report the most commonly analyzed spectral features (mean pitch, spectral purity, frequency modulation) complicated interpretation of the negative results. A second study reported similar results using mice deafened by systemic injections of diphtheria toxin in a transgenic line expressing diphtheria toxin receptors in inner ear hair cells. Mice deafened on postnatal day 2, before the onset of hearing, showed no major difference from their wildtype littermates in terms of repertoire composition or spectral features of syllables. This study used a more complex syllable classification scheme to reduce the chance of missing an effect of learning on subtle syllable characteristics and reported comparisons for a comprehensive set of acoustic parameters. Although based on negative results, the combined results of both studies significantly strengthen the conclusion that the gross acoustic features of mouse songs are not learned through auditory experience.

A different study obtained results that are seemingly contradictory to the negative effects of the early deafening experiments. When adult male mice were deafened by cochlear removal after developing normal vocalizations, a progressive worsening of the spectral purity and changes in the acoustic parameters of their songs occurred (Arriaga et al. 2012). The same study also reported strong effects on vocalizations from knockout of the caspase-3 gene, which results in deafness by loss of inner ear hair cells; however, the knockout was non-specific and could have affected non-auditory systems as well. Importantly, the deafening-induced deficits in adult mice that have been reported appear less dramatic than those observed in species that rely heavily on audition for vocal development such as humans and song learning birds (Doupe and Kuhl 1999; Heaton et al. 1999; Marler and Sherman 1983; Okanoya and Yamaguchi 1997; Waldstein 1990; Watanabe et al. 2006; Woolley and Rubel 1997).

One important difference between the seemingly conflicting studies is that the mechanically deafened mice were tracked for months after deafening. This longitudinal approach was adopted because research in songbirds has shown that the deleterious effects of deafening on vocalizations can be quite slow to develop (Heaton et al. 1999). It would be interesting to determine whether otoferlin knockout and selective elimination of inner ear hair cells with diphtheria toxin have long term effects on adult USVs. In any case, there is an apparent paradox regarding auditory experience in the ontogeny of adult mouse songs, whereby audition may not be necessary for initial establishing the overall structure of syllables but could be necessary for maintaining their finer qualities.

There is also considerable debate regarding the role of social experience in shaping acoustic output. Consistent with reports that audition is not necessary for normal vocal development, the first study on tutoring mice with songs from a different strain reported no differences between normally reared and cross fostered mice (Kikusui et al. 2011). However, several methodological issues make it difficult to draw strong conclusions from this negative result: the learning paradigm used for cross-fostering did not ensure or test for vocal production by the foster father, which may have prevented the young males from acquiring a template to mimic; pups were tutored at a very early age and for a short period; after tutoring, the mice were not acoustically shielded from other males of their own strain. A later study used a different social paradigm and arrived at seemingly contradictory results (Arriaga et al. 2012). Male mice that had previously only heard songs of their own strain were housed with a male of different strain and a female. In this triad, the subordinate males systematically altered the pitch of their songs over the course of 2 months to match that of the dominant strain. Importantly, the males were motivated to sing throughout the study by the female presence, were only exposed to songs of their own strain prior to pairing, and only heard the songs of their cage-mate after pairing.

Given the differences in design between the initial cross-fostering and pitch-matching studies (Arriaga et al. 2012; Kikusui et al. 2011), and between the early deafening and longitudinal adult deafening studies, it is likely that the gross morphology of syllables is innately specified, but the fine details of pitch and perhaps syllable sequencing may be adaptively modified to a moderate degree over time. The issue of social context may be critical in these studies, and there is already evidence that social conditions can strongly affect song production (Chabout et al. 2012; Hanson and Hurley 2012). Thus, studies properly designed to investigate songs produced in behaviorally relevant contexts and perceived by expert listeners for whom the communication signals are designed may yield surprising results. What stimulates a male to alter his song, and which brain pathways support this process? Do females prefer the ultrasonic courtship songs of hearing-intact males to the songs of deaf or experimentally manipulated males? Does female preference select for particular song types? Given the high sensitivity of females to adult USVs (Hammerschmidt et al. 2009; Musolf et al. 2010), it is possible and quite likely that even a small but reliable change in repertoire composition, syllable sequencing, pitch, or spectral purity could carry enough information to affect behavioral outcomes.

4 Function of Mouse Songs

Ultrasonic communication offers some significant advantages over communication by audible vocalizations. Perhaps most importantly, many predators, including birds of prey, cannot hear USVs. Additionally, USVs propagate more directionally than audible sounds and they dissipate easily due to environmental obstacles, making the sound source difficult to detect and localize. Aside from such defensive benefits, it is unclear what function adult songs may serve, as they have not been shown to indicate negative or positive affect. There is considerable debate regarding possible territorial defense and courtship roles adult songs may serve in social interactions, because adult mice of both sexes will produce USVs in certain dyadic social encounters (Gourbal et al. 2004; Hammerschmidt et al. 2012a; Moles et al. 2007; Moles and D'Amato 2000; Nyby 1983). Males typically sing in response to the perceived presence of a sexually mature female (fresh urine, and soiled bedding will trigger singing) (Guo and Holy 2007; Hoffmann et al. 2009; Musolf et al. 2010); these songs are sexually selective and release appears to be mediated through the vomeronasal olfactory system (Bean 1982; Guo and Holy 2007; Holy et al. 2000; Thompson et al. 2004). Sensory neurons in the vomeronasal organ (VNO) express the Trpc2 channel, which is essential to VNO function (Zufall 2005; Zufall et al. 2005). Genetic ablation of this channel eliminates the sex selectivity of mouse courtship behaviors including songs, and releases these behaviors in females (Kimchi et al. 2007; Stowers et al. 2002). The results of these studies suggest that a fully functional circuit for the expression of male sexual behaviors, including USV production, is present but repressed in females during male-female dyadic encounters.

Although most recent studies have focused on male songs produced in encounters with a sexually mature female, there are various reports of female mice with normal VNO function using somewhat similar vocalizations (Hammerschmidt et al. 2012a; Moles et al. 2007; Moles and D'Amato 2000). Like males, female mice will vocalize when another female enters their home cage in a typical resident-intruder paradigm. Some studies report that females actually vocalize more than males under such conditions (Hammerschmidt et al. 2012a). The existence of significant female USV production in dyadic social encounters has been taken as evidence against a courtship function for male USVs. However, the value and function of a communication signal cannot be reduced to the acoustic parameters of the signal itself. The same acoustic signal could serve distinct communication functions in male-female and female-female interactions. Indeed, the responses of females to male songs provide some clues that these songs are functionally distinct from acoustically similar vocalizations. Female mice are capable of distinguishing male songs from other ultrasounds, such as pup isolation calls (Hammerschmidt et al. 2009; Musolf et al. 2010). Given the choice, females selectively approach the source of the songs instead of the source of the isolation calls. Preference for male songs is striking given that pup calls are considered a very strong and reliable stimulus, and the frequency ranges and spectral parameters of the two signals overlap significantly. Moreover, wild females exhibit a slight tendency to prefer the songs of non-kin males (Musolf et al. 2010).

This kin-based discrimination by female listeners is not surprising given recent evidence of individual and kinship signals in the spectro-temporal features of wild male songs (Hoffmann et al. 2012). It remains unclear whether males maintain this differentiation under laboratory rearing conditions, or whether familial cues are hereditary or learned.

5 How Are Mouse Songs Produced?

5.1 Laryngeal Source

Gross laryngeal anatomy is well conserved among mammals, as described in studies that found the organization of the mouse larynx is very similar to that of humans (Harrison 1995; Thomas et al. 2009); most of the laryngeal cartilages and muscles are similarly positioned in both species. Early evidence supporting a laryngeal USV source in rodents came mainly from laryngeal nerve transection and electrophysiology studies. Premotor signals to the larynx are transmitted via the superior and recurrent laryngeal nerves whose shared root is the brainstem nucleus ambiguus (Amb). Bilaterally severing the recurrent laryngeal nerve abolished pup and adult USVs (Nunez et al. 1985; Roberts 1975). Electrical recordings in anesthetized rats showed that a majority of the Amb motoneurons sampled displayed little background activity and tonic bursts tightly coupled to and preceding sound production by 46 ms (Yajima et al. 1982). Recent unpublished observations indicate that the explanted mouse larynx is capable of producing sounds displaying the non-linear dynamics characteristic of natural USVs (Berquist et al. 2010); however, these sounds were in the human audible spectrum and it remained unclear if they depend on vibrations of the vocal folds or a whistle mechanism. The most recent evidence, albeit from rats, shows that the predictions of a whistle mechanism do not hold for ultrasound production in rodents (Riede 2011). Specifically, subglottal pressure and tracheal airflow patterns were not consistently related with fundamental frequency. In contrast, the laryngeal muscles showed high amplitude bursts at rates approaching 150 Hz during USV production. These results strongly support a sound production mechanism that relies on precise control of the vocal folds via central regulation of the laryngeal musculature.

5.2 Central Control

All vocalizing mammalian species studied to date possess a basic circuit for the gating and programming of innate vocalizations which includes midbrain premotor structures, and brainstem motoneuron pools for motor control of phonation and respiration. The typical vocal circuit present in mammalian brains begins with the caudal periaqueductal gray (PAG) which projects to brainstem respiratory premotor nuclei including RAm for control of respiration, and cranial nerve nuclei including Amb which directly innervates the larynx (Ennis et al. 1997; Jürgens 1998, 2002a, 2009; Mantyh 1983). Decades of work mostly by Uwe Jürgens and colleagues using anatomical tracing (Dujardin and Jürgens 2005; Hannig and Jürgens 2005; Jürgens 1982, 1983, 1984; Jürgens and Alipour 2002; Müller-Preuss and Jürgens 1976; Müller-Preuss et al. 1980; Simonyan and Jürgens 2002, 2003, 2004, 2005; Thoms and Jürgens 1987), brain imaging (Brown et al. 2008; Jürgens et al. 2002; Simonyan and Horwitz 2011; Simões et al. 2010), electrophysiology (Coudé et al. 2011; Düsterhöft et al. 2003; Hage and Jürgens 2006a, b; Jürgens 2002b; Lüthe et al. 2000; Shiba et al. 1997), electrical (Jürgens and Ploog 1970) and chemical (Lu and Jürgens 1993) brain activation, lesions (Jürgens et al. 1982; Jürgens and Pratt 1979; Kirzinger 1985; Kirzinger and Jürgens 1982, 1985), and reversible inactivations (Jürgens and Ehrenreich 2007; Siebert and Jürgens 2003) has produced a detailed description of the pathways involved in controlling innate mammalian vocalizations . The general conclusions drawn from this body of work are as follows: (1) limbic regions regulating arousal and the drive to vocalize including the amygdala and cingulate cortex converge on the PAG; (2) the PAG serves a gating function to activate motor programs for specific calls associated with different arousal states; (3) the spectral structure of calls is primarily determined at the level of medullary premotor circuits that coordinate the activity of phonatory motoneuron pools in various cranial nerve nuclei. This interpretation of the pathways suggests that what is truly indispensable for vocalization is the PAG and downstream circuits of the brainstem.

Consistent with the general model of vocal control described above, USV-related activity-dependent immediate early gene expression was found in the cingulate and motor cortices and the basal ganglia in mice (Arriaga et al. 2012). When males were stimulated to sing by female urine cues, neural activity was detected in these regions, providing the general outline of a forebrain vocal production system that includes limbic, motor cortical and striatal components. Unfortunately, data regarding the roles of forebrain, especially premotor and limbic, structures in vocal production in mice are lacking. In fact, there is quite little data on the functional organization of mouse motor cortex in general. Some information comes from an electrical microstimulation study, but this technique generated disjointed and overlapping representations with poor spatial resolution for broad muscle groups of the limbs and face (Pronichev and Lenkov 1998). Motor control circuits have been mapped with good detail in the rat, especially the motor representations in the barrel cortex controlling whisker movements (Brecht et al. 2004). Additionally, forebrain contributions to vocal behavior of adult rats have been established for limbic structures connected to the dopaminergic mesolimbic system (Brudzynski 2009; Burgdorf et al. 2007), and the infralimbic medial frontal cortex-PAG-Amb pathway (Depaulis et al. 1992; Frysztak and Neafsey 1991). Similar forebrain contributions to adult mouse USVs from either limbic or premotor systems, however, remain largely unstudied. Only one study to date has investigated the role of limbic structures on USV production. This study demonstrated that bilateral ablation of the amygdalae altered the distribution of syllable types in the vocal repertoire, as mice that suffered lesions produced more short notes than sham operated controls. According to the standard model of mammalian vocal control described above, these findings are likely to reflect changes in the regulation of copulatory behavior including USV production by emotionally salient information transmitted through the limbic-PAG axis. Although there is some evidence that different syllable types may correlate with different parts of the mating interaction, it remains unclear how the repertoire changes reported map back to changes in the processing of emotional stimuli.

In addition to the limbic-midbrain-brainstem pathway for innate vocal production, species that are capable of vocal-learning have evolved cortico-striatal-thalamic loops and cortico-bulbar pathways for learning and generating novel vocalizations, respectively. Specifically, a projection from vocal premotor regions to the vocal motor neurons is thought by many researchers to be critical to the evolution of vocal learning abilities (Deacon 2007; Fischer and Hammerschmidt 2010; Fitch et al. 2010; Jarvis 2004; Kirzinger and Jürgens 1982; Kuypers 1958; Okanoya 2004; Simonyan and Horwitz 2011; Wild 1994, 1997). The underlying assumption is that the unique capabilities of songbirds and humans derive from improved vocal control as a result of direct cortical control of the vocal apparatus. That is, reorganization of neural architecture was the basis and precondition for the reorganization of function. In songbirds this precise control corresponds to the descending projection from the nucleus robustus archistriatalis to the tracheosyringeal motor nucleus, and in humans the analogous projection is from laryngeal motor cortex to nucleus ambiguus. Interestingly, a similar but sparse projection was found in mice from the region of primary motor cortex that is active during singing to laryngeal motor neurons in nucleus ambiguus (Arriaga et al. 2012). The discovery of a direct motor cortical vocal pathway greatly increases the utility of the mouse model for vocalization. Even the rudimentary projection from motor cortex to Amb can be leveraged to test various hypotheses regarding the genetic specification of this pathway and its relevance to the evolution and complexity of vocal learning.

It appears that the primary motor cortex is not critical for the production of adult USVs, as lesions to this region left the gross song structure intact (Arriaga et al. 2012). However, there were significant changes to some spectral features of the song syllables, including greater frequency modulation and a wider distribution of frequencies produced. These changes to the songs suggest a loss of fine control over the acoustic output, and the resulting changes appear to reflect a reversal of the refinement that occurs during the transition from adolescent to adult USVs (Grimsley et al. 2011). One interpretation of the effects in mice is that mouse USV song syllables are similar to male zebra finch long calls, which contain both learned and innate components. Lesions of the analogous vocal premotor pathway in zebra finches eliminate the modified features of calls and leave only a basic innate template (Simpson and Vicario 1990).

Thus, mouse songs may not necessarily be entirely ‘learned’ or ‘innate’. Previous studies of vocal learning have focused entirely on systems that are either innate and dominated by the limbic-PAG vocal pathway (suboscine song, calls of chickens and pigeons, non-human primate calls) or dominated by the direct motor cortical vocal pathway (human speech, birdsong). According to the recently proposed Continuum

Hypothesis (Arriaga and Jarvis 2013), it is conceivable that an intermediate neural organization exists in mice as a step from a phylogenetically older vocal system focused on the PAG to a system controlled by motor cortex capable of greater vocal flexibility and eventually generation of novel sounds. Thus, the mouse song system could provide a valuable model for investigating the integration of motor commands from the cortical and limbic-PAG vocal premotor pathways.

The same motor cortical region that projects to the laryngeal motor neurons also projects to the subjacent dorsal striatum. Current research on the mammalian basal ganglia suggest that the sensorimotor striatum is involved in the learning of action sequences in response to behavioral contexts (Barnes et al. 2005; Graybiel 2005). Additionally, basal ganglia circuits that are specialized for and active during singing in the avian "song system" are critical for the variability critical for vocal exploration during songbird development (Brainard and Doupe 2000; Kao et al. 2005; Olveczky et al. 2005). Given that the dorsal striatum in mice both receives input from the singing-activated motor cortex and is active during song itself, these cortico-striatal circuits can provide a key substrate for studying the basal ganglia contribution to learning of contextual social communication behaviors. These circuits and associated vocal behaviors may also benefit research on some neuropsychiatric disorders, such as Parkinson's disease (PD), which result from basal ganglia dysfunction and are associated with speech and voice disorders.

6 Genetic Basis of Vocal Communication

Perhaps the greatest benefit of using mouse models to study mammalian vocal communication is the abundance of readily available, optimized techniques for genetic manipulation in this species. Such tools allow the molecular, circuit, system and behavioral levels of complexity to be connected in ways that are difficult in other model systems. The best example to date has been the foxP2 gene that encodes a forkhead-box transcription factor. Multiple studies have linked specific foxP2 mutations to severe speech deficits in human patients (Vernes et al. 2006) and vocal production in mice and songbirds (Enard et al. 2009; Fischer and Hammerschmidt 2010; Fujita et al. 2008; Gaub et al. 2010; Groszer et al. 2008; Haesler et al. 2004, 2007; Miller et al. 2008; Rochefort et al. 2007; Shu et al. 2005; Teramitsu and White 2006; White et al. 2006). Although foxP2 is regulated during singing and development in songbirds (Haesler et al. 2004; Miller et al. 2008; Teramitsu and White 2006), there has been little progress directly linking gene sequence, and protein function to phenotype in this system. Knockdown of foxP2 was achieved in the avian striatum and affected the quality of song learning (Haesler et al. 2007), but required the relatively inefficient technique of lentiviral injection. By comparison, multiple studies rapidly leveraged the tools available for generating transgenic mouse models to test the effects of targeted disruptions of the foxP2 gene on neural circuits and vocal production (Enard et al. 2009; French et al. 2007; Fujita et al. 2008; Gaub et al. 2010; Groszer et al. 2008; Mizutani et al. 2007; Shu et al. 2005).

Given their roles in motor-skill programming and foxP2 expression patterns (Lai et al. 2003), the striatum and cerebellum are two sites where foxP2 may be linked to vocal development and USV production. In the cerebellum, mice carrying the R522H mutation identical to one that causes verbal apraxia in the human KE family produced fewer ultrasonic pup calls and suffered improper development of the cerebellum associated with numerous Purkinje cell abnormalities (Fujita et al. 2008). In the basal ganglia, humanizing the foxP2 gene through two amino acid substitutions resulted in altered pup call structure associated with less extracellular dopamine, greater dendritic length of medium spiny neurons, and increased long-term synaptic depression (Enard et al. 2009; Reimers-Kipping et al. 2011). In contrast, synaptic plasticity via long-term depression in the dorsolateral striatum is strongly impaired in mice lacking a functional foxP2 gene (Groszer et al. 2008). Because homozygous inactivations of foxP2 are typically lethal before weaning, most studies have focused on pup calls. However, a preliminary experiment has shown that the R522H also results in changes to the spectral characteristics of adult mouse songs (unpublished data). Because foxP2 is expressed in layer V of M1 (Campbell et al. 2009), in what appears to be the same region where singing-related IEG expression has been reported (Arriaga et al. 2012), it may soon be possible to directly link specific genetic mutations, protein function in identified subsets of neurons, and neural activity in a vocal premotor pathway to features of acoustic output within the adult mouse song system.

In addition to the study of foxP2 and the related verbal dyspraxia, mouse vocalizations are also beginning to be studied in models of psychiatric disorders involving communication deficits. Some genes involved in the regulation of social behavior have also been implicated in USV production in mice including vasopressin (Scattoni et al. 2008b) and neuroligins (Jamain et al. 2008; Radyushkin et al. 2009). And some researchers have proposed using the well-documented effects of various genetic manipulations on the production rate and quality pups USVs as reliable phenotypic markers for mouse models of neurodevelopmental disorders (Scattoni et al. 2009). This approach is particularly useful for the study of disorders with a clear genetic component (Kang and Drayna 2011), especially the monogenetic heritable forms of autism (Fischer and Hammerschmidt 2010; Jamain et al. 2008; Radyushkin et al. 2009; Scattoni et al. 2008a). For example, pups of one inbred mouse strain (BTBR) that exhibits social deficits and repetitive behaviors similar to some symptoms of autism also displays abnormal vocal behavior (Scattoni et al. 2008a). The BTBR pups produced more USVs and had a different vocal repertoire than three control inbred strains. The authors propose that such changes in early vocal behavior can be diagnostic of the impaired communication symptoms of autism. Similarly, USV production has been proposed as part of a diagnostic autism severity composite score using a different model of heritable monogenic autism, the neuroligin (Nlgn4) null mutant strain, which features decreased production of both adult male and female USVs (El-Kordi et al. 2012). By extending this approach to other models of communication disorders, or neuropsychiatric conditions with a strong vocal component, mouse USVs may provide a reliable and easily measured index of social communication for diagnostic behavioral phenotyping.

7 Final Considerations

Although interest in mouse ultrasonic communication has only recently surged, there are many opportunities for significant discoveries at all levels of neuroethological study. Mouse models can clearly serve to cover the gap in understanding the molecular basis of vocal production, social communication dysfunctions, and the evolution of brain systems that form the basic substrates of speech. On the latter point, the finding that adult males can adaptively modify their pitch is already challenging assumptions about the distribution of the vocal learning trait by suggesting that vocal modification abilities may be expressed along a spectrum with vocal mimics and so-called vocal non-learning species at the extremes, and mice somewhere in between. Having vocal modification abilities expressed along a spectrum may make it easier to select for or against a convergent, advanced vocal imitation trait in multiple taxa. It has been proposed that positive selection for adaptive vocal modification can occur by sexual selection for more complex vocalizations, but that this could be strongly countered by negative selection by auditory systems of predators that habituate less to complex and variable vocalizations (Jarvis 2004; Okanoya 2004). One important caveat is that the laboratory mice most commonly studied have been bred in captivity for many generations, possibly allowing positive sexual selection for complex vocalizations without negative predatory pressure. Therefore, it will be useful to determine if wild mice display similar neuroanatomical and behavioral features.

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Chapter 7
Vibrational Communication: Spiders to Kangaroo Rats

Jan A. Randall

Abstract An amazing variety of animals communicate by vibrational signals. The behavior is common, diverse and occurs in multiple taxa ranging from spiders and insects to rodents and elephants. Production of vibrations is a mechanical event of stomping, tapping, drumming, rubbing surfaces together (stridulation) and trembling the body (trembulation) to transmit both airborne and seismic signals. Groundborne vibrations are transmit through a diversity of substrates, including soil, rocks, leaf litter and plant stems and leaves. Receptors for the signals consist of ears and mechanoreceptors in mammals and specialized structures in arthropods. Mate attraction is an important function of substrate-borne vibrations, which are often combined with visual displays in multimodal courtship displays. In spiders substrate-borne vibrations function as sexually selected signals of fitness. Besides attracting mates, insects use vibrations to communicate between parent and offspring, members of the social group, food recruitment and in predator defense. Substrate-borne vibrations also are important in predator–prey interactions. Footdrumming as a communication system is the most developed in territorial kangaroo rats (*Dipodomys*). The species specific drumming patterns can be complex, and the bannertailed kangaroo rat (*D. spectabilis*) drums individually distinct footdrumming signatures to communicate territorial ownership. Kangaroo rats also drum during competitive interactions and courtship. In the presence of snakes the kangaroo rats footdrum in individual defense to inform the snake the kangaroo rat is aware and will no longer be easy prey.

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1 Introduction

Animals ranging from mammals to worms have evolved as many unique ways to communicate by substrate vibrations as there are different taxa (See Hill 2008, 2009; O'Connell-Rodwell 2010 for comprehensive reviews of vibrational communication). Because substrate-coupled vibrations are not subject to the same constraints as airborne signals, very small animals such as spiders and insects are able to communicate using low-frequency signals via a substrate. With an estimated 195,000 described species of insects in at least ten different orders generating substrate vibrations, the potential for diversity is huge (Stewart 2001; Cocroft and Rodriguez 2005). Some familiar examples of insects that communicate with substrate-borne vibrations include ants, grasshoppers, crickets, katydids, cockroaches, stoneflies, booklice, true bugs, leafhoppers, lacewings, heelwalkers, stoneflies and caddisflies (Stewart 2001; Eberhard and Eberhard 2012). Besides attracting mates, insects use vibrations to communication between parent and offspring (Nomakuchi et al. 2012), members of the social group (Boucher and Schneider 2009), food recruitment and in predator defense (Hill 2008; Crocroft and Hamel 2010). In an unusual function, pupae of the Japanese rhinoceros beetle, *Trypoxlus dichotoma*, issue substrate-borne vibrations to deter conspecific larvae from burrowing into them and breaking their cells, which leads to death (Kojima et al. 2012). Crustaceans comprise another group of arthropods that communicate by seismic signals. Fiddler crabs drum (rap) the substrate with the lower base of their major claw (chelae) and with multiple pairs of walking legs (Taylor and Patek 2010). Recent research has revealed how spiders use their well developed adaptations for generating and sensing substrate vibrations in multiple ways (See below and reviews in Uhl and Elias 2011; Elias and Mason 2010).

Vibrational communication is also common in mammals. Rodents from at least three different families of fossorial (ground-dwelling) and seven families of semi-fossorial rodents communicate by vibrational signals (See review in Randall 2001). These signals function mainly in territorial defense, competitive interactions and predator defense. Substrate-borne vibrations are also a good way for burrow-dwelling, fossorial rodents (mole rats) to keep track of their neighbors (Rado et al. 1987; Narins et al. 1992). The generation of substrate vibrations has also been reported in elephant shrews (Rathbun 1979), 75 species of Bovidae, 46 species of macropodoid marsupials, two species of Camelidae, two species of Giraffidae, seven species of Cervidae and elephants (Caro et al. 2004; Rose et al. 2006; Randall 2010). Little is known, however, about the function of these behaviors.

2 Vibrational Signals: Drumming, Stridulation and Trembulation

Production of vibrations for communication is basically a mechanical event of hitting, stomping, tapping, drumming, rubbing surfaces together (stridulation) and trembling the body (trembulation) to transmit vibrations to a substrate to generate both airborne and seismic signals. Usually no special structures are required, and animals use what moveable body parts are available to them to produce the sounds. The most common structures are those used for locomotion such as feet and legs. Insects and spider also use other segmented appendages to generate vibrations, including antennae and pedipelps respectively. Mice and termites bang their heads (Hill 2008).

A spider's acoustic world consists of substrate-borne vibrations that can be produced in three different ways. Percussion, described in 12 different families of spiders, occurs when the animal hits an appendage against a substrate (footdrumming) or another appendage. 'Web plucking' behavior is included in this category (Uhl and Elias 2011). Stridulation, described in 34 families, is when an animal rubs two rigid body parts against each other. Tremulation occurs when an animal oscillates its body or appendages and the energy from the oscillation is transferred to the substrata through the animal's legs (Elias and Mason 2010; Uhl and Elias 2011). Insects generate vibrations similar to spiders.

Mammals produce vibrations by hitting feet, arms, legs and head against a substrate. The substrate is usually the ground, but it can also include tree trunks and the animal's own body as in the case of the mountain gorilla (Randall 2001, 2010). Mammals most commonly drum their feet to generate low-frequency vibrations transmitted through the ground and air. The behavior ranges from single foot thumps or stamps to striking the feet repeatedly in rapid succession. Larger mammals, such as ungulates, employ a single foot. They lift the forefoot to strike the ground suddenly with the hoof one or more times (Caro et al. 2004). Macropodoid marsupials strike the ground with one or both hind feet to produce single or double thumps (Rose et al. 2006). Elephants, *Elephas maximus*, *Loxodonta africana*, bang their trunks and feet on the ground (O'Connell-Rodwell et al. 2000, 2007). Elephants can produce low-frequency vocalizations at such high amplitudes that they couple with the ground and become substrate-borne (O'Connell et al. 2000).

Fossorial mole-rats in the family Bathyergidae communicate to conspecific inside the burrow by footdrumming vibrations (See review in Mason and Narins 2001). Another fossorial rodent, the Blind mole rat (*Spalax ehrenbergi*) (the genus is now *Nannospalax*), drums the flattened anterodorsal surface of the head on the roof of the burrow in response to vibratory signals from conspecifics (Rado et al. 1987). The European mole vole (*Microtus pyrenaicus*) drums with its front incisors, and water voles (*Arvicola richardsoni*) run on three legs simultaneously using one hind foot to scratch a flank gland and drum it on the substrate to deposit the scent (Randall 2010).

Kangaroo rats (genus *Dipodomys*) have the most elaborate drumming behavior of any mammalian species studied thus far. They drum their feet in species-specific patterns that diverge in four important ways: (1) the number of individual pulses (footdrums) grouped together to create a footroll, (2) the number of footrolls grouped together in a sequence, (3) the drumming rate (drums/s) and (4) the total number of individual drums (pulses) of the feet in a bout of drumming (Randall 1989, 1997) (Fig. 7.1). These bipedal rodents generate the drums by hitting their large hind feet on the ground. The bannertailed kangaroo rat, *D. spectabilis*, props

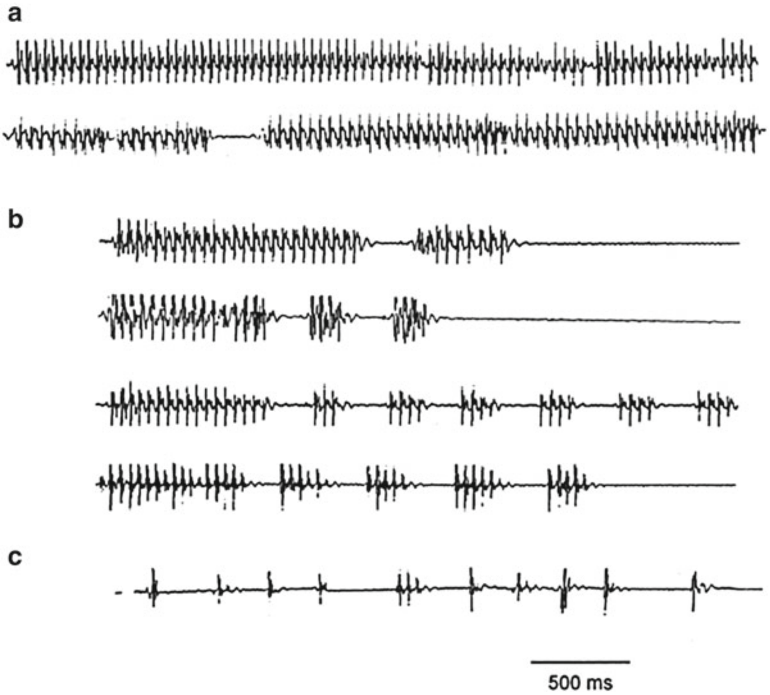

Fig. 7.1 Footdrumming patterns of three species of kangaroo rat (**a**) giant, *D. ingens*, (**b**) bannertailed, *D. soectabilis*, (**c**) desert, *D. deserti*

on its tail and hits the front of both hind feet together to generate a footdrumming signature consisting of a longer initial footroll followed by 1–12 shorter footrolls at an average rate of 17 drum/s. The giant kangaroo rat, *D. ingens,* alternates feet to generate 1–2 long foot rolls at 18 drums/s. The first footroll averages 69 individual foot-drums with the longest one recorded consisting of about 300 individual drums (Fig. 7.1) (Randall 1997, personal observation). The Heermanns kangaroo rat, *D. heermanni*, can produce several footrolls in a series at 20 drums/s (Shier 2003). The simplest drumming pattern in kangaroo rats is by the desert kangaroo rat, *D. desert*, with single drums at 0.25 s intervals (Randall 1997) (Fig. 7.1). Size is a limitation to drumming in kangaroo rat species. All species of kangaroo rats that communicate by drumming their feet have an average body size in excess of 60 g. Species weighing less than 60 g have not been observed drumming in any consistent way.

The bannertailed kangaroo rat also footdrums in the presence of snakes with modifications to the drumming signature (Randall and Matocq 1997). The kangaroo rats changes the two signal elements that account for the individual drumming signature: the number of footdrums in the first footroll and the number of footrolls in a sequence to make the footdrumming pattern less structured, more intense and longer.

Male wolf spiders, *Hygrolycosa rubrofasciata*, produce footdrumming signals during courtship. Although less complex, the spider's drumming signal shares some characteristics with the footdrumming signal of kangaroo rats. There are two main components of the spider's drumming signal: length (ms) and pulse rate (pulses/ms). A typical drumming bout lasts about 1 s with an average of 29 separate pulses. In comparison, kangaroo rats drum sequences considerably longer than 1 s, but the fastest drumming rate is much shorter (4–20 drums/s). Despite the simplicity of the drumming pattern of *H. rubrofasciata*, there are differences among the males. Pulse rate is highly repeatable within males so that individual males differ consistently from each, but the relative difference between males is small. Signal length and signal volume are also highly variable between males and repeatable for individuals. Females prefer the longer and more intense drumming (Rivero et al. 2000).

Although much less common than in arthropods and mammals, some species of amphibian use seismic vibrations to communicate. The white-lipped frog (*Leptodactylus albilabris*), with its body buried partially in the mud, produces seismic vibrations while vocalizing when the frog rapidly expands its vocal sac to generate a low-frequency thump as the sac strikes the substrate (Lewis et al. 2001). In contrast, calling male *L. syphax* beat their forefeet on the ground (Gridi-Papp and Narins 2010). Recently, toe twitching in frog and toads has been described and hypothesized to function as a vibrational, as well as a visual, lure to attract prey (Sloggett and Zeilstra 2008).

3 Substrates and Signal Transmission

Animals transmit vibrations through a diversity of substrates, depending on what is available in their habitat. A common substrate for transmission of vibrational signals by terrestrial vertebrates is the ground consisting of a variety of soils ranging from sand to clay. Energy is transferred through the ground in waves that vary in velocity and type with characteristics of the substrate (See Hill 2008 for review).

Among the substrates used to receive or transmit information by terrestrial insects, the stems and leaves of plants are the most widespread (Cocroft and Rodriguez 2005). Larger insects propagate vibrations along trunks and branches of trees (McVean and Field 1996). Aquatic insects and crustaceans transmit vibrations through the water (Hill 2008; Taylor and Patek 2010). Spiders send vibrations on webs they or another spider constructs, and bees communicate on honeycombs. These substrates have different transmission properties that must be taken into account when an animal wishes to maximize its ability to transmit information to a receiver (Cocroft et al. 2006; McNett and Cocroft 2008; Hill 2008; de Groot et al. 2011).

Recent research illustrates how the type of substrate can sharply affect the transmission and propagation of seismic vibrations and male mating success of spiders (Elias et al. 2004, 2010a; Hebets et al. 2008). Male jumping spiders, *Habronattus dossenus* Griswold 1987 (Salticidae), generate seismic signals during courtship on three different substrates in their environment: rocks, sand and leaf litter. Rocks and sand attenuate the signal, while leaf litter is the most favorable for signal transmission and mating success. Males, however, do not modify their courtship behavior to display only on the substrate with the best signal propagation, and they display on all three substrates as they encounter them (Elias et al. 2004).

Male wolf spiders, *Schizocosa*, display with visual and seismic signals on different substrates in their natural environments. *S. retrorsa*, court via drumming on their natural substrate of pine needles and red clay, where they experience the greatest mating success. They also court on leaf litter, where they are not normally found and have much lower initial mating success than on the natural substrates (Hebets et al. 2008). Rundus et al. (2010) found that *S. retrorsa* pairs, are equally likely to copulate in all signaling environments (Rundus et al. 2010). In contrast, *S. stridulans* normally inhabits leaf litter and courts females the most frequently there. Leaf litter transmits the vibrational signal the most effectively, and males are the most successful in obtaining copulations on the leaf litter. The substrate-borne vibrations are very important to mating success, because muted males unable to produce vibrational signals do not mate on any substrate (Elias et al. 2010b). Seismic feedback cues from female *S. stridulan* also affect where males court. Males that receive seismic feedback cues from females are more likely to optimize signal transmission by altering their use of signaling substrate than males without the feedback (Sullivan-Beckers and Hebets 2011). Another species of wolf spider, *S. ocreata*, occupies a complex microhabitat that includes leaf litter, wood, bark, soil and rocks. Mating success is the best on leaf litter, the substrate that has the best transmission properties for vibrational signals, and 85 % of successful matings occurred on this substrate. On substrates that attenuated seismic signals, males compensate by using more visual signals as a ‘backup’ (Gordon and Uetz 2011). Taken together, these studies demonstrate that male spiders exhibit flexible and opportunistic behaviors in their selection of substrates on which to generate vibrational signals during courtship. Although they may not always have access to the substrate that generates the best vibrational signal, they are able to compensate by seeking out a better substrate or by increasing the visual signals when on the substrates that limit the transmission of substrate-borne vibrations.

Insects also adjust vibrational signals to transmit well in their respective environments (Cocroft et al. 2006; McNett and Cocroft 2008). This response would be especially beneficial for plant-dwelling insects that are restricted to a single host. Plant stems and leaves, however, present limitations to signal transmission that could lead to mistakes in locating mates (McNett et al. 2010; de Groot et al. 2011). Because insects are much smaller than the structures on which they vibrate, the amplitude of the signal can be low and the vibrations dampened. The stems and leaves also are subject to wind-induced noise and act as frequency filters that can substantially alter the amplitude spectrum of a signal (Čokl et al. 2005; McNett et al. 2010). In contrast to the 3-dimensiononal space of airborne signals, vibrational signals are transmitted via a 1D environment on plant stems and a 2D space on leaf surfaces. Vibrational signals transmitted through plants in a 1D environment may carry very little, if any, information about source direction and distance (McNett et al. 2006; Čokl et al. 2007;

De Luca and Cocroft 2009) and lead to problems locating the source of the signal and mistakes in location of mates (de Groot et al. 2011).

Another accepted limitation to communication via substrate-borne vibrations in insects and spiders is that signal range is low and transmission is limited to a continuous substrate. A recent study demonstrated that the communication range of vibrational signals emitted by small insects is not limited to physically interconnected substrates. Grapevine leafhoppers, *Scaphoideus titanus*, are able to communicate between leaves on different cuttings up to 6 cm apart. Such signals may be detected by mechanosensory hairs or the Johnston's organ in the antennae (Eriksson et al. 2011).

4 Signal Reception

The diversity of animals that communicate by vibrations on multiple substrates has led to the evolution of diverse adaptations for signal reception. Animal "ears" consist of two basic types, pressure and mechanoreceptors. The mammalian ear, which is a pressure receptor highly specialized for reception of airborne vibrations, is the major receptor of the vibrations produced via footdrumming in both large and small mammals. Kangaroo rats and Gerbilline rodents have enlarged tympanic bullae and hypertrophied middle ear volumes specialized for hearing low-frequency airborne sounds that correspond to the frequencies in the drumming signal (Randall 2001, 2010). The use of drumming as a major signal modality may have led to ears better adapted to hear low-frequencies, because the bannertailed kangaroo rat has better low-frequency auditory sensitivity than a kangaroo rat species that does not drum, *D. merriami* (Shaffer and Long 2004).

Reception of seismic vibrations thorough an ear adapted to receive airborne vibrations led Randall and Lewis (1997) to ask the question: How does the bannertailed kangaroo rat with a well-adapted ear for hearing airborne sounds receive seismic signals? The kangaroo rats engage in footdrumming exchanges underground from burrows less than10 m apart, and kangaroo rats in the burrow footdrum in response to footdrums and disturbance on top of the burrow. The kangaroo rats apparently hear each other because they time their drumming responses not to overlap (Randall personal communication). A series of experiments revealed an answer to the question (Randall and Lewis 1997). Footdrums cause seismic vibrations that are transmitted directly through the ground from the site of drumming to the burrow wall and then radiated as an airborne sound into the burrow chamber. These vibrations are about 40 dB greater inside the burrow than airborne sounds outside the burrow. The kangaroo rats can use their sensitive ears for airborne reception of low-frequency sounds to hear the seismic signals when they become airborne in the burrow chamber.

Bone conduction is the usual route by which vibrations are transmitted to the inner ear of mammals. This may be a direct route to the inner ear through the cranial bones, or it may involve the middle ear. The blind mole rat, which is solitary and highly aggressive, receives information about the location of neighbors via seismic vibrations transmitted from their lower jaw pressed against the side of the burrow to the incus in the middle ear, thus bypassing the tympanic membrane (Rado et al. 1987, 1989). Blind mole rats may use somatosensory receptors to determine the direction of seismic vibrations in their tunnels (Kimchi et al. 2005). The massively hypertrophied mallei found in some golden moles is also an adaptation for receiving seismic vibrations by bone conduction. Although the human ear is highly specialized for reception of airborne sounds, another pathway of hearing could be through bone conduction via the skull to the sensory epithelium of the cochlea (Stenfelt and Puria 2010).

Snakes detect the substrate-borne vibrations via their mandible in direct coupling with the ground. Vibrations are transmitted from the mandible to the stapes via the quadrate bone to the inner ear (Young 2010). Much of the body of reptiles is in contact with the substrate, and mechanoreceptors in the skin are another possible avenue of vibration detection for these animals (Proske 1969).

Mechanoreceptors associated within deep skeletal structures such as joints and ligaments comprise another avenue of transmission of vibrations from the ground to the ear (Hunt 1961; Gregory et al. 1986). Pacinian corpuscles, which are pressure receptors consisting of lamellated bundles of cells, may transmit vibrations from the feet up through the legs and shoulders into the middle ear cavity or directly to the inner ear of placental mammals (Hunt 1961; Bouley et al. 2007). Kangaroos (Wallaby, *Thylogale billardierii*) have structures similar to Pacinian corpuscles in their legs (Gregory et al. 1986). The feet of elephants are rich in Pacinian corpuscles that could be used to detect ground-borne vibrations (Bouley et al. 2007), and the tip of the Asian elephant trunk is also rich in Pacinian and Meissner corpuscles, which may enable the elephant to detect very subtle vibrations with its trunk (Rasmussen and Munger 1996). There is no information on reception of seismic vibrations via the feet of kangaroo rats, but the possibility seems worth an investigation. The large hind feet of bipedal mammals provide a large amount of contact between the substrate and body. This coupling of the substrate with Pacinian corpuscles could act as a direct receptor of substrate-borne vibrations generated by footdrumming and facilitate reception of the seismic component of the signal.

Spiders are extremely sensitive to vibratory signals. Their main vibration receptor consists of slit sensory organs unique to spiders and found on virtually every part of the body, but especially legs and pedipalps (See comprehensive review of this system in Fratzl and Barth 2009). Slit sensilla are mechanoreceptors consisting of a hole in the cuticle of the exoskeleton covered by a membrane with a dendrite connected to the internal surface of the membrane (Hill 2008). These small grooves deform in response to mechanical stimuli imposed by movement and vibrations. The most sensitive of the slit sense organs is the metatarsal lyriform organ. Substrate vibrations cause the tarsus to move against the distal end of the metatarsus to compress the slits and stimulate the mechanosensory cells associated with them (Gingl et al. 2006). Spiders also use mechanosensitive hairs for seismic reception.

Insects have evolved a diversity of mechanoreceptors to receive substrate-borne vibrations (Hill 2008). The primary vibration receptors of insects are found in their legs. Campaniform sensilla, which are usually located near the joints, have comparatively low sensitivity, whereas the subgenual organ in the tibia is extremely sensitive. Its structure is complex and varies between different groups. Signals that are perceived by insects as substrate-borne vibrations also have a low intensity airborne component (Čokl and Virant-Doberlet 2003; Kavcic et al. 2013) that potentially may be detected over a few centimeters by antennal receptors (Kirchner 1994; Kavcic et al. 2013).

5 Footdrumming as Territorial Defense

Kangaroo rats use footdrumming as a mammalian version of individual acoustic signals to advertise territories analogous to bird song. In both birds and kangaroo rats, long range signals for territorial advertisement, rather than physical contact, communicate competitive ability and identity and minimize the cost of territorial defense (McGregor 1991; de Kort et al. 2009).

The bannertailed kangaroo rat is unique in its ability to generate individually distinct footdrumming signatures to communicate identity to territorial neighbors (Randall 1989, 1997) (Fig. 7.2). In playback experiments, territory owners footdrummed at higher rates in response to the footdrums of strangers compared with

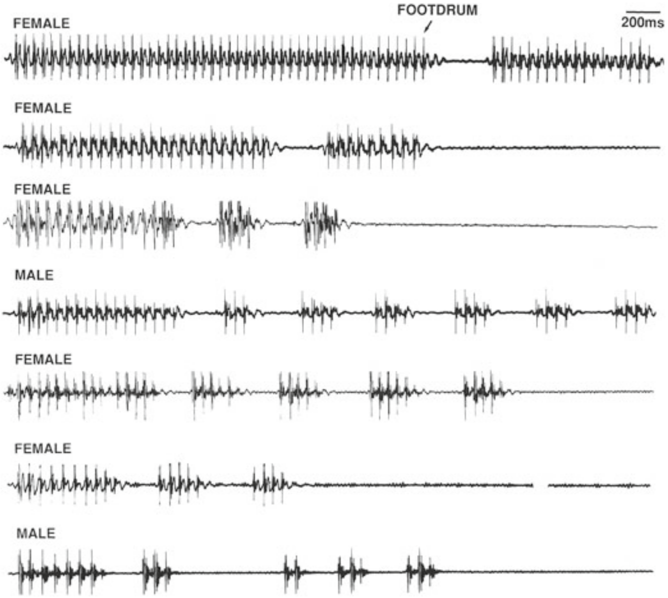

Fig. 7.2 Individual footdrumming signatures of adult male and female bannertailed kangaroo rat, *D. spectabilis*. Reprinted from Animal Behaviour, Vol 38, JA Randall, Individual footdrumming signatures in bannertailed kangaroo rats *Dipodomys spectabilis*, pp 620–630, 1989, with permission from Elsevier

neighbors (Randall 1993). Footdrumming signals of territorial owners differed the most from close neighbors compared with non-neighbors. Neighbor groups exhibited higher percentages of correct classification of footdrumming signals than non-neighbors (Randall 1995). The drumming patterns are flexible. The kangaroo rats can modify footdrumming signatures in response to changes in their social environment when they move into a new territory to distinguish themselves from their new neighbors (Randall 1995). This flexibility in communication is important to respond to constantly changing conditions of population density and proximity of neighbors. At higher densities, when there is more overlap of neighbors, more signal elements of the footdrumming signature are changed than in years when densities are low (Randall 1995).

In general, however, the individual footdrumming signatures of the bannertailed kangaroo rat tend to remain relatively constant from year to year. Adults that remained in the same territory had the most consistent footdrumming signatures. Of footdrumming signatures of 46 animals analyzed over two or more years, 37 % showed no change in the four structural signal elements (number of footdrums in the first, second and third footroll and footrolls in a sequence) while 63 % changed at least one signal element. Over the long term, however, no kangaroo rat radically changed its drumming signature. Kangaroo rats that drummed a long first footroll or a long footdrumming sequence continued to drum a long first footroll or footdrumming sequence with modifications, while kangaroo rats with shorter first footrolls and sequences also remained consistent within the general pattern (Randall 1995). The kangaroo rats possess the flexibility to alter drumming signatures to differ from new neighbors while still maintaining elements of their individual signature.

Greater variation in the footdrumming signatures of juveniles compared with adults suggests that young bannertailed kangaroo rats develop their individual drumming signatures as they mature (Randall 1995, 2010). The mothers' footdrumming provides an opportunity for young kangaroo rats in a litter (usually 1–3) while still in the burrow to learn the drumming patterns of their mothers during the 5–6 weeks before they begin to drum themselves. When about 0.25–0.50 % adult body weight, the young bannertaileds begin to exit the burrow to forage and footdrum at high rates (footrolls/h) (Randall 1984).

Do young bannertailed kangaroo rats copy the footdrumming signatures of their mothers? In a comparison of five signal elements of the drumming signatures of mother-offspring pairs, mother-daughter footdrumming signatures were similar, but the footdrumming signatures of sons tended to differ from their mothers. Daughters and mothers differed in one or less signal element while sons' footdrumming signatures differed on average from 2 to 4 signal elements from their mothers (Randall 2010). The reason for this difference is unclear, but it could lead to inbreeding avoidance (See discussion in section on mating).

Another highly territorial kangaroo rat, the giant kangaroo rat, *D. ingens*, drums individually distinct drumming patterns (Randall 1997). Whether the variation in the signatures communicates identity is less clear for *D. ingens* than for *D. spectabilis*. Although *D. ingens* footdrums in response to visual and auditory contact with neighbors, during playback tests in the field they footdrummed equally to playbacks of footdrumming from conspecifics and *D. spectabilis* and *D. deserti* (Randall 1997). A territorial signal can communicate "someone lives here" or "I live here". Kangaroo rats that drum single thumps, *D. deserti*, or simple patterns, *D. heermanni*, communicate that someone lives in the territory, but there is no information about identity (Randall 1997; Shier and Randall 2007). Thus far, only the bannertailed and giant kangaroo rats seem able to communicate identity via footdrumming signatures.

Invertebrates can use substrate-borne vibrations in territorial disputes similar to kangaroo rats. Larvae of the common hook-tip moth, *Drepana arcata* (Deoabiudea), detect approaching conspecific intruders by vibratory cues (Guedes et al. 2012). In response to the vibrations the larvae drum and scrape mandibles and anal "oars" against leaf surfaces in territorial defense. Territories consist of nests that require an energy cost to construct and are valuable to own. The drumming and scraping appear to mediate the encounters and allow the resolution of conflicts without physical harm, and the intruder usually responds by leaving the leaf (Yack et al. 2001). The vibrations are considered to be ritualized displays to warn another caterpillar not to waste time pursuing an occupied territory (Yack et al. 2001).

6 Vibrations in Multimodal Signals

Multimodal displays are favored by selection because they transmit more complete and reliable information to allow for faster and more accurate decisions. Many animals communicate using complex multi-component displays that contain signals or components made from different sensory modalities (chemical, visual, vibrational) (Partan and Marler 1999, 2005; Candolin 2003; Hebets and Papaj 2005; Taylor et al. 2007; Bro-Jorgensen 2009). Because researchers frequently study only one communication modality at a time, the complexity of signaling in animal communication has been under appreciated until recently. In terms of using vibratory signals in a multimodal signal, the best examples have been in spiders.

Jumping spiders, genus *Habronattus*, exhibit some of the most elaborate multimodal displays in the animal kingdom (Elias et al. 2012). The spiders employ sex-specific, colored ornaments that they coordinate with combinations of motion displays and substrate-borne vibrations. Vibrations consist of up to 20 elements organized in functional groupings (motifs) that change as courtship progresses, analogous to a musical composition. In a comparison of 11 species of *Habronattus*, Elias et al. (2012) found that displays ranged from no complex display (*H. borealis*) to a species with the most complex communication system yet described in arthropods. *H. coecatus* has 18 different morphological structures it can use as ornaments to combine with a diversity of vibrational patterns. Future comparative research on this diverse communication system in jumping spiders has a good chance to lead to a better understanding of the evolution of substrate-borne vibrations in complex multimodal systems.

The peacock spider, *Maratus volans*, is a charming example of another spider that combines vibrational and visual signals in elaborate, multimodal courtship displays (Girad et al. 2011). Males of this jumping spider from Australia unfurl a brightly colored flap that resembles the fan of a peacock, which they prominently displays while vibrating the abdomen by trembulation to produce substrate-borne vibrations. Three different types of vibrations are transmitted during the courtship in conjunction with the visual displays (Girad et al. 2011). The elaborate courtship of the peacock spider is unusual in its complexity. Besides being interesting to watch, the display might be a good model for studies of how female choice drives elaboration of sexually selected traits in spiders.

Seismic signals are also an important component of multimodal signals in wolf spiders, and their use varies among species. Male wolf spiders use both seismic and visual components of courtship displays that range from unimodal (seismic only) to multimodal (seismic and visual) (Hebets and Uetz 1999; Uetz and Roberts 2002; Uetz et al. 2009). Signal modes are species specific and can vary between even closely related sibling species (Hebets et al. 2013). The individual or complex components of multimodal signals interact to contribute to the efficacy of communication in many functional ways (Hebets and Papaj 2005).

Species of wolf spider in which females use mostly vibrational cues in assessing conspecific males tend to have vibration-based male courtship displays (*S. duplex* and *S. uetzi*) while the opposite is true for species in which females use more visual cues in male assessment (*S. stridulans* and *S. crassipes*) (Hebets and Uetz 1999). In a comparison of seven species of wolf spider (*Schizocosa* spp.), five of seven species of female preferred the vibrational to the visual signal. In the other two species the preference was equal (Uetz and Roberts 2002). When sibling species, *S. ocreata* and *S. rovneri*, were compared, females of both species detected multimodal stimuli faster than visual or seismic cues alone, but they differed in responses to cues once they became oriented (Uetz et al. 2009). In another species of wolf spider, *S. stridulans*, the seismic signal was sufficient for successful copulation, whereas the visual signal was neither necessary nor sufficient. Females preferred the more energetically expensive signal. In this example only the seismic signal is important for mating success, thus representing an example of a seismic signal dominating a multimodal communication system (Hebets 2008) Taken together, these results suggest multimodal signaling increases detection of males by females and that vibrational components are an important, and sometimes essential, part of the signal.

Although multimodal communication in mammals has not received as much attention or research as in arthropods, mammals often employ more than one signal modality in communication. Acoustic signals are often combined with visual. Wild chimpanzees drum on buttresses and trunks of trees to produce low-frequency sounds in environments of low visibility. The drumming occurs in discrete bouts that may be integrated into the chimpanzee's pant hoot as a multimodal signal for long distance communication (Arcadi et al. 2004). Drumming or thumping by ungulates is usually described as part of combination of visual and vocal signals when alarmed by predators (Caro et al. 2004). Red squirrels, *Tamias hudsonicus*, confront predators with loud vocalizations, stomping their hind feet and tail flicks (Digweed and Rendall 2009). Footdrumming accompanies visual and vocal signals in great gerbils (*Rhombomys opimus*) during mating interactions (Randall personal observations) and anti-predator behavior (Randall et al. 2000).

7 Vibrational Communication and Mating Success

For courtship signals to evolve, signals used during mating should convey honest information about male quality, be costly to produce, and be reliably detected and processed by female receivers (Zahavi 1977; Maynard-Smith and Harper 2003). Failure of a male's signal to stimulate a female's sensory system may cause serious fitness costs for the male (Guilford and Dawkins 1991). Females should prefer males with the more elaborate and energetic displays as a signal of male condition and fitness. High quality males are better able to afford the costs associated with the displays and their vigorous displays communicate to the female that she will have good genes for her offspring (Kotiaho et al. 1998). Furthermore, besides losing a mating opportunity, a male's survival may depend on his courtship performance. Female spiders can be very aggressive, and males that perform poorly may be in danger of becoming the female's next meal, and opportunity for future mating is eliminated (Elgar 1992; Prenter et al. 2006; Stoltz 2008; Roggenbuck et al. 2011).

The importance of vibrational signals in mating success and eliciting female receptivity is well established among numerous wolf spider species (Hebets and Uetz 1999; Uetz and Roberts 2002; Maklakov et al. 2003; Hebets 2005, 2008; Gibson and Uetz 2008; Sullivan-Beckers and Hebets 2011; Hebets et al. 2013). Variation in male vibration signals also influences female mate choice decisions in several other spider species (Kotiaho et al. 1996; Gibson and Uetz 2008; Soltz et al. 2008, 2009). Female choice in redback spiders*, Latrodectus hasselti*, is especially unambiguous. Females favor prolonged vibratory courtship that can last hours. Males attempting rapid mating without the prerequisite courtship pay a large cost. They are cannibalized before mating can be completed (Soltz et al. 2008). But this is not always the case. Sand-dwelling wolf spiders *Allocosa brasiliensis*, show a reversal in sex roles, and males sometimes cannibalize females of low body condition (Aisenberg et al. 2011).

Perhaps the best example of how drumming rate leads to mating success is the wolf spider, *H. rubrofasciata*. The extensive research on this species found that females prefer the most actively drumming males (Kotiaho et al. 1996), and males that drum at higher rates are selected by females over males with lower drumming rates (Kotiaho et al. 1996; Parri et al. 1997; Ahtiainen et al. 2004). During the short mating season (April–June) males drum while wandering around the habitat searching for receptive females. Once they locate a female the males increase the drumming rate to high intensity (Rivero et al. 2000). These high drumming rates are costly. They require large amounts of energy and compromise the immune function (Mappes et al. 1996; Kotiaho et al. 1998; Ahtianen et al. 2005). Males in better physical condition, therefore, are able to drum at higher rates than males in poorer condition (Kotiaho 2000), and females likely choose the high drumming males as an indicator of good genes for their offspring (Parri et al. 2002). These results demonstrate that production of substrate-borne vibrations via drumming are condition-dependent and function as honest signals of male quality in *H. rubrofasciata* (Kotiaho et al. 1996, 1998, 1999; Mappes et al. 1996; Alatalo et al. 1998).

Recent research demonstrates the importance of substrate-borne vibrations for female mate choice in another species of wolf spider (Wilgers and Hebets 2012). For male *Rabidosa rabida*, the seismic signal is critical for female mate choice. Males use both seismic vibrations and visual ornaments in mating interactions. When signals are separated, females respond to the seismic signal alone, but not to the visual signal. When females are able to detect both signal components, variation in visual ornamentation influences mate choice, and the females prefer ornamented males. These results suggest that the seismic signal of male *R. rabida* is necessary for female mate choice and that both the visual and vibratory components of the courtship display interact to influence female mating decisions (Wilgers and Hebets 2012).

Drumming in wolf spiders has a duel function. The males drum during courtship and in competitive interactions with other males (Delaney et al. 2007). In *S. ocreata,* signaling rates, which include foot tapping, are much higher in male–female interactions than in male-male contests and higher for males that successfully mated than for those that did not mate. Mean duration of some male displays is also greater for males that successfully mated. However, male size was not associated with probability of mating. Taken together, results suggest an intersexual selection context for the current function of male signals in these wolf spiders and that increased display vigor is associated with male mating success (Delaney et al. 2007). In contrast, in *S. lineatus* the presence of male vibrations was shown to stimulate females to mate, but had no other function (mate recognition and indication of mate quality) (Maklakov et al. 2003).

Female choice seems to be a driving force on the substrate-borne vibrations used in courtship displays of male jumping spiders. Mating success of *Phidippus clarus* males depends on signaling rate of the vibrations (Elias et al. 2005). These high intensity rates are correlated with male size, and both virgin and mated females assess male size through the courtship vibrations (Sivalinghem et al. 2010). Size is likely an important predictor of fitness in this species as larger, heavier males are more successful in male competition (Elias et al. 2008; Kasumovic et al. 2009).

Seismic feedback from females to courting males can be important for successful courtship. Males of the wolf spider *S. rovneri* court females with seismic signals transmitted through the forest floor. If females provide positive feedback with visual and seismic displays, males increase their overall signaling effort while males with no feedback maintain their signaling rates (Sullivan-Beckers and Hebets 2011). In addition, males receiving only seismic responses from females change the substrate on which they display (Sullivan-Beckers and Hebets 2011). These males have the flexibility to adjust their courtship behavior to optimize transmission of seismic signals and possibly obtain higher mating success.

Sometimes experience is a factor in female responses. In the pholcid spider, *Holocnemus pluchei,* females with previous mating experience generate substrate-borne vibrations most frequently. Intensity was higher in females that did not accept new copulations compared with those that copulated, and there was no difference in response to elaborate and non-elaborate courtship by males. Females probably communicate levels of sexual receptivity and may assess indirectly a male's ability to persist in courtship (Dutto et al. 2011).

Many insects communicate during courtship with substrate-borne vibrations (Hill 2008). For instance, when a female *Drosophila* senses vibrations generated by male abdomen shakes, she becomes receptive and stops walking. These abdominal quivers and associated vibrations, as well as their effect on female receptivity, are conserved in other Drosophila species (Fabre et al. 2012). In another recent example, treehoppers, *Enchenopa binotata* (Hemiptera: Membracidae), duet during mating interactions with plant-borne vibrational signals. A female's likelihood of responding to a male corresponds to the likelihood of her mating with him (Rodríguez et al. 2004, 2006). *Enchenopa* females are most selective when they experience vibrational signals with high variability. Females are adapted to adjust selectivity in response to the degree of variability in potential mates. The observed pattern of plasticity in mate preferences suggests that the benefits of selectivity increase as variability in potential mates increases (Fowler-Finn and Rodriguez 2012).

Footdrumming has been described during mating in rodents to function as a courtship signal performed in close proximity to the female. Fossorial mole-rats exchange footdrums during mating, including social *Cryptomys damarensis* (Jarvis and Bennett 1991) and the solitary Cape-mole-rat, *Georychus capensis* (Narins et al. 1992). Both the Mongolian gerbil, *Meriones unguiculatus* and great gerbils, *Rhombomys opimus*, engage in footdrumming exchanges during mating (Randall 2001, personal observation).

Bannertailed and giant kangaroo rats (*D. spectabilis* and D. *ingens*) footdrum during mating in intersexual exchanges. Neighborhood males enter the territories of estrous females on the night of mating, and females that would normally chase the male out of her territory instead engage in footdrumming exchanges. Males may drum softly as they approach a female and attempt to engage in contact. Many of these exchanges and mating occur in the burrow as the male and female move in and out of it. Females of both species exhibit less aggression toward familiar neighbor males and engage in more nonaggressive contact with close neighbors (Randall 1991; Randall et al. 2002).

The tendency of bannertailed kangaroo rats to mate with neighbors poses the danger of inbreeding. Both males and females are philopatric and continue to reside in their mother's natal territory for many months after weaning. When they do disperse, it is to a territory in their neighborhood or they may inherit the territory of their mother (Jones 1984; Waser et al. 2005). This dispersal behavior increases the likelihood that neighbors are related and that mating would occur between relatives. Molecular data show, however, that inbreeding is lower than expected if females were mating with their sons (Waser et al. 2005, 2012). Mother-son offspring were underrepresented in an analysis of long-term data of mating relationships, and offspring from first and second-degree relatives were also under represented to suggest that inbreeding does not readily occur and there is precopulatory mate choice (Waser et al. 2012). Waser et al. (2012) conclude that the kangaroo rats are more likely to discriminate kin by familiarity developed via association early in life than by spatial cues or phenotype matching.

There is some evidence to suggest that differences in footdrumming signatures between mothers and sons could be at least one mechanism of kin recognition and inbreeding avoidance in the bannertailed kangaroo rat. Sons develop footdrumming signatures to differ from their mothers while daughters and mother footdrumming signatures are similar (Randall 2010). If the kangaroo rats discriminate kin by familiarity developed via association early in life, mother-son pairs could learn to recognize each others' footdrumming signatures and avoid mating. Potential mates have ample opportunity to test for recognition of familiar footdrumming patterns during the vigorous footdrumming exchanges that occur during courtship (Randall 2010 and personal observation). Further study is necessary to determine why there are these sexual differences in learning footdrumming signatures. A comparison of paternity with footdrumming signatures might reveal whether males mate more frequently with unrelated females that have a different footdrumming signature from their mothers (Randall 2010). If so, this would be the first example of kin recognition by footdrumming signatures.

8 Vibrational Signals and Contest Assessment

Bannertailed kangaroo rat males compete vigorously for access to estrous females by footdrumming and chasing. Some of the longest and most vigorous footdrumming occurs during these contests. When the operational sex ratio favors males, up to six males may converge at the territory of the estrous female and compete for access to her (Randall 1991, 2010). A female is only in estrus a few hours, and males limit their total time in the female's territory to correspond with the time she is in estrus. Males footdrum and chase a majority of the time they are in the estrous female's territory, and when other males are present they drum at very high rates (1,128 ± 156.4 footrolls/h) (Randall 2010). Mating interactions in the giant kangaroo rat are similar. Footdrumming increases with the number of males present. The more males the higher the drumming rate (Randall 2010). In matings with two or less males, little footdrumming occurs, but when two or more males compete drumming increases exponentially (Hekkala 1995; Randall 2010). There is no evidence that the male that footdrums the most and longest has a mating advantage. Mating success seemed determined more by age than size (Randall 1991).

Because aggressive contests can be costly, assessment of fighting ability is important to competitors. The ability to sustain production of vibratory signals is probably a good predictor of fighting ability. Male jumping spiders, *Phidippus clarus*, use multimodal signals (visual and substrate-borne) to assess their fighting ability during aggressive encounters. Substrate-borne vibrations are important predictors of the winner, and heavier and more actively signaling males are contest winners. Furthermore, the duration of pre-contest phase is based on differences in vibration behavior between males. Bigger males are more willing to escalate towards contact phases even though the outcome of escalated fights is based made more on weight than on size (Elias et al. 2008).

Agonistic drumming activity of the wolf spider, *H. rubrofasciata*, is related to fighting ability (Kotiaho et al. 1999). *H. rubrofasciata* fights begin with agonistic drumming, and the winner of the fight drums at a significantly higher rate than the loser of the fight. About a third of the encounters were settled prior to escalation into a contact fight, probably by the difference in agonistic drumming rate between the opponents. Difference in agonistic drumming rate between the opponents was significantly greater than in those trials that did escalate to contact fighting. This suggests the spiders drum to transmit an honest signal of fighting ability, size and motivation.

Disputes in caterpillars (family Drepanidae) are solved by ritualized displays that are only used in territorial defense. The solitary larvae of the common hook-tip moth (*Drepana arcuata*) defend a silk nest on a leaf from conspecifics. They engage in ritualized "duels" with intruders, during which they produce vibrations by drumming and scraping their mandibles as well as specialized anal structures against the leaf (Yack et al. 2001). Most conflicts are resolved quickly, and the resident caterpillars generally wins the territorial disputes, but, relatively large intruders can displace a resident from its nest (Yack et al. 2001).

9 Predation

9.1 Predators Locate Prey

Predators are able to locate prey by responding to substrate-borne vibrations. They may respond to vibrations produced by some aspect of the habitat in which the prey is found or an incidental vibration from a natural activity such as eating (Hill 2008). The Namib desert golden mole, *Eremitalpa granti namibensis*, responds to incidental vibrations generated by motion of dune grass. The blind mole detects wind-caused vibrations of the grass transmitted through the sand and orients and swims through the sand to the source of the vibrations to hunt for termites associated with the grass (Lewis et al. 2006). Predatory stinkbugs (*Podisus maculiventris*) feed on caterpillars they locate by vibrational cues the prey makes when chewing plant material (Pfannenstiel et al. 1995).

Besides attracting mates, vibrational signals used in courtship attract predators (Parri et al. 1997; Ahtiainen et al. 2004; Lindstrom et al. 2006; Roberts et al. 2007). A recent study illustrates the importance of vibrational signals in sexual communication as a mode of prey detection by predatory spiders and provides a technique to analyze for predation events that cannot be observed readily in the field. Virant-Doberlet et al. (2011) used molecular techniques to analyze gut contents of the predatory tangle-web spiders, *Enoplognatha ovata* (Theridiidae), for the presence of leafhoppers as prey. Results revealed that leafhopper nymphs that signaled by plant-borne vibrations were preyed on at a greater rate than nymphs that were non-signaling. Playback experiments illustrated that the predatory spider used vibration signals to find their prey, and they killed significantly more displaying males than females. These results are important for two reasons. First, the innovative use of molecular techniques to analyze gut contents creates an opportunity to investigate previously untested predator–prey association, and second, the study demonstrates that exploitation of vibrational signals by predators may be important drivers of the evolution of predator–prey interactions (Cocroft 2011; Virant-Doberlet et al. 2011).

The ultimate predatory spiders that use vibratory deception to capture prey are in the family Salticidae, genus *Portia* (Nelson and Jackson 2012). They are jumping spiders that feed on other spiders using fascinating behavioral adaptations that minimize detection and identification by the prey and thereby prevent a counter-attack. *Portia* is unusual because it exploits a wide range of spider species by using a trial-and-error method (Jackson and Wilcox 1990). They capture prey by invading their webs and mimicking the vibrational signals of caught insects or approaching mates. *Portia fimbriata* masterfully mimics the behavior of an insect ensnared in the capture zone of a web by making faint vibrations on the periphery of the web. In webs of more dangerous, large prey *Portia* vibrates vigorously on the web to create a disturbance (“smokescreen”) to mask its approach (Tarsitano et al. 2000).

A predatory strategy of the fringed jumping spider, *P. fimbriata*, is to imitate the vibrational signals of males to lure out females. *Euryattus sp*. females, another saltacid spider species, are unusual because they nest inside suspended rolled-up leaves. During courtship, *Euryattus* males perform a specialized vibratory display (shuddering) while standing on a suspension nest of a female, causing the leaf to rock back and forth. The female exits the leaf and either mates with the male or drives him away. *P. fimbriata* mimics the courtship display by standing on the leaf and shuddering in a similar vibratory displays to lure *Euryattus* females from their nests so they can prey on them (Jackson and Wilcox 1990; Nelson and Jackson 2012).

The predatory strategy of invading the webs of web-building spiders has been adopted by an insect predator, assassin bug, *Stenolemus bituberus*. The assassin bug plucks the silk to generate vibrations that mimic prey of the spider. The vibrations have a temporal structure and amplitude that is similar to those generated by prey and different from a courting male. If the spider ventures within striking distance of the plucking assassin bug, it becomes the bug’s dinner (Wignall and Tayler 2011). The assassin bugs’ problem is how to access the web and move close enough to ambush without alerting the prey, because web silk is extremely proficient at transmitting vibrations and web-building spiders have acute ability to detect vibrations on the web. To overcomes this difficulty the assassin bugs have developed a simple strategy to avoid detection. They use natural event of wind to function as a ‘smoke screen’ to mask their approach (Wignall et al. 2011).

There is ample evidence that snakes are capable of responding to substrate-borne vibrations (Young 2010). It is possible, therefore, that snakes could eavesdrop on the territorial footdrumming of kangaroo rats to locate them as prey, especially when they are very hungry after hibernation. Results of playback tests of gopher snakes, *Pituophis melanoleucus affinis*, to territorial footdrumming of the bannertailed kangaroo lend some support to this hypothesis. Six of six snakes that had not eaten for an indefinite period and were very hungry moved toward a buried, mechanical thumper playing territorial footdrumming and repeatedly struck at the kangaroo rat positioned on top of the thumper in a protective cage. In contrast, 5 of 7 snakes that had eaten within 4 weeks and were presumably less hungry moved away and avoided the territorial footdrumming, and only one snake struck at the kangaroo rat (Randall and Matocq 1997). There were mixed results with snakes that had not eaten in 6 weeks. Four approached and 5 avoided the thumper. Because hungry snakes often have to travel long distances to locate patchily distributed prey (King and Duvall 1990), it would be to a hungry snake's advantage to use the drumming to locate areas where they could wait in ambush for a kangaroo rat dinner.

9.2 Prey Fight Back

Predation is a strong selective force on the evolution of defense behavior of prey, and an appropriate defensive response is critical to survival. An unique example of an animal that responds to specific substrate-borne vibrations created by the approach of a predator is the red-eyed tree frog, *Agalychnis callidryas*. Egg-eating snakes attack the egg clutches that mature on vegetation hanging over a pool. Vibrations generated by the snake trigger an immediate synchronized response to propel the embryos from the egg capsule into the water below. The response by the frogs is very specific, and natural disturbances in the environment such as wind and rain do not trigger release of the embryos. This specificity is important because there is an abundance of predators in the pond below that will prey on the embryos, and immature embryos would be especially vulnerable (Warkentin 2005; Caldwell et al. 2009, 2010). Even caterpillar larvae (*Semiothisa aemulataria* (Geometridae)) can distinguish the vibrations generated from different sources. They defend themselves from specific predators by hanging on a silk thread in response to wasps (*Polistes fuscatus*) and stink bugs (*Podisus maculiventris*), but not in response to birds, other herbivores or abiotic factors (Castellanos and Barbosa 2006). The masked birch caterpillar (*Drepana arcuata*) does not respond to disturbances caused by wind and rain but does respond to vibrations caused by the approach of predators (wasps) and conspecifics (Guedes et al. 2012).

Sexually selected signals attract mates and provide an advantage in courtship, but they can also attract predators to cause a disadvantage in survival (Zuk and Kolluru 1998; Rosenthal et al. 2001). Animals using multimodal signals in courtship displays may be especially vulnerable. In spiders, the benefit of increased signaling efficacy of large visual ornaments and complex, multimodal signaling may be countered by increased predation risks. For instance, wolf spiders, *S. ocreata*, are more vulnerable to predation by jumping spiders (*P. clarus*) when the multimodal signal of both visual and seismic vibrations are used in mating displays than when there is only the visual signal (Roberts et al. 2007). Higher drumming rates during mating encounters attract predators. Female wolf spiders, *H. rubrofasciata*, will not mate with non-drumming males and prefer males with the higher drumming rates (Parri et al. 1997; Ahtiainen et al. 2004), but male spiders with higher drumming rates are more prone to predation by pied flycatchers (*Ficedula hypoleuca*) (Lindsrom et al. 2006). Because these males are in better condition and have higher mobility, they are able to escape predator attacks better than males with lower mobility. The males in good condition, therefore, can compensate for the predation risk generated by higher drumming rates and bear the energy costs and predation risks of signaling better than males in poor condition.

An interesting insect example is the response of ants to the vibrational alarm signals of insects that provide them with food. In this mutualistic association, the ants protect the prey from predators, the prey survive the approaching predator, and the ants are given nectar as food by the insect prey (DeVries 1990; Travassos and Pierce 2000). Adult treehoppers, *Publilia concava,* generate distinct substrate-borne vibrations in response to the approach of the ladybird beetles. Ants respond with increased activity that is interpreted as anti-predator behavior directed at the beetle (Morales et al. 2008).

Predation pressure is a strong evolutionary force that has led to a diversity of anti-predator behaviors in mammals. Small mammals, mainly rodents and elephant shrews, drum their feet in the presence of snakes (Randall 2001, 2010). A large number of hoofed mammals strike their feet on the ground when they encounter a predator (Caro 1995; Caro et al. 2004). Macropoid marsupials, kangaroos and wallabies, thump their feet when disturbed and in the presence of predators (Rose et al. 2006). Male and female adult eastern grey kangaroos, *Macropus giganteus*, generate loud thumps with their hind feet, Because solitary kangaroos thump more than grouped kangaroos, the thumps may function to startle a predator or to communicate it has been detected (Bender 2006). It seems surprising given the number of macropods that thump their feet and the commonness of the behavior that it has not been studied in more detail.

Kangaroo rats employ an active defense against snakes. After detecting a snake, territorial kangaroo rats (*D. spectabilis, D. ingens, D. deserti*) approach to within striking distance, jump back and begin to footdrum. The kangaroo rats often continue to approach a snake and footdrum until the snake leaves or is removed (Randall and Stevens 1987; Randall and Matocq 1997; Randall and Boltas King 2001). This would seem a very dangerous, non-adaptive behavior, but for kangaroo rats the drumming is adaptive because it functions as an individual defense to thwart further hunting by the snake. The kangaroo rats actually reduce risk to themselves by their apparently risky behavior. This conclusion was supported by experiments with bannertailed kangaroo rats and gopher snakes, *P. m. affinis* (Randall and Matocq 1997). In laboratory encounters gopher snakes decreased stalking behavior in response to increased footdrumming by the kangaroo rats. Snakes avoided footdrumming playbacks in field tests, unless they were very hungry (Randall and Matocq 1997). The drumming communicates to the snake, which hunts by surprising its prey in an ambush, “I am not easy prey so get out of my territory”, and in natural observations snakes did leave the territory (Randall and Stevens 1987). The hypothesis that the footdrumming in the presence of snakes is directed to warn adult neighbors was rejected because neighboring kangaroo rats did not respond to playbacks of the anti-snake drumming of a neighbor (Randall and Matocq 1997). Mothers, however, footdrummed at higher rates and came closer to the snake than nonmothers to suggest that the footdrumming warns vulnerable offspring in the burrow of danger.

Both social and solitary rodents drum their feet in the presence of predators (Randall 2001). The great gerbil, *Rhombomys opimus*, is a social rodent that lives in family groups consisting of an adult male, related females and their offspring (Randall et al. 2005). Adults and juveniles of both sexes emit alarm calls and foot-drum in the presence of terrestrial predators (Randall et al. 2000; Randall and Rogovin 2002). This well-organized alarm system communicates degree of risk and response urgency to family members (Randall and Rogovin 2002). All alarm calling occurs out of the burrow, but when the gerbils footdrum they change the location of their drumming in response to the type of predator and its ability to enter the burrow (Randall et al. 2000). When a large terrestrial predator such as a fox or monitor lizard, *Varanus griseus caspius*, that is unable to enter the burrow is sighted, the gerbils vocalize and enter the burrow and footdrum from inside the burrow. In response to a sand boa, *Eryx miliaris*, that can enter the burrow, the gerbils footdrum outside of the burrow in closer proximity to the snake than when encountering either a wolf hound (represents a fox) or monitor lizard (Randall et al. 2000). Response to the snake suggests the gerbils may be communicating directly to the snake that its chances of ambush are thwarted much in the same way as in kangaroo rats.

10 Evolution of Vibrational Communication

The path of evolution of vibrational communication is unclear. We know that it is a very ancient system dating back in vertebrates to ancient amphibians (Hill 2008). Signaling by tremulation of the body or of some of its parts is one of the most widespread and, presumably, primitive modes of mechanical signaling in insects (Stritih and Ĉokl 2012).

We can only speculate about how vibrational signals originated in arthropods, but it seems logical that drumming, tapping and rubbing originated from incidental actions associated with walking. A slightly higher leg lift, louder foot step or accidental thump of the abdomen might capture the attention of a potential mate and eventually become part of a mating display. Females often have a preference for novel signals, and female jumping spiders, *H. pugillis*, prefer novel forms of seismic signals (Elias et al. 2006). The current diversity of communication by substrate-borne vibrations in arthropods illustrates a high radiation in which the behavior evolved multiple times at a fairly fast rate (Rodríguez et al. 2008).

Changes in habitat and its affect on mating signals may be a driving force in the radiation of some spiders and insects. Elias and Mason (2010) suggest that the diversity of substrate-borne, sexually-selected signaling in spiders, insects and other arthropods is associated with "sensory drive" mechanisms. This theory predict that females evolve preferences for mating signals that are efficiently detected and decoded (Endler and Bosolo 1998). The heterogeneity of spider habitats drives the modification of signal production for efficient signal transmission leading to evolution of female perception to match the changing signal leading to assortative mating and species divergence (Hebets et al. 2013). In a similar interpretation for insects, Cocroft et al. (2010) propose that plant host shifts led to divergence in mate communication systems in insects because differences in male advertisement signals of *Enchenopa* treehoppers covary with differences in resource use. Once differences in signal traits have appeared female mate choice is likely to reduce gene flow and promote further divergence (Cocroft et al. 2010).

The path of evolution of footdrumming as communication in mammals can only be speculated, but the diversity of mammals that drum suggests the behavior evolved independently in different lineages (Randall 2001). It seems logical to speculate that footdrumming or stomping in some lineages evolved from incidental behavior. A cow or horse stomping its feet when swarmed by flies on a hot summer day or a rodent or bird trying to dislodge a mosquito are familiar sights (Darbro and Harringron 2007). Deer mice, *Peromyscus maniculatus* stomp their feet in defensive behavior during attacks by biting stable flies, *Stomoxys calcitrans* (Kavaliers et al. 2005). Defensive responses to the biting flies are acquired through social learning, and observers learn faster when the demonstrator is familiar or related. This recognition of incidental signals that communicate threatening stimuli could become a precursors of anti-predator behavior through the social learning of fear-induced avoidance responses.

When mammals become excited and agitated by stressful situations, they may drum or stomp their feet (Randall 2001). Foot shock and novel stimuli induce drumming in Mongolian gerbils (Routtenberg and Kramis 1967), and footdrumming rates in kangaroo rats are especially high in stressful situations (Randall 1991; Randall and Matocq 1997). Drumming, therefore, could have originated from responses to stressful situations when animals become fearful in the presence of a predator or a competitor. The original drumming may have been a result of displacement behavior by a fearful animal in conflict about whether to chase or flee (Randall 2001).

Drumming also may have originated by ritualization of behavior associated with digging and running. The drumming could be an extension of digging in fossorial rodents where the digging becomes ritualized (Francescoli and Altuna 1998). Kangaroo rats often engage in a brief drumming bout of 2–4 drums before they chase another kangaroo rat. The behavior appears to be an intention movement to indicate a high probably of locomotion toward another animal. This behavior is seen in kangaroo rats that are too small in body size to drum in extended bouts for communication as well as in the larger territorial species (Randall 2001). Drumming to communicate territorial ownership evolved in the larger-sized kangaroo rats that overcame energetic limitations from size constraints (Randall 2001).

11 Concluding Remarks

Vibrational communication is an important mode of communication that requires more recognition and investigation. Although its diversity parallels or surpasses other communication modalities, a strong body of research has only recently begun to develop. Studies of vibrational signals have a very broad base because invertebrates and vertebrates use vibrational signals as a major modality of communication in both intra- and inter-specific communication in many different contexts. It is my hope that recent attention to vibrational communication in the comprehensive book by Peggy Hill (2008), an edited volume by Caitlin O'Connell-Rodwell (2010) and this review where I have included the latest research will generate the interest that the subject deserves and that a strong theoretical and empirical base for the behavior will be developed.

The diversity and sophistication of vibrational communication is quite interesting and surprising. Substrate-borne vibrations are the only mode of communication, with the possible exception of chemical, that can be accomplished by animals ranging from a simple caterpillar to an elephant. The idea that developing beetle pupae could signal conspecific larvae with substrate-borne vibrations to deter being run into or caterpillar larvae discriminate vibrations from different predators would not have been considered only a few years ago. Considering the large number of insect, spiders and mammals that communicate with vibrational signals in one form or another, there is still much to learn about many interesting adaptations for communication that involve these signals.

The diversity of how vibrational signals are produced and the substrates on which animals produce them is rather surprising. It seems animals can produce vibrational signals on almost any substrate, including water. For example, jumping spiders in Damian Elias's lab readily vibrate on flesh-toned pantyhose pulled over an embroidery hoop (Randall personal communication). The assumption should be avoided, therefore, that no communication is occurring because the substrate seems unlikely or there is no discernable sound. There are many substrates used by animals for vibrational communication that require investigation. Much more is to be learned about transmission properties, behavioral preferences for types of substrates and the mechanisms for the choice.

The importance of and variation in vibrational signals used in mating behavior has become well established in arthropods. We find the flamboyant sexually selected signals of spiders of great interest. There is strong evidence that female choice in spiders is related to the intensity and duration of drumming and other substrate-borne vibrations generated by courting males. These vibrations are sexually selected signals that are probably under intense selection for honesty, especially considering that female spiders are able to attack and kill males that have not communicated effectively. This picture of spider mating, however, is based on only a few species, and there are examples of role reversal. The task ahead is to learn about mating behavior in many more species from different locations and habitats if comparisons of different mating tactics are to be good models for understanding the evolution of the behavior.

Evidence for vibrational signals as important component of multimodal signals in insects and arthropods is becoming well established. Unfortunately, the same cannot be said for mammals. Seldom is the foot stomping or drumming a focus of an investigation. Often the act of drumming is treated as an incidental occurrence and not studied as a component of behavior. For instance, we know that many ungulates drum or stomp a foot when alarmed, but the reason for the behavior and what is communicated remains to be studied in any detail. The same is true for macropoids. Despite the description of drumming in multiple species of kangaroos, there has been little effort to study them in any detail. The only mammal where a complete picture of drumming as communication has been established is in kangaroo rats.

One reason that the field of vibratory communication did not advance until recently was the lack of ability to "hear" and record the signals for analysis. Within the past 10 years the vast world of vibratory communication in small invertebrates has been discovered with sensitive instruments such as the laser Doppler vibrometers. (See references of Elias and Cocroft for details). Geophones have been used in various arrangements to record substrate-borne vibrations in mammals for many years (A nice summary of the technical aspects of studying vibrational communication can be found in Wood and O'Connell-Rodwell 2010).

Molecular techniques create new research opportunities for studies of vibrational signals. The use of molecular techniques to determine what prey a spider has been eating is innovative and promises to be a new avenue of research for predator–prey relationships in spiders and insects. Paternity tests could be used to make the connection between reproductive fitness and courtship intensity. Is the spider or kangaroo rat that drums the most and at the greatest intensity really preferred by females and fathers the most offspring? The large number of insects, spiders and mammals that communicate by vibrations provides much opportunity for much future research. There is extensive opportunity, especially in insects and spiders, to conduct comparative research on vibrational communication in closely related species to tease out the pathways that evolution of the behavior might have taken (Cocroft et al. 2010; Elias et al. 2012). The use of molecular techniques promises to add a new and fruitful area of research in future studies.

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Chapter 8
Communicative Coordination in Bees

Guenther Witzany

Abstract Since Karl von Frisch's work it has been evident that the highly complex social behaviour of bee swarms is organised and coordinated by sign-mediated interactions, i.e. communication. If communication processes are disturbed this may have fatal consequences for bee colonies. As in every other natural language the same sign sequences may have different meanings in different contexts. This means that bees with a limited repertoire of signs can transport different messages which trigger different response behaviours with far-reaching consequences. As in every other natural language, bee languages also differ in habitat-dependent dialects. The language of honey bees in colder hemispheres is the only known non-human language which uses body movements that represent symbolic meaning functions.

1 Introduction

Twenty years before Karl von Frisch received the Nobel prize for his research into the bee language, he was embroiled in a controversy involving so-called animal languages. He was accused of improperly using the term language to describe specific behavioural features. His opponents argued that a very simple form of animal communication was involved, but certainly not language. In his response "Sprache" oder "Kommunikation" der Bienen? (von Frisch 1953) Karl von Frisch proves that it is justified to speak of the language of bees because a system of signs is involved. In the early 1970s the controversy was updated by a group of American biologists that bees does not communicate but find their goals by using their olfactory sense.

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This was refuted again by Karl von Frisch through careful constructed experiments (Wenner 1971; von Frisch 1992).

Communication processes inherently depend on a repertoire of signs. According the capability of bees to communicate these signs has been identified as behavioural movement sequences. Communication serves to coordinate action and behaviour as well as to form associations between linguistic-competent individuals. This sign-use takes place in regulative, constative and – less frequently – in generative linguistic action as well, or in linguistic behaviour that is also characterised by regulative, constative and generative features. Without sign-use there would be no coordination processes.

The rules that govern linguistic behaviour stem largely from the practice of *social interactions*. Nevertheless there are some indicators that interpretation processes occur not only according to swarm vectors but also to individual needs (Grüter et al. 2008).

The individual's genetic make-up gives it the ability to communicate in a species-specific environment. Additionally it is necessary to learn and remember real-life experiences, which orientate inherited abilities by concrete social interactions, i.e. swarm behavioural patterns.

The interorganismic communication we will discuss here demonstrates the rule-governed, sign-mediated interaction between conspecifics. The increased skill in following these rules goes hand in hand with the improved ability to use linguistic signs within rule-governed interactions between individuals of a real, species-specific, life-world (*Lebenswelt*). Living 'Beeings' in general are unaware of these underlying rules nor are they able to explicate the rules as rules. Only humans are able to identify and explicitly reflect on these levels of rules.

The language and communication of the honeybee, which has been studied in great detail, can serve as an excellent example of non-human language (von Frisch 1952, 1953, 1955, 1965, 1970, 1971; Lindauer 1975, 1981; Seeley 1982, 1992, 1995; Heinrich 1981). This can be illustrated by two cases in which communication, coordination of behaviour, and the formation of associations are achieved through linguistic signs.

In contrast with the investigations on language and communication in the other organismic kingdoms outlined in this book, I will focus in the case of the honeybees only at the interorganismic level, i.e. sign-mediated interactions between the same or related species. This is because, in contrast with all other cases of biocommunication we can mention, here we have the rare phenomenon that bodymoving patterns act as symbols (von Frisch 1953; Sherman and Visscher 2002). In contrast, indexical or iconic sign-use symbols do not represent by themselves what they mean, but are a kind of natural convention. Their correct use must be trained within in vivo social interactions.

2 Colony Formation

Honeybees originally stem from the warm regions of the Earth. The extension of their range into the northern hemisphere brought with it the problem of how to deal with longer cold periods. Winter requires the development of a specific survival strategy that was unnecessary in the geographic and phylogenetic origins of honeybees.

Searching for and finding suitable over-wintering sites are critical for the survival of honeybees in temperate and more northern latitudes. The complex communication and behavioural coordination of individuals in this community requires correspondingly differentiated communication abilities and skills; without these, no suitable housing could be selected. A mistake in the selection of a hive leaves no opportunity for a second attempt: the correct choice is a life-or-death situation for the bee colony. Today we know that only one-quarter of all newly-established bee colonies survive the first winter (Seeley 1982). Once the bees survive the first winter in a well-chosen site, the probability of surviving for another 5 years is high. How does the selection of an appropriate site take place?

In the cold season, the bee colony forms a tight aggregation in its hive. A great number of bees join to form a type of outer shield; fine quivering movements of their flight muscles help maintain an ambient temperature of at least 10 °C in the colony. Abundant supplies of honey ward off starvation. Spring marks the beginning of an intensive phase of brood rearing, and newly-emerging bees lead to dense colonies and reduced space in the hive. Precisely this condition is a sign (social clock) for the worker honeybees to construct queen cells in which a number of future queens can be reared simultaneously (Seeley 1982; Bloch 2010). The old queen uses sound signs to communicate with the enclosed future queens. If one imitates the sounds of the enclosed future queens with the appropriate instruments, then the old queen answers these artificially produced sounds quite specifically. Although the queen is known to communicate with the future queens, the subject of the communication remains unknown. Before the replacements emerge and decide the future leadership of the colony in a stinging duel, the mother queen leaves the nest with half the original colony.

The initial flight is rather short, in any case less than 50 m (Seeley 1982). The queen alights on a more or less suitable object and is immediately surrounded by a cluster of bees. As soon as the cluster is completed, a few hundred so-called scouts swarm out to search the terrain for a suitable new hive. These scouts are the oldest bees in the colony, i.e. those that have already collected food for the original colony and are therefore already familiar (memory) with the surroundings (Thom 2003; Zhang et al. 2005; Menzel et al. 2006; Gros et al. 2009).

The selection criteria for the new home are quite differentiated (Seeley 1992; Lindauer 1975). The height of the entrance hole must lie at least 2 m above the ground in order effectively to rule out any disturbance of the colony by other animals. The opening of the hole should be no larger than 50 cm in order to permit reliable regulation of the hive's internal climate in winter, even if the temperatures drop to very low values. The hole should also face south: this enables the bees to swarm out and defecate at even the slightest outside temperature increases in winter. The volume of the entire hive should not be fewer than 100 l in order to provide sufficient room for the honey stores the colony needs to over-winter; at the same time, volumes in excess of 100 l make the regulation of the inside temperature difficult. The presence of old honeycombs is a positive criterion because it considerably reduces or even eliminates the time- and energy-consuming effort of honeycomb construction (Seeley 1992; Lindauer 1975).

Each of the scouts that have swarmed out returns to the colony as soon as it has found a site that seems suitable. She lands in the swarm and begins to carry out the characteristic movements that researchers have termed dances (Lindauer 1975). Such dances are displayed not only during the search for new hives, but also in locating suitable feeding sites. The dances have a communicatory character and represent linguistic signs whose expression enables comprehensible information to be relayed to other bees. Because the scouts do not return with pollen or nectar, the dance is not a message about feeding sites but rather about where and in which direction a suitable place to build a hive can be found. These so-called waggle dances resemble a figure-of-eight in whose central section the abdomen is waggled. The waggle dance can be defined as constative linguistic behaviour (Lindauer 1975). The constative behaviour may be stopped in the case of external danger by nest mates also (Srinivasan 2010). The direction of the central section of the danced figure-eight points to the direction of the new site in relation to the respective position of the sun (Lindauer 1975; von Frisch 1965).

The greater the distance to the prospective site, the longer the waggling motion for that particular stretch lasts. This is interconnected with increasing inexact message transfer (Beekman et al. 2005). Three or four other scouts observe the waggle dance from close quarters. Each scout advertises her discovery with her own dance. The more suitable she believes her discovery to be, the more vigorous the dance. The greater a scout's doubt about her own discovery, the more subdued her dance. The latter are quickly attracted to the dances of their more agitated neighbours and follow up on the communication of one such dancing bee: they fly to the site indicated by the dance and inspect the keenly promoted hive. After the inspection, these scouts return to the swarm: each scout that is more convinced of the new hive than of the one she originally found begins an agitated dance to promote the new site. One after the other, all sites that were keenly promoted by scouts are visited by the other scouts. This consensus-building process gradually leads to agreement on one site (von Frisch 1965; Lindauer 1975; Seeley 1982; Visscher 2007).

It should be mentioned that the inspection of a potential hive site is quite a precise process: the bee walks up and down the entire hollow, often covering a distance of 50 m (Seeley 1982). This allows her to cover the entire inner surface of the cavity. When a scout gives up her original, first discovery and *consensually* agrees with the other scouts on another site, then the experienced scouts are in true agreement (Seeley 1982).

The new beehive can be up to 10 km away from the original site. The search lasts no more than 3–4 days. If no suitable place is found, then the bees begin constructing a hive directly at the first landing site and, since such hives cannot withstand the winter weather, the colony dies during the first cold spell.

If, on the other hand, the scouts have agreed on a new site, they force their way to the surface of the bee cluster in a zigzag course. At this point the entire colony begins to beat its wings in order to raise its temperature to 36 °C (Seeley 1982; Heinrich 1981). This is a necessary precondition for the bees to be able to fly after this quiescent state (Seeley et al. 2003). If the colony is knocked off-balance before this temperature is reached, the whole swarm falls to the ground. When, after a few minutes, the correct temperature is reached, the scouts give the sign to take off: they force the aggregated bees apart in a series of so-called buzzing runs. The entire swarm disperses and ascends into the air, forming a cloud of bees with a diameter of approximately 10 m. Within this cloud, the scouts repeatedly take off in the direction of the new site, thereby showing the other bees the correct bearing of the destination. In the first 30 m the swarm makes only very slow progress, but it picks up speed dramatically over the next 200 m.

Upon reaching the newly-selected site, the scouts emit a sign (von Frisch 1965 with a reference to Lindauer 1975). The nature of this sign is still unknown. The swarm reacts to this sign, however, and comes to a standstill above the new hive. The scouts drop from the stationary swarm, alight on the entrance of the new home, and mark it precisely with a scent. Shortly thereafter the entire swarm takes over the hive. Within hours they remove all dirt, begin immediately to build the combs, and fly in search of pollen and nectar. This marks the end of this specific communication process until the following year.

3 The Sign-Mediated Interaction of Foraging

The second display of honey-bee language that I describe here picks up where the first left off. It plays an equally important role in enabling the bee colony to survive over the winter.

So-called foraging bees are responsible for finding suitable food sources. Foraging bees are experienced and possess memory (Menzel et al. 2006; Towne 2008). Upon finding such a site, the forager returns to the surface of the hive and begins her own waggle dance (Rohrseitz and Tautz 1999). She brings along pollen and nectar, which not only informs the other bees that the dance refers to a feeding site and not to a new hive site (von Frisch 1955, 1970), but also provides information on the quality and quantity of the food (Farina et al. 2005). The linguistic signs and the sequence of these signs are the same as in the first communication process described above (in which only scouts were involved). In this case, however, the waggle dance sequences are relevant to all encountered foragers, prompting them to collect food in the described direction and described distance (Beekman and Lew 2008). The constative linguistic behaviour has changed into regulative linguistic behaviour. The linguistic behaviour is different, the communication processes pursue different goals, yet the linguistic signs that are employed have remained the same. Additionally the food-gathering honey-bees now begin to produce special volatiles to recruit other honey-bees (Tautz 1996; Tautz and Rohrseitz 1998; Dyer 2002; Thom 2003; De Marco 2005; Thom et al. 2007).

The above scenario refers only to information on feeding sites that are more than 25 m away. The bees again dance a figure-of-eight. The orientation of the central section of the figure signals the direction of the feeding site in relation to the position of the sun. If the dance takes place on a vertical honeycomb, the deviation in direction between the feeding site and the sun's position is accurately recreated as the deviation from the vertical (von Frisch 1965). As in the case of the first communication process, distances are depicted temporally: the waggling in the central section of the figure lasts longer for longer stretches than it does for short ones. Thus, waggling for 1 s can indicate a distance of 500 m, while waggling for 2 s can indicate 2 km. Other bees follow the waggle-dancing bee at close quarters, and certain odours provide additional information about the site. Rather than approaching such places directly, the individual bees take small detours. They orientate themselves according to distinctive landscape features (Srinivasan et al. 1996; Capaldi et al. 2000; Towne and Moscrip 2008; Pahl et al. 2011). These orientations are determined in an arbitrary manner and are specific to the individual bee: they are not communicated to the others. If certain orientational features are experimentally altered, some bees can briefly become disoriented (Menzel et al. 2006).

Although honey-bees in most cases are diurnal – most of them are colour-blind in moonlight – one species which flies on moonless nights has been observed. It recognises landmarks in starlight (Somanathan et al. 2008).

4 Bee Dances and Their Meanings

Karl von Frisch identified nine different dance types have been identified as linguistic signs (von Frisch 1965):

1. The round-dance is a call to search for food in all directions within a radius of 25 m.
2. The waggle-dance describes the direction of the destination in terms of the respective position of the sun and defines the distance.
3. The tremble-dance describes a conspicuous type of movement made by successfully returning foragers. They hastily make their way across the honeycomb, bumping into colony members and informing them that something is going on, e.g. that food is available.
4. The ruck-dance is carried out by foragers that are emptying their honey sacs and involves intermittent, directed tail wagging. It serves more to indicate a general dancing mood than to impart any specific message.
5. The sickle-dance has been observed in every bee species (with one exception) in the transition between the round-dance and the waggle dance (figure-of-eight). The opening of the 'sickle' in the dance pattern denotes the direction to the feeding site.
6. The buzzing run is the sign to disperse. Scouts barge through the interlocked bees in the swarm in an undirected, zigzag course and audibly buzz their wings.
7. In the "cleaning run" the bee shakes its body from one side to the other.
8. In the vibration-dance, one bee takes up contact with another, whereby it rapidly vibrates its abdomen. The meaning of this dance has not yet been deciphered, although there is strong evidence that it involves a communication form combining dance and acoustic signals.

9. Finally, the jitter-dance is an expression of neurotic behaviour and is disregarded by the surrounding bees. Research has shown it to be a result of a traumatic experience such as severe impact, poisoning, injury to appendages, or extreme state of alarm.

The type of sign use that we designate as dances is a genetically acquired linguistic competence: even without prior socialisation, i.e. the presence of older bees, juveniles develop the ability to dance. These kinds of dances are not able to transport messages. Subsequent social interaction with bees of the same age is important to develop meaningful dances: carrying out linguistic behaviour and heeding the calls for specific action require some degree of practice and experience in participating in mutual interactions.

While the ability of bees to take their bearings according to the respective position of the sun is innate, the specific skills are gained and perfected in the course of a few days of flying experience. Interestingly, bees recognise the sun as having a 24-h course, so that they can carry out their dance at the correct angle vis-à-vis the sun even in the dark (von Frisch 1965; Lindauer 1975).

5 Forms of Communication Beyond Dances

Honey-bees exhibit other forms of communication that are either combined with or separate from the communicatory dances themselves. Various wing-beating frequencies or abdominal vibrations can transmit movement frequencies on suitable substrates (Kirchner 1993); other bees are able to identify their meaning. This is evident in the specific reactions to certain frequencies (von Frisch 1965).

Odours, which are actively employed, are apparently an even more significant form of danceless communication (von Frisch 1965, 1970). During her nuptial flight, the queen bee emits scents that attract the males (drones). The bees positioned at the entrance hole of the hive beat their wings to waft the smell of their scent glands toward the arriving workers and thus guide them to the entrance. The scent glands are also used to mark certain food sources, enabling other bees to find these sites more easily (Breed 1998). Bees that are threatened or attacked extend their sting and whirr their wings to exude an alarm scent which is not identical with bee poison. The alarm induces members of the colony to attack. This attack is generally directed at moving objects in the vicinity.

6 Context Determines Meaning of Language Signs

Twenty years before Karl von Frisch received a Nobel prize for his research into bee language, he was embroiled in a controversy involving so-called animal languages. He was accused of improperly using the term language to describe specific behavioural feats. His opponents argued that a very simple form of animal communication was involved, but certainly not language. In his response (von Frisch 1953), Frisch proves that it is justifiable to speak of the language of bees because a system of signs is involved.

In this chapter I have discussed only two of many sign-mediated communication processes that can serve as examples of rule-governed, sign-mediated interactions between individual bees in a colony. Each of these communication processes encompasses a series of characteristic sign uses and sign combinations, whereby the context of usage clearly determines the meaning of the utilised sign sequences. Furthermore, various forms of behaviour evidently take on sign character and, when combined, can take on meaning and be understood as signs. The habitat specificity with which such language communities apply their stock of signs is reflected in the different dialects of bee communities.

The communication of honey-bees (a) with one another and (b) about something is necessary to exchange information, coordinate behaviour, and form associations between individuals of such social animal communities (Lindauer 1975). Survival without the sign-mediated interactions described above would be impossible. At the same time, this example vividly illustrates how certain behaviour can take on sign character within behaviour sequences.

Beyond using linguistic signs in regulative and constative linguistic behaviour, bees must originally have been able to perform generative linguistic behaviour, thereby ultimately constituting new life-forms. In order to survive the winter, the swarm first had to have selected the correct over-wintering site through appropriate communication. At some point, the rules underlying this communication were innovatively generated, much in the same way as the transition from signs with mere reference character (honey-bees of warmer latitudes) to symbolic sign systems (northern hemisphere bees) must have been a marked innovative step. The ability to survive the winter eventually became fixed in the genetic text of these surviving bee generations. We know that this happened, but can only guess at how it happened.

The survival strategy of honey-bees in colder latitudes clearly shows that communication experience in generative linguistic behaviour, which substantially and permanently supersedes the originally innate language competence, can constitute an expanded communication competence. This competence is hereditary in an expanded (or at least modified) form; in the context of social animals, it can be differentiated as broadened language play skills, for example, through learning processes (Lindauer 1975). Learning processes depend on the capability to memorise and short-term as well as long-term memory has been proven (Menzel and Muller 1996).

6.1 New Colony Building

As demonstrated in our treatment of two sign-mediated communication processes in the language of northern hemisphere honey-bees, in certain situations the behavioural context determines the meaning of the linguistic signs used. The bees' ability to interact socially is no doubt genetically fixed. The constitution of the specific performance, however, i.e. of the actual communication process, is contingent on the actual situational demand.

In the sign-mediated communication process underlying the foundation of a new colony, only scouts participate in the search for a new home. They are the oldest bees in the swarm and have already gathered food for the parent hive; they are fully familiar with the features of the local terrain. Why do only these experienced scouts swarm out and not the inexperienced ones as well? Does the flight of the queen cause certain genetic text sequences in the scouts to be expressed, i.e. those that code for and initiate such behaviour? Or does the rule governing the participation of experienced scouts alone underlie some other species-specific, intersubjective communication?

The criteria that a prospective hive must fulfil are so differentiated that one can reasonably assume a genetically determined inspection and evaluation behaviour. On the other hand, these evaluation criteria clearly do not exist from the onset: they must have been constituted by experience, followed by subsequent genetic fixation. Pragmatic situations formed the evaluation pattern for the combination or creation of genetic sequences that then coded these experiences as text sequences. Naturally, there is no reason to doubt that natural genome editing agents competent in genetic text processing and integration carried out this fixation, i.e. have structured and, above all, inserted the respective sequence at the appropriate site in the genome.

No haphazard change or deformation of genetic text sequences can shape the highly differentiated selection criteria for the winter hives of northern hemisphere honey-bees: they are simply too rigorous. The failure of the hive selection process to match the required hive features closely can kill off the entire swarm in one winter. The argument that this involves the natural selection of many chance mutations would imply the extinction of all northern hemisphere bee populations before they ever had the opportunity to develop sufficiently differentiated selection criteria for suitable winter hives.

As demonstrated earlier, the process by which a potential winter home is scrutinised is itself incredibly complex and exact. The bees pace the entire length and breadth of the new site: not a millimetre is left out. This explains why a single bee covers a distance of nearly 50 m in the course of this inspection, even though the cavity itself is relatively small.

The sign-mediated communication process underlying the founding of a new bee colony also points to numerous other pragmatic situations that must be or, if they are genetically fixed, must have been vital for the evaluatory function. The consultation between scouts about the potentially most suitable new home – in this case the tail waggle dance – raises the question: what induces bees that have identified a potential site as being less satisfactory to dance less vigorously, and bees that have identified a site as being highly suitable to dance more vigorously and to 'symbolically code' (Todt 1986) the direction and distance of their discovery? What induces the less lively dancers, those who are less convinced of their discovery, to take up the invitation of the more vigorously dancing bees to inspect the site they consider to be particularly suitable, especially when this involves repeating the same complex and time-consuming inspection procedure? What subsequently enables these bees to decide in favour of the recommended, inspected, and perhaps more highly-evaluated site and themselves promote this site with an appropriately intense dance (Seeley and Visscher 2008)? Furthermore, this new decision may itself be temporary, and another, even better, home may trigger a renewed inspection process, etc. At any rate, the final decision is a consensual decision by all scouts, all of whom have by then inspected the most highly-advocated home. If no consensus can be reached, no decision is taken and the swarm freezes to death at the site of their deliberations during the first cold spell.

Provided that the decision-making process represents sign-mediated communication, then it cannot be of the algorithmic type; rather, it must be a truly communicative process between conspecifics in a shared life-world (*Lebenswelt*). They represent subjects for one another because they use the same linguistic signs in the same sign-mediated communication process to achieve understanding, form associations, and coordinate behaviour. The fact that language is involved, i.e. language and not merely a formal procedure, opens the potential for generative and therefore entirely new linguistic behaviour. Otherwise, colder hemisphere bees would never have been able to differentiate the necessary sign-mediated communication processes (processes outside the repertoire of warmer hemisphere bees). Whereas southern hemisphere bees use behaviour to constitute signs with direct indicatory or invitational character, northern hemisphere bees employ movements to constitute and utilise a symbolic sign character for these movements; understanding these signs permits more differentiated messages to be deciphered (messages that even humans can understand, provided that they can determine the rules underlying the use of these movement signs).

Todt, a sociobiologist whose research was instrumental in initiating an interdisciplinary dialogue with semiotics in Germany, expressly underlines the use of symbols by bees of the colder hemisphere.

The specific sign-mediated communication process involved in searching for a home is terminated only when consensus has been reached. The process is completed when a new home (one selected exclusively by scouts) is inhabited and developed.

6.2 Foraging

This marks the onset of the second sign-mediated communication process described above – food-gathering. Again, the waggle dance is used to convey information. The rules underlying the movement sequences as well as the indication of direction and distance remain the same as in the preceding example. The sequence of signs is also the same. Their meaning, however, is different because they take on new meaning within the pragmatic context of a new communication process. The waggle dance may well be a rule-governed, genetically fixed behaviour that is expressed as the need arises: nonetheless, the actual situation in which the signs are used within a population of communicating conspecifics lends meaning to the signs themselves and determines their sequence in a dance.

In addition, the target group addressed by these expressions is not the same as in the preceding case. All foragers, not just the scouts alone, are called upon to search for food sites. One situation-specific feature is responsible for the fact that foragers (and not just scouts) are being addressed, even though the mode of expression and the utilised linguistic signs are the same as in the previous example in which scouts were prompted to swarm out: only when the dancers carry flower pollen – which is not the case when the task involves searching for a new hive – is the call valid for foragers as well. In the absence of pollen, the foragers do not react to the messages or invitations. Understanding (*Verständigung*) between bees is not limited to dance movements alone. These movements are combined with (the very important) vibratory movements (Kirchner and Towne 1994) of the wings and abdomen along with the rule-governed use of olfactory signs. This marks the limits of our comprehension of the bee language. Human beings can never hope to progress much beyond a passable understanding of the rules governing the bees' use of linguistic signs: beyond a certain complexity of sign combinations, mastering the specific modes of use would require becoming involved in the bees' communication process as interactional subjects. This inherently transcends human capabilities and points to the limits in the compatibility of trans-specific forms of communication, for example, in meta-organismic communication.

6.3 Bee Dialects

Bee colonies form relative language communities that are distinguished by dialects (Sen Sarma et al. 2004). Experimentally-mixed colonies of Austrian and Italian bees revealed clear differences in the interpretation of the dance tempo, which indicates the distance to the feeding site. When the Austrian bees communicated a suitable feeding site at a distance of 300 m, for example, the Italian bees executed the instruction in exactly the right direction, yet over a distance of 500 m. Vice versa, a 200-m dance by the Italian bees meant a much shorter distance to the Austrian bees. Thus, despite identical rules being applied to the same linguistic signs, distinct differences existed in the meaning of the signs (von Frisch 1965). Interestingly, these differences in bee language dialects are even compatible over longer time distances. It depends on the capability of social learning of the bee populations. Longer time enables processes of training of different meanings of identical moving patterns (Su et al. 2008).

In stingless bees, the use of symbolic signs in regulative and constative linguistic behaviour to indicate direction and distance is not developed. These bees must accompany and guide inexperienced conspecifics to every discovered food site.

One final pragmatic criterion for the signifying function of the utilised linguistic signs deserves mention: the occurrence of various bee dialects. The same sign (or the same sign sequence) can exhibit slightly different rules of usage in bee colonies that are geographically widely separated yet belong to the same species. In the case of the Austrian and Italian bees described earlier, the form in which the same symbolic (behavioural) sign is expressed can translate into site deviations of several hundred metres. The pragmatic context, in this case the bee colony's actual life-world (*Lebenswelt*), determines the semantic rules according to which this sign is interpreted. As we know now, these rules which depend on cultural customs of honey-bee populations are subject to learning and memory capabilities. After a certain time-span honey-bees can change their sign using practice according to new situational contexts (Su et al. 2008).

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Chapter 9
Social Association Brings Out the Altruism in an Ant

Kenji Hara

Abstract The carpenter ant which is a social insect depends on olfactory (chemical) cues for most of the communication between the nestmates. The care of the worker is essential for a larval survival of the carpenter ant. Brooding behavior of workers accumulating larvae lying scattered under the queen is the altruistic behavior which is essential in social maintenance. The development of this brood-accumulation behavior in a worker requires 'social experience' in early time after the eclosion. The essence of this behavior is olfactory attention switching.

1 Introduction

In the humid and sticky evening of one day of May, before the more than 10 years, I happened to meet a marriage flight of the carpenter ant *Camponotus japonicus*. A myriad of the queens which finished copulation covered over the ground. I took one of them home with me and have begun to breed it indoors. The queen laid eggs a few days later, and a few workers emerged more in several weeks. With careful observation of this tiny colony, I noticed that the larvae and the pupas were always collected near queen (Fig. 9.1). When the queen moved, the workers had a larva in her mouth in a hurry and followed the queen. The worker is sterile; her own gene is not inherited in the next generation but, nevertheless, she takes care of the larvae which are her younger sisters for 'the welfare of the colony'. Such 'altruistic' actions due to the workers are indispensable for their social maintenance. This brooding behavior of ants which reminded of a totally human family was very impressive for me.

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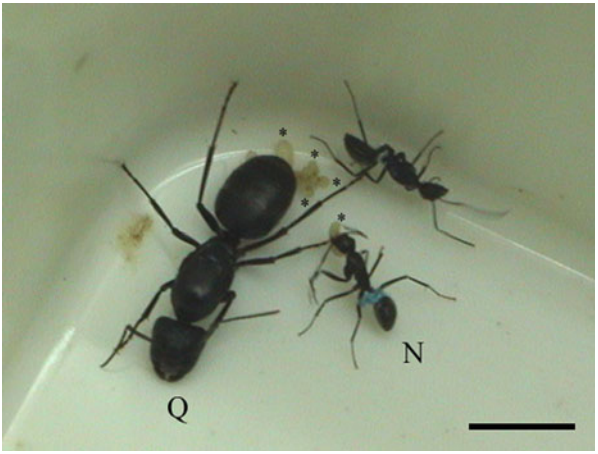

Fig. 9.1 Brood-accumulation behavior of the ant *Camponotus japonicus*. Age-related division of labor is a trait of the ant society. A child care is the work that a worker of the ant engages in after eclosion first. The younger worker in charge of the child care is called a 'nurse' (*N*). Brood-accumulation is a key behavior of the child care that nurses carry larvae (*asterisks*) to the side of the queen (*Q*), repeatedly. Scale bar = 1 cm

Ants employ the most complex forms of chemical communication of any animals. To behave as a social member the individual ants depends on chemical sense for most of the communication among the members. At first in this essay, I briefly introduce the ant society and the chemical communication required for the social life of ants. Then, I give outlines about the physiological basis on such the chemical communication. Finally I discuss about "attention to odor cues" on the brood-accumulation behavior which is one of basic reactions for larval cares performed by the worker.

2 The Ant Colony

The ants are classified as a single family, the Formicidas, within the order Hymenoptera, which also includes the bees and wasps. The known living ants comprise 11 subfamilies, 297 genera, and approximately 8,800 species, and dominate many terrestrial ecosystems (Hölldobler and Wilson 1990).

Their tremendous ecological success is based predominantly on division of labor among colony members. The ant colony is an almost exclusively society of workers reproduced from a (or a few, in some species) queen, whereas there are three different castes, queens, males, and workers, that can be distinguished by several morphological traits. The worker is a 'non-reproductive' female. The altruistic behaviors of this caste, i.e. the trade-off between individual sacrifice and colony welfare, are the most important feature of ant society.

The ant colony is a superorganism. Each worker of a colony specializes in a subset of all tasks required for successful group functioning. Individual experience and behavioral plasticity of workers lead to distinct task allocation, resulting in an adaptive and flexible colony response. Within an colony of the carpenter ant *Camponotus japonicus*, for example, two main modes of labor specialization of workers can be distinguished, nurse and forager (Hara 2002; Nemoto and Hara 2007). It has traditionally been thought that one of the mechanisms whereby an ant colony achieves a proper labor allocation is the adoption by workers of different specializations at different ages; Young workers nurse their sister. Older workers typically leave the nest to search for food outside it for colony members, namely, nestmates, where they find life very dangerous. These altruistic actions integrate the colony tightly and make possible advance forms of labor specialization.

3 Communications

The modes of communication used in the ants are extremely diverse (Hölldobler and Wilson 1990). The several behaviors, such as tapping, stridulation, stroking, glasping, antennation, tasting, puffing and streaking, are demonstrated the means of communication to conspecific individuals in the ants. These behaviors have impacts to others via the visual, auditory, tactile, and chemical senses.

For ants, the chemical sense is the most prominent modality. Ants have a well-developed olfactory system, and their complex behaviors are mediated in large part by chemical substances. Pheromone is the substances used in communication within a species. Volatile-retardant pheromones are usually employed as the labels (long-term signals) for nestmate, caste, and physical state (e.g. age). They are present on the body surface of ants as a part of cuticle lipid, and are sensed by direct contact with antenna (contact chemosensory). Volatile pheromones play a role for the releasers (temporal signals) such as recruitment, alarm and trail.

An extremely diverse array of exocrine glands is found on the ants (Billen and Morgan 1998). A major social function of exocrine gland is the production of pheromones, for which many glands have become specialized. Individual glands usually produce mixtures of substances, which are moreover often complex in both constitution and function. The ‘vocabulary’ of this communication in the ants can be enriched by variation not only of chemical substances, but also in the response according to the concentration of pheromones.

4 Nestmate Recognition

When an alien ant enters the nest, the residents attack this stranger with extreme violence, locking mandibles and appendages while spraying with formic acid from poison gland of the abdominal tip. Such the aggressive behavior against non-nestmate is a fundamental feature of social life, and the ability to discriminate the nestmates from other non-nestmates allows the individual to be integrated into the colony.

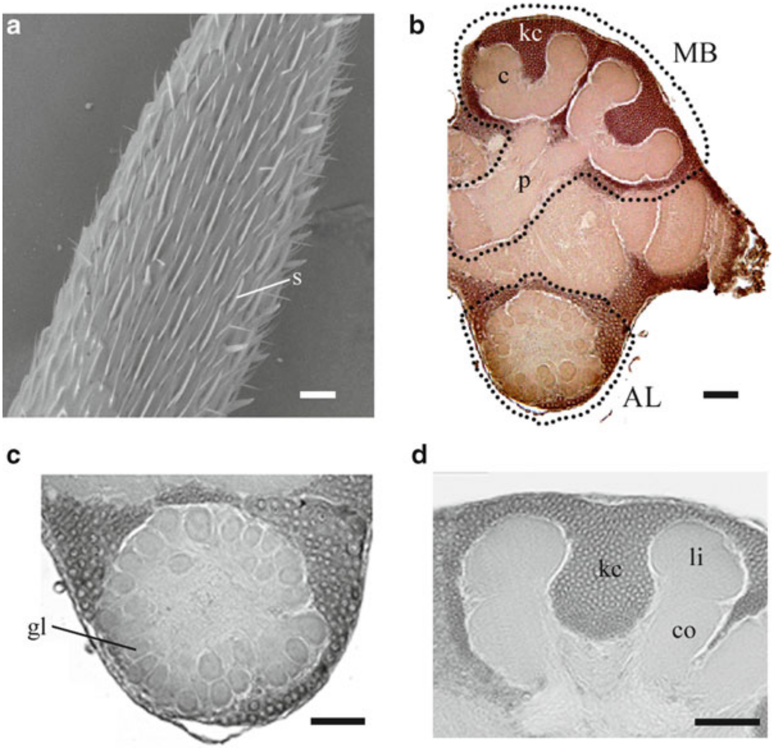

Fig. 9.2 Neuronal basis on the chemical communication of the ant *Camponotus japonicus*. (**a**) Scanning electron micrograph of antennal surface. Various types of sensillum (s) are on the antenna. Each of sensilla houses a large number of receptor neurons. (**b–d**) Histological sections of (**b**) brain hemisphere, (**c**) antennal lobe and (**d**) mushroom body in the adult worker (nurse). *Dotted outline* in (**b**) indicate mushroom body (*MB*) and antennal lobe (*AL*), respectively. *kc* region of Kenyon cells, *c* calyx, *p* peduncle, *gl* glomerulus, *li* lip region, *co* collar region. Scale bar in (**a**) = 20 µm, and in (**b–d**) = 50 µm

4.1 Colony Label

Nestmate discrimination is mediated by chemical cues that constitute a 'colony label' common to all colony members (e.g. Bonavita-Cougourdan et al. 1987; Morel et al. 1988; Hölldobler 1995). The colony label resides in differences in cuticular hydrocarbon (CHC) profiles among colonies, both between and within species. The CHC blends produced by non-nestmates elicit overt aggression.

Chemosensory information assumed to be involved in nestmate recognition is perceived by the olfactory receptor neurons in various kinds of sensillum on the antennae (Fig. 9.2a). The specialized sencilla appear to have almost all-or-non sensitivity to non-nestmate or nestmate CHC blends (Ozaki et al. 2005). The receptor neurons are always desensitized to stimulation by own (i.e. nestmate) CHC blends, whereas the ratio of CHC blends is thought not to be constant and gradually change over time. The sensory adaptation of receptor neurons could be a candidate for the desensitization.

4.2 Learn of the Colony Label

In ants as in most social animals the first days after emergence of the adult insect seem crucial for the integration and the socialization of individuals into their maternal colony. As is known in many ant species, newborn workers (callows) can be successfully cross-fostered between colonies. The resulting callows are accepted as nestmates by the sisters of their foster nurses. And also they recognize their foster nurses and foster queen as nestmates and start to perform social behaviors for an alien conspecific colony (Carlin and Hölldobler 1983). These suggest that colony-specific recognition cues were transmitted from the nurse to the adopted callow. Early experience is thus involved in the development of a social preference of a young animal.

The early post-eclosion period is seems to be special in regard to the system formation of processing the colony-specific CHCs. The fostered callow ants have never encountered the CHC pattern which shared by all members in the foster colony. Therefore, its receptor neurons are naturally expected to be ‘sensitized’ to the stimulus. But why the callow ant never decides the foster colony-specific CHC as a non-nestmate signal, and learns it as a template of nestmate recognition cue. The neuronal correlate with this early learning of CHC pattern and the differences with a peripheral recognition mechanism in the adult ant are not known and pose challenging questions.

5 Neuronal Basis on the Chemical Communications

5.1 Antennal Lobe: Primary Olfactory Center of the Insects

Axons of antennal olfactory receptor neurons synapse onto dendrites of a variety of interneurons in the glomeruli of the first-order olfactory center, the antennal lobe (AL) (Fig. 9.2b). Glomeruli are densely packed spherical structures constituting the functional units of the AL. Glomerulus is the spherical neuropile that contain the synaptic contacts between axon terminals of a large number of olfactory receptor neuron and the dendritic ramifications of local interneurons and projection neurons.

Studies on the fruit fly *Drosophila melanogaster* have shown that each olfactory receptor neuron expresses a single and specific olfactory receptor (OR) gene (one neuron-one receptor rule), and the neurons expressing the same OR gene converge into individual glomeruli of the AL (one glomerulus-one receptor rule)

(Dobritsa et al. 2003; Fishilevich and Vosshall 2005). As a consequence of this sorting of the olfactory receptor neurons, odors are represented as spatial patterns of neuronal activity in the AL (Galizia et al. 1999). Such the insect AL displays strong structural similarities with the olfactory bulb of vertebrates (Hildebrand and Shepherd 1997). The glomerular number varies according to the species of the insect; an average of 166 glomeruli in the brain hemisphere of honeybee (worker), 125 glomeruli in the cockroach, 64 glomeruli in the tobacco hornworm, and 43 glomeruli in the fruit fly. The carpenter ant (worker) has over 400 glomeruli in the brain hemisphere (Fig. 9.2c; Nishikawa et al. 2008). This appears to be the largest in insects so far. Such a large number of glomeruli may reflect the broad spectrum of chemicals received by olfactory receptor neurons on the antennae and complexity of sensory processing in the AL.

Local interneurons, which possess an arborization devoid of an axon and strictly located within AL, modify the odor reply of the projection neurons. Projection neurons, which ramify into the AL and send their axon to various brain target such as the mushroom body and the lateral protocerebrum, transmit odor information to these higher brain centers.

5.2 Mushroom Body: Insect Brain Centers Involved in Multimodal Sensory Integration

Insect mushroom bodies (MBs), pair brain compartments situated in the dorsal protocerebrum, are the center of multimodal sensory integration involved in behavioral modulation (Menzel 2001). The general design of MBs, including the internal circuitry and connections with other brain regions, is highly conserved in all insects (Strausfeld et al. 2009). The MB consists of a population of intrinsic neurons, referred to as Kenyon cells, whose somata occur in the cortex lying dorsally to the MB (Fig. 9.2b, d). The axons of Kenyon cells all run in parallel, thus forming a dense structure called the peduncle (Fig. 9.2b). Distally, the peduncle divides into two or more major subunits, referred to as the vertical and medial lobes, which are major output regions of the system. Most MB efferents project into the protocerebral neuropile surrounding the MB, from which they also receive some input. Kenyon cells have their dendrites organized within a dense neuropile referred to as MB calyx which is situated around the proximal segment of the peduncle (Fig. 9.2b). In most insect families, the calyx receives direct olfactory input from the antennal lobes and has therefore often been perceived as a secondary olfactory center.

In advanced Hymenoptera, such as ants and bees, have particularly large and elaborately organized MBs which are comprised of a large number of Kenyon cells (Fig. 9.2d). Their calyxes are subdivided into three sub-compartments (Fig. 9.2d; Gronenberg 1999). Olfactory projection neurons from the antennal lobes project to the calyx' lip region while visual fiber tracts originating in the optic lobes (medulla and lobula) innervate the collar region of the calyces. The collar also receives input from the mouthparts (probably gustatory; Durst et al. 1994). A third calycal region, the basal ring, receives segregated visual, antennal and probably other sensory input, whereas it is difficult to discriminate in the carpenter ant (Ishii et al. 2005). In addition to sensory input, the calyx also receives efferents from the MB lobes, referred to as feedback neurons (Gronenberg 1987; Grünewald 1999).

In contrast to the compartmentalized sensory input to the calyx, the separation between sensory modalities is abolished at the MB output level by the prolific interconnection of the MB with surrounding neuropiles. In an ant species, Kenyon cells exist with dendrites invading both lip and collar, assumed to synapse onto visual as well as olfactory input neurons (Ehmer and Gronenberg 2004). These complex recurrent network formed by the MBs and the surrounding protocerebrum is thought to be capable of integrating and associating information of different sensory modalities.

6 Postnatal Environment and Social Behaviors

6.1 Brood-Accumulation Behavior

It is often observed in a colony of the carpenter ant that larvae and pupae were always collected by the side of the queen. Larva and pupa of the ant do not have locomotiveness. With our careful observation, when a queen moves, we notice that a worker (i.e., nurse) has a larva in its mouth in a hurry and follows the queen (Fig. 9.1). After having put the larva by the side of the queen, the nurse takes next actions immediately to search in the nest and then takes care of the alike to left larvae. Repetition of these actions leads to accumulation of larvae scattered in a nest beside the queen. We refer to this child care as the brood-accumulation behavior. Nurse is a sterile female. Therefore, this brood-accumulation behavior is a typical altruism task in the ant society.

We have analyzed the brood-accumulation behavior in the carpenter ant with our original test (Fig. 9.3; Hara 2002). This test (brood-accumulation test, afterword) led a conclusion that a chain of four behavior elements, [hold → queen search → release → larva search], is the basic unit of the brood-accumulation behavior. (1) At first the worker has a larva in its mouth (hold). (2) Then, the cue having a larva performs induces the exploratory behavior of the queen to the worker (queen search). (3) When the worker finds the queen and recognizes her as ‘Mother’ (nestmate recognition), the worker lets go of a holding larva beside the queen (release). (4) The worker loiters around subsequently while looking for the next larva (larva search). As a result of repetition (loop) of the unit, all the larvae are accumulated beside the queen.

In general, ‘selective attention’ is to take out specific information from a large number of sense information, and to recognize it (Aston-Jones et al. 1999). As for the selective attention, some domains of the brain including the basic network about

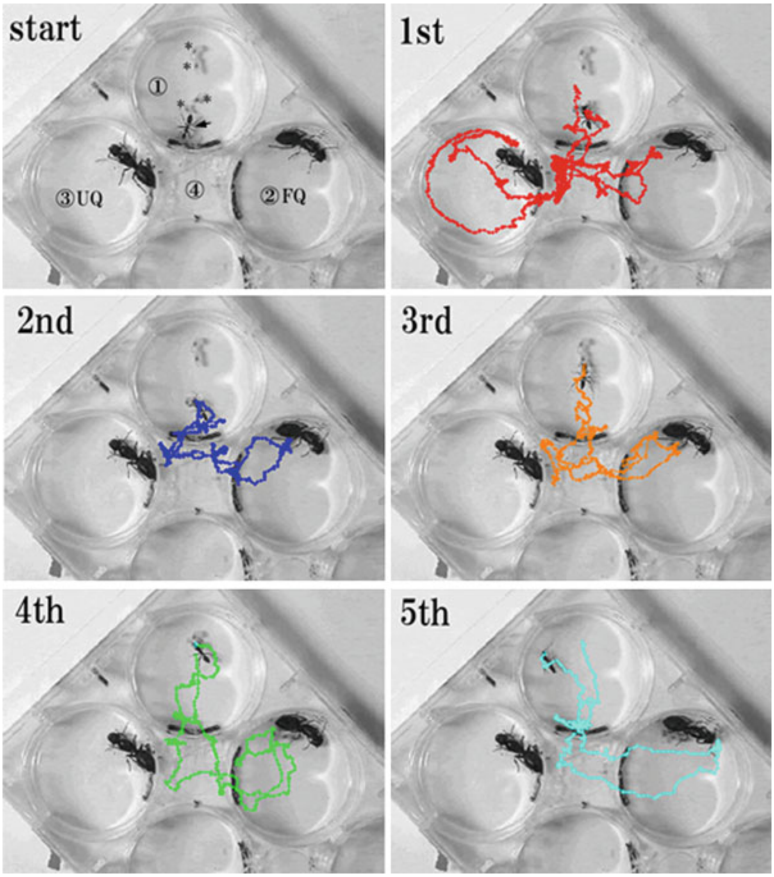

Fig. 9.3 Brood-accumulation test. (***start***) A subject (*arrow*) has a first larva in its mouth. Other four larvae (*asterisks*) are scattered in the room ①. (***1st–5th***) Behavior traces of the subject in every larva. The larvae are accumulated to the foster queen (*FQ*) in the room ②. During the test, the subject shows interest in the unfamiliar queen (*UQ*) in the room ③, but does not release any larva near the UQ

"orientation of the attention", "event detection" and "maintenance of the warning state" are thought to be in condition to have been connected by one circuit. An important characteristic is to be able to change this focus of attention flexibly among other things (attention switching).

The worker recognizes a larva and queen as the chemical cues of pheromones peculiar to each. Therefore, 'search' under the brood-accumulation behavior is in condition to pay attention to specific pheromone, and the conversion of the behavior element shows that the worker changed attention to another chemical cue. The loop mediated by the attention switching is a conformation peculiar to social behavior, and is not found in behavior of solitary insects such as a fly or the cricket.

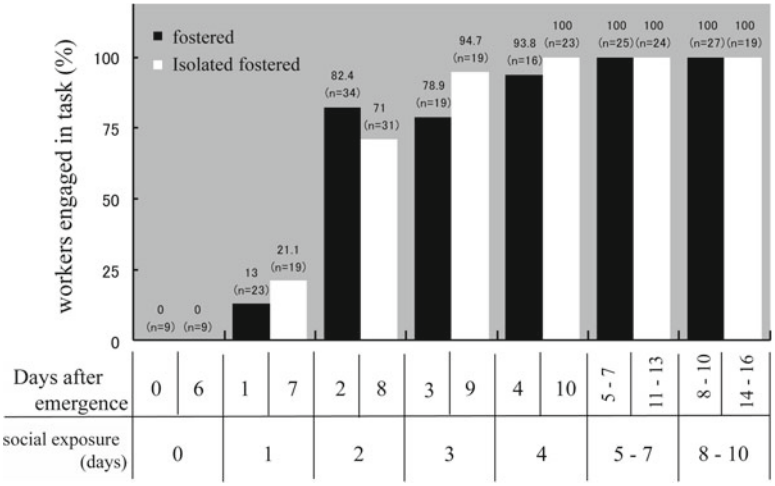

Fig. 9.4 Social contact accelerates a development of the brood-accumulation behavior. For each day in the foster colony, the percentage of workers engaged in brood-accumulation was compared between two different groups, 'fostered' and 'isolated fostered' (see text). The 'isolated fostered' workers were 6 days older than the 'fostered' workers. There were no significant differences between them ($p > 0.05$), indicating that the development of the brood-accumulating behavior is depend on the time spent in foster colony rather than age. The percentage (ordinate) is shown above each bar; *n* denotes the number of subjects tested

6.2 *Ontogeny of Brood-Accumulation Behavior is Necessary for 'Social Experience'*

The worker just after the adult eclosion keeps still near the queen and does not perform brood-accumulation behavior. What kind of condition is necessary for development of the brood-accumulation behavior? We carried out following experiments in order to approach this question.

Two experimental groups, 'fostered' and 'isolated fostered', were tested for the brood-accumulation behavior, regarding day after emergence (age) and experience in social communication (social exposure). 'Fostered' workers were transferred to a new nest (foster colony) within 6 h of emergence and were reared with a foster queen. 'Isolated fostered' workers were isolated within 6 h of emergence and were maintained in isolated until they were 6 days old, then they were transferred to a foster colony and reared with a foster queen.

The 'drive' to engage in brood-accumulation behavior develops over time and appears to require social contact as the isolated workers engaged fully in this task only after the third day in the new foster group (Fig. 9.4). This result indicates that workers without any social experience do not pay attention to brood or engage in brood-accumulation behavior. Perception both of queen and brood is likely to be important for brood carrying to the queen.

6.3 Nestmate Recognition and Brood-Accumulation Behavior

As described before, the nestmate recognition is the ability that is essential in running social life. For the newly-emerged workers, therefore, the learning of the colony label is necessary for their social life, and to that end, the maturation of at least antenna lobe is essential. Then, is the ability of the nestmate recognition necessary for development of brood-accumulation behavior?

The relationship with the age in day after eclosion and nestmate recognition ability was examined using brood-accumulation test (Hara 2003). Older workers took significantly less time to develop the ability to discriminate queens than newly emerged workers even when the amount of social exposure was identical in the two groups. The finding that the worker lacking the ability to recognize the foster (i.e. nestmate) queen is available for normal brood-accumulation behavior shows that queen discrimination ability is not necessary for the maturation of this behavior.

7 Conclusion

Every vital phenomenon progresses in bumper fluctuation. The social behaviors of the carpenter ants are no exception, too. Even if it was in the same worker, for example, we often observe that sometimes it performs brood-accumulation behavior positively but do not sometimes look to a larva at all. The larvae are always accumulated near a queen surely, regardless of the numerical increase or decrease of workers in their society. This indicates that the society as a whole level shows stable character for environmental variation. In other words, the individual wobble becomes small by the coaction among the individuals in their society and, as a result, the society is thought to be robust in total. The individual ability of social members decides a capacity of the society, and the other, individual ability changes depending on the whole society as an agent. “Communication”, as described in this paper, has a key role for realizing such the robustness in the ant society.

Why does “communication” have a function to join personality together each other and create a social robustness? What is difference in the neuronal processing between “communication” and any other stimuli? The sociobiology of the ants is a very appropriate model in order to address this question, whereas we are not given enough explanation for it scientifically at present. To analyze the complicated phenomenon with the experimental science, we must simplify the element which there is innumerable. In the case of a social insect in particular, we mistake an essence if we do not mind a method of this simplification enough. We intended to assemble experimental designs while examining this point closely enough until now and, however, expect the collaboration with a more novel idea. What is “communication”? Our challenge for the goal continues still more.

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Chapter 10
Termite Communication During Different Behavioral Activities

Ana Maria Costa-Leonardo and Ives Haifig

Abstract This chapter reviews the communication that occurs among termites performing different behavioral activities. Termites are social insects, and social activities require communication signals that are emitted by signaler individuals and perceived by receiver individuals. Termite castes are mostly blind, and the communication among individuals occurs predominantly through chemical and mechanical cues. The chemical communication involves pheromones that elicit behavioral responses from the individuals; these semiochemicals signal the trail from the nest to food, the presence of enemies, the location of reproductive partners and provide cues for the recognition of nestmates. In addition, indirect communication occurs during building activities through a self-organized mechanism in which the information that elicits termite behavior comes from changes in the environment and does not require direct contact among individuals.

1 Introduction

A termite colony is comprised of castes belonging to two distinct lines: the reproductive line, which is composed of nymphs, alates and the king and queen, and an apterous line, which is composed of workers, soldiers and their precursors (Grassé 1982; Roisin 2000).

Functional reproductives are generally the king and the queen, also known as primary reproductives, which are derived from alates that lose their wings after the

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Table 10.1 Classification of termite families and subfamilies after Engel et al. (2009) and Engel (2011)

Family	Subfamily
Mastotermitidae	
Hodotermitidae	
Archotermopsidae	
Stolotermitidae	Stolotermitinae
	Porotermitinae
Kalotermitidae	
Stylotermitidae	
Rhinotermitidae	Coptotermitinae
	Heterotermitinae
	Prorhinotermitinae
	Psammotermitinae
	Termitogetoninae
	Rhinotermitinae
Serritermitidae	
Termitidae	Sphaerotermitinae
	Macrotermitinae
	Foraminitermitinae
	Syntermitinae
	Nasutitermitinae
	Apicotermitinae
	Cubitermitinae
	Termitinae

nuptial flight. In addition to these individuals, a termite colony may present neotenic reproductives, which are young individuals that replace or complement the reproduction of the royal couple (Grassé 1982; Myles 1999; Roisin 2000). Workers are the individuals responsible for performing various tasks in the colony, such as foraging, construction and feeding, and soldiers are the individuals specialized in defense. In certain basal termites, the individuals that perform the functions of workers are known as pseudergates because they play a role as helpers in the colonies, but they may also differentiate into any other castes, i.e., alates, neotenic reproductives or soldiers (Roisin and Korb 2011).

After the updates that were contributed by Engel et al. (2009) and Engel (2011), the order Isoptera currently comprises nine families. A summary of the current classification status is shown in Table 10.1.

2 Types of Communication

Insects use colors, tastes, smells and mechanical vibrations to communicate. Based on these cues, insects search for and select foods, meet sexual partners, identify enemies, search for nesting locations and recognize nestmates. To perform these different activities, insects execute behaviors to adjust their interactions with the environment (Matthews and Matthews 1978).

According to Ali and Morgan (1990), insects communicate directly with one another through visual, mechanical and chemical signals. In termites, direct communication most commonly involves chemical cues because the majority of castes are blind and exhibit cryptic habits. However, termites also use mechanical signals, although these signals are not yet fully understood. Visual signals are not as important in termite communication as in the communication of the order Hymenoptera, which includes species with well-developed compound eyes (Billen 2006). Grassé (1959, 1984) also described a form of indirect communication among termite workers during building activities, known as stigmergy, that is a self-organized process.

2.1 Direct Communication

2.1.1 Visual Communication

In general, termite workers are blind, but in the family Hodotermitidae, the workers of *Hodotermes mossambicus* have compound eyes. Unlike the majority of termite species, these workers use their functional eyes for photo-menotactic orientation, and can recognize the light of the sun or the moon (Heidecker and Leuthold 1984). For this reason, these termites may be active in foraging during both the day and the night (Leuthold et al. 1976). These workers also communicate through chemical substances and use pheromonal orientation in the absence of light or when light is difuse. However, visual orientation predominates over pheromonal orientation during the foraging activities of the *H. mossambicus* workers. The visual function of this termite caste seems to be more closely related to the orientation of foraging groups than to communication.

Although a study had previously suggested that the male alate of *Odontotermes assmuthi* uses visual cues to locate the female (Sen-Sarma 1962), further studies have not corroborated the use of visual cues in communication among the alate reproductives of the Isoptera. These reproductives have compound eyes, which are functional at a specific time in their lives, including during the period when they swarm to find their partners. However, there is no evidence of visual communication prior to mating, as these reproductives use chemical signals to attract their partners. The alates of *H. mossambicus* do not use visual cues to locate a partner; the females were attracted to males, even when they were not visible (Leuthold and Bruinsma 1977). According to Pearce (1997), there are no morphological differences between the compound eyes of male and female alates, although the degeneration of these eyes has been verified in functional primary reproductives (Noirot 1969; Grassé 1982).

2.1.2 Mechanical Communication

Mechanical signals may be acoustic, vibrational or tactile. Vibrational communication is wide spread in social insects, and termites use these signals for alarm communication

(Stuart 1969; Inta et al. 2009). Drywood termites also use vibroacoustic signals to evaluate the size of a food source (Evans et al. 2005). The most common tactile communication between individuals occurs through antennation. However, egg recognition by the workers of *Reticulitermes speratus* occurs through egg morphology, including egg size and smooth surface texture, and is an additional example of tactile signaling (Matsuura 2006).

2.1.3 Chemical Communication

Chemical communication is the most important type of communication for termites, and it may involve either olfactory or gustatory stimuli. A wide variety of chemical substances may act as semiochemicals, including pheromones for intraspecific communication and allelochemicals for interspecific communication. Almost all social activities in termites require one or more chemical substances for communication between individuals.

2.2 Indirect Communication

The concept of stigmergy was defined by Grassé (1959) to describe the indirect communication among individuals during the building activities of termites. Building activity is a decentralized process that depends on the nest structure and not on direct interactions among workers. A specific structure, such as pellets of soil or pillars, stimulates a termite to start building. This termite modifies the existing structure by adding building material, and this change elicits building behavior in other termites. Therefore, stigmergy is the information from the local environment in which previous actions guide subsequent worker activities, in other words, the progress of construction provides new information to guide builder workers (Camazine et al. 2003).

3 Communication in Behavioral Activities

Communication is extremely important to social insects, such as termites. Social activities require communication signals that are emitted by signaler individuals and perceived by receiver individuals. These activities require cooperation among individuals, and for this mechanism, the recognition of conspecifics is necessary. Nestmate recognition is associated with hydrocarbons on the cuticular surface, which have endogenous (genetic) and exogenous (environmentally acquired) origins (Kaib et al. 2002). The collective action of nestmates may affect foraging decisions, defense, brood care and other behaviors that are coordinated by signals and/or cues. Building has been determined to be the result of self-organization, which has been applied for mass communication in large colonies. Divisions of labor generated task specialization that was of great benefit for the termite society (Crosland et al. 1998). With task specialization, specific types of communication, principally chemical, arose, which resulted in an increased efficiency in the performance of activities. However, most of the compounds that are involved in chemical communication in termites are still relatively unknown when compared to what is known about other social insects, such as ants and bees.

3.1 Foraging

Isoptera can be grouped into two life types according to their feeding habits: one-piece nest and multiple-piece nest (Abe 1987, 1990; Korb 2008). One-piece nest termites are found in the Archotermopsidae, Kalotermitidae and Rhinotermitidae families. Multiple-piece nest termites are found in the Mastotermitidae, Hodotermitidae, Stolotermitidae, Stylotermitidae, Rhinotermitidae, Serritermitidae and Termitidae families. While the first lives in their food (a piece of wood), the others leave the nest to collect food and search for new food resources (Korb 2008).

In multiple-piece nest termites, foraging is a collective activity that is composed of integrated individual actions (Traniello and Leuthold 2000). In general, termite foraging is associated with a division of labor among the nestmates. Communication during foraging is signalized by semiochemicals, in which the trail pheromone performs a primordial function. The trail pheromone is a blend of different substances, including decadienol, dodecanal, dodecenol, dodecadienol, dodecatrienol and neocembrene, that may vary in number and quantity in the different species (Table 10.2) (Costa-Leonardo and Haifig 2010; Bordereau and Pasteels 2011).

All of the actions that are related to termite foraging begin with trail-pheromone laying, and this semiochemical is produced in the sternal gland (Stuart 1961; Costa-Leonardo 2006, 2008). Studies investigating communication by trail pheromones indicate that recruiting pheromones are ephemeral and orienting pheromones are persistent. These different pheromones are responsible for the different phases of foraging (Traniello and Leuthold 2000).

Subterranean termites excavate a network of tunnels and galleries to search for food. Once food is discovered, additional foragers are recruited, and when the food has been chosen for consumption, the termite workers will deposit a phagostimulant pheromone that elicits the feeding of their worker nestmates (Reinhard et al. 1997; Reinhard and Kaib 2001; Casarin et al. 2003). Termite foraging is coordinated by the trail pheromone that is laid when workers press their abdomen against the substrate and discharge their sternal gland secretion. During the search for new food sources, termites lay exploitation trails that are reinforced by recruitment trails when food is found. When scout workers explore a new territory, they walk in curves and constantly move their heads and antennae, laying an exploitation trail (Reinhard and Kaib 2001). The excavation of new tunnels is performed by individuals that repeatedly sweep the tip of the tunnel with their antennae. The termite

Table 10.2 Principal chemical components of trail pheromones in termites

Family	Chemical component	References
Mastotermitidae	Undecadienol	Sillam-Dussès et al. (2007)
Hodotermitidae	Aldehyde	Bordereau and Pasteels (2011)
Archotermopsidae	Undecanol + dodecanal	Bordereau and Pasteels (2011)
	Hexanoic acid	Hummel and Karlson (1968)
	Dodecanal	Bordereau et al. (2010)
Stolotermitidae	Undecadienol	Sillam-Dussès et al. (2007)
Kalotermitidae	Dodecenol	Sillam-Dussès et al. (2009b)
	Nonanol + decanol + undecanol + dodecanol	Klochkov and Zhuzhikov (1990)
Stylotermitidae	n.i.	
Rhinotermitidae	Dodecatrienol	Matsumura et al. (1968), Tai et al. (1969), Tokoro et al. (1989, 1991), Laduguie et al. (1994), Wobst et al. (1999), Robert et al. (2004) and Sillam-Dussès et al. (2006)
	Neocembrene	Sillam-Dussès et al. (2005, 2009a)
Serritermitidae	n.i.	
Termitidae	Dodecenol	Peppuy et al. (2001a, b)
	Dodecadienol	Deng et al. (2002) and Robert et al. (2004)
	Dodecadienol + neocembrene	Bordereau and Pasteels (2011)
	Dodecenol + dodecadienol	Bordereau and Pasteels (2011)
	Dodecatrienol	Bordereau et al. (1993) and Sillam-Dussès et al. (2006)
	Dodecatrienol + neocembrene	Kotoklo et al. (2010), Sillam-Dussès et al. (2010) and Bordereau and Pasteels (2011)
	Dodecatrienol + neocembrene + trinervitatriene	Sillam-Dussès et al. (2010)
	Neocembrene	Moore (1966), Birch et al. (1972) and McDowell and Oloo (1984)

n.i. not identified

excavators have direct tactile interaction with the tunnel walls and each other (Bardunias and Su 2010). After a few centimeters of exploiting, the workers stop and quickly return to the nest using the marked trail. When a scout termite discovers food, it returns to the nest while laying a recruitment trail, which is continuous and is different from the dotted exploitation trail.

Traniello and Busher (1985) described three phases of foraging organization for *Nasutitermes costalis* (Termitidae). In the initial phase, soldiers leave the nest to exploit the area and inform other soldiers about the food resources that were found. A relatively small number of workers appear in the foraging trails or at the food within 1 h of the detection of a food source. The recruitment of a large number of workers characterizes the second phase of foraging, and the caste ratio in the trails tend to workers. In the third phase, the recruitment of soldiers decreases, while the recruitment of workers increases. The increase in the bidirectional flow of workers leads the soldiers to their positions along the borders of the trails. The differential recruitment of soldiers and workers suggests that the soldiers perform an essential role in food exploration as scouts. They are also important for the communication of the food location to workers. This communication seems to be predominantly chemical and the differences in behavior between workers and soldiers may be related to their perception for the trail substances. In another Nasutitermitinae termite, *Velocitermes heteropterus*, the patterns of exploration and recruitment during foraging differ from *N. costalis*. The scouts leave the nest as a unit composed of both minor and major workers and soldiers (Haifig and Costa-Leonardo unpublished).

In the majority of one-piece nest species, the search for food, which is also the nest, is performed only by alate reproductives (Traniello and Leuthold 2000). Although drywood termites live in the wood that they use as food and do not execute foraging expeditions, their workers are very noisy, generating acoustic emissions by chewing the wood and using vibroacoustic signals to determine the quantity of food (Evans et al. 2005).

3.2 Building

Termite nests are conspicuous in certain environments, and they are notable for their diverse sizes and architectures. In some species, most commonly in the largest African nests of the genus *Macrotermes* (Termitidae), the king and queen are restricted to a nest compartment known as the royal chamber, which is generally located above the nest center. In termites, building behavior may also be considered to be a protective and defensive tactic (Stuart 1967, 1969; Prestwich 1983).

The process of termite nest building involves a behavioral collective and cooperative activity of great complexity. Evidence indicates that a termite colony is a non-centralized cooperative system, comprised of autonomous unities that are distributed in the environment and display a stimulus–response behavior (Grassé 1984). The termite nest-building process is an example of self-organization, consisting of an automatic process of spontaneous order that generates a repetitive pattern of structures, such as pillars and arcs (Camazine et al. 2003).

Population size is important in termite building, and construction behavior may not occur if this stimulus is below a certain threshold. According to Stuart (1967), building is an answer to stimuli of low intensities, such as air movement, odor, light, heat, etc., that disturb the normal state of the colony environment. Additionally, an important stimulus for termite building is ongoing construction, and as has already been noted, this process of indirect communication among individuals is known as stigmergy. The stigmergy process consists of a few termites building simple structures in the beginning of the nest construction, and later, other termites are stimulated to perform the same task. Therefore, stigmergy may be understood as a succession of responses to stimuli that are quantitatively different. Stigmergy may be considered to be a self-organized mechanism because it produces complex

Fig. 10.1 Building activity in *Silvestritermes euamignathus*. Note the fresh pellets deposited by the workers

structures without the need for planning and control and because each individual acts only on the basis of local information.

Experimental evidence of termite building is scarce, but it is known that termites continuously lay trail pheromones during building activities and that these trails may recruit additional nestmates to this task (Bruinsma 1979). Additionally, tactile stimulus initiates building activity, as in the *Nasutitermes* genus, which constructs in the presence of surface irregularities (Stuart 1967). Bruinsma (1979) used tiny steel balls in experimental arenas to elicit building behavior in *Macrotermes* workers. According to Torales (1982–1984), the *Cornitermes cumulans* species marks the previous building location with feces. In nest building, termites use small pellets of soil and feces (Fig. 10.1). These small pellets are embedded in saliva produced by the salivary glands (Fig. 10.2), which seems to contain a "cement" pheromone that stimulates building (Bruinsma 1979). This salivary pheromone is a methanol-soluble volatile that can be extracted from freshly built soil and, when moistened, elicited pillar construction (Prestwich 1983). The building behavior and termite movements are locally controlled by the concentration of the pheromone, which is likely a component of the saliva from the builder workers. The initial deposit of soil pellets stimulates workers to accumulate more material through a positive feedback mechanism (Grassé 1984).

According to Bruinsma and Leuthold (1977), the physogastric queen of *Macrotermes subhyalinus* produces a pheromone that stimulates the building of the royal chamber. The communication between the queen and the builder workers occurs through a threshold concentration of the queen pheromone, which works as a template for the construction of the royal chamber (Camazine et al. 2003). The workers that are below the threshold concentration are engaged in the normal construction that is induced by stigmergy. Workers of Apicotermitinae (Termitidae) also build a chamber around their unsheltered queen (Fig. 10.3) when they are experimentally removed from their host nest (Costa-Leonardo and Haifig unpublished). Trail pheromones orient the movement of builder workers around the queens

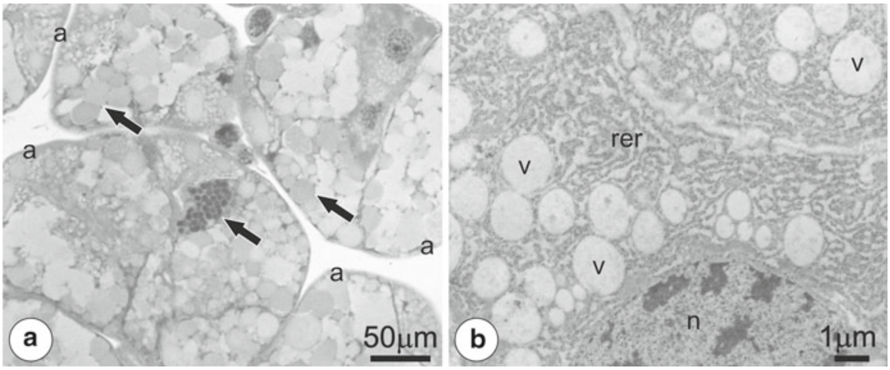

Fig. 10.2 Salivary glands in *Cornitermes cumulans* worker. (**a**) Salivary acini (*a*) with the various secretory cells filled with different secretions (*arrows*). (**b**) Ultrastructure of a secretory cell, showing the round electron-lucent vesicles (*v*) of secretion and the richness in the rough endoplasmic reticulum (rer). *n* nucleus

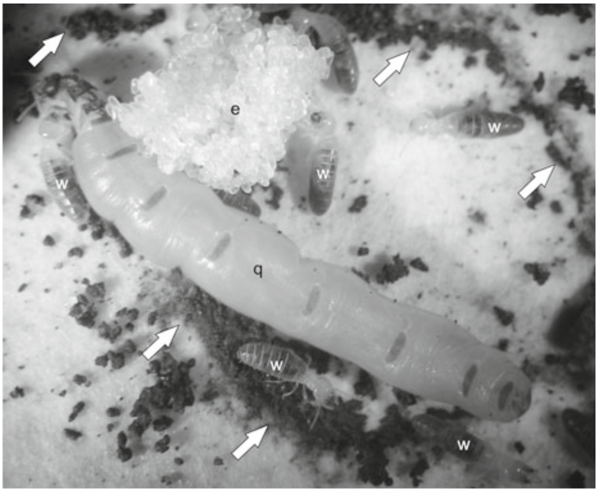

Fig. 10.3 Termite workers building walls of the royal chamber around the physogastric queen and eggs. *Arrows* indicate the pellets that have been deposited by the workers during wall construction. *e* eggs, *q* queen, *w* workers

and dictate the shape of the royal chamber (Camazine et al. 2003). The simulation study of Ladley and Bullock (2005) investigating royal chamber and tunnel network construction demonstrated that simple behavioral rules are sufficient to generate complex structures in a completely self-organized way.

None of the pheromones that are involved in the construction have been identified, although palmitoleic acid was thought to be one of the constituents of the pheromone produced by the queen of *Macrotermes michaelseni* for the construction of the royal chamber (Prestwich 1983; Grassé 1984).

3.3 Defense

The defense of a termite colony is a collective behavior that is coordinated by a variety of signals (Kaib 1999).

3.3.1 Alarm

According to Landolt et al. (1998), alarm behavior generally occurs as a result of a threat that is communicated to the colony by chemical signals or otherwise produced by nestmates. Alarm signals are produced after various disturbances, including breaking or violation of the nest, light, air flow and the presence of pathogens (Stuart 1963; Rosengaus et al. 1999; Inta et al. 2009; Hertel et al. 2010). Workers of *Zootermopsis angusticollis* avoid termites that have been exposed to the spores of the fungi *Metarhizium anisopliae* through the perception of the vibrational signals that are emitted by the exposed nestmates (Rosengaus et al. 1999).

Alarm pheromones are normally produced in large amounts and are highly volatiles (Blum 1969). Šobotník et al. (2010) stated that termite alarm is elicited by mechanical signals (vibrations on the substrate), by the pheromones of the frontal gland of soldiers or by physical contact between nestmates. A combination of these factors during alarm behavior is common, as in the soldiers of the *Coptotermes* species, which often combine intense jerking with the ejection of the fluid from their frontal gland (Hertel et al. 2010). Alarmed workers of *Hodotermes mossambicus* defecate, and this fecal material seems to contain an alarm pheromone (Wilson and Clark 1977).

Termites exhibit varied convulsive movements to communicate alarm, and this body vibration is a behavior that occurs in all of the castes (Stuart 1963; Šobotník et al. 2010). The head-banging movement is more developed in soldiers and consists of a vibration of the entire body with an up-and-down movement of the head against the substrate or parts of the galleries or nests. This movement is accompanied by a characteristic sound, which is sometimes very loud, because many soldiers are often alarmed together. Other alarm movements of termites have been designated as bumping or jittering and in these cases, no sound is involved (Stuart 1963). Several researchers consider both movements to be the same, but conveying different degrees of alarm. According to Stuart (1963), the sound is incidental in alarm communication, and the alarm is transmitted by the mechanical contact of alarmed termites with un-alarmed ones.

Vibrational signals are interpreted as alarm in many termite species and are perceived by the subgenual organ of these insects (Howse 1970; Šobotník et al. 2010). Ohmura et al. (2009) showed that termite tremulation (especially back-and-forth movement) and tapping behavior (head bumping) are species-specific. In one-piece nest termite species, alarm signals involve one or a few termites that are close to the site of the disturbance. In multiple-piece nest termite species, for example, in the case of the *Macrotermes* species, there is a sophisticated system of vibrational

Table 10.3 Principal substances identified as alarm pheromones

Species/Genus	Pheromones	References
Nasutitermes costalis	Carene (monoterpenes) Limonene (monoterpenes)	Vrkoc et al. (1978)
Nasutitermes rippertii	α-Pinene (monoterpenes) Limonene (monoterpenes)	Vrkoc et al. (1978)
Velocitermes velox	α-Pinene (monoterpenes) Limonene (monoterpenes)	Valterová et al. (1988)
Schedorhinotermes lamanianus	Monoterpenes	Kaib (1990)
Nasutitermes princeps	α-Pinene (monoterpenes)	Roisin et al. (1990)
Reticulitermes	Monoterpenes Sesquiterpenes	Reinhard et al. (2003)
Prorhinotermes canalifrons	(E,E)-α-farnesene (sesquiterpenes)	Šobotník et al. (2008)

long-distance alarm communication. The soldiers drum their heads against the substrate when their nest is disturbed. Other soldiers are extremely sensitive to vibrations and begin to drum themselves, indicating the existence of positive feedback in signal production and resulting in the escape behavior of termites into their nest (Röhrig et al. 1999). In *Pseudacanthotermes spiniger* and *Pseudacanthotermes militaris* (Termitidae), the vibrational signals elicit polyethic responses. Workers react to head-banging by escaping, whereas minor soldiers may escape, become immobile or begin head-banging (Connétable et al. 1999).

Alarm signaling after the spray of the stick frontal secretion that alerts soldiers to the battle site was first described in soldiers of the *Nasutitermes* genus by Ernest (1959). Table 10.3 shows the chemical substances, known as alarm pheromones, that are produced by the frontal gland of termite soldiers, including diverse terpenoids. The volatile compounds that are responsible for alarm signaling in the *Nasutitermes* species are mostly monoterpenes and sesquiterpenes (Prestwich 1984; Pasteels and Bordereau 1998; Šobotník et al. 2010). In addition, immobilized enemies may be covered with soil and feces by *Nasutitermes exitiosus* workers, and this behavior seems to interrupt the alarm signal (Eisner et al. 1976).

The response of termites to the alarm pheromones may differ in the workers and the soldiers. According to Šobotník et al. (2008), soldiers are attracted to the alarm source, while the other castes hide. Alarmed soldiers propagate the alarm by physical contact, increasing their walking speed or releasing their frontal gland secretions. Figure 10.4 shows the morphology of the head and nasus in the termite soldiers that spray the frontal gland secretions. Alarm pheromones also induce polyethic responses. The major soldiers of *Nasutitermes exitiosus* and minor soldiers of *Schedorhinotermes lamanianus* are not involved in attacking the enemies and are exclusively responsible for the dissemination of the alarm inside the nest (Kriston et al. 1977; Kaib 1990).

Alarm communication may also occur through physical contact between alarmed termites and their recruited conspecifics. When the forager termites of *Macrotermes subhyalinus* meet the foragers of *Macrotermes bellicosus*, a significant recruitment

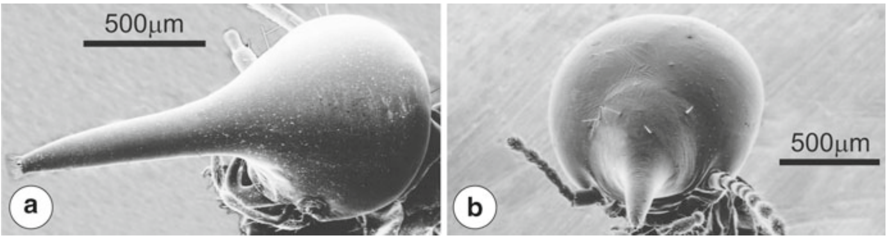

Fig. 10.4 Scanning electron micrograph of the head of a *Rynchotermes nasutissimus* soldier (**a**) and of a *Nasutitermes jaraguae* soldier (**b**)

of workers and minor soldiers occurs. This recruitment is initiated by the major workers, which return to the nest while laying a trail pheromone that will guide the nestmates that were stimulated by tactile signals (Kettler and Leuthold 1995). In *Zootermopsis*, the direct physical contact occurs simultaneously with the vibratory movements (Stuart 1963). Alarm may be elicited by vibrations, pheromones from the frontal gland secretions and physical contact. Furthermore, these stimuli may act alone or in combination, and they are not exclusive to termite soldiers (Šobotník et al. 2010).

3.3.2 Competition

Competition is an important factor in termite population dynamics and may occur at intra- and interspecific levels. In the Isoptera, most of the studies investigating competition evaluated this process in laboratory conditions (Jmhasly and Leuthold 1999; Li et al. 2010; Jost et al. 2012). Bioassays that promote physical contact between competitors immediately result in agonistic behavior, with soldiers opening their mandibles and biting the individuals of the opposing species (Thorne and Haverty 1991; Polizzi and Forschler 1998; Li et al. 2010; Jost et al. 2012). However, when termites of different species encounter each other in experimental foraging arenas that have space, they normally block the passages of the territory intersection (Uchima and Grace 2009; Cornelius and Osbrink 2010; Li et al. 2010; Jost et al. 2012). Dead termites of other colonies or species that are found inside the exploratory tunnels lead to the isolation of the area and the formation of new tunnels (Lima and Costa-Leonardo 2012).

Jmhasly and Leuthold (1999) observed the overlapping territories of the *Macrotermes subhyalinus* and *Macrotermes bellicosus* species in the field and did not find aggressive behavior. These termites withdraw and block their passages without deadly conflicts. The opposite was inferred by Darlington (1982) in the analysis of the foraging territories of *Macrotermes michaelseni* colonies because cemetery pits were observed between nearby tunnels. Messenger and Su (2005) also observed that agonistic encounters between different colonies of *Coptotermes formosanus* (Rhinotermitidae) may cause a fight, which is preceded by a physical communication through antennal inspection between the individuals. This fight may be followed by a behavior known as “suicide cramming”, in which some termites tightly squeeze into the foraging tunnel connection and die, blocking the passages and ending the agonistic activities. According to Li et al. (2010), termite cadavers resulting from agonistic behavior appeared to induce sand deposition that blocks tunnels and deters the reopening of these blockages. Ali and Morgan (1990) described funeral pheromones, which are chemical compounds produced by dead ants that stimulate living ants to remove the corpses of their nestmates from the nest. In ants, these funeral pheromones include saturated fatty acids, esters derived from these acids and unsaturated fatty acids. However, such pheromones have not been identified in termites.

Recent studies have demonstrated that vibroacoustic cues are important for communication in some drywood termites, such as *Cryptotermes secundus*, and that these cues help to avoid competitors (Evans et al. 2009). According to these authors, vibrational cues are fast, operate over distance and do not require direct contact. Drywood termites distinguish their own species from others using vibration cues that are generated through wood chewing.

Reproductive replacement may generate competition among nestmates, and the struggle for the heritage of the colony may lead to the elimination of competitors. In Kalotermitidae, numerous neotenic reproductives develop in the absence of the primary reproductives, but only one couple is accepted by the society, while the others are eliminated by the colony (Grassé 1982). Korb et al. (2009) observed that the communication among workers in orphaned colonies of *Cryptotermes secundus* occurs through physical contact, and the individuals that exhibit more butting against the others will become reproductives.

3.4 Reproduction

The reproduction of Isoptera is influenced by semiochemicals, and the variation in these substances includes different termite species and feeding habits. Mature termite colonies liberate alate reproductives that disperse and found new colonies (Nutting 1969). This seasonal phenomenon is known as swarming and is always preceded by a pre-swarming phase, which occurs inside the natal nest. Sex pheromones induce the meeting of sexual partners in termites and are generally produced by the sternal gland of the 5th sternite.

Some of the sex-attractive components are identical to the trail pheromone; however, they are produced in larger quantities when acting as sex pheromones (Kaib 1999). These compounds belong to three chemical classes: aldehydes, alcohols and hydrocarbons (Bordereau and Pasteels 2011). In the family Rhinotermitidae and the subfamilies Macrotermitinae and Syntermitinae, the sex pheromone includes the alcohols dodecenol, dodecadienol and dodecatrienol. In the subfamily Nasutitermitinae, neocembrene is the major component of the sex pheromone. Additionally, dodecanal is the principal component of the sternal gland secretion in the male

Fig. 10.5 Immature alates of *Velocitermes heteropterus* aggregated in a flower shape

alates of *Zootermopsis* and most likely represents the major component of the male sex-pairing pheromone (Bordereau and Pasteels 2011).

3.4.1 Pre-flight Behavior and Dispersal Flight

In the pre-flight period, the alates of many species become gregarious, separating into groups in superficial chambers or galleries close to the nest exit (Nutting 1970). In this pre-flight phase, the alate reproductives seem to produce specific pheromones which maintain the group in a gregarious state, but stimulate hostility from the other nestmates (Buchli 1961). When they withdraw from the nest, immature alates of *Nasutitermes fulviceps* exhibit an aggregation behavior in the shape of geometric figure or flower (Grassé 1984). The same behavior may be observed in other termitids, for example, in immature reproductives of *Velocitermes heteropterus* (Fig. 10.5). However, there are no data about the chemical composition of this possible pheromone that elicits alate aggregation.

Sometimes, the pre-flight period is quite long because for the nuptial flight to occur, the alate reproductives must be physiologically mature and the adequate meteorological conditions must be present. The alate maturation requires tactile and chemical social interactions with nestmates and changes in phototaxis, which become highly positive (Grassé 1982).

During the nuptial flight, the sexual partners (males and females) meet in spotlights because in this phase, they exhibit a positive phototaxis. In many termite species, principally among the neotropical termitids, the females attract the males by exposing the sternal gland of the 5th sternite in a process known as the "calling position", and this period is named the "calling phase". In the *Macrotermes annandalei* and *Macrotermes barneyi* species, long-range attractants are produced by the posterior sternal glands present in female imagos (Peppuy et al. 2004). In the termite *Trinervitermes bettonianus*, the tergal glands are responsible for the production of the long-range attractants (Leuthold 1975). In *Nasutitermes ephratae*, both the tergal and the sternal secretions seem to be involved in sex attraction (Bordereau and Pasteels 2011). According to Leuthold and Bruinsma (1977), only the males of *Hodotermes mossambicus* call female imagos by exposing their sternal gland. Calling pheromones may be secreted by female and male termite reproductives, but the non-calling sex individuals produce lower quantities of the pheromone, as in *Pseudacanthotermes spiniger* (Bordereau et al. 1991). In some species, as in the case of *Coptotermes gestroi*, this phase of calling is absent (Costa-Leonardo and Barsotti 1998).

3.4.2 Post-flight Behavior and Mating

In general, the reproductives lose their wings before beginning the tandem or nuptial dancing. After the calling phase, the reproductives initiate the pairing behavior. The most common pattern in the beginning of tandem behavior is the males placing their palps in the abdominal tergites of the females, as occurs in *Reticulitermes* (Howse 1984). According to Eliyahu et al. (2008), mature females of *Blatella germanica* produce a pheromone of lipid composition that elicits courtship behavior when males contact their abdomens with antennae. Males of the *Reticulitermes lucifugus* and *Coptotermes formosanus* species touch the lateral regions of the females with their antennae before initiating tandem behavior (Buchli 1960; Raina et al. 2003a).

Afterwards, the pair excavates together a nuptial chamber that is appropriate to rear the brood and initiate the colony. Tergal glands are involved in the formation of the sexual pair after the dispersal flight (Noirot 1969; Grassé 1982; Costa-Leonardo and Haifig 2010). Figure 10.6 shows a male reproductive of *Procornitermes araujoi* following a female, which possesses three tergal glands. It is still not clear if the tergal glands are the only glands related to this function because some termite species that lack these structures display tandem behavior (Park et al. 2004). The principal compounds that are secreted by the tergal glands, which act as sex-pairing pheromones, are dodecatrienol, dodecenol, neocembrene and trinervitatriene (Bordereau and Pasteels 2011). Reproductives of the species *Anacanthotermes ochraceus* do not exhibit calling or tandem behaviors, but Clément (1956) observed a brief antennation between the individuals prior to the digging of the nuptial chamber.

Various environmental factors affect the selection of a suitable nesting site. The mating only occurs after the establishment of the royal pair in the copularium, days or weeks after the dispersal flight. According to Bordereau and Pasteels (2011), sex-mating pheromones have not yet been described, but they most likely elicit copulation. Copulation is always preceded by mutual grooming in the *Coptotermes formosanus* (Raina et al. 2003b) and *Odontotermes formosanus* species (Tian et al. 2009).

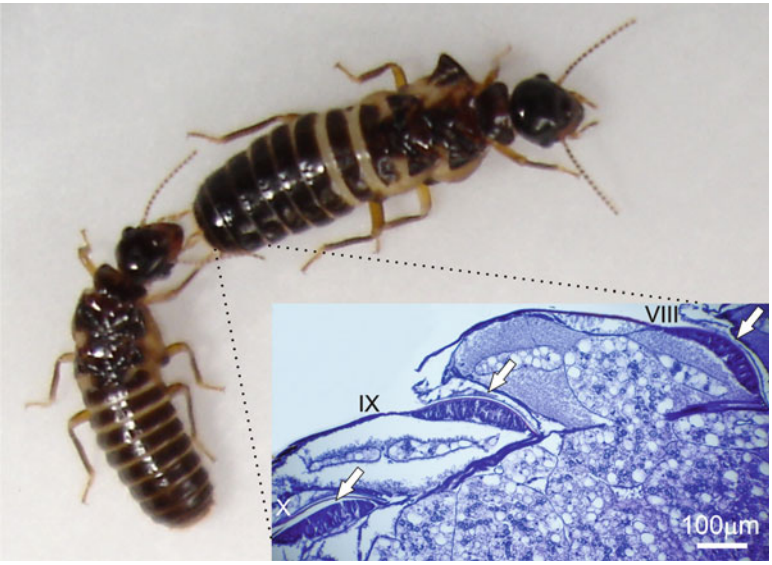

Fig. 10.6 Alate reproductives of *Procornitermes araujoi* exhibiting tandem behavior. The *insertion* shows the abdomen of the female with three tergal glands (*arrows*) under the *VIII*, *IX* and *X* tergites

4 Communication in Social Interactions

During social interactions, termites must recognize their nestmates. The discrimination system avoids social parasitism (Wallace 1964) and increases the success of the termite society. The extended period of young termite maturation allows larval retention within the natal colony and the communication between these individuals and their nestmates is poorly understood. However, recent data has made clear the communication of eggs and other components of the colony. The nature of the queen's control of a termite colony is not completely understood, but some chemical signals that inform her nestmates of her reproductive status are being discovered.

4.1 Nestmate Recognition

Nestmates and non-nestmates are recognized by termites through chemical communication. Chemical cues allow colony recognition, and these cues consist mainly of hydrocarbons from the termite cuticle (Clément and Bagnères 1998; Costa-Leonardo et al. 2009). Termites, like other insects, have a lipid layer on the cuticle that provides protection from desiccation, and is partly composed of hydrocarbons (Lockey 1988). In termites, the colony odor is the result of genetic and environmental factors

(Dronnet et al. 2006; Shelton and Grace 1996). Among the environmental factors are termite diets and intestinal bacterial composition (Matsuura 2001; Florane et al. 2004). A recent study added pure hydrocarbons to the diet that was experimentally offered to *Reticulitermes flavipes* and they were incorporated into the cuticular and internal hydrocarbon pools (Rawlings 2012). Nest paper in wasps and comb wax in bees are environmental factors that contribute to the colony odor of these social insects (Breed et al. 1988; Singer and Espelie 1996). In ants, the colony odor is due to the hydrocarbons that are present in the cuticle and in the secretion of the postpharyngeal gland, which is spread to nestmates through trophallaxis (Vander Meer and Morel 1998). In general, grooming behavior spreads cuticular hydrocarbons among termite nestmates (Costa-Leonardo and Haifig 2010). The phenotypes of the cuticular hydrocarbons may vary within the colonies of a termite species, and this may generate inter-colonial aggression (Bagine et al. 1994; Kaib et al. 2004).

Different hydrocarbon profiles are present in different castes and sexes (Pasteels and Bordereau 1998). White larval termites seem not to exhibit discrimination cues that are found in the cuticle; it is likely that this is because their cuticle is unsclerotized and seems to differ from that of their mature nestmates and/or because they have a different diet, composed exclusively of stomodeal salivary food (Thorne and Haverty 1991). Larvae from a nest of the termite species *Cornitermes cumulans* were not injured when placed together with workers and soldiers from another nest (Costa-Leonardo et al. unpublished), suggesting that these individuals lack a chemical identity. Shelton and Grace (1996) propose that young termites are capable of interpreting the recognition cues and integrating with the individuals from the new colony, as occurs in the ant species *Manica rubida* and *Formica selysi* (Errard 1994). In these species, each individual possesses a template encoding the allospecific and the conspecific cues needed to characterize nestmates.

Hydrocarbon profiles also indicate fertility and dominance status in colonies of the Hymenoptera and Isoptera (Liebig 2010; Costa-Leonardo and Haifig 2010). Significant amounts of four polyunsaturated alkenes indicate the reproductive status of both sexes of the functional reproductives of the termite *Zootermopsis nevadensis* (Liebig et al. 2009). Qualitative differences in the cuticular hydrocarbon profiles were found between the queens and the workers of *Cryptotermes secundus* (Weil et al. 2009).

4.2 Egg and Brood Care

In the establishment of a termite colony, both the king and the queen take care of the eggs and larvae. These reproductives groom and move the eggs from one site to another. This behavior keeps the embryos free of fungi and bacteria (Edwards and Mill 1986). According to Bordereau (1985), egg grooming cleans the eggs and transmits pheromones that are produced by the queen.

In the termite *Reticulitermes speratus*, the eggs of neotenic queens produce volatile substances that act as an attractant to workers and an inhibitor of

Fig. 10.7 *Velocitermes heteropterus* workers transporting eggs and assisting the queen

reproductive differentiation. These substances were identified as n-butyl-n-butyrate and 2-methyl-1-butanol, respectively, and help the workers to locate the eggs (Matsuura et al. 2010).

The workers regularly transport (Fig. 10.7) and groom the eggs in mature colonies (Crosland et al. 1997). Termite eggs will not survive without the protection of workers because after they are laid by the queen, they are carried by the workers to the egg chambers, where these individuals groom and coat them with saliva and antibiotic substances (Grassé 1982; Matsuura et al. 2000).

Termite workers recognize the eggs by morphological cues and by their pheromones, which consist of the antibiotic protein lysozyme and the digestive enzyme β-glucosidase (Matsuura et al. 2007, 2009). The palpation of the eggs by termites provides tactile cues of their surface texture, shape and size (Matsuura et al. 2007). Social factors, such as the number of workers, influence egg number and size. Queens of *Reticulitermes speratus* produce larger eggs in lower quantities in the beginning of the colony, when workers are still absent. Larger eggs require shorter hatching periods and develop into larger larvae (Matsuura and Kobayashi 2010).

The termite larvae are dependent individuals and, therefore, they are unable to survive without being fed by other individuals. In incipient colonies, the larvae are fed by the royal couple, and with the growth of the colony and the appearance of the first workers, these individuals assume this task, and the king and queen become involved only with reproduction (Matsuura and Kobayashi 2010). This idea is corroborated in a recent study by Shimada and Maekawa (2010) which showed that when workers are present, the levels of cellulase gene expression decrease in reproductives.

Table 10.4 Pheromones present in neotenic queens

Species	Neotenic queen pheromones	nv/v	References
Cryptotermes secundus	Long-chain and branched CHC	nv	Weil et al. (2009)
Zootermopsis nevadensis	Polyunsatured alkenos	nv	Liebig et al. (2009)
Prorhinotermes simplex	Polar compounds of proteinaceous origin	nv	Hanus et al. (2010)
Reticulitermes santonensis	Polar compounds of proteinaceous origin	nv	Hanus et al. (2010)
Kalotermes flavicollis	Polar compounds of proteinaceous origin	nv	Hanus et al. (2010)
Reticulitermes speratus	n-butyl-n-butyrate 2-methyl-1-butanol	v v	Matsuura et al. (2010)

CHC cuticular hydrocarbons, *nv* non-volatile, *v* volatile

4.3 Queen Dominance and Attendance

According to Matsuura (2012), the queen's dominance is perceived by the nestmates through releaser pheromones (behavioral activators) and primer pheromones (physiological primers).

Releaser pheromones may elicit queen-tending behavior in workers, causing these individuals to groom and feed the queen as well as to collect the oviposited eggs (Fig. 10.7). Some releaser pheromones may also elicit aggressive behavior by non-reproductive nestmates against individuals that produce reproductive signals inside the colony and may become competitors of the queen (Liebig et al. 2009). A functional queen may secrete primer pheromones, which suppress the development of the reproductive apparatuses of other individuals from the nest and maintain its reproductive dominance (Brent et al. 2005). There is no evidence to indicate whether the inhibitory signals are spread through trophallaxis or on an olfactory basis (Korb 2005; Weil et al. 2009). The chemical signals that affect the endocrine system and control reproductive development disappear when the queen is absent (Matsuura 2012).

To date, the dominance of the primary queen has not been clarified in termites, and the pheromones involved in this communication are unknown. However, recent studies demonstrate that both volatile and non-volatile substances act as pheromones in neotenic queens of different termite species, maintaining the dominance of these individuals inside the colonies (Table 10.4). Basal termites inhabit small nests (one-piece nest) and use more non-volatile pheromones, while the termites of the Termitidae family, which have larger colonies, use both specific cuticular hydrocarbons and volatile pheromones (Matsuura 2012).

Volatile pheromones that are present in the neotenic queens of *Reticulitermes speratus* are the following: one ester, n-butyl-n-butyrate, and one alcohol, 2-methyl-1-butanol, which are the same pheromones that are emitted by the eggs (Matsuura et al. 2010). It is surprising that eggs of *Reticulitermes speratus* emit volatile pheromones that are identical to those produced by the queens. Specific cuticular hydrocarbons of the *Cryptotermes secundus* and *Zootermopsis nevadensis* species (Weil et al. 2009; Liebig et al. 2009) and specific proteinaceous compounds in the *Prorhinotermes simplex*, *Reticulitermes santonensis* and *Kalotermes flavicollis* species (Hanus et al. 2010) have already been described as non-volatile pheromones in neotenic reproductives.

5 Sensory Structures Involved in Communication

The various termite tasks are performed by diverse castes or individuals of different ages. Grooming and trophallaxis are notably important in termite society, and they are necessary for spreading contact and chemical communication throughout the colony. To monitor changes in the external environment, the termite body has sensilla that vary in function, number and distribution (Pearce 1997; Yanagawa et al. 2009a, b). The majority of these sensilla are bristle-like, but some are characteristic, such as campaniform sensilla. These different sensilla compose the sensory system of termites, which allows them to perceive different tastes, odors, touch, pressure, temperature, humidity and vibrations. These sensory structures are essential for communication and allow termites to enjoy the benefits of community life.

Termites perceive chemical stimuli, such as sex and trail pheromones, through chemoreceptors located in the antennae, maxillary palps, labial palps and other parts of the mouth (Fig. 10.8a–d). The antennae possess different sensilla, including olfactory, gustatory, hygrosensory, thermosensory and mechanosensory sensilla, which provide the termite with information about its environment (Yanagawa et al. 2009a). Mechanoreceptors, such as the campaniform sensilla, are present in all antennal segments, while chemoreceptors are located only in the distal segments (Tarumingkeng et al. 1976; Costa-Leonardo and Soares 1997). Scout workers of subterranean termites are able to deform their antennae because of their moniliform shape, and this ability allows them to perceive the relief of the tunnel walls with the mechanoreceptors located on the base of the antennae (Bardunias and Su 2010). In addition, movement and gravity may be perceived by the chordotonal sensilla, which are also present in the antennae of termites (Pearce 1997). According to Ziesmann (1996), olfactory sensilla possess numerous pores that distinguish different odors. Termites detect fungal odors and remove fungal conidia from the body surfaces of their nestmates through mutual grooming (Yanagawa et al. 2009b).

Physical contact is detected by termites through the sensory bristles and the campaniform sensilla, which are mechanoreceptors that are spread on the cuticle, principally in the antennae and mouthparts (Kirchner et al. 1994). As has been previously described, tapping alerts are detectable by subgenal organs (Howse 1970; Šobotník et al. 2010). Additionally, important sensory organs called cerci exist in both sides of the termite abdomen (Fig. 10.8e–f), although it is not known whether they participate in communication. These appendages possess filiform sensilla that are arranged in rows and are responsible for the detection of faint air currents and low-frequency sound or medium vibration (Ishikawa et al. 2007). In roaches, the cerci

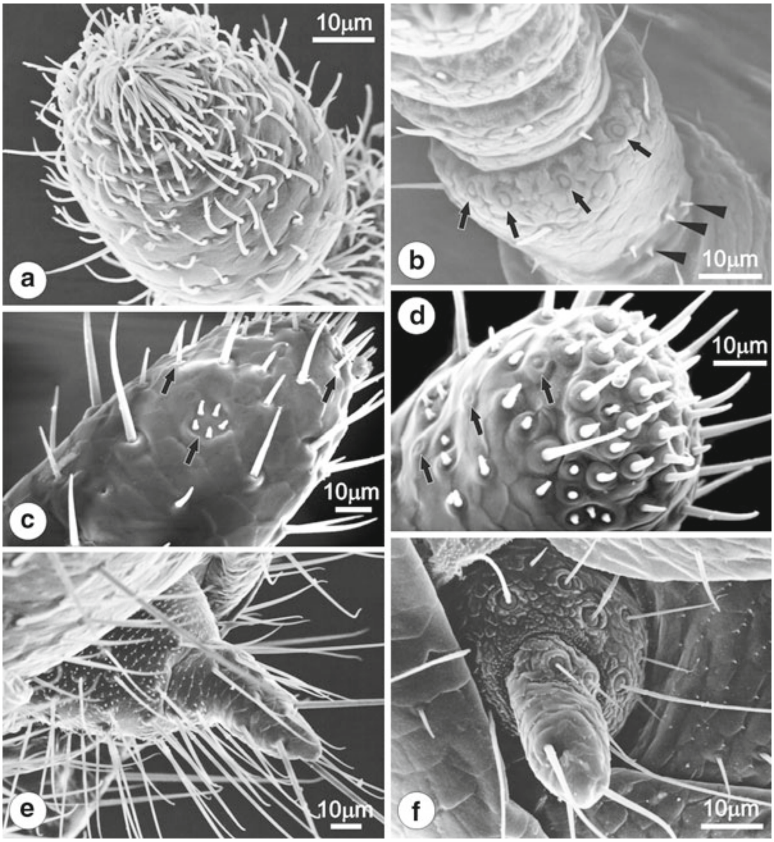

Fig. 10.8 (**a**) Antennal tip of a worker of *Serritermes serrifer*. Note the numerous long bristle sensilla. (**b**) Detail of the campaniform sensilla (*arrows*) present in the antennal pedicel of the termite *S. serrifer*. Note the short bristle sensilla (*arrowhead*). (**c**) Maxillary palp of a *Cryptotermes brevis* soldier. The *arrows* indicate different sensilla. (**d**) Labial palp of a *C. brevis* soldier. The *arrows* indicate campaniform sensilla. (**e**) Cercus of a female alate reproductive of *Heterotermes tenuis*. (**f**) Cercus of a worker of *S. serrifer*

play an important role in the escape behavioral movements of these insects from a predator (Camhi and Tom 1978).

In general, reproductive alates have two compound eyes and two ocelli, and these individuals exhibit positive phototaxis; they are attracted by lights during swarming flights. When they land and establish pairs, they exhibit negative phototaxis. The development of the compound eyes varies according to the termite species and their reproductive strategies, which are related to ecological conditions, including food resources (Katoh et al. 2007). After the royal pair initiates a life inside wood or soil, the eyes begin to degenerate. The role of the compound eyes of alates is more likely for the orientation of these individuals than to visual communication between them.

6 Concluding Remarks

Termites are eusocial insects that are composed by castes that perform different activities in the colonies. Table 10.5 summarizes termite communication during different behavioral activities and the actions that are exhibit by the termites during

Table 10.5 Summary of termite communication during different behavioral activities

Termite behavior		Types of communication	Actions[a]	Source
Foraging		Mechanical	Tunnel wall antennation	–
			Mutual antennation	–
			Chewing the wood	–
		Chemical	Lay trail pheromones	Sternal gland
			Lay phagostimulant pheromones	Salivary glands
Building		Mechanical	Antennation of the substrate	–
		Chemical	Lay "cement" pheromone	Salivary glands
			Lay trail pheromone	Sternal glands
		Stigmergy	–	–
Defense	Alarm	Mechanical	Head-banging, bumping or tapping	–
			Jittering or tremulation	–
			Physical contact	–
		Chemical	Spray alarm pheromones	Frontal gland
	Competition	Mechanical	Antennal inspection	–
			Biting	–
			Butting	–
			Chewing the wood	–
		Chemical	Nestmate recognition	Cuticle
Reproduction		Mechanical	Antennation	–
			Palpation	–
			Allogrooming	–
		Chemical	Sex pheromone emission	Sternal gland, posterior sternal glands, tergal glands
Nestmate recognition		Chemical	Surface pheromone emission	Cuticle Exocrine glands?
Egg care		Mechanical	Grooming	–
			Palpation	–
		Chemical	Grooming	Eggs
			Olfaction	Eggs
Queen attendance		Chemical	Trophallaxis	Unknown
			Grooming	Unknown

[a]Action was defined as an activity developed by termites to communicate with nestmates, non-nestmates and sometimes with the environment itself

communication. Sensory structures present in the individuals are responsible for the perception and interpretation of the different signals and cues, which stimulate and modulate individual and collective behaviors. The ecological success of termites is dependent on their different communication strategies, which establish a social organization that is dependent on the signals and cues released by conspecific individuals while performing their various activities.

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Chapter 11

Crows and Crow Feeders: Observations on Interspecific Semiotics

John M. Marzluff and Marc L. Miller

> *He gets fat with ruffles and has a different walk when I tell him how handsome he is in a certain tone.*
>
> – Crow Feeder

Abstract Biosemiotic studies include those which focus on systems of signs linking humans and animals. We review the general roots of interspecific communication with emphasis on biosemiotic studies. Beyond domestic animal—human communication, humans are known to communicate closely with a few wild animals with which they have mutualistic foraging relationships (dolphins, honeyguides). We reveal another such relationship in a pilot field study of American crows (*Corvus brachyrhynchos*) and human crow feeders. Our study illustrates an interdisciplinary consideration of interspecific communication goals, tactics, rewards and signals. Always alert to threats in searches for food, crows responded to a repertoire of messages and behaviors of crow feeders they recognized. Crow feeders—motivated to attract, feed, and spend time with particular crows—fall into two categories. Crow friends talk and behave with crows as they might with people. Crow observers are more detached, wanting unobtrusive interaction without emphasis on personal identities or feelings. We propose that the crow feeding events can be usefully studied with a strategic engagement model. We encourage future biosemiotic projects to

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(1) employ an interdisciplinary approach, (2) examine genetic in addition to biological and cultural processes, (3) explore variation across biosemiotic systems, and (4) consider real-world implications of findings.

1 Introduction

Communication across species boundaries is inevitable and common throughout the animal kingdom. Natural selection favors distinctive, unambiguous, and species-specific signals for conveyance of intraspecific messages, but often members of other species perceive these signals (Smith 1977; Danchin et al. 2004). This perception may favor differentiation of signals among species so that the signaler's time and energy are not wasted on inappropriate receivers. However, when the benefits of communicating with a larger audience are substantial, then natural selection may favor convergence of signals among species or elaboration of signals so that effective communication across species evolves.

1.1 Biosemiotics

Broadly speaking, s*emiotics* refers to a field of inquiry which concentrates on systems of messages. Within the field, Witzany and Yip (2007, p. 295) have defined *biosemiotics* as:

> …a transdisciplinary science which investigates sign processes (semioses) within and among living organisms with theoretical and empirical studies.

Biosemiotics is a framework to consider interspecific communication. In the simplest form this communication includes the mutual recognition of urgent signals regularly given by species that live closely together. In this way many small birds that seasonally flock together appropriately respond to each other's alarm and mobbing calls (Templeton and Greene 2007; Magrath and Bennett 2012). Similarly, a host of vertebrate and invertebrate prey, from plovers and antelope to hog-nosed snakes, opossums, and sphingid moth caterpillars, have evolved distraction, threatening, or deceiving signals honed by natural selection to fool or warn would be predators (Smith 1977).

Overt, on-going, and nuanced interspecific communication is apparently rare among animals other than humans, and seems to be limited to cases of mutual advantage (Smith 1977). This might include the advantage of play (e.g., crows respond to the play initiation postures of dogs and cats with whom they tussle; Marzluff and Angell 2012), or the more direct advantages of cooperative maintenance and foraging behavior. The pistol shrimp (*Alpheus djiboutensis*) and gobiid fish (*Cryptocentrus cryptocentrus*) that live together in burrows exchange signals across at least two sensory modalities for mutual benefit (Smith 1977). Flicks from the fish's tail inform the blind shrimp about nearby predators and chemicals from the fish attract the shrimp to clean its skin.

1.2 Anthropological Zoosemiotics

A special case of biosemiotics concerns sign exchanges between humans and animals. Martinelli (2010) employs the term *anthropological zoosemiotics* to denote this focus.

When humans communicate with other species in anthropological zoosemiotic fashion, elaborate ritualized dialogues are possible. Seboek (1998, pp. 67–73) has developed a non-exclusive (and, incomplete) listing of eight relationships linking people and animals. Martinelli (2010, pp. 131–133) slightly modifies Seboek's list and adds four of his own at the end[1]:

1. *Predator/Prey Relationship*: Depending on the species in question and the situation, the human being and the animal can play the roles of predator or prey in their interaction.
2. *Partnership Relationship*: Here Seboek (1998, pp. 68–69) notes four kinds of partnership: (a) host-guest partnership (as with pets), (b) mutual dependence partnership (as with bee-breeding), (c) sexual relationship partnership (as in some cultural practices), and (d) partnership relations aimed at social facilitation (as when pets or domestic animals are used to help people communicate with other people).
3. *Sports/Entertainment/Hobby Relationships*: The human being can utilize/exploit other animals in sporting, hobby, and entertainment activities.
4. *Parasitic Relationship*: The human being can have a parasitic relationship with of other animals, playing the dominant role (as in reindeer-breeding). It is also possible for the human being to play the subordinate role (as with fleas).
5. *Conspecificity Relationship*: The animal can establish a relationship of conspecificity with the human being. This phenomenon—known as zoomorphism—occurs when animals identify the human as part of their species (or, in some instances as they identify themselves as part of the human species).
6. *Insentience Relationship*: The human being and the animal can establish a relationship of insensibility in which one species (the animal) considers the other as an inanimate part of their *Umwelt*, or environment.
7. *Domestication Relationship*: The human being can domesticate other animals.
8. *Training Relationship*: The human being and other animals can have a training relationship in which one teaches the other. Heidger (1968, p. 120) describes two

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[1] For readability and consistency, we have re-phrased the labels of these categories.

types of training relationships where humans take the lead: (a) *apprentissage* or laboratory training, and (b) *dressage* or circus-like training.

9. *Manipulation Relationship*: The human being manipulates other animals.
10. *Source of Knowledge Relationship*: The human being and the animal can be a source of knowledge for the other. (See, for example, Shepard 1996.)
11. *Significational Source Relationship*: The animal and the human being can inspire each other. Thus, the animal can be transformed *via* an allegory, metaphor, or myth.
12. *Defender/Protector/Promoter Relationship*: The human being and the animal can defend, protect, and/or promote the other.

Anthropological zoosemiotics is most obvious between humans and their domestic species. Dogs and horses, for example, attend to our verbal, chemical, and gestural signals, and we theirs' as we hunt, herd, and recreate together (Jakovcevic et al. 2012; Proops and McComb 2012). These examples illustrate a range of Seboek-Martinelli categories (*Partner*; *Sports/Entertainment/Hobby*; *Domestication*; *Training*; *Manipulation*; *Source of Knowledge*; *Significational Source*; and *Defender/Protector/Promoter*).

Humans also communicate with wild species, most eloquently with the honeyguide bird in East Africa. There, the greater honeyguide (*Indicator indicator*) leads Boran people to hidden beehives that require human muscle and tools to open. Both bird and human benefit from cooperating as the honey provides important calories to the nomadic people and the bird eats wax and larvae. These benefits have resulted in a series of mutually understood signals (Isack and Reyer 1988). The bird attracts people by approaching them, perching restlessly nearby, and giving a characteristic two-note, persistent call. Loud whistles are used by the Boran to attract the bird and whistles, loud voices, and banging on wood keep the bird intent on guiding. As people follow, the bird calls, conspicuously displays its white outer tail feathers, perches in view, and flies in an undulating pattern in the direction of the hive. Both distance and direction to the hive are reliably signaled by the bird and understood by the people. The Boran-greater honeyguide example illustrates a number of Seobek-Martinelli possibilities (*Partner*; *Parasitic*; *Manipulation*; *Source of Knowledge*; *Significational Source*).

In Brazil, artisanal fishers and dolphins (*Tursiops truncates*) communicate to mutual benefit while fishing (Pryor et al. 1990; Simões-Lopes et al. 1998; Zappes et al. 2011). Dolphins initiate cooperative fishing by seeking out humans fishing from shore with cast nets. Dolphins perform stereotypical rolls in front of lines of fishermen that move fish from deep water into shallows where cast nets are effective. As the men stand with nets in hand, facing away from shore the dolphins swim rapidly toward them, and if fish are present, they stop 4 m away and signal the location of fish by nodding their head, slapping the water, and pointing toward fish with their nose. At that signal, the fishermen cast their nets and the dolphins dive down to catch fish that break from the school to avoid the net. As with the other examples discussed, fisherman-dolphin communication arguably illustrates a range of Seboek-Martinelli relationship categories (*Partner*; *Parasitic*; *Manipulation*; *Source of Knowledge*; and perhaps *Domestication*; *Training*; and *Defender/Protector/Promoter* as well).

1.3 Communication Among Equals

Interspecific communication among long-lived, social, and sentient species, such as dolphins and people may be influenced by social politics, shared trust, personality, and cultural norms. In fishing cooperatives among wild dolphins and Brazilian fishermen, dolphins recognize individual people and preferentially communicate with those they have established relationships with. Likewise, fishermen recognize that some dolphins are unreliable and deceptive fishing partners (Zappes et al. 2011). Researchers in the Bahamas who were studying the two-way communication between humans and wild Atlantic spotted dolphins (*Stenella frontalis*), discovered that mutual gaze and synchronized swims were important precursors to successful communication sessions (Herzing 2010). These mimicked behaviors may build mutual trust.

Crows and ravens (corvids; birds of the Family Corvidae) have lived closely with humans for tens of thousands of years (Marzluff and Angell 2005; Finlayson et al. 2012). These sentient birds (Marzluff and Angell 2012) recognize individual people (Marzluff et al. 2010) by individual and social learning (Cornell et al. 2012), attend to their gaze (Bugnyar et al. 2004; Clucas et al. 2013), and utilize a wide range of individualistic and graded vocalizations (Marzluff and Angell 2005) including mimicked human voices (Marzluff and Angell 2012). Corvids regularly scavenge from people and during the course of our long-term studies we have met several people who actively encourage scavenging by providing foods especially for their corvid neighbors. Here we offer a preliminary description of these feeding associations with the aim of discovering and describing the interspecific communication that is included.

2 Crows and Crow Feeders

2.1 Interspecific Communication

We conducted a pilot study on eight people and the crows they routinely feed. All crow feeders resided in the greater Seattle, Washington (USA) area and were selected by convenience from a pool of people who told us of their feeding habits. On average, the eight feeders had been feeding crows for 5.2 years (range 0.75–10 years; Table 11.1). All people fed crows in a consistent location ranging from their backyard to their place of work. All but one fed at a consistent time, and six of eight identified a focal crow. Those with focal crows could identify the bird by injury (1 case of a bird with a missing foot), or by the bands they wore as part of our previous studies. Those that did not identify a focal bird were engaged with feeding a flock. We joined each crow feeder for 1 or 2 feeding sessions during which time we observed the interaction and interviewed the crow feeder.

People initiated a feeding session with a variety of signals meant to attract the attention of crows (Table 11.1). Most people presented a conspicuous and consistent

Table 11.1 Characterization of interactions between eight people and the crows they feed

Characteristic of Interaction	Occurrence in feeder (CF)—Crow (C) interaction								Total/average
Duration (years)	0.75	1	2	4	6	8	10	10	5.2
Consistent location	Y	Y	Y	Y	Y	Y	Y	Y	8
Consistent time	Y	Y	Y	Y	Y	Y	N	Y	7
Focal bird	Y	Y	Y	N	N	Y	Y	Y	6
Initiation phase									
CF: call to crow	X	X	X					X	4
CF: exaggerate feeding motions		X			X	X			3
CF: conspicuous food container	X	X		X	X	X	X	X	7
CF: rattle food container	X	X				X			3
CF: tap on window			X						1
C: vocalize staccato kaw sequence	X			X		X	X	X	5
C: perch in traditional location	X	X	X	X	X	X	X	X	8
C: peer in window	X		X			X	X	X	5
C: bill wipe						X			1
C: swoop over feeder and land ahead				X		X	X	X	4
C: circle flight around feeder							X		1
Feeding phase									
CF: exaggerate feeding motions		X	X		X	X			4
CF: talk softly with crow	X	X	X	X	X		X	X	7
CF: lock gaze with crow	X		X	X			X	X	5
CF: move along set route		X		X		X	X	X	5
C: swoop over feeder and land ahead				X		X	X	X	4
C: walk aside feeder		X		X	X		X	X	5
C: walk behind feeder				X		X	X	X	4
C: perch close (<5 m) to feeder	X		X	X	X	X	X	X	7
C: call softly	X	X					X		3
C: kaw sharply in sets of 2, 3, or 4		X	X	X	X	X		X	6
C: return gaze from feeder	X		X	X			X	X	5
C: increase blinking of nictitating membrane	X		X	X			X	X	5
C: erect head feathers	X	X	X	X			X		5
C: pound on substrate if feeder too close							X		1
C: bow and give unique *woo* call	X								1
Ending phase									
CF: wipe hands							X		1
CF: close/remove feeding container		X	X	X	X	X	X	X	7
CF: talk softly to bird				X	X				2
CF: show bird empty, palm up, hand				X					1
CF: close entry to feeding area			X			X			2
C: fly or walk to station at end of route	NA	NA	NA	X	NA	NA	X	X	3
C: look in building for feeder	X		X			X	X		4

food container (a large purse, can, tub, or bag) and either shook it to make a rattling noise, called verbally to the crows, or waved their arms in exaggerated feeding movements. Crows responded to these signals by coming to the person, but often crows met the crow feeders before they were overtly attracted. In every case we observed, crows perched in habitual locations (on lamps, trees, fences) at the traditional places they were fed. Over half of the crows anticipated the feeder, and peered in the window of the building from whence the crow feeder would emerge prior to a feeding session. A majority also called loudly with a short staccato sequence of 3–5 kaws at the start of the feeding session. This served to attract other crows to the area and was appreciated by the crow feeders. In half of the cases, as the crow feeder entered the feeding area, crows swooped low from behind and flew right over the head of the feeder in a characteristic pattern before landing slightly ahead, usually along the path traversed by the feeder. This was the most overt signal we observed by the crows to the crow feeders.

We observed a variety of interspecific signals exchanged between crow feeders and crows during the actual feeding session (Table 11.1). People kept crows engaged by talking softly to them, gazing directly at them, making exaggerated feeding motions, and walking with them along a set feeding route. Crows perched closely to the crow feeder, returned the person's gaze, increased the blinking rate of their nictitating membrane, kawed sharply in sequence, and often erected their head feathers in a typical subordinate posture (Heinrich 1989). Crows walked alongside, or behind mobile crow feeders and swooped over them as was done during the feeding initiation phase. In a few instances crows modulated human behavior with soft calls and sharp pounding on the substrate they perched upon (to stop approach). In one case, that involving the crow with an injured leg, the bird bowed and gave an unusual call (video available upon request) to its crow feeder.

The rapid blinking of nictitating membranes by crows as they interacted with crow feeders suggests a social response to a valued conspecific. This behavior was noticed by 5 of 8 crow feeders, and we recorded blink rates at each of these locations as crows were interacting with crow feeders. The average rate per minute of observation was 29.4 (n = 13 counts, range = 17–50/min), which is consistent with lab and field recordings of blinking in non-fearful settings (Marzluff et al. 2012).

At the end of feeding, crow feeders typically closed or removed the feeding container and left the site (Table 11.1). Four people gave additional signals such as saying "that is all" or "goodbye", wiping their hands conspicuously, or signaling their hands were empty by showing their open, upturned palms. After eating, crows individually left the area without obvious signals. In the cases where people provided food along a set route, the crows anticipated the end of the route by flying ahead of the crow feeder and perching at the terminus. In half of the associations, after the person entered their home or building, crows peered into the window and attempted to spot the feeder.

2.2 *Crow Motivations*

Our previous research suggests that crows quickly associate the sight of a known caretaker with the reward of food (Marzluff et al. 2012). Upon seeing the person who had fed and maintained their cage for 2–4 weeks, crows activated portions of the forebrain associated with hunger (preoptic area; POA) and reward (medial

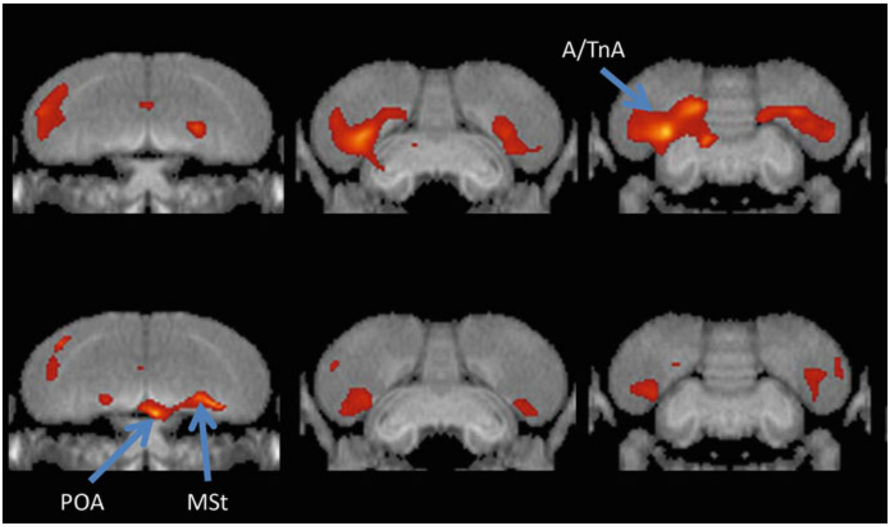

Fig. 11.1 Crow motivations of hunger, reward, and fear. Crows that see the crow feeders activate brain regions distinct from those activated by the sight of a feared person (one who previously captured them). In this summary image from Marzluff et al. (2012) we present voxel-wise subtractions converted to z-score maps superimposed to a structural MRI template of the crow brain for better anatomical localization. *Top row* shows the activation pattern of crows viewing a threatening face ($n=5$) compared to a group shown an empty room ($n=3$), and the *bottom row* indicates the activation pattern of crows shown a caring face ($n=4$) compared to the empty room group. Coronal slices (from anterior to posterior) illustrate peak activations in one or more group subtractions (voxels with $Z>1.64$ are colored, those with $Z>3.8$ are considered significant with associated structures as indicated). Activated structures for threatening face versus empty room: *A/TnA*: arcopallium/nucleus taeniae of the amygdala, 11 % increased $Z=4.42$, $p=0.00000425$. Activated structures for caring face versus empty room: *POA*: pre-optic area, 7.6 % increased, $Z=3.99$, $p=0.000011$, *MSt*: medial striatum, 5.9 % increased $Z=3.94$, $p=0.000052$. Slight differences in perception in the rostral forebrain were also found, but not shown here (Marzluff et al. 2012)

striatum; MSt; Fig. 11.1). Left hemisphere bias suggests this is a positive social experience (Tate et al. 2006). This is in contrast to activation of right hemisphere fear-learning circuits (including the amygdala) when crows sight a person who has previously harmed them (Fig. 11.1). Given the rapid nature with which crows make the association between food and crow feeders and the long-term nature of all the crow-crow feeder relationships we investigated, we suggest that in the wild, crows also formed mental associations between the individual crow feeder and the likelihood of a food reward. It is also likely that associations were formed between the locations of feeding and the likelihood of a reward, thus enabling crows to anticipate where, and often when, feeding would occur.

2.3 *Crow Feeder Motivations*

The labeling of the relationship between crow feeders and crows is a difficult riddle to resolve. On the one hand and with the somewhat conventional utilitarian view, this relationship is characterized by a producer (the crow feeder) and a consumer or scrounger (the crow). On the other hand a mutualistic view allows for the possibility of complex positive payoffs to both parties. With this perspective, crow feeders get the personal and social satisfactions of feeding and engaging crows, and crows get food, increased fitness, and arguably, social benefits having to do with companionship.

Employing the Sebeok-Martinelli inventory of human-animal relationships, we find that the crow feeders in our pilot study could arguably fall in eight or so categories (*Partner*; *Sports/Entertainment/Hobby*; *Domestication*; *Training*; *Manipulation*; *Source of Knowledge*; *Significational Source*; and *Defender/Protector/Promoter*). We add that crows could perhaps also play several additional roles (*Conspecificity, Insensibility*).

2.3.1 Serious Leisure

From a sociological point of view, our crow feeders showed a commitment to what Robert Stebbins has termed "serious leisure." Stebbins (1977, 1979, 1982, 1987, 1992, 2007) has established that people increasingly want more out of leisure than a relief from work, or spectator and sensual diversion. His work shows that the intensity and quality of the commitment of people who participate as amateurs, hobbyists, and volunteers in the fields of sport, entertainment, science, and the arts as leisure pursuits very often matches that of others who are paid to do the same thing. This led to the development of his concept "serious leisure."[2]

We found that the serious leisure of our crow feeders had features which mirrored those of serious leisure elsewhere. Thus, the serious leisure of our crow feeders, as subjectively experienced, was (1) engaged in for its own sake, hence *an end in itself*; (2) *inspired and passionate*; (3) marked by *a personal commitment* of time, energy, and other resources; (4) *ritualistic*, entailing the veneration of sacred objects and the implementation of interdictions against inappropriate behavior; (5) *transcendental*, or superior to other human endeavors; and (6) *separate* from other leisure and *exclusive*.

2.3.2 Ritual Solidarity

We further found that the serious leisure of our crow feeders exhibited a ritual phase-structure in which a kind of prototypical social solidarity (between crow feeders and crows) is produced in the manner described by Emile Durkheim (1912) in his seminal volume—*The Elementary Forms of Religious Life*. With serious leisure, solidarity is a ritual product of the Durkheimian kind which becomes evident in (1) the respect participants develop for one another, (2) the generation of sacred objects (e.g., technologies and apparel, memories, special events and personalities,

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[2] To clarify the connotation, Stebbins (1992, p. 8) intends the adjective "serious" to embody "such qualities as earnestness, sincerity, importance, and carefulness, rather than gravity, solemnity, joylessness, distress, and anxiety."

etc.), and (3) the potential participants have to direct righteous indignation toward those who would criticize or denigrate the ritual in question.

Of course, the prototypical social solidarity we noted is that reported by our crow feeders, and presumed by us from watching crow feeding routines. This is to say that our crow feeders often behave in a manner which suggests that social solidarity is a valued goal (certainly for them, if not the crows).

2.3.3 Social Roles of Crow Feeders

In our discussions with crow feeders, we asked how they might describe their relationships with the crows they feed. Very generally, we found that the social roles of crow feeders fall into two categories—*Crow Friends* and *Crow Observers* (Table 11.2, Fig. 11.2). Both Crow Friends and Crow Observers are motivated by more than merely wanting to provide nutrients to crows; they also want to spend time with crows. As will be seen, Crow Friends extend a human-centered model of friendship in their communications with crows. In this, they are relying on similarities (for example, in the facility to have social relationships) between crows and people. By contrast, Crow Observers use their time with crows in a different way. They expect less interest by crows in people (and people's personalities). They are especially keen to acknowledge differences (in abilities, in goals) between crows and people (Table 11.2).

2.3.3.1 Crow Friends

The Crow Friend role characterizes crow feeders who have developed a personal commitment to the well-being of crows. Of the six Crow Friends in our small sample, four had developed friendships with particular crows (as opposed to having only a generalized friendship with the species), and three of the four had names for their crows (Fig. 11.2).

The Crow Friend behaves as a good partner to crows in the same manner as he or she might to a human. Throughout the ritualized process of attracting and feeding crows, the Crow Friend nurtures an interspecific relationship. This is accomplished with signals conveying (in the mind of the Crow Friend) recognition of crows; approval, praise, and encouragement; but also—and depending on the situation—disapproval and disappointment, sadness, and hope.

Of course, the Crow Friend is often motivated to improve a friendship. Thus, crow feeders experiment with different tactics of attraction, social engagement and communication, and learning. Crow Friends select and refine a variety of goals to make the friendship more meaningful and exciting. Crow Friends find that they too can learn through friendships. The Crow Friends we studied very much valued a symmetric relationship—one in which neither the human nor the crow dominates the action. Crow Friends want the co-participation of both parties to be balanced.

Fig. 11.2 Crow feeders in action. (**a**) Crow feeder approaches favored feeding spot in backyard. (**b**) Crow feeder sitting at favored spot. Crows later walked up the stairs with crow feeder. (**c**) Crow food here consisted of baloney strips and unsalted peanuts. Other crow feeders offer catfood, tunafish, bread crumbs, raw egg in the shell, cheese rinds, squirrel trailmix, and table leftovers. Crow feeders reported that their crows did not like tomatoes, rice, or sweet potatoes. (**d**) Crow feeder at favored spot

Table 11.2 Social roles of crow feeders. Some crow feeders (CF) have developed a relationship with a particular crow (+) while others have not (−). Further, some crow feeders have given names to their crows (+) while others have not (−). Most, but not all, of the Crow Friends have given names to their crows. Crow Observers have not developed relationships with particular crows and, accordingly, have not given names to crows

		Relationship with a particular crow	
		−	+
Names for particular crows	−	CF5, CF6 CF3, CF4	CF1
	+		CF2, CF7, CF8

Crow Observers *Crow Friends*

Although there are variations among the six Crow Friends—in the scheduled time and length of interaction, in the choice and preparation of food for crows, in the selection of feeding sites and routes, and in the micro-styles of interspecific communication—we find that Crow Friends shape their routines with crows in much the same way as they do when they manage friendships with humans. Crow Friends talk about crow friendships with a vocabulary familiar to us all. Reflection by Crow Friends on the details of their successes and failures with crows invests meaning and value in the friendship routines and rituals they design.

A few direct quotations taken from our field notes illustrate a range of concerns of Crow Friends covering feelings and sympathies; communication goals, strategies, tactics, and experiments; curiosities, speculations, and hunches; expectations, obligations, and responsibilities; and (dis)satisfactions and celebrations:

- *Crow Friend Motivation*
  - "I go out (to feed crows) for pleasure. To interact." [CF7]
  - "They make me happy. They give me a lot of joy." [CF3]
  - "I have tried to show that I care about them. I try to convey that I am a friend. And that they are safe. They have gotten that message over the last two years." [CF3]
  - "I'll just go around and see who comes [to be fed]. It's probably the best part of my day. … They can totally make my day. Just by feeding. They are interesting that way." [CF4]
  - "I started when there was a big snow. I noticed him limping and I was worried about him." [CF1]
  - "They know I love them." [CF8]
  - "They need their freedom. They are my friends." [CF8]
- *Crow Personality*
  - "I tried to get too close the kids. Isabella scolded me.[3] Now I am more passive. Her anger has no bounds." [CF7]
  - "I fed the wrong crow! He yacked at me and took off." [CF8]
  - "I [by oversight] did something bad. I brought red-hot peanuts, not honey-coated. He would drop the highly seasoned ones." [CF8]
- *Crow Friend Bonding*
  - "I know his voice. Anywhere." [CF7]
  - "I know the [crow] parents are telling them [the offspring] they don't have to be afraid of me. … Only those that know me, come close." [CF8]
- *Crow Friend Language*
  - "Hey, hoo, hoo, come! … Edgar, you are so handsome! … You like that baloney, don't you?" [CF2]

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[3] Crow names are pseudonyms.

  - "Pretty pretty bird! Come on. There you go. …Oh, you're back! Come on, sweetheart. There we go." [CF3]

- *Crow Friend Tactics*

  - "It took me one day to train them to stay away from cats, bluejays. … I started out with peanuts, then baloney. Pancakes. And toasted cheese sandwiches." [CF3]
  - "I tried to feed one with my hand. He didn't like it." [CF4]
  - "You are sharing the same space [with the crows]. I try to blend in with them."[CF4]
  - "He's up there. He is the only one that just hangs out. He hasn't talked to me yet. I see him. He sees me. We talk. I say, 'OK.'" [CF1]

- *Crow Friend-Crow Communication*

  - "I take it as my friend. He wants to acknowledge me. He does it in this tiny voice. Usually he initiates the conversation. …We go back and forth. He shows me his inner eyelid. Looks like his eye is flashing white." [CF1]
  - "There was a three-way thing going on between Kau, me and a robin. I can't believe how aggressive robins are. He starts talking to me, like about the robin." [CF1]
  - "It's so soft. It's such an intimate little noise [which he makes to me]. Can you see why it makes me so fond of him?" [CF1]
  - "I just like the recognition. They treat me like I'm a special person. … I felt he was protecting me, that I belonged to him." [CF8]
  - "One time he followed me for a couple of blocks." [CF1]

2.3.3.2 Crow Observers

The Crow Observer differs modestly from the Crow Friend in that the former is less personally involved in interspecific communication with crows than is the latter. Our Crow Observers respected the autonomy of crows and specifically did not want to foster friendships in which one actor was a subordinate, a family member or dependent, a pet, or a kind of property. Instead, our Crow Observers wanted to be physically close to crows and they prefer to interact with crows in a relatively unobtrusive and passive way. With these priorities, crow observers are neither bound, nor benefit by the responsibilities and social obligations associated with friendships.

Of the two Crow Observers in our sample, one showed a kind of scientific curiosity in the life of crows. The second Crow Observer was less interested in studying crows and more motivated to simply provide food as an element in an ecological system.

The Crow Observer values the food provision function he or she plays in sustaining crow well-being, but is not interested in crows understanding his or her psychological condition or personal opinions, insights, and suggestions. The Crow

Observer is useful to crows because the observer provides food on a regular basis. But the Crow Observer does not care if the crow comprehends his or her humanity or even if the crow can distinguish him or her from a mechanical crow feeder.

As with Crow Friends, the two Crow Observers in our sample were seen to have overlapping styles of interspecific communication. For the Crow Observer, there is satisfaction in attracting and feeding crows, but there is no interest in teaching crows something new, in sharing feelings with crows, or in developing friendships with crows. The Crow Observer, compared to the Crow Friend, interacts with crows from a detached posture. The Crow Observer is comfortable with the knowledge that crows, in their biology and sociology, are not of the human species. Crows are interesting to Crow Observers for representing an Other which is—at this point in time—not entirely understood and perhaps never entirely knowable.

Direct quotations from our field notes illustrate the respect Crow Observers have for crows and their disinclination to anthropomorphize:

- *Crow Observer Detachment*
  - "They all look alike to me. I used to name them." [CF6]
  - "I am the agency of food." [CF5]
- *Crow Observer Motivation*
  - "I make it my business to stay the hell out of their business. I just supply the goodies and get out of the way." [CF5]
  - "I am most happy when they all come in, when the lawn is black. I hate waste. I like to watch their interaction. I like to see what they do. … Crows want a minimum to do with humans." [CF5]
  - "It's symbiotic. [The opportunity] give me insight into how they react. To me, it's fair trade. … I imagine that they are happy because I'm doing something for them. … I'm helping them. If they could smile, they would." [CF6]
- *Crow Observer Tactics*
  - "I feed crows all sorts of stuff. Catfood, table scraps including chicken carcasses." [CF5]
  - "[A feeding tactic] and something I have been toying with [is offering] peanuts in a bag. They can't figure it out." [CF6]
- *Crow Observer Observations*
  - "Crows have what I would call a convocation. They all come together, for a half an hour or more. It's like they're coming together and discussing things. Sometimes it is like they are choosing sides." [CF5]
  - "[When they congregate] they are not vulnerable. It's like they are a team. Unfortunately, they are noisy. [For my neighbors] they are flying rats." [CF6]

2.4 Coupled Relationship Between Crows and Crow Feeders

The behaviors of crows associated with anticipation of a reward, including waiting for crow feeders where feeding occurred, moving ahead of feeders to the next stop on a feeding route, and peering into structures occupied by the crow feeder are consistent with conditioned responses to learned associations. Much as Pavlov's dog responded to the sound of a bell, crows responded to the sight of a reliable feeder. These conspicuous crow behaviors, especially waiting, following, and looking for the feeder, were recognized and responded to by the crow feeders.

This set up a strong feedback loop, which shaped this example of interspecific communication. As crows learned to recognize individual crow feeders and behave differently toward them relative to other humans, the crow feeders became more responsive often exaggerating some of their feeding motions and staying near the crows to closely observe them. The ability of crow feeders to lock gaze with the crows they fed is especially remarkable, given the tendency of crows to quickly flee from gazing humans (Clucas et al. 2013).

While crows and crow feeders appear responsive to each other's subtle signals, what we observed is far short of the ritualized and symbolic communication that has been documented between honeyguides and Boran people or between dolphins and Brazilian fishers. We suggest that the crow and crow feeder communication is an early stage in the evolution of interspecific communication. Currently only a few humans are crow feeders and they employ a variety of signals to make their intentions known to crows. The ability of crows to understand the signals given by crow feeders may easily spread among local crow populations by social learning, just as does information about the identity and habits of dangerous humans (Cornell et al. 2012). However, there is little opportunity and even less apparent desire for humans living near crow feeders to learn the local crow feeding signals. As such, the crow-crow feeder relationships we observed were restricted to a few people and the crows that resided nearby. Without a consumptive benefit to humans, such as the food provided by communicating with honey guides or dolphins, the next stage of a universally recognized semiotic system appears unlikely to develop across species.

3 Viewing Interspecific Communication as a Strategic Engagement

Interspecific communication involving humans and social, sentient animals may best be understood by considering more than simply the signals involved. Complex and varied motivations, adjustments, and history of the participants can shape communication. As these species are typically long-lived, we would also expect dialogues to change through time and be quite individualistic. To conceptualize more fully this sort of interaction, we thought it useful to consider communication as a part of a strategic engagement.

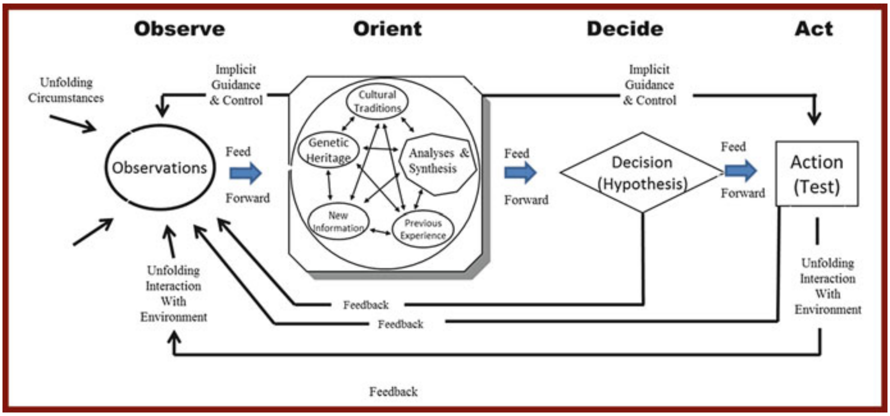


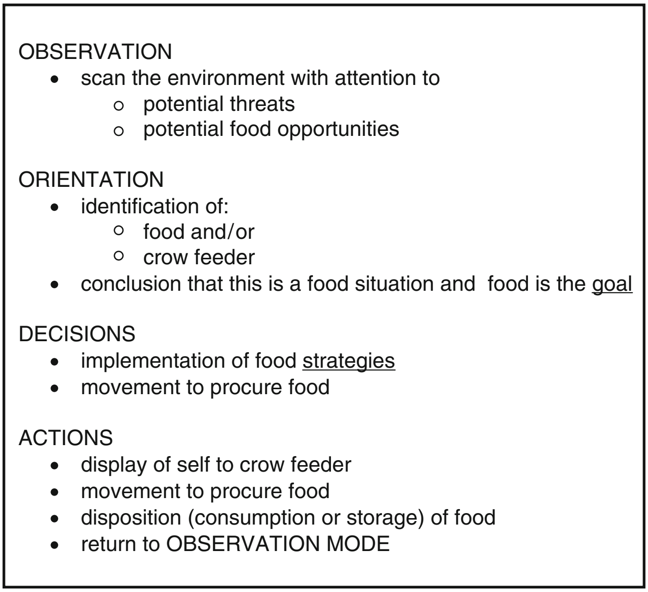
Fig. 11.3 Dynamics within and among the four major components of the OODA loop. *Arrows* illustrate feedbacks and iterations in the process of OODA loop reasoning (Adapted from a 1995 oral briefing by Col. J. Boyd)

In the 1990s, the writings of retired Air Force Colonel John R. Boyd—which provided the foundation for Warfighting, the official doctrine of the United States Marine Corps (1994)—developed a framework which emphasized an iterative and fractal sequence of reasonings broken into the phases of Observation, Orientation, Decision, and Action (Boyd 1996). The OODA Loop, as the framework was called (Fig. 11.3), has inspired command and control analysts, and warfare strategists of many nations (Fadok 1995; Schechtman 1996; Fairweather 2004; Osinga 2005; Ford 2010). In recent years, OODA loops have diffused to shape decisions by academics and practitioners interested in business (Bower and Hout 1998; Ullman 2005; Box et al. 2007; Fingar 2011).

In the Observation phase, the actor surveys the environment, ready to concentrate attention on phenomena which could influence—positively or negatively—the very short-term survival of the actor. In the Orientation phase, the actor sharpens the analytical focus in determining the qualitative nature of the situation at hand. This results in a conclusion as to whether actor survival is likely to be enhanced or degraded by the situation. In the Decision phase, the actor commits to a general goal. Finally, in the Action phase, the actor implements strategies and tactics to achieve the general goal and supporting objectives.

It is important to point out that the negotiation of an OODA loop is not a linear (that is, rigidly sequential) undertaking. Rather, OODA loops are flexible structures characterized by feedback branches. OODA loops also demonstrate a fractal aspect in that there are OODA loops nested within OODA loops.

OODA loops help actors achieve their goals in the context of uncertainties associated with threats and opportunities. In our research, we have found that engagements of crows and crow feeders can be modeled with OODA loops. An understanding of



OBSERVATION
- scan the environment with attention to
    - potential threats
    - potential food opportunities

ORIENTATION
- identification of:
    - food and/or
    - crow feeder
- conclusion that this is a food situation and food is the goal

DECISIONS
- implementation of food strategies
- movement to procure food

ACTIONS
- display of self to crow feeder
- movement to procure food
- disposition (consumption or storage) of food
- return to OBSERVATION MODE

Fig. 11.4 Key activities within the four major components of the crow OODA loop

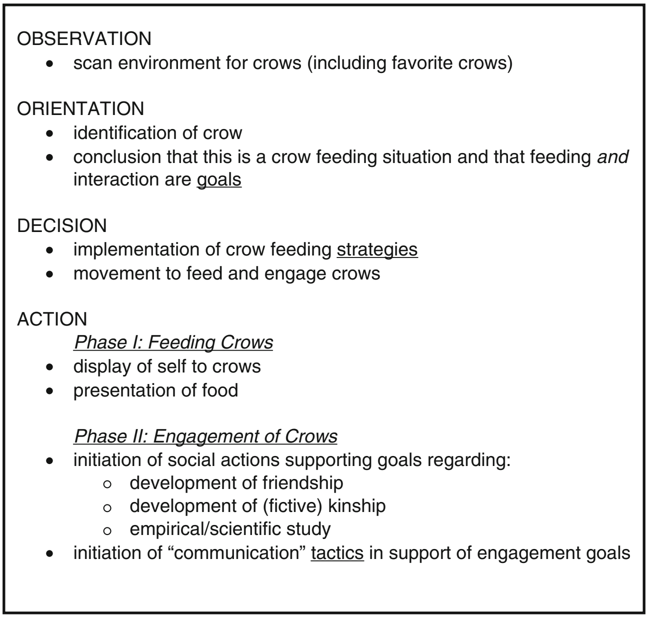
crows and crow feeders begins with a specification of how the crow OODA loop “fits” (or fails to “fit”) with the OODA loop of crow feeders.

3.1 The Crow OODA Loop

A conceptualization of the basic crow OODA loop is depicted in Fig. 11.4. We show that crows daily face the challenge of finding and obtaining food without falling victim to threats, which abound in the environment. Behaving in ways coded by the OODA loop framework, crows must identify food (and crow feeder attractors), determine that the goal of pursuing food is warranted, procure and eat or store food, and then again adopt a mode of search and observation.

3.2 The Crow Feeder OODA Loop

A conceptualization of the crow feeder OODA loop is shown in Fig. 11.5. For crow feeders the goal of successfully feeding a crow is often augmented with a goal of interacting further with crows. Feeding crows, then, can function as a means to



OBSERVATION
- scan environment for crows (including favorite crows)

ORIENTATION
- identification of crow
- conclusion that this is a crow feeding situation and that feeding *and* interaction are goals

DECISION
- implementation of crow feeding strategies
- movement to feed and engage crows

ACTION

Phase I: Feeding Crows
- display of self to crows
- presentation of food

Phase II: Engagement of Crows
- initiation of social actions supporting goals regarding:
  - development of friendship
  - development of (fictive) kinship
  - empirical/scientific study
- initiation of “communication” tactics in support of engagement goals

Fig. 11.5 Key activities within the four major components of the crow feeder OODA loop

another end such as the creation of opportunities to study crows, to develop “friendships” with crows, to help to wounded crows, and so forth.

3.3 Critical Moments in Cross-Species OODA Interactions

Inspection of Figs. 11.4 and 11.5 show that crows and crow feeders are not quite engaged in a competition or a conflict (as with fighter pilots and business firms), nor are they quite seen as engaged in a cooperation (as with humans working with other humans). At one level, it is true that both parties benefit from the interaction, yet this *mutualism* is interpreted as such by the analyst and not necessarily by the actors.

We can talk to crow feeders and ask what goals they have and what kinds of satisfactions are motivations. If, for example, a crow feeder reports that she considers a crow as a friend, or even as a fictive family member, we can understand motivation as based on the value of friendships and kinship.

But, we cannot yet know all of what the crow thinks. Certainly, the crow must be satisfied with the food, but what does the crow make of the crow feeder? Here it remains an open question whether the crow has distinct feelings for a human crow feeder that it does not hold for an automated machine dispensing food. Brain scanning technology (e.g., Marzluff et al. 2012) could be used to test for such differences.

With this in mind, we note that a particularly critical moment in the OODA loop interaction of crows and crow feeders is the time immediately following the successful procurement of food by the crow. It is at this time the crow feeder hopes that the second goal of engagement can be realized. And it also is in these moments that crows have a window of time—which is similar to the times crows have been documented to play—in which they can perhaps consider experimenting with social relationships with the crow feeders. These moments may be characterized as moments of incipient communication where communication is defined as relatively shared and common understandings by the crow and the crow feeder about mutualistic outcomes of the interaction.

4 A Way Forward in the Study of Interspecific Semiotics

In this chapter, we have reported on a pilot study of crows and crow feeders. We have introduced a variety of concepts, literatures, and frameworks that we believe are promising and not regularly considered by ethologists. Looking ahead, we now make several suggestions regarding the ways in which interspecific semiotic investigations might be usefully structured.

First, we strongly encourage interdisciplinary research. This will allow the complexity of each species to be evenly examined. Our collaboration of a natural and social scientist enabled critical investigation of both crows and humans. While either perspective alone may unravel the basic of communication between these species, our simultaneous observation of humans and crows interacting stimulated interdisciplinary discussion and informed evaluation of distinct literatures particular to each perspective. Investigation of the human motives and rewards while interacting with humans would be incomplete without a strong social science perspective.

Second, we promote research which examines not only the biological and cultural components of biosemiotic systems, but the genetic components as well. Such a focus permits understanding not only of structures and process in the short-term (for example, over a few generations), but of the evolutionary change. We have not considered the long-term affects of prolonged crow-human interactions here, but future studies that compared communication between these species in places where interactions have been ongoing for millennia (as opposed to decades in our area) would be interesting.

Third, we advocate the study of variation in semiotic interactions in order to reveal the possible evolution of the most extreme forms. In our work, this fostered a general discussion of how our crow semiotics fits in with dolphin/human or honeyguide/human semiotics. We note that the point in our case is that the human is not getting a direct food benefit out of participating; what the crow feeder gets out of the interaction is much more complex than mere nutrition and ranges from serious leisure to other benefits.

Finally, we encourage interdisciplinary researchers to consider the real-world implications of their research design and findings. Species selected for semiotic study often have practical value (food source, income source, basic science resource), but other values are also important to society. Rare and endangered species bring into play environmental justice and ethical values. Charismatic and sublime species—as well as those which are notably unattractive—raise matters of environmental aesthetics.

Acknowledgments We express our gratitude to the crow feeders who participated in our pilot study. Their hospitality greatly facilitated our work. We greatly benefitted from their insights, speculations, and questions about the lives of crows. We thank Anne Clark, who many years ago suggested that we look closely at the behavior of people who regularly interact with crows.

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Chapter 12
Interspecies Communication with Grey Parrots: A Tool for Examining Cognitive Processing

Irene M. Pepperberg

Abstract For over 35 years, I have examined Grey parrot cognition via a modeling technique, whereby birds are trained to use elements of English speech referentially, so they can be questioned vocally, much like young children. The oldest bird, Alex, labeled >50 objects, seven colors, five shapes, quantities to eight, three categories (color, shape, material) and used "no," "come here," "wanna go X," and "want Y" (X, Y being appropriate location or item labels) intentionally. He combined labels to identify, request, comment on, or refuse >150 items and to alter his environment. He understood concepts of category, relative size, quantity, presence or absence of similarity/difference in attributes, showed label comprehension and a zero-like concept; he demonstrated some understanding of phonological awareness and a numerical competence more like that of young children than other nonhumans. He could be queried about optical illusions in ways directly comparable to humans. Younger birds are acquiring similar competence.

1 Introduction

Many studies have aimed to establish symbolic interspecies communication. The best-known primarily used nonhuman primates and marine mammals (e.g., Gardner and Gardner 1969; Kellogg 1968; Miles 1978; Premack 1976; Richards et al. 1984; Rumbaugh 1977). Of these, Premack seemed most interested in using this communication system as a means to examine nonhuman cognitive processing, as suggested by Griffin (1976). The idea of replicating such studies with an avian subject such as a Grey parrot, a species evolutionarily far-removed from humans and with a brain the size of a shelled walnut, was initially met with skepticism (Pepperberg 1999, 2012b). Not only were parrots considered mindless mimics (e.g., Lenneberg 1967)

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but investigators using what were then-standard operant conditioning techniques had already tried and failed to establish any form of symbolic communication with mimetic birds (e.g., Grosslight and Zaynor 1967; Mowrer 1950, 1952, 1954). Furthermore, prior to the 1970s, researchers argued that birds lacked, to any great extent, a cerebral cortex (the so-called mammalian organ of intelligence; e.g., Jerison 1973), had examined few avian species other than pigeons in studies that concentrated primarily on topics such as delayed match-to-sample, and generally agreed that avian abilities were inferior to those of mammals (for a review, see Premack 1978). My rationale for attempting to counter all these objections, my initial choice of subject (the Grey parrot, Alex) and training procedure, have been discussed in detail elsewhere (e.g., Pepperberg 1999, 2012b); my goal in this chapter is to describe (briefly) the techniques that I adapted and developed, and the cognitive abilities of these birds that were consequently uncovered.

2 Training Techniques

2.1 Model/Rival (M/R) Procedures

The primary instructional procedure, described in detail elsewhere (Pepperberg 1981, 1999) and known as model/rival or M/R training, is based primarily on methods developed by Todt (1975) and Bandura (1971). It involves three-way *social* interactions among two humans and a parrot to demonstrate the targeted vocal behavior. The parrot watches and listens as one trainer presents objects and queries the other trainer about them (e.g., "What's here?", "What color?"), giving praise and transferring the named object to the human partner to reward correct answers. Incorrect responses are punished by scolding and temporarily removing items from sight. Thus the second human is both a model for the parrot's responses and its rival for the trainer's attention, and illustrates consequences of errors. The model must try again or talk more clearly if the response was deliberately incorrect or garbled; that is, the model is subject to corrective feedback, which the bird observes. The parrot is included in interactions, being queried and rewarded for successive approximations to correct responses; training is adjusted to its performance level. If a bird is inattentive or accuracy regresses, trainers threaten to leave.

Unlike other modeling procedures (reviewed in Pepperberg and Sherman 2000, 2002), the M/R technique exchanges roles of trainer and model. The parrot thus sees how questioner and respondent interchange roles, and how their interactions result in environmental change. Role reversal also counteracts an earlier methodological problem: birds whose trainers always maintained their respective roles responded only to the human questioner (Todt 1975). Here, birds respond to, interact with, and learn from any human.

To ensure the closest possible link between labels or concepts to be learned and their appropriate referent, M/R training uses only *intrinsic reinforcers*: Reward for uttering "X" is X, the object to which the label or concept refers. Earlier unsuccessful attempts to teach birds to communicate with humans used *extrinsic* rewards: a single food neither relating to, nor varying with, the label or concept being taught (see Pepperberg 1999). This procedure delayed label and concept acquisition by confounding the label of the targeted exemplar or concept with that of the food reward. Initial use of labels as requests also demonstrates that uttering labels has functionality; later, birds learned "I want X," to separate requesting and labeling (Pepperberg 1988a) and to enable them to request preferred rewards while learning labels for items of little interest.

Notably, in subsequent studies with additional birds, use of techniques that eliminated aspects of M/R training—reference, functionality, or various levels of social interaction (i.e., omitting joint attention of humans and bird on the targeted item, or using a single trainer)—failed to engender symbolic communication. Thus, when birds were exposed to audiotapes, videotapes (with and without human co-viewers, with and without live feeds), one model with various levels of interaction, or the use of Alex as a semicompetent model (i.e., as one who, at the time, could not exchange roles and act as questioner), they failed to acquire referential labels but learned labels taught simultaneously during standard M/R training (see Pepperberg 1994b, 1999, 2012b; Pepperberg and McLaughlin 1996; Pepperberg et al. 1998, 1999, 2000) (NB: Alex did eventually learn to exchange roles fully, and thereby helped train a younger bird, Griffin).

2.2 Indirect Training Procedures

My Grey parrots also actively engaged in learning outside of formal training. Students and I tracked one such form of Alex's learning, sound play (Pepperberg et al. 1991), in which he derived novel targeted speech patterns from existing ones. He seemed able to separate specific phonemes from the speech flow *and* produce them so as to facilitate production of upcoming phonemes ("anticipatory co-articulation"; Patterson and Pepperberg 1994). In humans, these abilities are taken as evidence for top-down processing (Ladefoged 1982), necessary for segmentation and phonological awareness (see later). He also practiced some utterances privately, specifically those completely-formed new labels or entire phrases that materialized after minimal training and without practice in his trainers' presence (Pepperberg et al. 1991). After learning to produce questions, he occasionally learned labels by asking us about the color, shape, or material of objects in his environment (Pepperberg 1999). He also often produced new vocalizations in the presence of trainers by recombining existing label parts, notably in their corresponding orders (Pepperberg 1990b). When we *referentially mapped* these spontaneous utterances—providing relevant objects to which they could refer—Alex rapidly integrated these labels into his repertoire. After acquiring "grey," for example (by asking "What color?" to his mirror image), he produced sound variants (e.g., "grape," "grate," "grain," "chain") that we mapped to appropriate referents (respectively, fruit, a nutmeg grater, seeds, a paper-clip ring; see Pepperberg 1990b, 1999). In contrast, he abandoned sounds whose combinations we couldn't map (e.g., "shane," "cheenut"), or for which mapped referents weren't of interest (e.g., dried banana chips used for "banacker"; Pepperberg 1990b). Thus, our bird's spontaneous utterances that initially lacked communicative, symbolic value could, as they do for children, acquire this value if caretakers interpreted them as such (Pepperberg 1990b). Alex and younger birds might also use a familiar label in a novel instance (e.g., Arthur, stating "wool", trained to a woolen pompon, as he pulled at a trainer's sweater, or Alex calling a piece of popcorn "paper"), learning either by approbation or by our providing instead an appropriate label (Pepperberg 1999).

3 Results

Using these techniques, Alex acquired significant symbolic communication. His early capacities are summarized fairly briefly, having been published elsewhere (e.g., Pepperberg 1999, 2012b); I discuss his and the younger bird, Griffin's, more recent data in somewhat greater detail.

3.1 Alex's Use of Labels

Alex acquired labels for over 50 objects, seven colors and six different shapes ("X-corner"); he used English number labels to distinguish quantities of objects, including collections of novel items, heterogeneous sets of objects, and sets in which items were placed in random arrays (see later). He combined vocal labels to identify proficiently, request, refuse, categorize, and quantify over 100 different items, including those varying somewhat from training exemplars. He had functional use of "no" and phrases such as "come here," "want X," and "wanna go Y" (X, Y being appropriate object or location labels). The requests, initially acquired via M/R training (Pepperberg 1988a), were spontaneously extended to any newly acquired labels. Requests were also intentional (Pepperberg 1987c, 1988a): If trainers responded incorrectly (e.g., substituting alternative items), he generally said "no" (86 % of the time), often coupling his refusal with a repetition of the initial request. His accuracy averaged ~80 % on tests of these abilities (for details and statistics, see Pepperberg 1981, 1987b, 1988a, 1994a, 1999).

3.2 Comprehension of Categories/Categorical Labels

Alex had a higher-order, hierarchical understanding of class concepts (Pepperberg 1983, 1996): he learned that various sets of responses—each of his color, shape, material, or object labels—could be subsumed under specific, different category labels, and that the labels for these categories had no intrinsic connection to the individual labels constituting the categories. He therefore could, depending on the question, describe the same item with respect to different categories (e.g., "What matter?": "wood"; "What color?": "green"; "What shape?": "4-corner"; "What toy?": "block").

3.3 Concepts of Same-Different

Understanding the concept of same/different requires more than learning match-to-sample or oddity-from-sample, identity or non-identity, or determining homogeneity versus nonhomogeneity; it requires understanding abstract relationships—ones that, although dependent upon absolute, perceptual qualities (e.g., color, shape), can be abstracted across any domain (Premack 1978, 1983). The subject must understand, for example, that the *same* relationship holds between the *different* pairs A-B and C-D, where A and B could be different colors and C and D could be different sounds. Such understanding also requires use of arbitrary *symbols* to represent *relationships* of sameness and difference between sets of objects *and* the ability to denote the attribute that is same or different (Premack 1983). Alex did learn abstract concepts of same/different. After M/R training to respond to queries of "What's same/different?" to a small subset of item pairs with the appropriate *category* label, he could respond appropriately to any two other objects that might vary with respect to all possible attributes of color, shape, and material, including objects/colors/shapes he could not label (Pepperberg 1987a). Notably, his responses were still above chance when, for example, the question "What's same?" was posed with respect to a green wooden triangle and a blue wooden triangle. If he had ignored the question and responded on the basis of prior training, he would have determined, and produced the label for, the one anomalous attribute (in this case, color). Instead, he responded with one of the two appropriate answers (i.e., shape or matter; Pepperberg 1987a).

3.4 Understanding Absence

Understanding absence relies on recognizing a discrepancy between the expected and actual state of affairs (e.g., Hearst 1984; Skinner 1957) and actively *reporting* the situation, not simply learning to avoid stimuli leading to absence of reward (e.g., Astley and Wasserman 1992). It may involve symbolic communication: Bloom (1970), for example, suggests that verbal production of terms relating to nonexistence is needed before an organism can be considered to have acquired the concept.

Alex was tested on his concept of absence in the context of same/different (Pepperberg 1988b). After training to respond "none" to an absence of similarity and difference for a small subset of, respectively, totally different or identical item pairs, he replied appropriately for a large variety of novel object pairs for which responses could now be "color," "shape," "matter," or "none." As before, objects could be items or have attributes he could not label.

3.5 Relative Size

Relational concepts are difficult: By definition, the basis for relative categorization changes constantly—what is the darker or smaller or heavier choice in one trial can be the brighter, bigger, or lighter exemplar in the next; choices based on specific, absolute criteria would be erroneous. Alex did succeed on this task. After M/R training on "What color bigger/smaller?" with a limited set of colors and objects, he was tested on a variety of familiar and unfamiliar items (Pepperberg and Brezinsky 1991). He transferred to objects of novel shapes, sizes, and colors not used in training, and that he often could not label. He also, *without training*, indicated when exemplars did not differ in size by responding "none," and answered questions based on object material as well as color (Pepperberg and Brezinsky 1991). Thus he was not limited to responding within a single dimension, was attending to our questions, and transferred information learned in one domain ("none" from the same/different study) to another. Such ability to transfer is a mark of complex cognitive processing (see Rozin 1976).

3.6 Comprehension of Vocalizations

Despite Alex's demonstrated label production and question comprehension, he had never specifically been tested on comprehension of individual labels. Some "language"-trained apes had demonstrated differences in production versus comprehension (note Savage-Rumbaugh 1986). Thus Alex was also tested. In this iterative task (see Granier-Deferre and Kodratoff 1986; Pepperberg 1990a), a subject is given one of several different possible queries or commands concerning the attributes of several different items shown simultaneously. Each query or command contains several parts, the combination of which uniquely specifies which item is targeted and what action is to be performed. Question complexity is determined by context (number of different possible items from which to choose) and the number of its parts (e.g., number of attributes used to specify the target and number of actions from which to choose). The subject must divide the question into these parts and (iteratively) use its understanding of each part to answer correctly. The subject demonstrates competence by reporting on only a single aspect (e.g., color, shape, or material) of, or performing one of several possible actions (fetching, touching) on, an object that is one of several differently colored and shaped exemplars of various materials. Alex was shown trays of seven unique combinations of exemplars and asked “What color is object-X?” “What shape is object-Y?” “What object is color-A?” or “What object is shape-B?” (Pepperberg 1990a). His accuracy on label comprehension was equal to that of production and comparable to that of marine mammals tested on similar tasks (dolphins, Herman 1987; sea lions, Schusterman and Gisiner 1988).

Alex also succeeded when a conjunctive condition was added (Pepperberg 1992). Here he was again shown a 7-member collection but was now asked to provide information about the specific instance of one category of an item that was uniquely defined by the conjunction of two other categories, for example, “What object is color-A *and* shape-B?” Other objects on the tray exemplified one, but not both, these defining categories. His accuracy, again comparable to those of marine mammals (Herman 1987; Schusterman and Gisiner 1988), indicated that he understood all elements in the question. The implications, that truly advanced cognitive process are involved, are discussed fully in Pepperberg (1999). (NB: Herman (1987) claimed that this task is recursive and thus demonstrated not only label comprehension but also linguistic competence—i.e., an understanding of embedded clauses with layered, hierarchical meaning. Premack (1986) argued, correctly, that the task is merely iterative. Following Herman, I used the term *recursive* in Pepperberg (1992), but did not make claims of linguistic abilities.)

3.7 Phonological Awareness

Alex’s sound play (see earlier) showed spontaneous combination of parts of existent labels to create new ones; was he also capable of true segmentation—understanding that his existent labels are comprised of individual sound units (phonemes, morphemes) that can be *intentionally* recombined in novel ways to create novel vocalizations? Such behavior would also imply some level phonological awareness (*sensu* Anthony and Francis 2005). Segmentation is not only considered basic to human language development (Carroll et al. 2003), but also a uniquely human trait by some researchers (e.g., Lenneberg 1967). Little evidence exists for such behavior in any nonhuman, including those taught elements of human communication systems (reviewed in Pepperberg 2007).

To determine what Alex might learn about morphemes and phonemes, he had received M/R training to associate the wooden or plastic graphemes B, CH, I, K, N, OR, S, SH, T with their corresponding appropriate phonological sounds (e.g., /bi/ for BI); the graphemes, which he would chew, were his reward. Although his accuracy was above chance ($p < 0.01$, chance of 1/9), it was never high enough (i.e., ~80 %) to claim he had mastered the task. Nevertheless, he demonstrated unexpected abilities with respect to sounds and labels after our youngest bird, Arthur, had acquired the label “spool” to refer to plastic and wooden bobbins.

Unlike Arthur, who used a whistle-like sound for the first part of the label (sonagrams in Pepperberg 2007) and unlike his usual form of acquisition (Patterson and Pepperberg 1994), Alex began by using a combination of existing phonemes and labels to identify the object: /s/ (trained independently in conjunction with the physical letter, S) and wool, to form “s” (pause) “wool” (“s-wool”;/s-pause-wUl/; figure 2 in Pepperberg 2007). The pause seemingly provided space for the absent (and difficult) /p/ (see Leonard 2001; Peters 2001). Note that Alex knew no labels containing /sp/, nor did he know “pool” or “pull,” or any other label that included /Ul/; he did know “paper,” “peach,” “parrot,” “pick,” and so forth, producing a viable /p/ via a form of esophageal speech (Patterson and Pepperberg 1998); /sp/ may have been even more difficult. He knew /u/ from labels such as “two” and “blue” (Pepperberg 1999, 2007). He retained this “s-wool” formulation for almost a year of M/R training, although normally only about 20–25 M/R sessions (at most, several weeks of training) were sufficient for learning a new label (Pepperberg 1999).

At the end of this year-long period, Alex spontaneously produced “spool,” perfectly formed (/spul/; see figure 3, in Pepperberg 2007). Thus, Alex added the sound—which humans heard, sonagraphically viewed, and transcribed, as—/p/ and also shifted the vowel toward the appropriate /u/. His utterance sounded distinctly human, differed from Arthur’s whistled version, and clearly resembled mine (Pepperberg 2007), although students had performed 90 % of the training.

Alex exhibited a similar pattern for “seven” (first in reference to the Arabic numeral, then to an object set; see later). His first production of the label could best be described as “s…..n”, a bracketing using the phonemes /s/ and /n/; he then quickly progressed to “s-one” (Pepperberg 2009; /s/-pause-/wən/) which looked sonagraphically quite different from my “seven,” but followed the form of “s-pause-wool.” Eventually, “s-one” became “sebun,” much closer to my “seven” (Pepperberg 2009).

Alex’s data demonstrate a functional understanding that his existent labels were comprised of individual units that could intentionally be recombined in novel ways to create referential, novel vocalizations (Pepperberg 2007, 2009). His combinatorial rule system was relatively limited, but was exceptional for a nonhuman.

3.8 Numerical Concepts

Alex also learned various numerical concepts over the course of many studies. The original question was whether he could learn a symbolic representation for exact quantity comparable to that of young children. The work actually took several decades, because the task has multitude components. Not only must nonnumerical perceptual mechanisms (e.g., contour, density, mass) be ruled out, but many other issues also must be addressed.

3.8.1 Initial Concepts: Basic Quantities, Simple Heterogeneous Sets

Alex would first have to learn that a new set of labels, “one,” “two,” “three,” etc. represented a novel classification strategy—one based on both physical similarity within a group and a group’s quantity, rather than solely by physical characteristics of group members (i.e., a set of “three” keys, no matter what kind). Unlike children, he was not trained in an ordinal manner but first learned to label sets of three and four, then five and two, then six and one (Pepperberg 1987b, 1994a). He was trained this way for two reasons. First, when number studies began, he knew "three" and "four" from his shape training ("three-corner" for a triangle, "four-corner" for a square), so that beginning with those numbers and existent vocal labels made practical sense. Second, lack of training in an ordinal manner was planned to avoid giving any cue that could be obtained by a number line; the initial goal was to ensure that only a direct connection existed between the number label and the appropriate set (Pepperberg 1987b).

Alex did indeed learn to label small sets of familiar different physical items, up to six, exactly (Pepperberg 1987b); his error patterns did not show a peak near the correct responses, which would have suggested only a general sense of quantity ("approximate number system"). Rather, his most common errors across all sets was to label just the object involved—to respond, for example, "key" rather than "four key." We could not however claim that Alex was "counting", because we could not yet show he understood the counting principles as would a child: that a stable symbolic list of numerals exists, numerals must be applied to individuals in a set to be enumerated in order, they must be applied in 1:1 correspondence, that the last numeral reached in a count represents the cardinal value of the set, and that each numeral represents one more than the previous numeral (Carey 2004; Fuson 1988; Gelman and Gallistel 1978; Mix et al. 2002; Pepperberg 1999). Nevertheless, items that Alex quantified need not have been familiar, nor been arranged in any particular pattern, such as a square or triangle; he maintained an accuracy of about 75–80 % on novel items in random arrays.

Moreover, if presented with simple heterogeneous sets—a mixture of X's and Y's, different exemplars of various sizes and of both familiar and novel textures and materials (e.g., corks and metal keys) often presented by simply tossing them in random arrays on a tray—he responded appropriately to "How many X?" "How many Y?" *or* "How many toy?" (Pepperberg 1987b). The design ruled out cues such as mass, brightness, surface area, odor, object familiarity, or canonical pattern recognition (Pepperberg 1987b, 1999). Alex was more advanced than some children, who, if they, like Alex, have been taught to label homogeneous sets exclusively, usually label the total number of items when asked about subsets in a heterogeneous set (see Greeno et al. 1984; Siegel 1982). These tests did not, however, determine if Alex had, for the smallest collections, used a noncounting strategy such as subitizing—a perceptual mechanism that enables humans to quickly quantify sets up to ~4 without counting—or, for the larger collections, a strategy of "clumping" or "chunking"—a form of subitizing (e.g., perception of six as two groups of three; see von Glasersfeld 1982)—to correctly label quantity without counting. The mechanisms that Alex was using were thus still unspecified.

3.8.2 Complex Heterogeneous Sets

To tease apart subitizing/clumping versus counting, we adapted tasks designed for humans (Trick and Pylyshyn 1989, 1994), who had to enumerate of one set of items embedded within two different types of distractors: (1) white *or* vertical lines among green horizontals; (2) white vertical lines among green vertical *and* white horizontals. Humans subitized for 1–3 in only the first condition, but counted, even for such small quantities, in the second. Subitizing thus fails when items to be quantified are defined by a collection of competing features (e.g., conjunction of color *and* shape; see Pepperberg 1999). Adapting our conjunction study (see earlier), we could ask Alex about the quantity of a similarly defined subset—e.g., how many red blocks in a set of red and blue balls and blocks.

Notably, Alex's accuracy (Pepperberg 1994a) matched human data (Trick and Pylyshyn 1989). His scores could be analyzed for subitizing because a subject with high accuracy on small numbers but lower accuracy for larger ones is likely subitizing small sets and using some other noncounting procedure for larger sets. So, if Alex were, for example, subitizing and clumping, rather than counting, he would make no errors for 1 and 2, few for 3, and more for larger numbers. Sequential canonical analysis, however, showed that errors were random with respect to number of items targeted (see Pepperberg 1994a). In fact, most errors seemed unrelated to numerical competence, but rather involved misinterpreting the defining labels, then correctly quantifying the incorrectly targeted subset: Eight of his nine errors were the correct number for an alternative subset (e.g., the number of blue rather than red keys). In those cases, the quantity of the designated set usually differed from that of the labeled set by two or more items, demonstrating that Alex's response was not simply a close approximation to the correct number label (Pepperberg 1994a). However, if Alex's perceptual capacities were more sophisticated than those of humans, the data, although impressive with respect to exact number, still would not justify claiming that he was counting.

3.8.3 Number Comprehension

Alex clearly labeled numerical sets, but had not been tested on number label comprehension. The issue is important, because young children who can label sets may still not comprehend the exact meaning of the number labels (Wynn 1990). He was thus tested with a variation of the previous task involving simultaneous presentation of several quantities, of 1–6, of different items—for example, X red cork, Y yellow cork, Z green cork, or X red paper, Y red wood, and Z red cork; queries were of the type, respectively, "What color Z?" or "What matter X?" (Pepperberg and Gordon 2005). Success required him to comprehend the auditorially presented numeral label (e.g., X = "six") and use its meaning to direct a search for the exact cardinal amount specified by that label (e.g., six things). Controls again eliminated issues of contour, mass, etc. Each query also retested his ability to identify the item or color of the set specified by the numerical label. To respond correctly, he had to errorlessly process all types of information. Some or all of this behavior likely occurred as separate steps, each adding to task complexity (Premack 1983). Our tests showed that, unlike young children (up to ~3 years old) described earlier, Alex understood the meaning of his number labels (accuracy close to 90 %, Pepperberg and

Gordon 2005). Most of his errors seemed to be a consequence of color perception or phonological confusion, not numerical misunderstanding.

3.8.4 A Zero-Like Concept

During the comprehension study, Alex spontaneously transferred use of "none," learned during the same/different task with respect to attributes (see earlier, Pepperberg 1988b) and spontaneously transferred to relative size (see earlier, Pepperberg and Brezinsky 1991), to the absence of a set of a particular quantity—a zero-like concept. On one query, when asked "What color three?" to a set of two, three, and six objects, Alex replied "five"; the questioner asked twice more, each time Alex replied "five." Finally, the questioner said "OK, Alex, tell me, what color five?", to which he immediately responded "none." He had never been taught about absence of quantity nor to respond to absence of an exemplar. Notably, Alex not only provided a correct, novel response, but had also manipulated the trainer into asking the question he apparently wished to answer (Pepperberg and Gordon 2005). He also correctly answered additional queries about absent sets, showing that his behavior was intentional and meaningful. Unlike chimpanzees, for example Ai, who had to be trained on the label "zero" (Biro and Matsuzawa 2001), Alex's use of "none" was spontaneous. Still, he might not have understood the concept of *zero* at the same level as do humans.

3.8.5 Addition of Small Quantities

Study of addition was based on that of Boysen and Berntson (1989) with chimpanzees, and used to examine further Alex's understanding of zero (Pepperberg 2006a). The only nonhuman to demonstrate true addition—the summation of two or more separate quantities *and* exact symbolical labeling of the sum—had been Boysen and Berntson's chimpanzee, Sheba; quantity, however, never totaled more than four. Other studies (summarized in Pepperberg 2012b) had important procedural differences so that no information was obtained on whether their subjects had "…a digital or discrete representation of numbers" (Dehaene 1997, p. 27).

Alex was shown a tray on which two small, upside down cups had been placed, each holding items such as randomly shaped nut or cracker pieces, or differently sized jelly beans. We occasionally used identical candy hearts to see if accuracy was higher when mass/contour cues were available. The experimenter brought the tray to Alex's face, lifted the left cup, showed what was under the cup for 2–3 s in initial trials, replaced the cup over the quantity, then replicated the procedure for the right cup. For reasons described later, in the last third of the experiment, Alex had ~10 s to view items under each cup sequentially before sets were re-covered. The experimenter then made eye contact with Alex, who was asked, vocally, and without any training, to respond to "How many total?" He was also queried with nothing under both cups. No objects were visible during questioning. To respond correctly, Alex had to remember the quantity under each cup, perform some combinatorial process, and then produce a label for the total amount. Appropriate controls were, as usual, in place. When nothing was under both cups, the goal was to see if he would use "none" without instruction (Pepperberg 2006a).

Alex scored above 80 %; identical tokens did not improve accuracy. Interestingly, when given only 2–3 s, he always labeled the 5 + 0 sum as "6"; when given ~10 s, however, his accuracy went to 100 %. Differences in accuracy between the shorter and longer intervals was significant *only* on the 5 + 0 trials. His data are comparable to those of young children (Mix et al. 2002) and more advanced than those of chimpanzees (Boysen and Hallberg 2000). His responses on 5 + 0 trials suggest, although cannot prove, that he actually used a counting strategy for 5: Only when beyond the subitizing range of 4 did he, like humans, need time in order to label the set exactly (details in Pepperberg 2006a). A final addition study showed he could add three sets of small items whose total summed up to eight (Pepperberg 2012a).

Alex failed to state "none" if nothing was under any cup. He refused to respond or said "one." He never said "two", the number of cups (Pepperberg 2006a). His responses of "one" suggests comparisons to the chimpanzee Ai, who confused "one" with "zero." Alex, unlike Ai, was never trained on ordinality (Biro and Matsuzawa 2001) but, like Ai, seemed to grasp that "none" and "one" represented the lower end of the number spectrum. Apparently, Alex's use of "none" was zero-like, but unlike his number labels (Pepperberg 1987b), did not denote a specific numerosity or empty set.

3.8.6 Ordinality and Equivalence

Alex's use of "one" for "none" in the addition study suggested knowledge about an exact number line—i.e., ordinality, which intrinsic to *formal* counting (Fuson 1988; Gelman and Gallistel 1978). To count, an organism must produce a standard sequence of symbolic number tags and know the relationships among and between these tags—i.e., that "two" not only comes before "four" in the sequence but also represents a quantity less than "four." Few animals use numeric symbols; thus symbolic ordinality is difficult to demonstrate. Even for chimpanzees that referentially used Arabic symbols, ordinality did not emerge as it does in children but had to be trained as a separate ability (e.g., Biro and Matsuzawa 2001; Boysen et al. 1993; Matsuzawa et al. 1991). Children learn cardinality for numbers <4 and a sense of "more versus less" while acquiring a meaningless, rote ordinal number series, then associate their knowledge of quantity in the small sets with this number sequence to form 1:1 correspondences that can be extended to larger amounts for both cardinal and ordinal accuracy (e.g., Carey 2004). Children may learn 1:1 associations that suggest full understanding of cardinality before they actually do, but cannot do so for ordinality (e.g., Bruce and Threfall 2004; Teubal and Guberman 2002).

Given Alex's background, might ordinality emerge as with children? A task involving equivalence relations tested this possibility (Pepperberg 2006b). Alex, after learning English labels for Arabic numerals (production and comprehension) in the absence of the physical quantities to which they referred, and without any training on a number line, used the commonality of these English labels to equate quantities (sets of physical objects) and Arabic numerals. He had to identify the *color* of one of a pair of Arabic numerals that was *numerically* (not physically) bigger *or* smaller (he already knew bigger/smaller and "none" for object pairs; see earlier). Thus he deduced that an Arabic symbol had the same numerical value as its *vocal label*, compared *representations* of quantity for which the labels stood, inferred rank ordering based on these representations, then stated the result *orally*. Controls ensured that the task tested number concepts exclusively (Pepperberg 2006b). Alex replied "none" for trials on identical, same-sized numerals of different colors (e.g., 6:6). For queries on differently colored and sized numerals of the same value (e.g., 2:2) he initially responded on a physical basis, but halfway through trials switched to a numerical basis. Mixing Arabic symbols and physical items showed he understood that, for example, one numeral (an Arabic 6) was bigger than four items (or Arabic 2 the same as two items), and cleanly separated mass and number (see Pepperberg 2006b).

Overall, Alex's understanding of symbolic number seemed far closer to that of children than to chimpanzees taught number labels (e.g., Biro and Matsuzawa 2001; Boysen and Hallberg 2000; Boysen et al. 1993; Le Corre et al. 2006; Matsuzawa 2009; Matsuzawa et al. 1991): He understood equivalence relations and inferred ordinality, despite being trained on numbers without respect to their ordinal value, unlike children and even other nonhumans.

3.8.7 Exact Integer System?

Despite all Alex's accomplishments, he, like nonhuman primates and unlike humans, had demonstrated no savings in his previous learning of larger numerals in our early training. Why? Might his issue be difficulty in learning to produce the English labels? To produce any given English utterance, he had to learn to coordinate his syrinx, tracheal muscles, glottis, larynx, tongue height and protrusion, beak opening, and even his esophagus (Patterson and Pepperberg 1994, 1998). Could vocal and conceptual learning be dissociated to test this possibility?

The plan was as follows (Pepperberg and Carey 2012): Alex was taught to identify vocally the Arabic numerals 7 and 8 in the absence of their respective quantities, then was trained that $6<7<8$; tests showed he inferred the relationships among 7 and 8 and his other Arabic labels. Could he then, like children (≥4 years old), *spontaneously* understand that "seven" represented one more physical object than "six," and that "eight" represented two more than "six" and one more than "seven," by labeling appropriate physical sets on first trials? That is, could he induce the cardinal meaning of the labels "seven" and "eight" from their ordinal positions on an implicit count list?

Interestingly, pretraining baseline trials suggested that Alex had some concept of quantity greater than six. When presented with sets of seven, eight, or nine items, he refused to answer on four of six trials. Only when forced to respond (badgered until he finally produced some utterance), did he use the available label ("six") that represented the largest currently trained quantity (Pepperberg and Carey 2012). His behavior suggested that he knew that a standard number answer would not be correct. Furthermore, when asked to provide the color of the (absent) set of six items on trays that held various numbers of differently colored items, including sets of seven and eight, Alex responded “none” on all four trials, but when subsequently asked on two of these trials for colors of smaller sets that were present, to ensure he was attending to the stimuli, he gave the appropriate labels. Thus, he demonstrated an understanding of the exact nature of the representation of his label “six” (Pepperberg and Carey 2012); it did not simply mean “the largest set present.”

Alex did label appropriately, on first trials, novel sets of seven and eight physical items. He, like children, created a representational structure that allowed him to encode the cardinal value expressed by any numeral in his count list (Carey 2004). Acquisition of symbolic communication, therefore, enabled a parrot, a nonhuman whose ancestors separated from the mammalian line ~280 million years ago, to demonstrate numerical competency comparable to children who understand cardinal principles, and in a manner not yet demonstrated by the phylogenetically closer chimpanzee.

3.9 Optical Illusions

The avian brain is anatomically distinct from that of mammals but, at least for birds such as parrots, differs at most quantitatively rather than qualitatively from mammals when processing certain cognitive tasks (see earlier); for tasks that primarily involve visual processing, however, differences may be more striking, as the avian and mammalian visual systems differ in many ways (reviewed in Pepperberg et al. 2008). Various experiments suggested that chickens (e.g., Regolin et al. 2004; Winslow 1933), ring doves (Warden and Baar 1929), pigeons (e.g., Aust and Huber 2006; Fujita et al. 1993; Nakamura et al. 2006), and both starlings and finches (Dücker 1966) perceive various optical illusions; some of these studies, however, involved training subjects to identify stimuli closely related to the eventual target and results often depended on, for example, on statistical averaging of pecking/touching behavior to a limited set of choices (e.g., for amodal completion, between a whole and closely-related partial figure). Results were often highly variable and dependent upon the details of the experimental design (review in Pepperberg et al. 2008; Pepperberg and Nakayama 2012, in prep). Symbolic communication, however enabled testing both Alex and our younger parrot, Griffin, on exactly how they saw the world, and testing them in ways more comparable to those used with humans—by simply asking them what they saw.

3.9.1 Müller-Lyer Illusion

Alex was presented with two-dimensional Müller-Lyer figures (Brentano form) in which the central lines were of contrasting colors. His responses to “What color bigger/smaller?" demonstrated that he saw the standard length illusion in the Müller-Lyer figures in 32 of 50 tests where human observers would also see the illusion and reported the reverse direction only twice. He did not report the illusion when (a) arrows on the shafts were perpendicular to the shafts or closely approached perpendicularity, (b) shafts were six times thicker than the arrows, or (c) after being tested with multiple exposures to conditions that also lessen or eliminate the illusion for human observers (Pepperberg et al. 2008). These data suggest that parrot and human visual systems process the Müller-Lyer figure in analogous ways despite a 175-fold difference in the respective sizes of their brain volumes and visual systems that are markedly different from each other. Because responses to the Müller-Lyer illusion may be a consequence of experience with significant examples of right-angled, parallel-perpendicular intersections (note Segall et al. 1966), something to which a captive born and bred parrot would be subject, we were also interested in a parrot's responses to types of illusions that might be less dependent upon experience in a laboratory.

3.9.2 Subjective Contours: Modal and Amodal Completion

Subjective contours involve ecologically relevant stimuli. Humans often fill in missing parts to facilitate the perception of objects in their environment. Early Gestalt psychologists (e.g., Kanizsa 1955, 1979) described two of the most common forms of this behavior: *amodal completion*, when the object of interest is occluded by some other item (Fig. 12.1a) and *modal completion*, when the object is actually illusory but nevertheless appears to exist (Fig. 12.1b). Many other creatures must experience this problem in their daily lives—'filling in the blanks' (perceptual completion) as a fundamental visual process. For example, processing partial clues about a potential predator and reacting is safer than not, even if some false alarms incur costs. As noted above, however, for most studies on nonhumans, subjects are not merely questioned about what they see, but undergo significant training prior to testing. Our parrot Griffin, however, because he, like Alex before him, knew labels for various colors and shapes based on three-dimensional objects, could simply be asked appropriate questions. Occluded objects were regular polygons (of one- to six-corners) of various colors, occluded mainly by black circles (which Griffin could not label either with respect to color or shape); occasionally occluders were other black polygons. Controls were colored polygons missing appropriate pieces

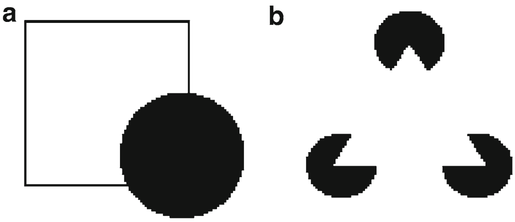

Fig. 12.1 (**a**) Occluded and (**b**) illusory objects

and black occluders appropriately displaced. In order to form illusory objects (again regular polygons of one- to six-corners), we used black 'pacmen' drawn on colored paper. Controls involved placing additional circles or 'pac-men' near the Kanizsa figure so Griffin could not simply quantify black objects. In both cases, Griffin was queried, "What shape X?", where X was the appropriate color of the targeted object. All test stimuli, notably, were two-dimensional. For both sets of objects, Griffin responded correctly with about 80 % accuracy (Pepperberg and Nakayama 2012). Interestingly, he inferred the need to "count" corners only when presented with nonregular polygons that were controls in the occlusion task (i.e., regular polygons with missing pieces). Thus he transferred, without any training, from three-dimensional to two-dimensional stimuli, and performed in a manner that eliminated issues of stimulus generalization or local processing (e.g., basing responses on the familiarity of angular parts of stimuli), which may have occurred for nonhuman subjects having received significant training in previous studies. He was not asked to choose by pecking at a limited number of options, but actually had to state vocally what he observed, based on a repertoire of *all* of his shape labels.

4 Conclusions

Whether acquisition of symbolic representation simply enables a nonhuman to express abilities that are already part of its cognitive "tool kit", or if such training actually alters the ways in which a nonhuman processes information, the results are, on the surface, the same: Data presented in this chapter demonstrate that the use of interspecies communication potentiates the discovery of cognitive abilities in avian subjects—cognitive abilities once thought to be the province of humans or, at most, nonhuman primates (Premack 1978).

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Chapter 13
Singing in Space and Time: The Biology of Birdsong

Marc Naguib and Katharina Riebel

Abstract The variation and complexity of songbird vocalisations is striking, with some birds singing up to 1,000 different song variants. Why do songbirds sing so much and such complex songs? This chapter will provide an overview over how song is controlled and acquired, how and what kind of information is coded in different singing styles and to what features receivers attend to, thereby showing how structure is linked to function. Bird song plays a crucial role in resource defense and mate attraction, allowing us to identify the potential fitness benefits of specific singing traits. Here we review and integrate some of the key contemporary topics such as advances in understanding how early development affects signals and receiver decision rules and how information is signalled in bird communities.

1 Introduction

The melodious beauty and complexity of birdsong is pleasing to our ears, intriguing to naturalists and an important model system for biologists studying animal communication. About half of the bird species are passerines ('true perching birds') with about an estimated 5,000 species of 'true' or oscine songbirds and another 1,000 species in the sister group of suboscines. In all oscine songbirds, which are the focus of this review, the species studied to date show the ability of vocal learning (Catchpole and Slater 2008). Bird vocalisations consist both of songs and calls.

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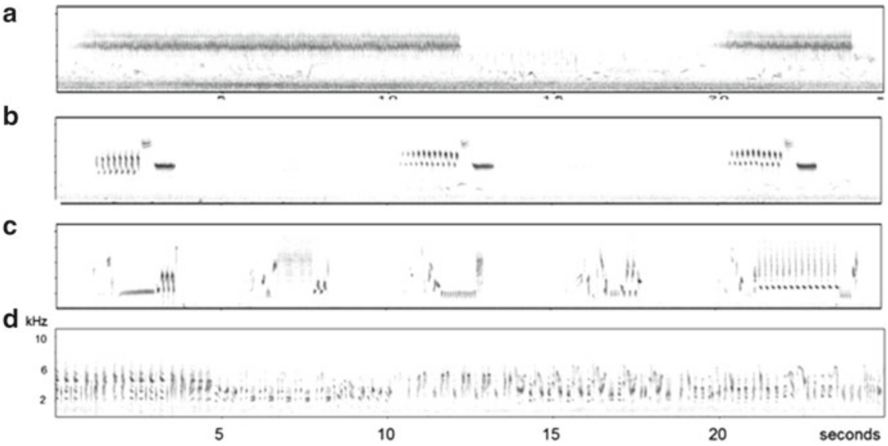

Fig. 13.1 Sound spectrograms of 25 s of singing sequences by males of four different species of songbirds illustrating structural and syntactical variety in birdsong. (**a**) Grasshopper warbler, *Locustella naevia*, (**b**) yellowhammer, *Emberiza citrinella*, (**c**) nightingale, *Luscinia megarhynchos*, (**d**) reed warbler, *Acrocephalus scirpaceus*

Calls are uttered by both sexes year round in a variety of contexts (Marler 2004) whereas the term 'song' is generally reserved for the more complex vocalisations given in reproductive contexts (see Sect. 3 and for extensive review Catchpole and Slater 2008). We will show how oscine birdsong allows us to study principles in communication from both a mechanistic and a functional perspective. Ever since Darwin, birdsong has been a textbook example for an extreme sexual dimorphism, based on the observations of predominant male song in the temperate zones of the Northern hemisphere (Kroodsma et al. 1996; Riebel et al. 2005) where most research on birdsong has been conducted on male songbirds. However there is an increasing awareness that in the tropics and neotropics, where most bird species breed, females of many species sing as regularly and vigorously as males do (Kroodsma et al. 1996; Hall 2009) or even outsing males (Illes and Yunes-Jimenez 2009). Looking for the developmental and ecological correlates of this biogeographic variation has shed new light on this fascinating communication system (Langmore 1998; Riebel 2003b; Hall 2004; Riebel et al. 2005). Moreover, recent studies on condition-dependent development of song and of song preferences (Lachlan and Feldman 2003; Holveck and Riebel 2010; Spencer and MacDougall-Shackleton 2011) provide a new understanding of the origin and maintenance of the high diversity in this sexually selected signal.

Birdsong structure varies strikingly among species, ranging from syntactically simple songs consisting of few different notes (song elements) such as in the grashopper warbler to highly complex songs as those of nightingales (*Luscinia megarhynchos*), where each male may have repertoires of hundreds of different vocal units (Fig. 13.1). Why is this so? How can we explain this variation and which signal traits provide which kind of information? Understanding the evolution of such a communication system requires understanding not only the functions of the signals and the constrains underlying their expression, but also the decision rules of

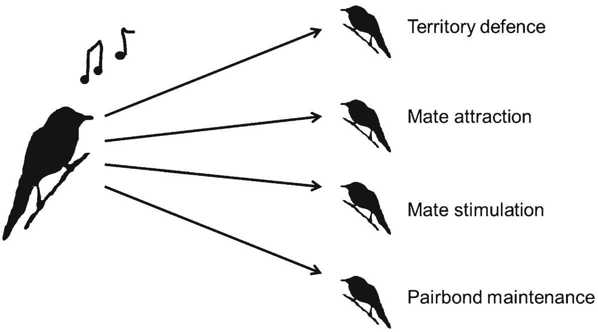

Fig. 13.2 The functions of birdsong. Singing is addressed at potential rivals and mates

the receivers (Naguib and Riebel 2006) because they exert the ultimate selection pressures on the singers. It is well documented that birdsong is an advertisement signal which functions in territory defence and mate attraction (Gil and Gahr 2002; Catchpole and Slater 2008) (Fig. 13.2). Recent developments on understanding decision rules by females (Riebel et al. 2009; Holveck and Riebel 2010), as well as their spatial behaviour to actually sample different males (Bensch and Hasselquist 1992; Roth et al. 2009), provide us with new fascinating insights into the complexity of animal communication. We here address the biology of bird song by integrating questions of causation and development with question on functions that are addressed in the following sections.

2 Development

2.1 Learning to Sing

The study of birdsong development is a beautiful illustration of the nature-nurture interplay of behavioural development (Slater 2003). Young birds do not simply learn the first best sound at hand. Instead, song learning is highly selective and a form of channelled learning (ten Cate 1989) – meaning that there are evolved mechanisms for *when* and *what* is learned. During a sensitive phase learning occurs without apparent external reinforcement and unlearned biases (varying in their specificity across species) guide what type of vocalizations are preferentially learned (Marler 1997). Like in human speech acquisition, perception learning precedes production learning in birdsong. Song is memorised during an early sensitive period and only after a period of prolonged motor practice develops into the adult form (Doupe and Kuhl 1999; Bolhuis et al. 2010). Without (early) exposure to species-specific song, young birds will develop very impoverished song. In normally raised and developing songbirds, the first auditory memories are laid down during the first weeks of life, often around the time when the young birds fledge from the nest. This called 'sensory learning phase' precedes the phase of extended motor practise, the so

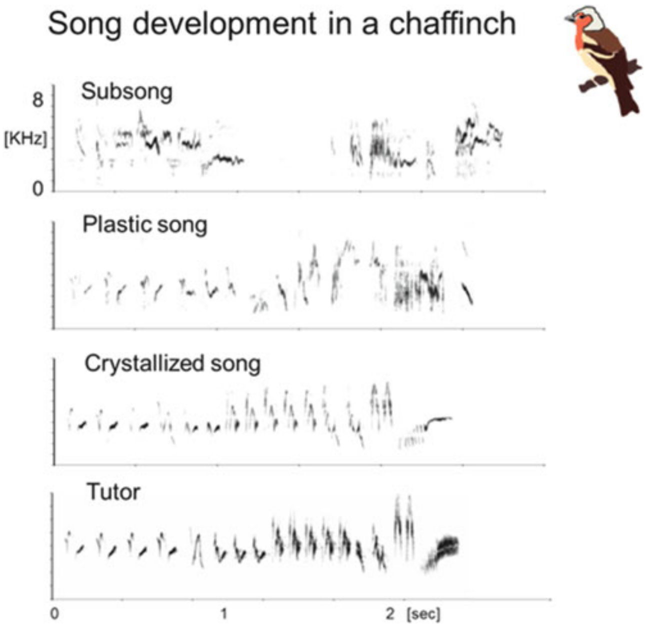

Fig. 13.3 Song development in a chaffinch (*Fringilla coelebs*). Chaffinches have a song type repertoire of 1–5 song types. The three *top panels* show the development of one of the bird's different song types. The *bottom panel* shows the tutor's song that was played back to the young bird the previous spring

called 'motor learning phase', but the exact timing of these two processes varies across species from slightly overlapping to completely separate in time, e.g. in many seasonally singing species, young birds might not start practising song until months after they heard adult birds sing for the last time. That first year birds indeed recall the specific songs heard the previous spring was first demonstrated in chaffinches (*Fringilla coelebs*), in William Thorpe's pioneering experimental studies where he exposed young chaffinches to tape recordings of adult song that they only started to sing the next spring (Thorpe 1954, 1958). Figure 13.3 illustrates how the early and first singing attempts consist of quiet amorph warbling (subsong) that still lack species-specific characteristics. Subsong will gradually proceed into more structured 'plastic song' getting more and more similar to the adult song in phonology and structure. While these first two phases often take several weeks to months and may partially overlap, the last transition to the fully crystallized song often occurs rather rapidly within a few days. After that, phonology, phonological syntax and timing fully correspond to adult song (Fig. 13.3).

Species differ in whether the song acquisition process is limited to their first year in life (which is the time to maturation in most songbird species) and with no additional learning after the first breeding season (so called 'closed-ended learners'). In other species learning might continue throughout life ('open-ended learners', e.g. canaries, *Serinus canaria*, or starlings, *Sturnus vulgaris*).

The good descriptions of the basic patterns non-withstanding, many questions regarding the when, from whom and what to learn are areas of on-going research (for an extensive overview see Catchpole and Slater 2008). Although most species show unlearned biases for the species-specific song, learning from non-specific models ('vocal mimicry') is widespread among birds (Garamszegi et al. 2007; Kelley et al. 2008), but there has been no systematic study of its functional significance. However, recent experimental studies demonstrate that an experimental approach to this phenomenon reveals unexpected functions of mimicry for example in mobbing contexts or to facilitate kleptoparasitism (Dalziell and Magrath 2012; Flower and Gribble 2012). Another long contested question namely how a culturally transmitted signal can honestly reflect the singers' (rather than the model's) quality has recently seen good empirical and theoretical progress: The developmental stress hypothesis suggests that the quality of the learning process itself could be informative of the singers' phenotypic quality (reviewed in Spencer and MacDougall-Shackleton 2011). Interestingly, the experimental tests of this hypothesis sometimes showed an effect on the actual learning from the model but often also marked effects on performance aspects of the learned signal (e.g. Holveck et al. 2008).

An unresolved and on-going area research is the question of whether the often-observed sex differences in song output are reflected in sex differences in learning (Riebel 2003b). The next section will show that female songbirds show learned preferences for male song independent of the sexual dimorphism in song production (Riebel 2003a, b). Song production in females ranges from no singing to showing more frequent and more complex singing than males (MacDougall-Shackleton and Ball 1999; Illes and Yunes-Jimenez 2009). The documented sex differences in the brain as studied so far suggest more quantitative (volume of song nuclei) rather than qualitative differences that seem to map on the differences in quality and quantity of song production (MacDougall-Shackleton and Ball 1999) and female songbirds may provide an unique system for disentangling production and perception learning (Bolhuis and Gahr 2006). Such comparative work should provide important pointers to the molecular basis of developmental flexibility of song control and vocal learning in birds (Fisher and Scharff 2009; Bolhuis et al. 2010).

Such comparative work on song learning capacity requires first identifying when and from whom they learn their songs as learning from sex-specific models can easily be mistaken for sex differences in learning capacity (Riebel 2003b).

2.2 Learning to Listen

Studies of song learning to date have mostly focussed on song production learning (Riebel 2003b). Yet it becomes more and more apparent that subadult song experiences also affect how adult birds decode songs as adults. Males memorise more songs than they sing: Territorial males show stronger reactions to the local variants of song, but it is unclear whether this is due to adult or subadult learning (McGregor and Avery 1986; Geberzahn et al. 2002). One important function of song is mate attraction (Catchpole and Slater 2008) (see below), raising the question as to how the cultural transmission process on the signal production side is mirrored on the receiver's side (Riebel 2003b). This process has only been studied in females to date but might also play an important role in male mate choice in species with singing females. The first experimental evidence for learned song preferences was found in laboratory raised zebra finch females that preferred to approach loudspeakers playing back their father's song over unfamiliar song (Miller 1979). These original findings have been replicated and expanded – rather than being specific for the father's song females can likewise develop a preferences for songs heard from foster fathers or flock mates or played back from loudspeakers during the period just around and after fledging (Riebel 2003a). As this period coincides with the sensitive phase for song (production) learning in this species it has been hypothesized that song preference learning also shows a sensitive phase (Riebel 2003a) an issue that clearly requires further study. Females do not only learn to prefer the specific and exact song variants they heard when young. The early song memories also seem to be generalised for songs similar to those experienced during the subadult stage. Female zebra finches crossfostered between the two geographically isolated zebra finch subspecies showed generalised preferences for songs sharing structural features with their foster subspecies (Clayton 1990). These laboratory findings are supported by observations in the wild: e.g. female great tits (*Parus major*) were found to be more often with a mate singing song variants similar to those of their fathers then expected by chance (McGregor and Krebs 1982).

Learning to recognise which songs to prefer seems but one way early experience affects adult preferences. In zebra finches, only song experienced females seem to discriminate against the impoverished song of males grown up without song exposure (Lauay et al. 2004). Only song experienced but not song isolates showed consistent preferences when tested repeatedly with the same songs (Riebel 2000). Song isolate canary females preferred different variants of complex trills than song experienced females (Draganoiu et al. 2002). Recent research also revealed an interesting interaction between females' early rearing environment and their adult song preferences. Brood size manipulations in zebra finches affect adult phenotypes: birds from large broods fare less well than those from small broods and their phenotypic quality is also reflected in their song (reviewed in Brumm et al. 2009; Riebel 2009). Adult females' preferences were depending both on their own and the males' rearing background: upon hearing songs from males from small and large brood sizes for the first time, females from small broods preferred songs from males from small broods (i.e. of high phenotypic quality) and females from large brood preferred songs from males from large broods (i.e. of low phenotypic quality). Females were thus able to discriminate between males from small and large broods further confirming the idea that song is an indicator of male quality (Spencer and MacDougall-Shackleton 2011). Female song preferences like male song thus develop in an intricate interplay encompassing their early song and social experiences as well as their own phenotypic quality. To understand the consequences of learned preferences on assortative mating and population dynamics, future work will have to address when and from whom females learn in natural settings.

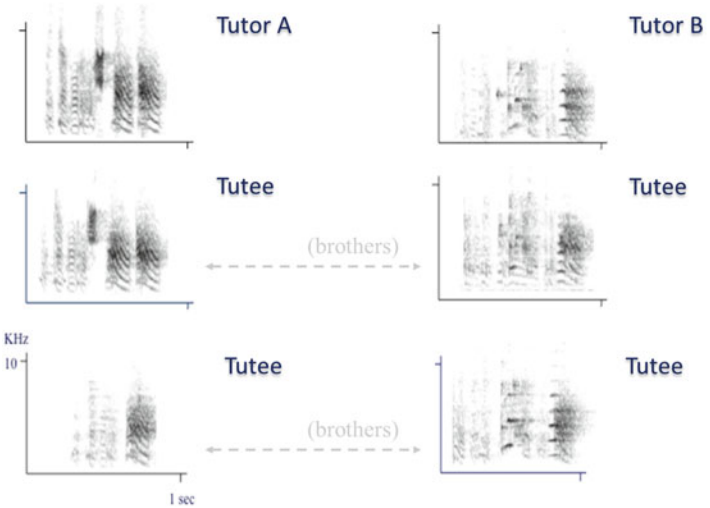

Fig. 13.4 Cultural transmission of song in male zebra finches. The *top panel* shows the songs of two adult males (labelled '*Tutor A*' and '*Tutor B*'). During the sensitive phase for song learning, the two young males (tutees) on the left were housed with tutor A and the two young males on the right were housed with tutor B and subsequently developed song motifs that were more similar to their tutors than to their biological brothers that had been exposed to different song motifs when young

2.3 From Individual Learning to 'Song Cultures'

One consequence of cultural transmission of song is that song not only varies between individuals but also between different geographic locations (Marler and Tamura 1964; Slater et al. 1984). Inter-individual and geographic variation arises from imprecise song copying (Fig. 13.4) but also from song variants disappearing, preferential learning of song types according to different transmission qualities of different habitats and influx of new song types of dispersing individuals (Slater 1986). In species with several different song types, individuals within a location will often share several song types (Slater et al. 1984) but also show individually distinct types. In such species geographical variation tends to be more continuous and is not referred to as dialects. In species with just one song type/song variant per individual all individuals in one location tend to share the same song variant. If these (sub) populations show a continuous distribution but a non-continuous pattern of song type sharing with sharp boundaries, they are referred to as dialects (Slater et al. 1984). Different populations of the same species have been documented to show different forms of unlearned biases (Balaban 1988; Nelson 2000). Songbirds thus provide an important study system for studies on the evolution of culture and its temporal and geographic changes such as dialect formation (e.g. Lachlan and Feldman 2003). A better understanding of female preferences in this process is an important target for the future, as females (learned) preferences for local song variants could result in mating barriers, which might lead to population divergence (Searcy and Yasukawa 1996; Verzijden et al. 2012).

3 The Social Function(s) of Song

Birdsong is an advertisement signal that functions predominantly in territory defence and mate attraction (Gil and Gahr 2002; Catchpole and Slater 2008). Female partner choice is affected by male song and, after having established social pair ponds, extra-pair copulations by females are also linked to the quality of the song of their extra-pair partners (Hasselquist et al. 1996). The function of song in female choice is supported by two main lines of evidence. (1) Field studies that demonstrated that song traits are linked to mating success and to paternity. (2) Laboratory studies that have shown that females are more responsive to specific song traits (Searcy and Yasukawa 1996; Catchpole and Slater 2008). In many bird species, males change their singing behaviour after pairing, suggesting that the function of song differs between the period of mate attraction and the period thereafter.

The territorial function of song, i.e. to advertise an area that will be defended against rival males, is well studied under field conditions. Simulations of singers using playback experiments in the field and observations of undisturbed singing in different contexts have shown that males obtain important information from a rival's song such as age or fighting motivation on which they decide how to respond to that rival (Catchpole and Slater 2008). As in all social behaviours which involve repeated encounters, individual specific information is of central relevance. Birds can indeed use such information to distinguish between familiar and unfamiliar individuals (Godard 1991) and assess qualitative and motivational characteristics of the singer (Gil and Gahr 2002) as well as to signal intrinsic characteristics such as personality traits (Amy et al. 2010). Familiar individuals are most commonly territorial neighbours, which are rivals in competition for space and matings. Although neighbours are competitors, once a relation is established, neighbouring males benefit by reduced aggression towards each other, a relation referred to as the "dear enemy effect" (Stoddard 1996). Moreover, recent studies have shown that having familiar neighbours has positive fitness effects (Grabowska-Zhang et al. 2012a, b). Neighbours can also act as an early warning system when a stranger starts singing somewhere in the territorial neighbourhood, an issue that has received specific attention in studies using birdsong as model in investigating communication networks (Naguib et al. 2004; Amy et al. 2010).

3.1 *Song Structure*

Birdsong with its high structural complexity can code a wealth of information about the singer. In addition to the structure of the song, the timing of songs and the singing activity also provide information to others (Fig. 13.5). Importantly, each of the various song parameters underlies different constraints and thus a different signalling potential. For instance, the production of the often very complex

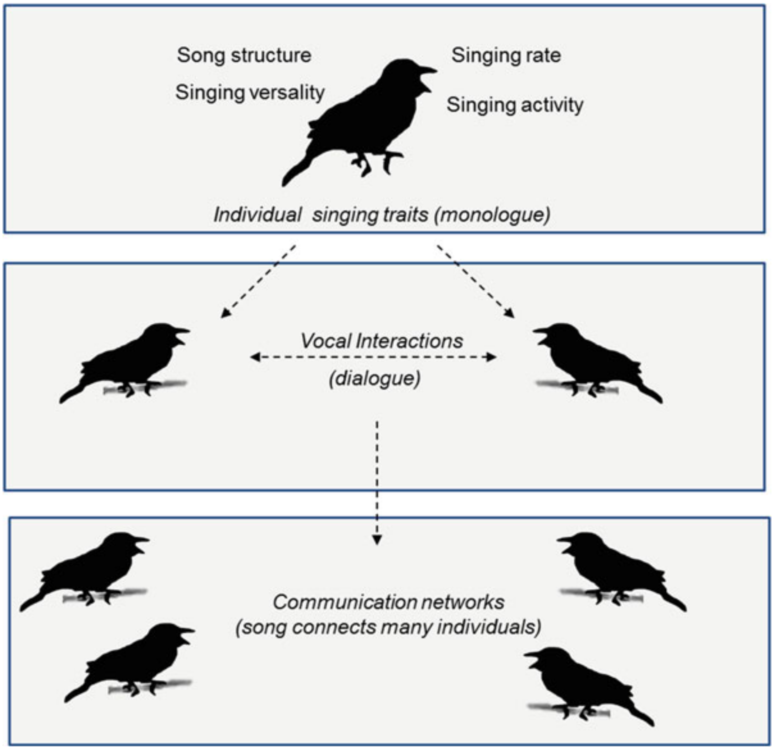

Fig. 13.5 Components of song bird (song) communication systems. (*Top*) The songs are the basic source of information. (*Centre*) When used in vocal interactions (dialogues) additional levels are added as the asymmetry and dynamic of interactions are meaningful and performance in these interactions can predict fitness. Bird song is a long range signal and birds are very mobile so that songs connect many individuals resulting in communication networks

notes birds sing, requires appropriate neuronal and motor control skills (Podos 1997; Hoese et al. 2000). Indeed dusky warblers (*Phylloscopus fuscatus*) that produce song elements at a higher relative amplitude, gain more extra pair matings than males that sing their elements 'less well' (Forstmeier et al. 2002), swamp sparrows (*Melospiza georgiana*) which can produce trills (trains of rapidly repeated elements, with high bandwidth and high repetition rate) are more attractive to females (Ballentine et al. 2004) and in nightingales, singing more trills elicits stronger responses by rivals and predicts mating success (Kunc et al. 2006; Schmidt et al. 2008; Sprau et al. 2010). Because song is learned, the specific song structure sung and the repertoire size have been suggested to indicate cognitive skills and the conditions experienced during early development, providing a window into the past (Nowicki et al. 1998), as well as current condition (Buchanan et al. 2003).

The potential for coding information in song complexity depends also on the species. In birds with a rather simple song, like swamp sparrows, parameters like the quality of trill production and quantitative traits like song rate, may be more important whereas in more versatile singers, complex parameters, such as repertoire size, syntactical organization, stereotypy or more global melody like performance traits may be more important. For instance, sedge warblers (*Acrocephalus schoenobaenus*) males become paired earlier when they have larger vocal repertoires, suggesting that repertoire size is a trait used by females in mating decisions and an indicator of male quality (Catchpole 1980, 1983). Great reed warbler (*Acrocephalus arundinaceus*) females display more to complex songs than they do to simple ones and have been shown to copulate specifically with those neighbours having larger vocal repertoire than their own mate, leading also to offspring with higher fitness (Hasselquist et al. 1996). Moreover, it is now also been suggested that overall performance characteristics, including features like melody and rhythm, may be features under selection pressure. Recent approaches taken from analysing human music have highlighted the possibility in intriguing ways (Araya-Salas 2012; Earp and Maney 2012; Rothenberg et al. 2013). These structural traits provide information on mechanical, developmental and cognitive mechanisms underlying signal expression. Yet, in order to be able to assess the traits, a bird has to sing in the first place and the quantity and timing of song will affect the availability of the information at a given time and space.

3.2 Singing Activity

The singing activity of a bird not only determines the availability of all the structural information discussed above but also has a signal value in itself. Singing makes a bird "visible" to others even at long distances. Hence the amount of singing will affect the quantity (and often quality) of information that is available to others. Singing costs time and energy and may also expose the singer to predators. Thus birds should sing specifically at those times where they can expect to achieve a benefit by receiver responses. Indeed, most songbirds vary substantially in singing activity over the year with a peak of singing at the onset of the breeding season (in seasonally breeding birds), which reflects its function in mate attraction and in territory defence (Fig. 13.1). Moreover, there is also substantial variation with time of day, and most temperate zone songbirds have a pronounced peak in singing around dawn, leading to the so called "dawn chorus" (Staicer et al. 1996). The dawn chorus presumably serves multiple functions (Kacelnik and Krebs 1983) and in several (but not all) species it has been linked at least in part to the fertile period of the female (Kunc et al. 2005). At the same time, dawn song can still play a role to advertise a territory, also in response to a potentially higher rival intruder pressure at dawn (Amrhein et al. 2004). Once birds sing, they vary substantially in song rate (i.e. the amount of song per unit time). High song rates can be a signal of quality, such as physiological condition, or also signal motivation such as to escalate a contest (Catchpole and Slater 2008).

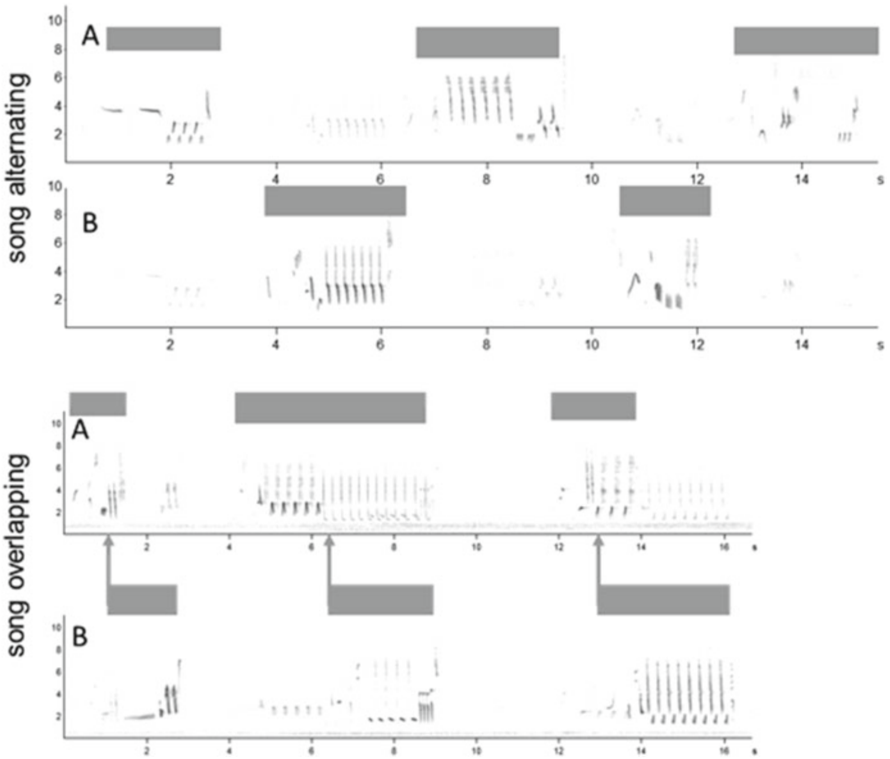

Fig. 13.6 Sound spectrograms of two nightingales interacting. *Top rows*: Birds *A* and *B* are alternating their songs (highlighted by *grey* bars). *Bottom rows*: Bird *B* is overlapping songs of bird *A*. Nightingales which overlap more in agonistic interactions have a higher mating success (Kunc et al. 2006)

3.3 *Vocal Interactions*

Often birds don't sing alone, i.e. perform a monologue, but use their song to interact with others, often over long distances across territorial boundaries. These vocal interactions are often highly dynamic where singers are responding to each other in various ways, either structurally by singing specific song patterns or by the timing of their songs. Most commonly, singers alternate their songs so that both can listen and can be heard. Yet, they may also overlap each other's songs, i.e. start to sing before the opponent has finished a song (Fig. 13.6). The function of song overlapping has been extensively studied and in almost all species studied to date song overlapping is used and perceived as an agonistic signal (Naguib and Mennill 2010). Another way of addressing a rival is to match his song type, i.e. to reply with the same song pattern the rival just sung (Todt and Naguib 2000). Song matching requires sharing of song types and in most species song matching has been associated with high arousal as birds match song more often in territorial conflicts.

Vocal interactions are interesting also from a broader perspective as they are usually asymmetric, meaning that one singer uses its song differently than the other singer. One singer may song-type-match more often or overlap more often than its counterpart. Theses asymmetries have been shown to reflect motivational or qualitative differences and can also be highly relevant to the broader audience leading to communication networks (Naguib 2005; Peake 2005). Assessing relative differences among others could be faster and more reliable when attending to the way they interact with each other and such information can then be further used in social decision making.

4 Summary

There is now good evidence that the structural variety in song between species surpasses variety required for species recognition and that much variation in structure and performance carries specific information about the sender and its intentions. An intriguing question in communication is how receivers integrate or weigh the different kinds of information. Some progress has been made in the relatively young research field that aims at understanding the development of song perception and this is a promising area for future research. But many questions regarding the communication process need further study, namely when is it more important to attend to traits reflecting current condition and motivation, such as song rate or the timing of songs in interactions and when is it more important to attend to structural traits, and if so to which? Experiments forcing receivers to make choices between such traits are rare but provide one of the avenues future research may take. Moreover, integrating the developmental history and song learning characteristics to communication under field conditions still remains a challenge worth to address. The interaction between learned song and learned preferences and their condition dependence has only recently become focus of modelling approaches (Ritchie et al. 2008; Lachlan and Nowicki 2012) that will need empirical data to increase their specificity. These data in combination with the advances made in tracking songbirds and thus identifying when and how they move around in relation to who his singing where and when will bring the study of avian communication to a new level integrating mechanisms and functions of singing as well as listening birds within the communication network (Naguib et al. 2011).

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Chapter 14
Chemical Persuasion in Salamanders

Lynne Houck

Abstract The mating system of group of terrestrial salamander species is described in detail, with a focus on the red-legged salamander (*Plethodon shermani*). A major feature of this system is the male production and delivery of a pheromone that is used during courtship. This pheromone is used only if the male encounters a less-than-receptive female. In this case, the male delivers specialized pheromones to this female. A female receiving these pheromones mates more quickly than a female lacking this pheromone stimulation.

1 Introduction

Communication between potential mates is critical if initial courtship interactions are to lead to reproductive success. In bower birds, for example, a female looking for a potential mate will visit a male's bower. This structure is an ornamented arena that the male constructs solely for the purpose of attracting and inseminating a female (Borgia et al. 1985). Moreover, the male readily will adjust his vocalizations to a visiting female (softer for inexperienced females) as part of his allure (Patricelli et al. 2002). If the female mates with the male, she then departs to build her nest and care for the young on her own. Meanwhile, the male continues to guard his bower, and perhaps adds a colorful leaf to its construction. The visual appeal of the bower, along with the male's behavior when a female is near, are the primary ways that this male communicates with a potential mate. In contrast, now imagine a pond in which a male Tungara frog boldly emits a "whine" vocalization that is meant to lure a gravid female to him (Ryan 1985). These examples of mating interactions are among the thousands of studies that report on reproductive communication that is based on the allure of visual or auditory cues.

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In contrast to vision or hearing, however, terrestrial salamanders have a silent approach to courtship persuasion. A courting male first makes careful physical contact with a female (often starting with her tail tip and working upwards). Should the female acquiesce to some preliminary physical contact (described below), the male will then deliver an aqueous mixture of pheromones to her nostrils. The inhalation of these pheromones stimulates neural signals that actually reach the female's brain.

Before describing the pheromone effects in more detail, consider the context in which these salamanders have evolved. The salamanders we studied are in the family Plethodontidae, and species in this family are characterized by having moist skin (as a frog has). Unlike most frog species, most plethodontid species are found not in the water but in moist terrestrial environments. No bowers or other structures are built for wooing females, nor do the males vocalize. Instead, the males are masters of chemical persuasion. Beginning well in advance of the mating season, an adult male begins to form new tissues under his jaw. These tissues become the structural support of what is termed a "mental" (= chin) gland. Subsequently, pheromone proteins are developed and can be expressed from this gland. Once the gland is fully developed, a male's goal during the multiple months to come is to locate and engage with as many females as possible. If the female is only somewhat interested (which is most of the time), the male will increase the intensity of his actions by delivering pheromones directly to her nose. A fluid mixture of pheromones then stimulates certain receptors in the female's nose. Professor Emmett Reid Dunn (an early and well respected herpetologist) termed the male mental glands "hedonic glands." As "hedonic" refers to pleasure-giving, we probably will never know enough about these salamanders to prove that the females actually are getting pleasure from the gland secretions. Nevertheless, the glands and their secretions certainly are the source of pheromones that the male uses to increase his chance of mating success.

My research over the years has focused primarily on one salamander species: the Red-legged Salamander (*Plethodon shermani*). The emphasis has been on pheromone effects on the female, but also the nature of the different pheromones produced by the males. Below are brief summaries of research projects involving salamander courtship pheromones. These summaries span three levels: (1) Pheromone persuasion during courtship, (2) The nature of salamander pheromone proteins, and (3) The unique evolutionary history of these pheromone proteins. Before summarizing this work, I describe a typical courtship for a male-female pair of red-legged salamanders.

2 Courtship Behavior of the Red-Legged Salamander

Red-legged salamanders are completely terrestrial and lay their eggs on land. The multi-month reproductive season can begin as early as May, when the salamanders first emerge from burrows that have shielded them from the freezing winter temperatures. From May or June through mid-September, animals are active at the surface whenever there is sufficient moisture on the ground. Long-term

Fig. 14.1 Male Red-legged salamander turning back to slap his chin gland onto the female's snout. Note the gland protruding from the male's lower jaw (With permission from Stevan J. Arnold)

droughts during this time prevent the salamanders from feeding, which can determine whether a female will have enough food to yoke a clutch of eggs. When conditions are cool and the ground is moist, males typically are searching for willing females. If a female is receptive, she will allow the male to contact her, ultimately leading to her assuming a tail-straddling walk (TSW) position (Fig. 14.1). During the TSW, the male typically turns back to the female and "slaps" his chin gland to her snout, delivering pheromones from his chin gland (Fig. 14.1). The male then turns forward and proceeds onward. If the female is receptive, she will continue moving forward in tandem with the male. During our experimental observations, a male typically would continue turning back to slap the female on multiple occasions. When the male was assured that the female was likely to remain with him in her tail-straddling position, he then lowered his body to the substrate and began to deposit a spermatophore (Fig. 14.2). A spermatophore is composed of a gelatinous base that supports a mass of sperm. When the male has finished depositing the spermatophore, he lifts up off of the spermatophore, moves his tail to one side, and starts moving forward (still with the female's head on his tail base). The female moves forward with the male, carefully holding her torso above the spermatophore. She stops moving forward when her cloaca is directly above the spermatophore. The female then lowers her cloaca over the spermatophore, lodging the sperm mass in her cloaca. She then lifts up (leaving the gelatinous base on the substrate) and moves away from the male. Note that, during the multi-month mating season, a female may become inseminated by as many as five males (Erika Adams, Ph.D. Thesis, Oregon State University 2005). Also, the female has a sperm-storage organ, the "spermatheca," which allows her to store viable sperm for multiple months (Sarah Eddy, Ph.D. Thesis Oregon State University 2011).

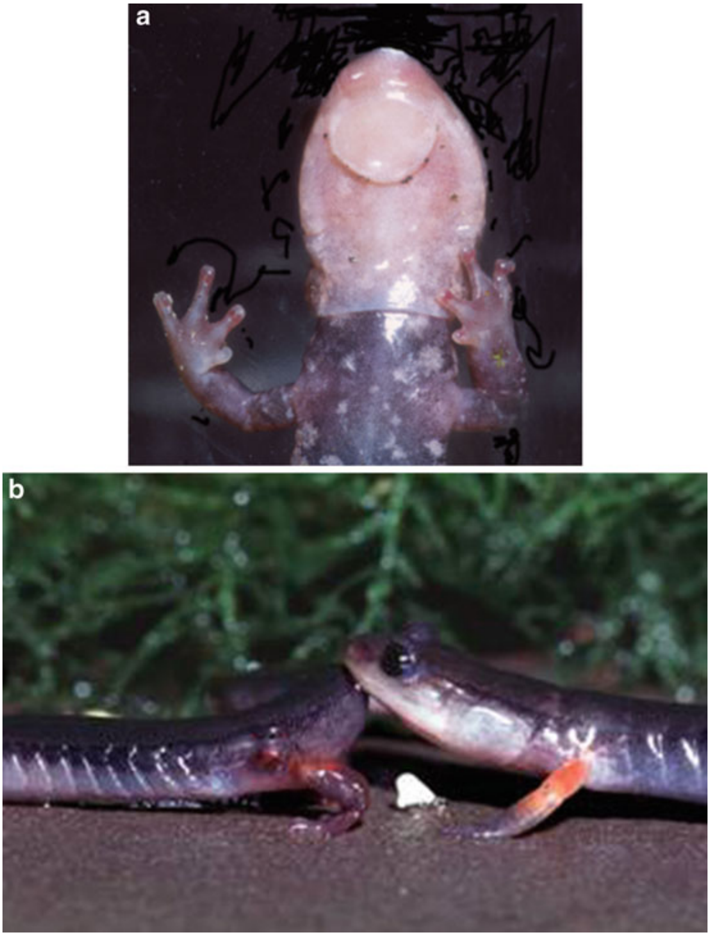

Fig. 14.2 (**a**) Male mental gland during the courtship season (With permission from Stevan J. Arnold). (**b**) Spermatophore deposited by the male during courtship (With permission from Stevan J. Arnold)

3 Pheromone Persuasion During Courtship

In the earliest experiment, our hypothesis was that a female treated with the male pheromone would be more receptive to the male, and thus the courtship duration would be shorter. For this initial experiment, we used the Ocoee salamander (*Desmognathus ocoee*), which are more likely to mate under laboratory conditions. We had 45 males and, using careful dissection, we removed the gland from each male's chin. After only 1 week of recovery, the glandless males were ready to mate again. The collected glands, however, were treated more roughly in order to release the pheromone fluid needed for our experiment. We used a tool that both sonicated and shredded the combined glandular tissue from all of the males. We then centrifuged the solution to remove any skin tissue, and then reserved the remaining fluid for our experiments. For 50 pairs, a glandless male was paired with an adult female in reproductive condition. In half of the pairs, the female received (on its nose) a drop of the pheromone solution; the remaining females received a drop of saline solution as a control. We put each male–female pair in its own box, and all the boxes were in a cool, darkened room. We allowed a 1-h "accommodation period" before starting observations so that each pair would have time to get used to being in their box. We then observed the boxed pairs for 6 h and, for each pair that was active, we recorded the time when the male and female were observed courting or actually mating. After that 6-h session, we left the pairs in their boxes for the rest of the night so they could continue courtship interactions. In the early morning, we examined each box, and recorded whether or not the pair had mated. Determining whether mating had occurred was very simple because a male lacks an intromittent organ and so he transfers sperm to the female by depositing a "spermatophore" (a gelatinous base that supports a mass of sperm on top). Sperm transfer occurred when a pair was aligned such that the spermatophore was deposited immediately in front of the female. Typically, the female then moved forward (while lifting herself above the spermatophore) and lowered her cloaca around the spermatophore. She then lifted herself up (with the sperm mass now in her cloaca) and moved off. The spermatophore base remained on the surface, bearing mute testimony to this mating ritual.

We staged courtship trials on four different nights, with both treatments (pheromone and saline) used each night. Our hypothesis was that females treated with the male pheromone would enter into the tail-straddling walk with a male more quickly than would females that only received a saline solution. This hypothesis not only was confirmed (Houck and Reagan 1990), it launched over 20 years of subsequent research.

4 Search for a Biochemist

At this point, I clearly needed help with the protocol of preparing a reasonable courtship pheromone solution. In search of a biochemist, I began attending the annual meetings of societies that might include biochemists. As it turned out, many other researchers had the same goal, but all to no avail.

4.1 Diversion into Study of Hormonal Effects

About this time, however, I had an opportunity to visit the Savannah River Ecology Laboratories (SREL) in Georgia, a place where a variety of animal research was taking place. At SREL, I met two colleagues: David Scott, who worked with many amphibians and reptiles at SREL, but focused primarily on the marbled salamanders

(*Ambystoma opacum*); and Mary Mendonça, a faculty member at Auburn University who was interested in the hormonal basis of animal behavior. Together, we measured testosterone (T) levels for marbled salamander males that were: (a) migrating to a breeding pond, (b) kept in the laboratory for a week, and (c) captured while actually courting a female. Surprisingly, the T levels for each group did not differ. We concluded that these male salamanders must totally disregard any other environmental cues (like laboratory conditions) during this once-a-year breeding bout (Houck et al. 1996).

4.2 Serendipity Provides Biochemist

On my next scientific trip, I attended a meeting that was held at a ski resort in Utah. We skied during the day, and the meetings were held later: from 4 to 10 pm each day (with a break for dinner). Everyone who attended gave a presentation. My presentation included a plea for any information about a biochemist willing to work with real animals. Still no luck. At the end of the meetings, however, I was in the plane flying back home when I happened to glance at the reading material of the fellow sitting next to me. How often do you see someone in an airplane reviewing a gas chromatogram? I remarked on this and, during the ensuing conversation, realized that I was talking to a real-life biochemist: Dr. Richard Feldhoff. I tried desperately to interest him in making salamander pheromones an important part of his research. No such luck, but he good-naturedly agreed *only* to try to process the first basic pheromone solution that I would send to him. Little did he realize that his agreement would be the start of a scientific relationship that would continue for more than 15 years.

The euphoria at finding a biochemist continued with the good news that Prof. Feldhoff's wife, Dr. Pamela Feldhoff, also was a biochemist and was willing to help. This willingness however, did not extend to accompanying me to North Carolina. As Prof. Feldhoff explained: "I like being in the lab." So, when we first started, I would drive to our collecting site (near Highlands, North Carolina), collect the salamanders, and then process the glands. Luckily, the Highlands Biological Station (HBS) was available, and HBS provided housing, kitchen facilities, and research space, and the Coker Laboratory was used to de-gland the salamanders. The processing procedure involved (a) placing the glands in a solution that caused the secretion of gland pheromones, (b) later removing and discarding the remains of the glands, and (c) centrifuging the remaining fluid. At this point, I sent the supernatant to Prof. Feldhoff for analysis. This process continued for a few years until Prof. Feldhoff decided that my processing was really not up to the strict biochemical standards of his laboratory. Although I tried hard, I must admit that occasional blood cells and other debris remained in the samples I sent to him. Accordingly, Prof. Feldhoff was forced to come to Highlands to prevent my blundering methods from contaminating the pheromone extract. I mentioned the lovely surrounding mountains and all the hiking trails in the area as compensation to his time and travel.

This initial trip soon was followed by others and, ultimately, both Prof. Feldhoffs were coming to the Highlands laboratory, along with their PhD students and undergraduates.

5 Successful Identification of Functional Protein Pheromones

The Feldhoff laboratory group worked hard to identify the protein pheromones obtained from the salamander glands, while the Houck group worked to stage observations of courtship behavior for females that were (and were not) treated with a pheromone protein solution. The courtship observations of our main study species, the Red-Legged Salamander (*Plethodon shermani*), were based on results from male-female pairs that mated in the laboratory. The two test groups were (a) a set of pairs in which the female received the pheromone, and (b) to different set of pairs in which females only received a dilute saline solution. The pheromone effect of increasing female receptivity was shown conclusively: for pairs in which the female had been treated with pheromone, their average courtship duration was significantly lower than the average time for pairs that only received the saline control. In particular, we isolated one of the most common pheromone proteins and tested that protein alone. This single protein affected female mating behavior. We named this pheromone Plethodontid Receptivity Factor (PRF), and published our results in the journal Science (Rollmann et al. 1999). This was a timely publication: (a) relatively few vertebrate pheromones had yet to be identified and biochemically synthesized (i.e., reproduced using synthetic cloning methods), and (b) a synthesized version of the pheromone was then tested, as verified by animal experiments that revealed a significant behavioral response to these synthesized pheromones.

5.1 Comparing Pheromones from Different Populations of P. shermani

The salamander population that we used to identify the PRF pheromone was from a well-known study site in North Carolina. But other sites of *P. shermani* populations were nearby, although distinctly separated. We wondered whether PRF might vary across populations, or whether this protein pheromone was highly conserved across all sites. We chose a nearby population and collected reproductive male salamanders. We deglanded the males and extracted the pheromone, which was analyzed using the Feldhoff's reverse-phase High Performance Liquid Chromatography (HPLC). We then obtained the elution profiles of these salamander gland proteins and identified discrete peaks. We compared HPLC profiles from males at our main study site with male profiles from a nearby site. We learned that (a) both sites showed the presence of the PRF protein, but (b) significant differences between the

PRF profiles were obvious. The significance of these results was that, not only were there PRF differences between the sites, but this result documented that our protein pheromones had evolved (Rollmann et al. 2000).

5.2 *Physiological Effects of* P. shermani *Pheromones*

At this point, we focused on how the physiological mechanisms of the female were being affected by male pheromones. What part of the nervous system was being affected by the pheromone? At a neuroscience meeting, I met Dr. Celeste Wirsig-Wiechmann, whose expertise included the study of neural responses to pheromones. Our behavior-modulating pheromones were of great interest to Dr. Wirsig-Wiechmann. She devised a procedure that ultimately allowed us to identify the neural areas affected by the male pheromones (Wirsig-Wiechmann et al. 2002). In particular, pheromone delivery revealed stimulation in a brain area called the "amygdala." This specific area of the brain performs a role in processing emotional (and other) reactions. To stimulate the amygdala, pheromone delivery starts with the male slapping his gland on the female's snout. The nasal cavity is divided into two different sections: (a) olfactory, which process airborne odorants; and (b) vomeronasal, which responds to liquid-borne pheromones. If the male gland was providing the female with pheromone stimulation, then the vomeronasal area should be stimulated. Celeste devised a method that attached a silent "marker" molecule to each molecule of the salamander pheromone. When a neuron responded to the pheromone, the marker molecule entered the neuron as a non-active part of the neural cell. Later, when the olfactory tissue was sectioned and stained, this processing revealed that only the vomeronasal areas were stimulated by the pheromone. This result showed that the vomeronasal neurons primarily were responsible for transmitting pheromonal information to the brain, ultimately to produce modifications in the female's behavior. Our study is one of very few to show actual brain response to pheromone stimulation.

5.3 *Effects of Pheromone on Conspecific Salamander Species*

Our next experiment built upon our earlier study (Rollmann et al. 2000) showing that pheromones in two separate (but nearby) populations of *P. shermani* pheromone effects were very similar. In fact, females from one population responded normally to pheromones from males in the other population. We expanded this comparison test: would *P. shermani* females respond to pheromones prepared from glands of other *Plethodo*n species? We predicted that species boundaries differences should promote a lack of female response to males of a different species. We obtained pheromone from two different *Plethodon* species (*P. yonahlossee* and *P. montanus*) not found near our main study population of *P. shermani*. In our experiment, *P. shermani* females were mated with *P. shermani* males, but the males all were deglanded and we used a pipette to mimic pheromone delivery to the females.

When a male turned back to "slap" a female, we would quickly deliver either a same-species pheromone or an "other-species pheromone" to our female *P. shermani*. To our surprise, *P. shermani* females responded robustly to male pheromones of both the *P. yonahlosee* and *P. montanus* (Rollmann et al. 2003). Although the pheromones were effective, we concluded that mate discrimination (and thus no courtship) would occur long before a female would actually enter the courtship phase when pheromones would be involved.

Segue now to other levels. The next experiments were produced with the support of an IRCEB grant from the National Science Foundation. Our initial group was joined by new colleagues, and our research topics branched out from initial behavioral and biochemical studies by adding a strong emphasis on how natural selection had acted on our system in many ways. We noted that the actual behavior of *P. shermani* pheromone delivery (male contacting the female's snout with his mental gland) a behavior that was did not change for over 20 million years. In contrast, the composition of pheromone secretions was rapidly evolving, with slight changes in the pheromone proteins occurring over and over. This epiphany influenced much of our subsequent research (e.g., Palmer et al. 2007a, b).

Our work so far had focused on the pheromone Plethodontid Receptivity Factor (PRF). But a second potential pheromone protein also was identified from the mental gland secretions. This second protein was less abundant, but continually present. We made a purified solution of this protein, and conducted behavioral tests to see whether female *P. shermani* would respond. As in earlier experiments we staged courtships between *P. shermani* male-female pairs, with females in half of the pairs receiving the *P. shermani* pheromone; in the other half of the male-female pairs, a female received only a saline control solution. Surprisingly, this second pheromone actually reduced female receptivity (i.e., it took longer for courtship to be completed for pairs in which the female experienced this pheromone). This second pheromone was named "Plethodontid Modulating Factor" (PMF). The complete male pheromone always included both PRF and PMF, and the combined effect of both proteins was to increase female receptivity. We also conducted additional experiments showing that both PRF and PMF solutions could activate receptor neurons in the female's nose (Wirsig-Wiechmann et al. 2006).

After focusing extensively on *Plethodon* salamanders, our team of dedicated biochemists devoted their pheromone-finding expertise to a very different plethodontid species, *Desmognathus ocoee*. One advantage of the *D. ocoee* species was that these animals were very abundant and were easily collected. On the other hand, the gland of each male was extremely tiny when compared with a gland from a *P. shermani* salamander. Despite the tiny gland size, the Feldhoff lab crew became experts on obtaining and processing the *D. ocoee* glands.

Not only did the *D. ocoee* salamanders have a different gland shape and different gland secretions, but their courtship behavior also differed. The *ocoee* male uses his top front teeth to scrape the female across her back. During the scraping, the male's courtship gland (located on his chin) is swabbing pheromone secretions on the female's back, directly over the area scraped by the teeth. The "swab and scrape" process is presumed to facilitate the entry of pheromones into the female's circulatory system. To date, however, no one has verified this assumption. Our courtship experiments with *D. ocoee*, however, have shown that females receiving the male pheromone were inseminated more rapidly than were females receiving a saline control solution.

In 2008, our salamander team published a paper describing our behavioral bioassay of the *Desmognathus ocoee* courtship pheromones. These salamanders have a different courtship pheromone, and a very different delivery system from the larger plethodontids.

The biochemical examination of the *D. ocoee* pheromone revealed that a 20–25 kDa molecular weight fraction of the pheromone was responsible for stimulating the females. This protein was very like the pheromone reported for newts, another group of salamanders. The newt pheromone was called "sodefrin", so we termed our protein "Sodefrin Precursor-like Factor" (SPF). Males of other plethodontid salamanders also expressed SPF, including species of *Plethodon*, *Aneides* and *Eurycea*. In all of these species, SPF was a highly variable protein that had undergone significant positive selection. The occurrence of the SPF pheromone in distantly related salamander genera suggests that this gene has been retained as a courtship signal throughout the evolutionary radiation of plethodontid salamanders, a span of more than 20 million years.

To date, our identified salamander pheromones include three proteins, each with its own evolutionary history. These proteins are among the very small group of pheromones known to affect female receptivity in vertebrates.

6 Conclusions

The salamander work continues, with the current focus on (a) the rapid rate of gene duplication in this system and (b) the effectiveness of other male signals (e.g. "foot dancing") that also seem to influence a female's choice to mate. Our salamander team attracts undergraduates and graduate students to join in annual collecting trips and observations of staged courtships. My hope is that one of these students will document how the *D. ocoee* pheromone (delivered into the female's circulatory system) actually affects her neural response.

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Chapter 15
Chelonian Vocal Communication

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Abstract Recently it was discovered that freshwater turtles communicate underwater by sound. The vocal repertoire of the Western Australian longneck turtle Chelodina colliei includes complex and percussive calls which are harmonically structured and frequency modulated, with dominant frequencies below 1 kHz and a range from around 100 to 3.5 kHz. Sounds with similar characteristics are used by the females of the South American river turtle Podocnemis expansa when migrating to nesting beaches and during communal nesting. Near term embryos inside eggs vocalize, and hatchlings emerging from nests and scampering across the beach and into the river continue to vocalize. In the water the adult females respond and the hatchlings then migrate with the females down the river, presumably to the flooded forests where they feed. Many unexplained aspects of aquatic turtles social behavior may eventually be explained when their vocalizations have been studied.

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1 Communication

Interactions among individuals are controlled, initiated, and regulated through communication between individuals. Males attract females and repel rivals; offspring solicit help from parents; individuals change behavior or color pattern to avoid predators. Communication is the interchange of information between two or more individuals, where it is clear who is the sender and who is the receiver of the signal (Krebs and Davis 1993). Signals are utilized with the objective to qualify and quantify the information interchanged between individuals, such as identity, position in the group, and behavioral information (Bradbury and Vehrencamp 1998).

Communication between animals in general involves vision, olfaction, tactile sensing, and hearing, some animals have the capability of electro reception as well (Halliday and Slater 1983).

1.1 Communication in Chelonians

Communication between chelonians is based on visual and olfactory signals (Kiester 1977; Alho and Pádua 1982; Galeotti et al. 2005a), tactile senses (Auffenberg 1977) and sounds (Campbell 1972; McCormick 1992; Sacchi et al. 2003; Galeotti et al. 2005a; Giles 2006; Ferrara et al. 2012).

The major part of the information available concerning communication in turtles indicates that visual and olfactory stimuli are the most commonly used and most important mechanisms used in these animals (Kiester 1977; Alho and Pádua 1982; Galeotti et al. 2005a, b). These signals have been identified during agonistic interactions and, principally, during courtship and copulation, when males and females are attracted by their movements and odors released (Auffenberg 1978; Galeotti et al. 2005b; Ferrara et al. 2009; Ibáñez et al. 2012).

Many examples of turtles using visual, tactile, and olfactory cues for communication have been published. Male freshwater turtles such as *Podocnemis erythrocephala* and *Mesoclemmys vanderhaegei* follow and bite the female during courtship (Ferrara et al. 2009; Brito et al. 2009). Head bobbing in a vertical plane is widely distributed in chelonian courtship (Kuchling 1999) and male North American Deirochelinae often add foreclaw vibration while swimming above the female or while facing her (Seidel and Fritz 1997). Male *Trachemys scripta elegans* and *Graptemys pseudogeographica* show a complex titillation behavior of vibrating the elongated foreclaws against the side of the head of the females (Jackson and Davis 1972; Vogt 1993). The number of vibrations per minute has been shown to be species specific in *Graptemys* species (Vogt 1993). Male and female terrestrial tortoises also interchange information during courtship when males enter in shell ramming disputes for females, or biting shells or following females (Auffenberg 1977). The cloacal odors are species specific in many species of tortoises (Carpenter 1980), or differentiate the sex of the turtle (Mahmoud 1967; Carpenter 1980) and may denote the level of receptivity of the female to the male's advances (Auffenberg 1977; Stacey et al. 1986; Ferrara et al. 2009; Ibáñez et al. 2012).

2 Acoustic Communication

For a long time documentation of sound communication between chelonians was mainly serendipitous observations (Campbell 1967, 1972; Campbell and Evans 1967; Mrosovsky 1972), and almost nothing is known about how these sounds are produced or how they function (Berry and Shine 1980; Olsson and Madsen 1998). In a review of stimuli involved in eliciting social behavior in turtles, Harless (1979) concluded "that most vocalizations simply occur in stressful situations and may or may not be eliciting or discriminative stimuli for other turtles". This lack of information is probably due to the fact that for many decades researchers assumed that turtles did not have an auditory sense (Pope 1955) and that the sounds produced were simply percussion noises made during copulation (Wever 1978; Mrosovsky 1972). However, recently, studies have shown that at least some species of turtles have a considerable auditory sense below 1,000 Hz (Campbell and Evans 1967), which permits these animals to perceive acoustic signals in the air or under water (Galeotti et al. 2004, 2005a, b).

Presently it is known that at least 47 species of turtles emit sounds during different contexts, 29 of those are terrestrial tortoises of the family Testudinidae (Table 15.1; see reference there) Most studies report sounds made during courtship and copulation and vocalization has been shown to have an important role in the reproductive behavior of some terrestrial chelonian species (Galeotti et al. 2004, 2005a, b).

2.1 Terrestrial Chelonians

Terrestrial tortoises vocalize in different contexts, during courtship (Jackson and Awbrey 1972; Galeotti et al. 2005a), when they are attacked (Campbell and Evans 1967), during combat displays with conspecifics (Ernst and Barbour 1989; McCormick 1992; Galeotti et al. 2005a, b) or when exploring new areas (Ernst and Barbour 1989). Even nocturnal choruses have been documented (Auffenberg 1964). However, it is the studies of courtship and copulation that are the most popular, once that vocalization was shown to play an important role in the reproductive behavior of *Testudo hermanni* and *Testudo graeca* (Galeotti et al. 2004, 2005a, b; Pellitteri-Rosa et al. 2011). It has been suggested that sound signals sent by individuals have qualitative information about the size of the turtle which could be used as a sign of reproductive fitness (Sacchi et al. 2003; Galeotti et al. 2005a, b). *Testudo hermanni* females favor fast-rate high-pitched calls which are typical for good-condition small-sized males, since the duration of the sound is directly related to the size of the male's carapace (Sacchi 2004; Galeotti et al. 2004).

Table 15.1 Presently it is known that at least 47 species of turtles emit sounds during different contexts; *A* adult, *H* hatchling, *J* juvenile (subadult)

Family/species	Context	Age class	References
Testudinidae			
Geochelone elegans	Courtship	A	Ernst and Barbour (1989)
Geochelone platynota	Courtship	A	www.startortoise.com
Geochelone pardalis	Courtship	A	Ernst and Barbour (1989)
Geochelone sulcata	Courtship	A	Grubb (1971)
Chelonoidis nigra	Courtship	A	Evans (1949); Jackson and Awbrey (1972)
Aldabrachelys gigantea	Courtship	A	Frazier and Peters (1982)
Astrochelys radiata	Courtship	A	Ernst and Barbour (1989)
Astrochelys yniphora	Courtship	A	Ernst and Barbour (1989)
Chelonoidis carbonaria	Courtship Foraging	A	Auffenberg (1965), Campbell and Evans (1967) Campbell (1967)
Chelonoides denticulata	Courtship	A	Auffenberg (1965)
Chelonoides chilensis	Courtship	A	Galeotti et al. (2005a)
Testudo gracea	Courtship Combat	A	Galeotti et al. (2005a) Ernst and Barbour (1989)
Testudo hermanni	Courtship Combat	A	Galeotti et al. (2005a) Ernst and Barbour (1989)
Agrionemys horsfieldii	Courtship	A	Cohen (1994)
Testudo kleinmanni	Courtship	A	Hoofien (1971)
Testudo marginata	Courtship Combat	A	Galeotti et al. (2005a) Hine (1982)
Gopherus agassizii	Courtship Exploration	A	Campbell and Evans (1967) Ernst and Barbour (1989)
Gopherus berlandieri	Courtship	A	Hosehoder in Wever (1970)
Gopherus polyphemus	Courtship	A	Carr (1952)
Kinixys belliana	Courtship Combat	A	Morris (1974)
Kinixys erosa	Courtship	A	Ernst and Barbour (1989)
Kinixys homeana	Courtship	A	Kirkpatrick (1998)
Kinixys natalensis	Courtship	A	Kirkpatrick (1998)
Homopus signatus	Courtship	A	Palmer (1994)
Psammobates oculifeus	Courtship	A	Ernst and Barbour (1989)
Manouria emys	Courtship	A	Mckeown et al. (1990)
Indotestudo elongata	Courtship Combat	A	McCormick (1992)
Indotestudo forstenii	Courtship Combat	A	C. Tabaka, personal communication (2009)
Indotestudo travancorica	Courtship Nocturnal chorus	A	Auffenberg (1964)
Trionychidae			
Nilssonia hurum	Courtship	A	Flower (1899)
Nilssonia nigricans	?	–	Annandale in Ernst and Barbour (1989)
Nilssonia gangetica	?	–	Gunther (1864)

(continued)

Table 15.1 (continued)

Family/species	Context	Age class	References
Kinosternidae			
Staurotypus triporcatus	?	–	Cope (1865)
Platysternidae			
Platysternon megacephalum	When disturbed	–	Campbell and Evans (1967)
Geomydidae			
Cistoclemmys flavomarginata	Courtship	A	Connor and Wheeler (1998)
Rinoclemys punctularia	When killed	A	Cope (1865)
Emydidae			
Emys orbicularis	Courtship	A	M. Zuffi, M. Lebboroni
Glyptemys insculpta	Courtship	A	Pope (1939) Kaufmann (1992)
Pseudemys floridiana	?	–	Neil (1950)
[a]*Emydoidea blandingii*	Swimming	A	Unpublished data
Cheloniidae			
[a]*Lepydochelys olivacea*	Nesting time Inside the nest and egg	A, H	Vogt et al. (unpublished data)
[a]*Chelonia mydas*	Swimming, and air	H	Unpublished data
Dermochelyidae			
Dermochelys coriacea	When attacked	A, H	Carr (1952)
	Diving		Kumpf (1964)
	Nesting time		Mrosovsky (1972), Cook and Forrest (2005)
	Inside the nest and egg		Ferrara et al. (in press)
Chelidae			
[a]*Chelodina colliei*	Swimming, resting	A, J	Giles et al. (2009)
Podocnemididae			
[a]*Podocnemis expansa*	Reproduction period (all life stages) Inside the nest and egg	A, J, H	Ferrara et al. (2012)
[a]*Podocnemis unifilis*	Inside the nest and egg	H	Unpublished data
[a]*Podocnemis sextuberculata*	Inside the nest and egg	H	Unpublished data

[a]Species added by us to a table adapted from Galeotti et al. (2005a).

2.2 Aquatic Chelonians

Even though there are a good number of publications concerning the acoustic behavior of terrestrial species, due to the easier methods for observing and recording the tortoises in a terrestrial situation, until quite recently no one believed that aquatic turtles use sound for communication. The few records of sounds from aquatic turtles were largely recorded in terrestrial situations. Carr (1952) mentioned sea turtles emitting sound when being hurt or killed. Some freshwater turtles were noted to emit sounds during defense or agonistic encounters (Goode 1967; Campbell and Evans 1967; Kaufmann 1992) and the leatherback seaturtle, *Dermochelys coriacea* was recorded to emit sounds during nesting (Mrosovsky 1972; Cook and Forrest 2005), but these were not considered to have functional importance.

3 Underwater Acoustic Communication in Chelonians

Recently it was discovered that both freshwater and marine turtles emit sound signals underwater and that vocalization is an important mechanism to exchange information within this group. So far only two species have been studied in detail, *Chelodina colliei* (Testudines; Pleurodira; Chelidae: the previously used name for this species was *Chelodina oblonga*), a longneck freshwater turtle endemic to the south-west of Western Australia (Giles 2006; Giles et al. 2009) and *Podocnemis expansa* (Testudines; Pleurodira; Podocnemididae), the largest river turtle in the Amazon (Ferrara 2012; Ferrara et al. 2012). People find it hard to believe, especially people that have been studying turtles for decades, that turtles are vocalizing under water and that the hatchlings are vocalizing when they leave the nest. One must realize that these sounds are very low frequency, near the lower range of the human perception range, thus hard to hear for people over 40. Also the sounds are usually very short, usually only fractions of a second and low volume. Thus if you are underwater the mere paddling of your feet or breathing through a snorkel is enough noise to obscure the sounds of turtles vocalizing.

3.1 Chelodina colliei

The underwater vocal repertoire of *C. colliei* consists of 17 vocal categories including complex and percussive calls (Giles 2006; Giles et al. 2009). The wetlands where this species lives are acoustically complex environments. They may contain logs, rocks, submerged and emergent vegetation, temperature stratification of the water, sand or silt sediments, water depths which may vary from month to month, and many contain gassy sediments, all of which impact the transmission of sound underwater. These wetlands are also predominantly shallow water environments and act as high-pass filters, where only higher frequencies propagate readily (Forrest 1994). The range and characteristics of vocalisations recorded for *C. colliei,* their frequencies as well as call structure appears to be influenced by the complex transmission characteristics of their aquatic environments (Marten and Marler 1977; Bradbury and Vehrencamp 1998; Tyack 2001) .

The vocal repertoire of *C. colliei* consists of clacks, clicks, squawks, hoots, short chirps, high short chirps, medium chirps, long chirps, high calls (Fig. 15.1), cries or wails, hoos, grunts, blow bursts, staccato's, a wild howl, drum rolling and even a sustained vocalisation (which lasted 9.5 min). Frequencies range from around

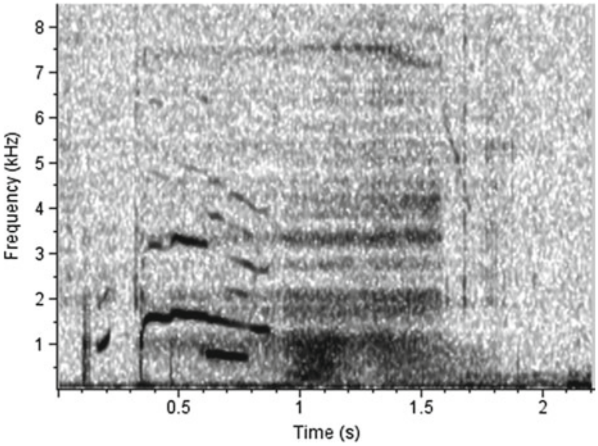

Fig. 15.1 Spectrogram of the 'High call' made by a large female *Chelodina colliei* (CL >24 cm). (DFT size 1024 points, overlap 49.9, Averaging of 1. Hanning window). Call begins with a short pre-syllable followed by a longer syllable with rapid up-sweep and slower down- sweep finish. The indistinct area at time 1–1.5 s indicates what has been called the 'breathy.' As no bubbles were recorded associated with this sound which would have indicated expulsion of air into the water, this sound is believed to be that of air circulating within the turtle respiratory/vocal apparatus

100 Hz in some of the percussive displays and extend as high as 3.5 kHz in some of the frequency modulated calls, but the dominant frequencies are below 1 kHz. Interestingly though, 'clicks' extended beyond the upper 20 kHz limit of the recording equipment (Giles 2006; Giles et al. 2009).

Turtles may be able to alter the distance of propagation of their calls by moving into deeper or shallower water when they signal. Although it is understood that cut-off frequencies are still determined by the shallowest position of the sender or the receiver (Forrest 1994). Not only were the majority of calls recorded for the *C. colliei* populations harmonically structured (which would enable transmission of at least part of the call, i.e. the higher frequency components as wetland water levels decline in summer), but additionally, these calls were also frequency modulated. As noted by Wiley and Richards (1978), frequency modulation is used to encode information which is a useful means to transmit information over longer distances and produces a signal pattern that is dissimilar to the background noise, thus making it stand out.

Frequency modulated calls, which we have categorized as chirp calls, were the most predominant of calls in the turtle repertoire and were particularly prevalent in spring and summer for both sexes. On several occasions when recording in the field with two or more turtles in view; 'short chirps' could be heard as turtles passed nearby to each other and on another occasion when several turtles were investigating a new object in their environment. These chirp calls appear to be their main contact calls. Preliminary play-back trials suggested some interest from swim-by turtles in chirp calls. Turtles were observed to stop swimming and maintain an alert posture where they held their necks either flexed or out-stretched. Many of the turtles also swam towards the underwater speaker (Giles 2006). Clearly sound is important for the long-necked freshwater turtles, but further research is needed to fully understand the biological function of their calls.

3.2 *Podocnemis expansa*

Adult females of the largest freshwater turtle in South America, *Podocnemis expansa*, emit sound signals during the entire reproductive period, from the migration of the females in the flooded forests to the nesting beaches, in front of the nesting beaches while basking, on the nesting beaches while nesting, in the deep holes in the river in front of the nesting beaches after nesting, and after the hatchlings emerge and migrate with the females back to the flooded forests (Vogt 2008; Ferrara et al. 2012, in press). During this period, 3–4 months, the behavior of the female is divided into six categories, migration, basking, nights without nesting, nights with nesting, waiting for the hatchlings to emerge, meeting the hatchlings as they enter the river, and migration with hatchlings (Fig. 15.2).

Among these behavioral categories it was possible to note a difference between the types of signal and the frequency (Hz). Lower pitched sound frequencies were used during migrations and basking (Ferrara 2012; Ferrara et al. in press). Sounds at lower frequencies travel over longer distances and are used by whales to communicate in the sea over great distances (Nummela and Thewissen 2008). Low frequencies of sound are also produced by turtles, suggesting they use this mechanism to form groups from distant localities to migrate to the nesting beaches.

During nesting the turtles use higher frequencies. This could be explained by the fact that the females are congregated in the shallow, 1.5 m, water in front of the nesting beaches before ascending the beach (Ferrara 2012; Ferrara et al. in press), and the use of higher frequencies in shallow water or air favors the propagation of the sound waves (Urick 1983; Forrest et al. 1993). In addition to this, shorter wavelengths increases the chance of a receiving female to localize the direction of the sound (Forrest 1994), which could be advantageous during synchronization of the females to ascend the beach to nest and to also not attract distant predators, caimans.

In systems of communication it is difficult to determine the significance or the function of different signals (Herzog and Burghardt 1977). The structure of the vocalization of one signal in particular can offer indications of the information that is being transmitted (Marler 1977). Noisy sounds and high frequencies have characteristics that induce proximity (Morton 1977) while short and repetitive sounds, that have characteristics that initiate and terminate abruptly facilitate the localization of the sound producer by another individual (Gelfand and McCracken 1986).

Two types of sound in the acoustic repertoire of adult *P. expansa*, in addition to the possibilities above, were the most frequent and the only ones that appeared in all of the categories of behavior, suggesting that they function to identify the species and locate the sender (Ferrara et al. in press). Sounds with similar characteristics to

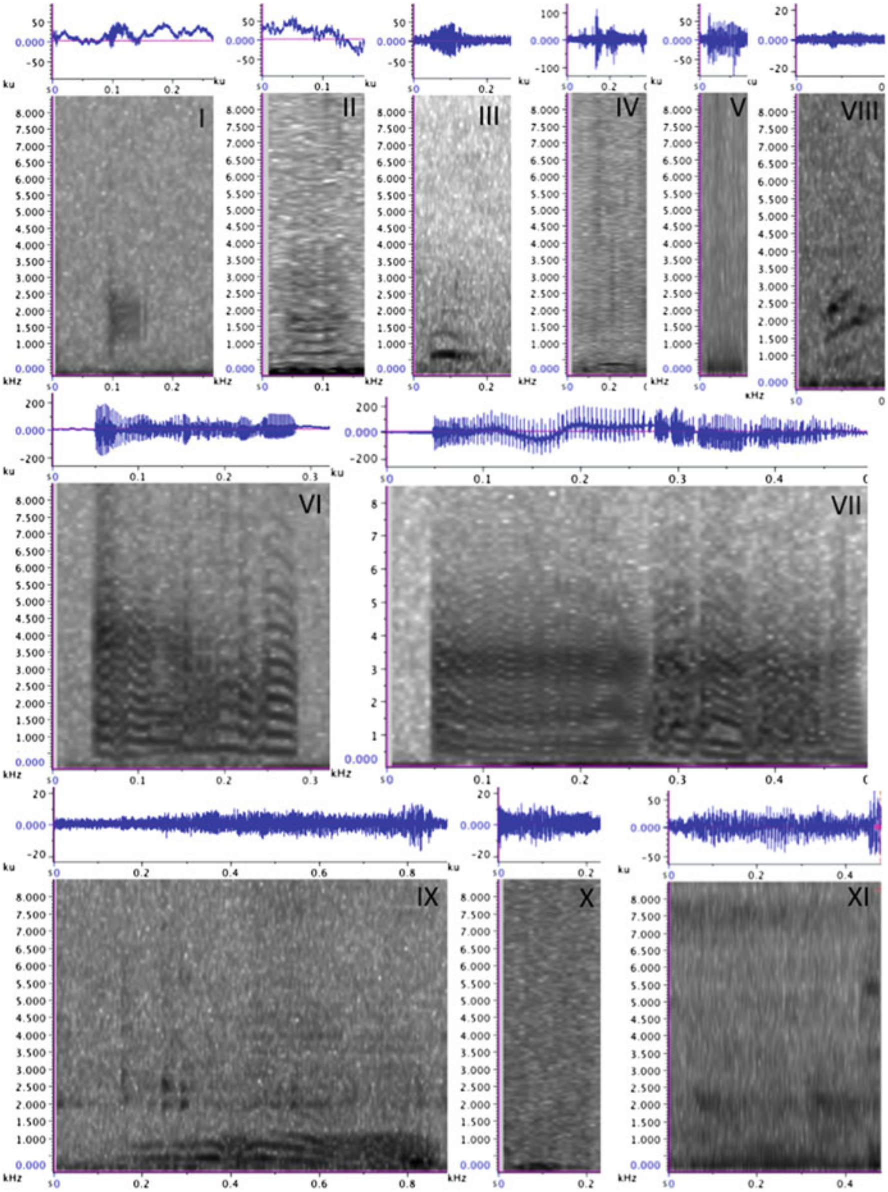

Fig. 15.2 Waveform and spectrograms of 11 types of sound produced by *Podocnemis expansa*. We used different fast Fourier transform (FFT) window sizes to generate the spectrograms (512-pt FFT for Sound Types *I*, *III*, *VI*, *VII*, *VIII*, *IX*, *X* and *XI*; 1024-pt FFT for Sound Types *II* and *IV*, and 256-pt FFT for Type *V*). All spectrograms were done using Hamming windows

these types of sound, were also found in the acoustic repertoire of *C. colliei*, birds, and crocodilians, they are known as "contact calls" (Vince 1968; Britton 2001; Marler and Slabbkoorn 2004; Giles 2006).

4 Vocalization of Turtle Hatchlings

Near term embryos and hatchlings of the aquatic species *Podocnemis expansa*, *Podocnemis unifilis*, *Podocnemis sextuberculata*, *Dermochelys coriacea*, *Chelonia mydas* and *Lepidochelys olivacea* also emit sounds (Ferrara et al. 2012; Ferrara and Vogt unpublished data). In *P. expansa* the near term embryos begin to vocalize 8–36 h before hatching (Ferrara et al. 2012) and in *D. coriacea* after 51 days of incubation (Ferrara et al. in press). The authors of these studies have three hypotheses of why the near term embryos and recently hatched turtles are vocalizing in the nest: (a) to synchronize hatching and induce communal digging to help move the siblings toward the surface and out of the nest; (b) synchronize emergence from the nest to dilute the predation pressure during hatchling dispersion to water; and (c) solicit females to approach so that the hatchlings can be lead and accompanied by the females in their migration to the flooded forest (Ferrara et al. 2012).

The last hypothesis suggested is in relationship to *P. expansa*, where it has been proven that there is postnatal parental care. Hatchlings were found to be vocalizing as they scampered from the nest across the beach to the river, once in the river they continued to vocalize and adult females responded. The hatchlings then migrate with females down the river, presumably to the flooded forests to feed (Ferrara et al. 2012). Hatchlings were found to migrate at least 62 km with females in 16 days (Vogt et al. unpublished data) This is not to say that the other species do not have a social relationship between the mothers and the hatchlings, only that it has yet to be studied and tested.

5 Conclusions and Outlook

The use of acoustic communication appears to be highly appropriate for aquatic turtles because the visibility in water is much lower than in air and turtles often occur in areas where the visibility is very low. The recent studies by Ferrara and collaborators open new directions for the study of social behavior and acoustic communication in freshwater turtles. The authors have demonstrated that acoustic communication in freshwater turtles is more broadly used than just during courtship and copulation. The sound signals are utilized in all life stages, from within the egg (the prehatchling vocalizes a few hours before hatching) to adults, demonstrating that the behavior of turtles is much more social than was imagined.

More specific and detailed studies need to be undertaken to better understand what role acoustic communication plays in the social behavior of all species of turtles. We know that some species are more social than others, and we imagine that these species have a larger vocal repertoire, but only two of the over 300 species of turtles in the world have been studied extensively and research with other species is needed. We propose that all turtles hear and vocalize and perhaps some species more so than others.

Sound absorption increases with frequency so that low frequencies are generally used for long-range communication. Although this has not been published, the late Ray Ashton was studying infrasound communication in tortoises in Florida. We have infrasound recording capabilities, but we have not found infrasound vocalizations in any of the aquatic turtles we have studied. Sound absorption is less in water than in air and in an aquatic environment sound travels approximately four and a half time faster than it does in air (Rogers and Cox 1988). Thus high frequencies can be utilised for communication under water over longer distances compared to similar frequencies in-air (Forrest 1994), making it unlikely that infrasound would be used by aquatic turtles in depth-restricted environments.

The field of acoustic communication in chelonians is quite new and we have just scratched its surface. We hope that this account will help to stimulate others to begin studying other species of turtles. We know that the Olive Ridley sea turtle (*L. olivacea*) vocalizes in the egg, during and after hatching, and the females during nesting and in the water in front of the nesting beaches. We suspect that all species of sea turtles are acoustically communicating underwater, migrating pods of adult sea turtles, possibly arribadas build up by turtles vocalizing, and dispersing hatchlings may maintain their groups through vocalizations. Many unexplained aspects of aquatic turtles social behavioral patterns may be eventually explained when their vocalizations have been fully studied. Despite these investigations into their vocalizations little is known how or where these sounds are produced.

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Chapter 16
Cetacean Acoustic Communication

Laela S. Sayigh

Abstract The mammalian order Cetacea, which contains the whales, dolphins and porpoises, is a highly diverse group with respect to life history patterns, social structure, social behavior and communication. This chapter reviews what is known about communication in each of the 13 cetacean families, and includes discussions of some of the better known communicative signals, such as the songs of several baleen whale species, and the group- and individual-specific signals of killer whales and bottlenose dolphins. The apparent anti-predator adaptations seen in the vocalizations of several families are also discussed. Overall, there is a great need for basic research on how calls are used in the natural communication systems of most cetacean species. Such research promises to shed light on both applied (e.g., effects of anthropogenic noise) and basic (e.g., evolution of vocal learning) research questions.

1 Introduction

The mammalian order Cetacea, which contains the whales, dolphins and porpoises, is a highly diverse group containing two suborders, the Mysticeti and Odontoceti, which are further broken down into 13 extant families. These families contain members as diverse in appearance as the largest animal ever to have lived, the blue whale, to the tiny harbor porpoise. Cetaceans also show a great amount of diversity in their life history patterns, social structure, social behavior and communication. Although prior reviews have highlighted differences between the two major groups, the baleen whales (mysticetes) and toothed species (odontocetes) (e.g., Tyack 1986a), or have focused on specific families or species (e.g., Janik 2009a), this review aims to summarize the current state of knowledge of acoustic communication in each of the 13 cetacean families. Although an additional goal is to highlight groups in need of further study,

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it will become apparent to the reader that this includes the majority of cetacean species, as most research on communication has focused on a small handful of species. For the most part, what we know about communication in the vast majority of species boils down to descriptions of call parameters, and even these are continually being revised and updated as techniques improve for recording cetacean sounds. In recent years, increasing numbers of studies are utilizing passive acoustic monitoring (PAM) as a tool for studying cetacean occurrence and abundance; these studies have increased our knowledge of descriptive parameters of cetacean calls. However, with respect to communication, measurements of call parameters are of limited usefulness when separated from information regarding the behavioral contexts of call production and responses to calls, data which are notoriously difficult to collect. In addition, although several studies have correlated certain call parameters with geographic variation or behavioral context (e.g., Azevedo et al. 2010; Bazua-Duran and Au 2004; Hawkins and Gartside 2010; Papale et al. 2013; Petrella et al. 2012; Sjare and Smith 1986b; Weilgart and Whitehead 1990), it is difficult to interpret such correlations without additional information, for example regarding whether or not individual or group specific call types may occur. Overall, there is a great need for basic research on how calls are used in the natural communication systems of most cetacean species.

Suborder Mysticeti contains four families of baleen whales: the Balaenopteridae, Balaenidae, Neobalaenidae, and Eschrichtiidae. Suborder Odontoceti contains nine families of toothed whales, dolphins and porpoises: the Physeteriidae, Kogiidae, Ziphiidae, Monodontidae, Delphinidae, Phocoenidae, Platanistidae, Iniidae, and Pontoporiidae. The status of our knowledge on communication in each of these families is discussed, in greater or lesser amounts of detail, below.

2 Mysticetes – The Baleen Whales

The four families of baleen whales share several unifying characteristics, the most noticeable being the presence of baleen plates that are used in feeding. Other key features that differentiate baleen whales from toothed whales include their tendency to undergo annual seasonal migrations (although these are far from universal, both among populations and age/sex classes), and other life history traits that are tightly linked to an annual cycle (e.g., Tyack 1986a). Communication is notoriously difficult to study in baleen whales, since the large spatial scales across which it may occur hinder our ability to observe both senders and receivers in communicative interactions (Edds-Walton 1997). In addition, it is logistically difficult to carry out controlled playback experiments over such large spatial scales.

2.1 Family Balaenopteridae

Members of the Family Balaenopteridae, often referred to as the rorquals, are for the most part similar in their overall sleek shape, except for the humpback whale, which

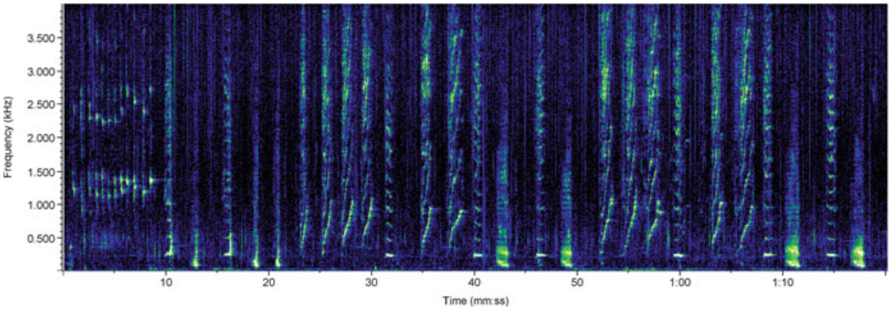

Fig. 16.1 Spectrogram of a segment of humpback whale song recorded off Australia, showing elements of song structure including repeating units and phrases. Spectrogram settings included an 8 kHz sampling rate and a 1,024 point Hann window with 90 % overlap (Recording courtesy of Ann Allen)

has a chunkier profile and extremely long flippers. With respect to communication, this latter species is probably the best studied among baleen whales, so we will start there.

One of the first cetacean communicative signals to receive a significant amount of research attention was the song of the humpback whale (*Megaptera novaeangliae*). A variety of factors likely contributed to this early research focus, including that humpback whale song consists of frequencies well within our hearing range and within the range of early acoustic recording systems, and that some humpbacks breed in accessible areas, such as near the Hawaiian islands. The earliest work focused on descriptions of song structure, which was found to consist of units, which combined to form phrases, which combined to form themes, in a repeating structure that could last up to 35 min in length (Payne and McVay 1971; Payne and Payne 1985; Payne et al. 1983; see Fig. 16.1). Later and ongoing work has focused on trying to elucidate the function of humpback whale song via behavioral observations and playback experiments on breeding grounds (e.g., Darling et al. 2006, 2012; Mobley et al. 1988; Smith et al. 2008; Tyack 1983). Surprisingly, now several decades after this research began in earnest there is still no consensus regarding how humpback whale song functions, other than that it is likely a form of reproductive advertisement. This assumption is supported by the observation that song is usually produced by lone males on the breeding grounds (Baker and Herman 1984; Darling and Bérubé 2001; Darling et al. 1983; Frankel et al. 1995; Glockner-Ferrari and Ferrari 1985; Tyack 1981; Winn et al. 1973). However, even these observations have been challenged, with recordings of song being made during migration (Norris et al. 1999), on feeding grounds (Clark and Clapham 2004; Stanistreet et al. 2013; Stimpert et al. 2012; Vu et al. 2012), and by males accompanied by females (Darling et al. 2006; Smith et al. 2008). Nonetheless, song is still believed to function in reproductive advertisement, but whether it functions in intersexual and/or intrasexual interactions continues to be debated (e.g., Darling et al. 2006; Smith et al. 2008).

An intriguing aspect of humpback whale song is that it changes over time, and all the males in a given breeding population appear to match these changes (e.g., Payne et al. 1983; Payne and Payne 1985; Cerchio et al. 2001). These changes are clearly derived from vocal learning, although Cerchio et al. (2001) speculate that innate templates for temporal features of song may also play a role. Until recently, these changes appeared to be gradual, resulting in a slow evolution of song structure over time (appr. 15 years for the song to change entirely). However, a faster pace of change was found among humpbacks in Australia, where new song types introduced by Western Australian whales into the Eastern Australian population were adopted by the vast majority of Eastern Australian males within 2 years (Noad et al. 2000).

Humpback whales also produce social sounds, which were found to attract whales from as far as 9 km away in playback experiments at the Hawaiian breeding grounds (Tyack 1983; Mobley et al. 1988). Although social sounds do not have a structure like song (Silber 1986), they do show varied frequency and temporal characteristics.

Other than humpbacks, all of the other balaenopterid whales share the same genus (*Balaenoptera*) and the same streamlined shape, but vary in size, with the blue (*B. musculus*) being the largest, followed by the fin (*B. physalus*), then sei (*B. borealis*), then Bryde's (*B. edeni*) and finally the minke whale (*B. acutorostrata*).[1] It has long been postulated that both blue and fin whales may produce sounds that are loud enough and low frequency enough to be heard across ocean basins (e.g., Payne and Webb 1971; Thomson and Richardson 1995; Charif et al. 2001; Širović et al. 2007). Long distance communication is facilitated by frequency sweeps and repetitions of calls (Edds-Walton 1997), which are both characteristic of blue and fin whale calling behavior. In the case of blue whales, the very low frequency vocalizations (<20 Hz) have frequency sweeps of only a few Hertz, but the calls are sustained for 10–20 s (Cummings and Thompson 1971; Edds 1982; Mellinger and Clark 2003). Fin whales produce low frequency, downsweeping calls, usually centered around 20 Hz (Watkins 1981), which can often also have a simultaneous higher frequency component (Simon et al. 2010). Watkins (1981) suggested that these 20 Hz calls function as contact calls. They have been recorded from single individuals and in vocal exchanges (Watkins 1981; Edds 1988; McDonald et al. 1995); Watkins (1981) described the approach of a fin whale from as far as 10 km away to another whale producing 20 Hz calls. Similarly, McDonald et al. (1995) reported call exchanges among three fin whales separated by several kilometers. Although transmission across ocean basins may be theoretically possible for the calls of fin and blue whales, more realistic estimates of the actual range of fin whale calls are on the order of 90 km (Simon et al. 2010), which make more sense from a biological perspective: animals travelling many hundreds of kilometers are unlikely to reach a calling whale in a biologically relevant time frame.

Watkins et al. (1987) described temporal patterning of 20 Hz calls, with either single calls or doublets being repeated for hours at a time. He suggested that this patterned calling represents a simple song, used for reproductive advertisement.

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[1] Only the Common minke whale is discussed here; the Antarctic minke whale is considered a separate species. In addition, the various subspecies of rorquals are not considered, nor is the recently described Omura's whale (*Balaenoptera omurai*).

This supposition has been supported by observations of callers being male (Croll et al. 2002) and of calling being associated with the breeding season (Lockyer 1984; Moore et al. 1998; Watkins et al. 1987; Simon et al. 2010). However, singing outside of the breeding grounds has also been documented (Simon et al. 2010), indicating either that breeding begins in high latitudes or that song may serve additional functions. Other fin whale call types have been speculated to be associated with feeding or agonistic interactions (Watkins 1981; Edds 1988; Širović et al. 2013).

Blue and minke whales have also been reported to sing on breeding grounds, and, like fin whales, minke whale song amounts to bouts of repetitive calling, which is perhaps a questionable use of the term "song" (Janik 2009b). Blue whale song is somewhat more complex, with more than one call type in a song lasting approximately 1 min. However, blue whale song structure appears to remain stable for decades (other than declines in tonal frequency; McDonald et al. 2009), and thus is not believed to be influenced by vocal learning. In addition to song, blue whales have also been reported to produce calls that appear to be associated with feeding (Oleson et al. 2007). Minke whale song can include calls that are unusual in structure and have been termed "star wars" vocalizations, based on their synthetic sound (Gedamke et al. 2001). Another call type described for minkes is the "boing," (Rankin and Barlow 2005); Delarue et al. (2013) reported high numbers of "boings" (3.5/min; lasting 30 min) during an apparent interaction with a predator.

Diel variability in vocalizations has been observed in blue, fin and sei whales, which may be related to feeding patterns linked to vertical migration of prey (Stafford et al. 2005; Wiggins et al. 2005; Baumgartner and Fratantoni 2008). Various hypotheses have been put forth for this pattern, including that whales could be, socializing or switching to another prey species involving coordination or defense of resources. Croll et al. (2002) also suggested that male fin whales may advertise prey resources to attract females.

Little is known about communication in sei or Bryde's whales, beyond a few descriptions of call parameters (e.g., Baumgartner et al. 2008; Rankin and Barlow 2007b; Edds et al. 1993). Limited data suggest Bryde's whales may produce contact calls (Edds et al. 1993). Alternating calls were recorded from a mother-calf pair when the calf was alone at the surface and while the female approached the calf; calling ceased when the pair joined (Edds et al. 1993). Adults have also been recorded producing call types described as frequency modulated, tonal moans as well as pulsed sounds, although nothing is known about the contexts of call production (Cummings et al. 1986; Edds et al. 1993).

2.2 Family Balaenidae

The Family Balaenidae contains four species: the bowhead whale, and three species of right whales (North Atlantic, North Pacific and Southern). The balaenids are markedly different in appearance from the balaenopterids; they are chunky in shape, with huge mouths containing very long baleen plates. This family has the dubious distinction of containing the two most endangered species of baleen whales, the North Pacific and North Atlantic right whales. This distinction has accelerated research on these species in recent years, and the calls of the North Atlantic right whale have become the basis for a ship alert system designed to avoid ship collisions. However, although a number of studies have described various call types produced by the balaenid species, little work has focused on how these calls function in the whales' natural communication systems.

Bowhead whales (*Balaena mysticetus*) have been reported to produce songs consisting of 1–2 themes that are repeated for up to 10 h (Ljungblad et al. 1982; Wűrsig and Clark 1990). Bowhead song appears to be intermediate in complexity between the simple call repetitions of fin whales and the much greater variety and structure of humpback song (Edds-Walton 1997). Wűrsig and Clark (1990) found that songs were linked to social and sexual activity during the spring migration, and Stafford et al. (2008, 2012) also found singing to coincide with the breeding period, indicating a role in reproductive advertisement. Like in humpbacks, songs change from year to year (Clark 1990), although there is evidence that bowhead song changes even more drastically than that of humpbacks, with whales producing songs that carry no resemblance to the song of the previous season (Tervo et al. 2011, 2012; but see Delarue 2011). The highly variable song repertoires of bowheads along with the changes between seasons are features consistent with a sexually selected reproductive advertisement display (Tervo et al. 2011, 2012). Unlike bowheads, there is no evidence for song production by any of the right whale species (Tyack and Clark 2000).

Vocalizations that appear to function as contact calls have been described in both bowhead and right whales. Wűrsig and Clark (1990) described a series of calls that were recorded while a bowhead mother and calf approached one another following a separation; these vocalizations ceased after joining. Clark (1991) also described call exchanges by three separated bowhead whales. For southern right whales (*Eubalaena australis*), Clark (1982, 1983) described frequency modulated upsweeps (between 50 and 200 Hz) called "upcalls" that appear to function as contact calls. Calling individuals were observed being joined by other upcalling individuals or groups, after which upcalling ceased. This call type was also recorded during vocal exchanges between mothers and calves during separations. Upcalls have also been recorded in the two other right whale species (northern rights, *E. glacialis*; e.g., Parks et al. 2007; see Fig. 16.2; N. Pacific rights, *E. japonica*; Munger et al. 2008), and it is this call type that is used to trigger alerts to mariners in New England waterways; however there are few behavioral data to go along with the acoustic recordings of these calls. In a tagging study, Parks et al. (2011) found that whales of all ages and both sexes produced upcalls as well as a variety of other tonal calls. Rates of upcalls were affected by behavioral state, with lower rates during periods of foraging, traveling, or logging, and higher rates during surface activity. Kraus and Hatch (2001) found that calling by right whale females attracts competitive males. A final call type that has been described for both southern (Clark 1983) and North Atlantic right whales (Parks and Tyack 2005) is the broadband, impulsive gunshot

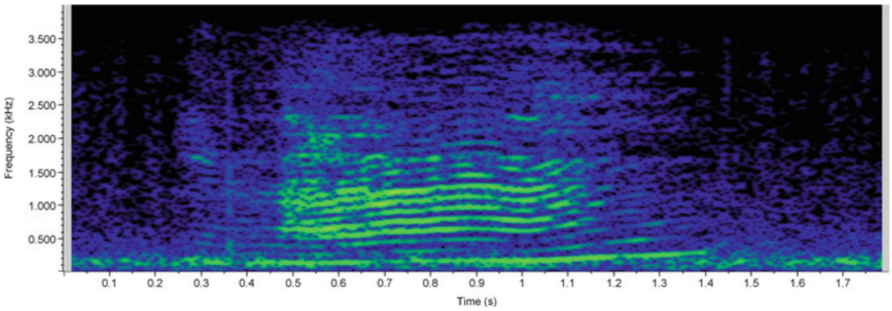

Fig. 16.2 Spectrogram of a Northern right whale up call. Spectrogram settings included an 8 kHz sampling rate and a 256 point Hanning window with 90 % overlap (Recording courtesy of Susan Parks)

sound. Parks and Tyack (2005) confirmed gunshot production only by mature males in a tagging study, and they hypothesized that these sounds may function as a reproductive advertisement display. Parks et al. (2012) analyzed bouts of gunshots and found that the whales producing them were either stationary or travelling, thus not identifying any clear context for their production.

2.3 Family Neobalaenidae

The Family Neobalaenidae contains just one species, the pygmy right whale, *Caperea marginata*. It is the smallest of the baleen whales and has little in common with the right whales. One published study describes recordings of a lone juvenile, which produced only one type of sound, “a short thump-like pulse or tone burst with a downsweep in frequency…with most energy between 60 and 120 Hz”; typically these occurred in pairs (Dawbin and Cato 1992). Nothing is known about how these sounds function in pygmy right whale communication.

2.4 Family Eschrichtiidae

The Family Eschrichtiidae also contains just one species, the gray whale, *Eschrichtius robustus*. There are several published descriptions of the acoustic characteristics of gray whale sounds. Crane and Lashkari (1996) found that most sounds have center frequencies below 200 Hz, and that they occur in repetitive patterns separated by long periods of silence. Gigi, a juvenile gray whale that was held in an aquarium for 1 year, was described to have produced higher frequency sounds, including “pulses” (100–10,000 Hz) and “clicks” (2–6 kHz; Fish et al. 1974). Similar call types were reported by Norris et al. (1977), and these were circumstantially linked to behavior that suggested that they function as contact calls. A captured calf produced "pulses" when released near the mother, who then swam to the calf. Two stranded male calves produced "click" sounds, which were also recorded when a mother approached her calf, and ended when they joined.

3 Odontocetes – The Toothed Whales

The nine extant families of toothed cetaceans are obviously unified by the presence of teeth, although in some species this trait is greatly reduced or even absent (e.g., in some female beaked whales). All species of odontocetes in which sound production has been studied to date have been found to echolocate, although the characteristics of their echolocation signals vary greatly. Echolocation may function in communication in some or all odontocete species, but this review will focus only on the (few) cases where a communicative function has been documented. Other than teeth and echolocation, there are few unifying features for this large and diverse group.

3.1 Family Physeteridae

The Family Physeteridae contains only one species, the sperm whale, *Physeter macrocephalus*, which is the largest odontocete. Sperm whales produce broad-band click vocalizations that function in both echolocation and communication. Stereotyped patterns of clicks, called codas, have a communicative function, and were initially proposed to serve as individual signatures (Watkins and Schevill 1977; Watkins et al. 1985). Later studies found evidence for shared coda types (Moore et al. 1993, Weilgart and Whitehead 1993; Rendell and Whitehead 2003), coda dialects, and large vocal clans (Weilgart and Whitehead 1997; Rendell and Whitehead 2003, 2005), seeming to contradict the idea of an individually specific function. However, several studies now indicate that sperm whale codas may serve both to identify individuals and groups. In a single group of seven sperm whales off the island of Dominica, Schulz et al. (2011) found that the vocal repertoires of both members of a mother-calf pair differed from those of other group members, and both Antunes et al. (2011) and Madsen (2012) found that there was reliable individual variability in the inter-click intervals of codas. Given that sperm whale social structure consists of stable matrilineal social units (Whitehead and Weilgart 2000; Mesnick 2001) in which individuals have preferred associates (Gero et al. 2008), it is logical that their communication could facilitate both group and individual recognition.

In addition to codas, male sperm whales have been found to produce low directionality, low frequency "slow clicks," that can be detected by conspecifics at distances of up to 60 km (Madsen et al. 2002). These clicks have been proposed to function as a reproductive advertisement display (Weilgart and Whitehead

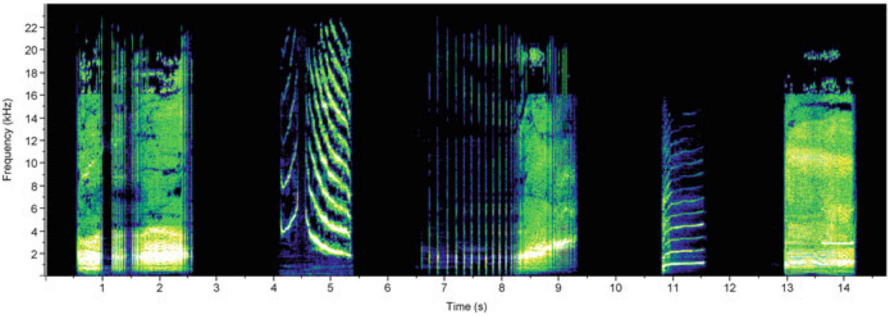

Fig. 16.3 Spectrogram of a variety of narwhal sounds; for ease of display these are shown as a sequence, although they were not produced as such. Spectrogram settings included a 44 kHz sampling rate and a 1,024 point Hann window with 90 % overlap (Recordings courtesy of Ari Daniel Shapiro)

1988), but recordings of these clicks from high latitude feeding areas where only mature males occur indicate that this must not be their only function. Madsen et al. (2002) speculate that they may also serve as an acoustic display related to competition for food.

3.2 *Family Monodontidae*

Family Monodontidae contains two arctic species, the beluga, *Delphinapterus leucas*, and the narwhal, *Monodon monoceros*. Beluga whales are highly vocal with variable, graded vocal repertoires (e.g., Belikov and Bel'kovich 2006, 2007, 2008; Sjare and Smith 1986a, b; Vergara and Barrett-Lennard 2008; Vergara et al. 2010), which include whistles, pulsed or noisy calls, and calls containing both whistle and pulsed components, as well as everything in between (e.g., Chmelnitsky and Ferguson 2012). Frequency ranges of beluga calls are unclear, as most studies were bandwidth limited. The majority of studies of beluga whale vocalizations are descriptive, with few insights into their communicative functions. There is evidence for a particular pulsed call type serving as a contact call (Chmelnitsky and Ferguson 2012; Vergara et al. 2010; Vergara and Barrett-Lennard 2008). In addition, Morisaka et al. (2013) provide evidence that a different pulsed call type may have individually distinctive pulse repetition rate patterns; this call type commonly occurs in vocal exchanges, similar to those of signature whistles of bottlenose dolphins (see below). For narwhals, Marcoux et al. (2011) found that whistles and pulsed calls were more similar within than between groups (or "herds"), and Shapiro (2006) reported calls with individual differences in pulse repetition rates (see Fig. 16.3). No associations were found between specific call types and behaviors (Marcoux et al. 2011). These data support the idea that narwhals produce individual- or group-specific calls.

Belugas are also capable of vocal learning, as evidenced by the spontaneous imitation of human speech-like sounds by a captive beluga described by Ridgway et al. (2012). This work confirmed earlier descriptive accounts of belugas producing speech-like sounds (e.g., Fish and Mowbray 1962). However, nothing is known regarding if or how belugas may use this vocal learning ability in their natural communication system.

3.3 Family Delphinidae

The Family Delphinidae is the most diverse family of cetaceans, containing at least 32 species in 17 genera, with the taxonomy continuously being revised (Committee on Taxonomy 2012). This family contains the famous common bottlenose dolphin, of "Flipper" fame, as well as a variety of other smaller and larger species, including pilot whales and killer whales. The three main categories of delphinid sounds are echolocation clicks, whistles, and pulsed calls; members of this family may produce one, two, or all three types of calls. Janik (2009a) recently wrote a comprehensive review of delphinid communication; thus, this review will focus only on a subset of delphinid species.

Two of the best studied species of cetaceans with respect to communication are delphinids: the common bottlenose dolphin, *Tursiops truncatus*, and the killer whale, *Orcinus orca*. The common bottlenose dolphin has been the focus of studies documenting individually distinctive signature whistles (e.g., Sayigh et al. 2007; Janik and Sayigh 2013; Fig. 16.4), although these signals have been documented in other delphinid species as well (Caldwell and Caldwell 1968, 1971b; Caldwell et al. 1973; de Figueiredo and Simão 2009; van Parijs and Corkeron 2001).

Signature whistles have been defined as the most common vocalization produced when individuals are isolated from their group members (Sayigh and Janik 2010), but they are also important vocalizations when animals are free swimming (e.g., Cook et al. 2004; Quick and Janik 2012). They are used for individual recognition (Sayigh et al. 1999) and for maintaining group cohesion (Janik and Slater 1998), and their development is influenced by learning (Tyack and Sayigh 1997). Dolphins are able to recognize the signature whistles of other individuals by means of the frequency modulation pattern of the whistle alone (Janik et al. 2006); whether or not voice cues (such as are used by most other non-human mammals for individual recognition) are also used is not known. Dolphins copy the signature whistles of close associates (Tyack 1986b; King et al. 2013), and copying appears to serve an affiliative function. Copies are imperfect, such that they are likely recognizable as copies, thus not affecting the capacity of signature whistles to serve as individual identifiers (King et al. 2013).

Bottlenose dolphins also produce a variety of non-signature, or variant whistles, as well as pulsed sounds (other than echolocation), but few of these vocalizations have been studied in detail. One of the better described sounds is the low frequency, pulsed "pop" vocalization described by Connor and Smolker (1996). These sounds were found to be associated with male alliances in consortships with females, and were hypothesized to be threat vocalizations used to induce females to remain close

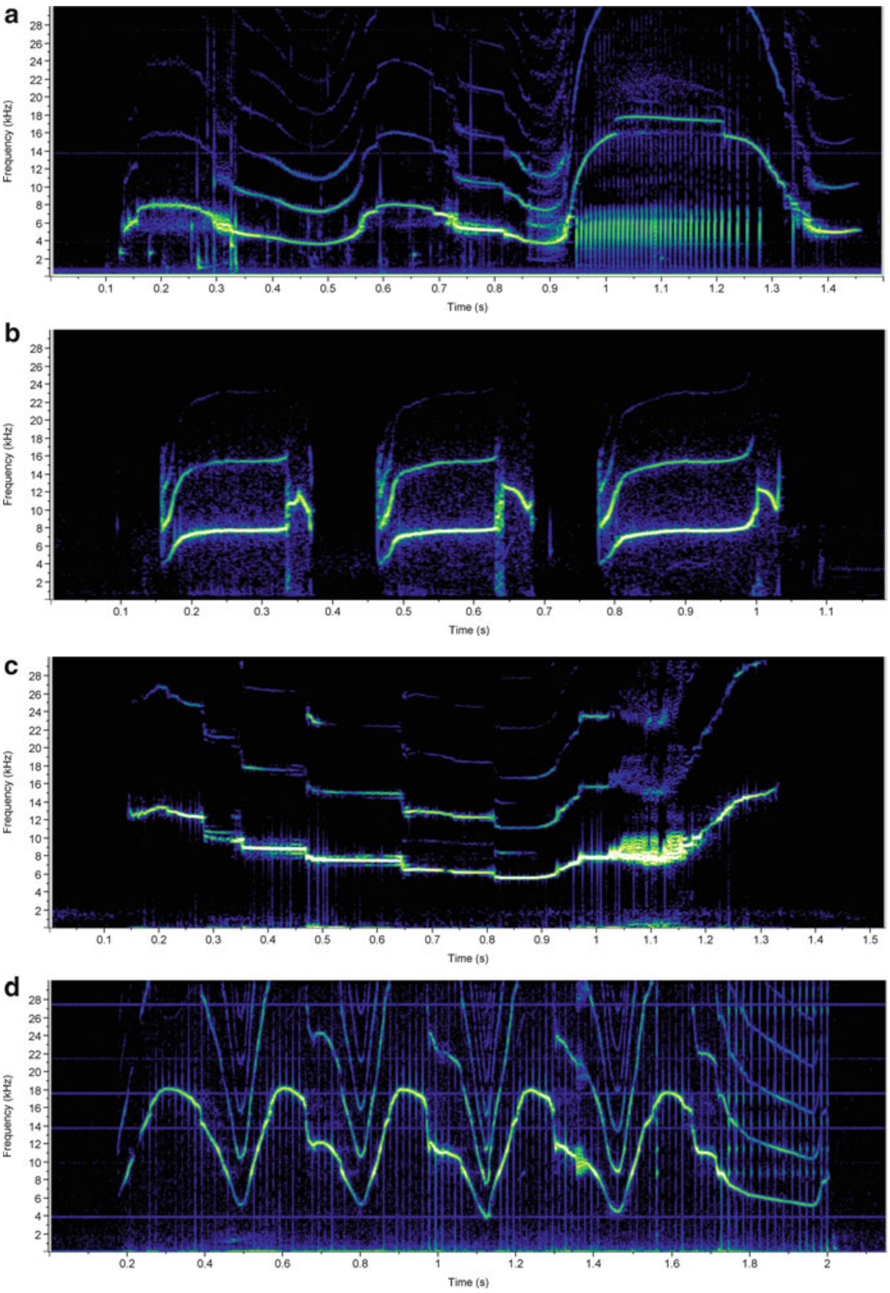

Fig. 16.4 Spectrograms of four different bottlenose dolphin signature whistles (**a**–**d**). Spectrogram settings included a 60 kHz sampling rate and a 512 point Hann window with 90 % overlap (Recordings by the author and Chicago Zoological's Society Sarasota Dolphin Research Program)

by. Female consorts turned toward males at a higher rate when males produced pops, and aggressive "head jerks" were also associated with pops. Another context-specific call is the "bray" described by Janik (2000). These calls mostly occurred while dolphins were feeding on salmonid fish. "Gulps," as described by dos Santos et al. (1995), commonly occurred after various types of vocalizations, including "brays"; these calls seemed to be associated with surface behaviors and agonistic interactions. Two studies have also described low frequency narrow-band sounds (Simard et al. 2011; Schultz et al. 1995), which may be associated with socializing behavior. Low frequency "moans" produced by captive dolphins were described by van der Woude (2009); these appeared to be associated with anticipation of human interaction.

Killer whales are top predators in the marine environment, preying even on the largest baleen whales (Ford and Reeves 2008). Of their communication signals, the best studied are the stereotyped or discrete pulsed calls of the resident (fish eating) killer whales near Vancouver, British Columbia (Ford 1991). These calls are specific to different pods of whales, which are highly stable matrilineally related groups. Discrete calls are believed to be learned, which leads to the formation of dialects between neighboring groups; the more closely related the matrilines, the more similar their dialects are (Ford 1991; Deecke et al. 2010). These dialects gradually change over time, and, like in sperm whales, they overlap to form acoustic clans (Deecke et al. 2000; Riesch and Deecke 2011).

Killer whales have also been reported to produce whistles, which in some cases are ultrasonic (Thomsen et al. 2002; Riesch and Deecke 2011; Riesch et al. 2006, 2008; Samarra et al. 2010; Filatova et al. 2012). These have been speculated to be designed for closer range communication than discrete calls, and may be designed to prevent eavesdropping. Even with these features, mammal-eating killer whales produce fewer whistles than fish-eating killer whales, which may be an adaptation to prevent being heard by potential prey (Riesch and Deecke 2011). Mammal-eating whales were also found to produce fewer pulsed calls, likely because these calls can be heard by their seal prey (Deecke et al. 2005).

3.4 Family Ziphiidae

Family Ziphiidae, or beaked whales, are the second largest family of cetaceans, with 21 species, but are among the most poorly known. There have been very few studies of beaked whale communicative signals. Pulsed sounds were reported from both a stranded Blainville's beaked whale (*Mesoplodon densirostris*) by Caldwell and Caldwell (1971a) and from a surface group by Rankin and Barlow (2007a), as well as from a Longmans' beaked whale (Rankin et al. 2011); Dawson et al. (1998) reported whistle vocalizations from surface groups of Baird's beaked whale (*Berardius bairdii*). None of these studies were able to link vocalizations to behavior. Recent studies that utilized digital acoustic recording tags have increased our understanding of beaked whale vocal behavior. For the most part, vocalizations

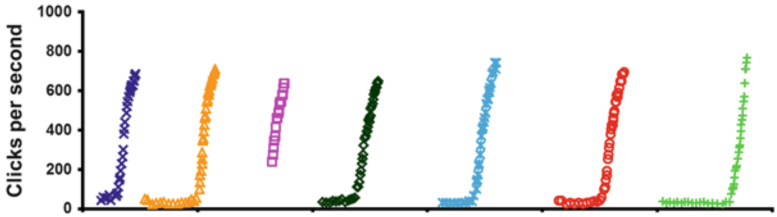

Fig. 16.5 Click repetition rate patterns for seven contact calls produced by a captive harbor porpoise calf (Figure courtesy of Karin Tubbert Clausen)

recorded on tags appear to be foraging-related echolocation (Johnson et al. 2004; Tyack et al. 2006). However, two studies reported calls that may have communicative functions. Aguilar de Soto et al. (2012) and Dunn et al. (2013) reported several distinctive call types, including whistles, produced by Blainville's beaked whales, usually during the descent portion of the dive. They proposed that the production of such calls only when at depth may be an anti-predation strategy, given that their predators (sharks and killer whales) are shallow divers. However, the study by Dawson et al. (1998) of Baird's beaked whale reported whistle vocalizations recorded near the surface, suggesting that there is likely diversity in beaked whale communication strategies.

3.5 Family Phocoenidae

The Family Phocoenidae contains six species in four genera. Those that have been studied produce narrow band high frequency (NBHF) clicks for echolocation (Møhl and Andersen 1973; Akamatsu et al. 1998; Villadsgaard et al. 2007), which have likely evolved to take advantage of a window of low ambient noise, and/or of the reduced hearing sensitivity of killer whales at these high frequencies (100+ kHz; Madsen et al. 2005). Communication in Phocoenidae has been little studied, and the few studies that have been attempted have focused on the harbor porpoise, *Phocoena phocoena* (e.g., Amundin 1991; Nakamura et al. 1998; Clausen et al. 2010). All of these studies found evidence for predictable patterns of click repetition rate in different contexts, suggesting a communicative function for clicks (Fig. 16.5).

It will perhaps not be surprising if porpoises, like beaked whales, do not have more complex communicative signals. These species are not known to be highly social, reducing the need for individual- or group-specific signals. In addition, the patterns seen in these species could also be influenced by risk of harassment and/or predation, as mentioned above for beaked whales. Several authors have raised the possibility that NBHF clicks may be an adaptation to reduce predation by killer whales, which rely on acoustic cues to find their prey (e.g., Andersen and Amundin 1976; Clausen et al. 2010; Madsen et al. 2005; Morisaka and Connor 2007), but whose hearing sensitivity drops off rapidly above 100 kHz (Szymanski et al. 1999).

Furthermore, bottlenose dolphins may kill or harass porpoises (Patterson et al. 1998; Cotter et al. 2012), and while porpoise clicks are within the hearing range of bottlenose dolphins, they are highly directional and relatively quiet, thus limiting the likelihood that they may be detected by other animals (Clausen et al. 2010).

3.6 Family Kogiidae

The Family Kogiidae contains just two species in one genus, *Kogia:* the dwarf and pygmy sperm whales. No studies have been carried out on their communication, and only a handful of recordings of *Kogia* vocalizations have been made (e.g., Marten 2000; Madsen et al. 2005). Both Marten (2000) and Madsen et al. (2005) found that *Kogia breviceps*, the pygmy sperm whale, produced narrow band high frequency (NBHF) clicks, similar to those reported for porpoises. As discussed above for porpoises, Madsen et al. (2005) speculate that these NBHF clicks may take advantage of a low-noise window at around 100 kHz, and/or may be an anti-predator adaptation.

3.7 Families Iniidae, Pontoporiidae, and Platanistidae

The remaining odontocete families are commonly grouped together as river dolphins, although not all are river dwellers; these are the Families Iniidae, Pontoporiidae, and Platanistidae. The Lipotidae, which contained the baiji, or Yangtze river dolphin, was recently declared extinct (Turvey et al. 2011). Several studies have described characteristics of river dolphin echolocation signals; Jensen et al. (2013) reported relatively low amplitude and low frequency signals from the Ganges river dolphin (Family Platanistidae), in contrast to the narrow band high frequency (NBHF) signals seen in Family Pontoporiidae (Melcón et al. 2012). Very few studies have looked at communicative signals of river dolphins. Podos et al. (2002) reported "heterogeneous series of short-duration notes" from the Amazon river dolphin, *Inia geoffrensis,* that were very different in structure to delphinid whistles. Although they found that these sounds were associated with foraging dives, their function remains unknown.

4 Conclusion

It will have become apparent to the reader that little is known about communication in the vast majority of cetacean species. The challenges involved in studying production and reception of signals in cetaceans are daunting; not only is the vocalizing animal difficult to localize, but the intended recipient may be miles away, or even if close by, is likely not visible to human observers. As mentioned earlier, non-invasive tags that record marine mammal sounds as well as movements and depth (e.g., Johnson and Tyack 2003) have the potential to increase our knowledge of communication, although this technology too is limited if not combined with behavioral observations and basic information such as group size and composition. In addition, these tags have so far mostly been used on larger species, and the challenges in attaching them to smaller species are substantial. Finally, the possibility that the tags themselves may affect behavior needs to be studied. All behavioral studies are also open to questions regarding the influence of the observers on the animals being observed; this may be especially true for cetaceans, which generally are observed from boats that generate potentially disruptive noise.

Even with so little data on the vast majority of cetacean species, several common themes emerge. Song, a patterned vocal sequence of varying degrees of complexity, is seen in several baleen whale species but no odontocete species to date. Among odontocetes, group or individually specific signals occur in some of the more social species such as the sperm whale, some delphinids, and possibly the monodontids. These key differences between mysticetes and odonotocetes were highlighted by Tyack (1986a), who related differences in communication to differences in social structure. Song plays a role in reproductive advertisement, whereas group and/or individually specific signals serve to maintain stable social relationships. Although some stable associations have been described among individual mysticetes (e.g., Weinrich 1991), mysticete social structure is less characterized by such associations than that of many odontocetes. The resident fish-eating killer whales off of Vancouver, British Columbia, live in the most stable groups known for any mammalian species, and long-term, stable associations have also been well described in sperm whales and several dolphin species (Mann et al. 2000).

Another recurring theme among cetaceans is the occurrence of narrow band high frequency (NBHF) clicks. These clicks, whether used for echolocation and/or communication, have been described in four diverse families: Phocoenidae, Kogiidae, Pontoporiidae, and Delphinidae (members of the genera *Cephalorhynchus* and *Lagenorhynchus*; Dawson 1991; Kyhn et al. 2010). As mentioned earlier, the acoustic crypsis hypothesis proposed by Madsen et al. (2005) and Morisaka and Connor (2007) proposes that these NBHF clicks (with an accompanying lack of whistle production) may be an anti-predator adaptation. Similarly, the tendency for some beaked whale species to vocalize only at depth has also been suggested to be an anti-predator adaptation (Aguilar de Soto et al. 2012; Dunn et al. 2013). These vocal adaptations in 5 of the 13 odontocete families speak to the strong selective pressure induced by predation.

Even with the immense challenges involved, there are huge potential benefits, both applied and basic, to studying cetacean communication. Applied research on effects of increasing levels of noise on cetaceans is urgently needed, but it is difficult to assess these impacts without more knowledge of how (e.g., what signals, over what ranges) and why (e.g., feeding, breeding, maintenance of social bonds) they communicate. With respect to more basic research questions, cetaceans are one of the few mammalian groups in which vocal production learning (Janik and Slater

2000) plays a role; such vocal learning skills have been so far documented in three cetacean families (Balaenopteridae, Monodontidae, and Delphinidae). An understanding of the role of vocal learning in cetacean communication could provide insights into the driving forces behind its evolution in diverse groups, thus potentially providing insights into the evolution of human language. Advanced cognitive skills are apparent in at least some cetacean species, and study of their communication may provide a window into the nature and flexibility of these skills (e.g., Griffin 1984). Future studies of communication promise to deepen our understanding of this fascinating and understudied group of mammals.

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Chapter 17
Communication in the Ultraviolet: Unravelling the Secret Language of Fish

Ulrike E. Siebeck

Abstract Ultraviolet vision is found in animals from across the animal kingdom including some mammals but excluding primates such as humans. Working under the assumption that what is conspicuous for us should also be conspicuous for other animals; scientists have often overlooked the role of UV vision in animal ecology. Indeed, despite the discovery of UV sensitivity well over a century ago, it has only been in the last 30 years that theoreticians and behavioural scientists have begun to interpret the world through the eyes of other animals, including the role UV light plays in signalling. Here, I discuss the conditions necessary for UV communication, focussing on its use in fish. I then go on to describe progress on the role UV plays in the language of fish.

1 Introduction

Fish have well developed sensory systems, such as olfaction, hearing, lateral line and vision. The corresponding cues of smell, sound, water movements and light (i.e. reflected light or colour signals) are all used for communication between and within species. Each of these cues has a different working range and is useful over different spatial and temporal scales. Water movements contain information about close range objects, such as other fish or obstacles and are particularly useful for fast direction changes in schooling fish. Olfactory cues can disperse over large distances and fish can follow a plume to its source. The speed of sound is five times greater in water than in air and attenuation is such that, in open water, sound can travel large distances. In shallow reef environments however, sound is most useful at close distances as sound signals are rapidly attenuated due to many boundaries, such as the reef structure and the surface of the water. Many fish produce sound and use it

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for communication during territorial interactions and courtship. The range of visual signals is restricted to meters to tens of meters at most depending on the clarity of the water. The use of visual signals has the great advantage that such signals are highly directional and can be detected rapidly, which is particularly important in habitats with high densities of fish, such as coral reefs. The visual system of fish develops rapidly after hatching (in some cases even before) and visual signals have been shown to be important for a large range of behaviours including feeding, predator avoidance and communication.

For a long time, it was assumed that other animals see the world in much the same way as we humans, and some people are still surprised to learn that other animals are sensitive to different parts of the spectrum. What is more, these animals often possess a greater selection of photoreceptors with different spectral sensitivities (for an extreme case see mantis shrimps; Cronin et al. 1994), meaning that they have the capacity to see the world in both different and often richer colours than we do. In the late nineteenth century, John Lubbock discovered that ants as well as small crustaceans could see outside the human visible range. He demonstrated this by splitting the spectrum of sunlight into spectral bands with a prism and recording which colour light (spectral band) the animals preferred and avoided. Ants (*Formica fusca, Lasius niger*) repeatedly removed their eggs from areas illuminated with ultraviolet light and, similarly, the crustacean *Daphnia pulex* avoided ultraviolet illuminated areas of an aquarium (Lubbock 1875, 1888).

In the 1930s, Merker published a series of works on ultraviolet sensitivity in animals, including several species of freshwater fish (Merker 1932, 1937, 1939). It took another 50 years before the first reports were published in which ultraviolet sensitive photoreceptors in fish were characterised (Avery et al. 1982; Harosi and Hashimoto 1983; Neumeyer 1984; Hawryshyn and Beauchamp 1985; Douglas 1986), which then triggered further research into UV sensitivity in fish (for review see Losey et al. 1999). UV sensitivity was also found in more invertebrates (von Frisch 1953; Autrum and von Zwehl 1964; Silberglied 1979; Koehler et al. 1987; Menzel et al. 1988; Cronin et al. 1994), and many other vertebrates, such as amphibians and reptiles (Govardovskii and Zueva 1974; Arnold and Neumeyer 1987; Perry and McNaughton 1991; Fleishman et al. 1993; Loew et al. 1996; Sillman et al. 1997), birds (Huth 1972; Goldsmith 1980; Chen et al. 1984; Palacios and Varela 1992; Bennett 1994; Bennett et al. 1996) and a few mammals (Jacobs et al. 1991; Jacobs 1992; Jacobs and Deegan 1994; Winter et al. 2003). In fact, looking across a wide range of species, UV sensitivity appears to be present more often than not, both on land and in the aquatic environment. This may not be surprising, considering that most UV sensitive pigments have been shown to be ancestral pigments that were lost in some animals, including birds (which regained UV sensitivity later) and man (for review see Hunt et al. 2001). UV sensitivity in teleost fish appears to be directly inherited from the ancestral pigment.

Interestingly, despite the knowledge of UV sensitivity in many animals, a large range of works continue to assess animal colours from the perspective of the human visual system. In early 1990s this flawed approach was so widespread, particularly in studies of sexual selection in birds, that it prompted the publication of a document, which not only pointed out the problem but also what is needed to be done to overcome it (Bennett et al. 1994).

I am often asked how we can test for something we cannot see and in the following section I will go through the different parameters that need to be considered for an investigation of underwater UV communication. Communication requires at least two participants, a sender and a receiver, as well as a signal or language that both are able to create, detect and understand. For an investigation of UV communication, we therefore need to understand UV light and how it is affected by water, how UV signals are created and transmitted between sender and observer, how animals detect and analyse UV signals and, then finally, we can look at the functional significance of UV signals (Lythgoe 1979).

2 The Communication Medium – UV Light

The sun emits radiation spanning a large range of wavelengths from radio waves to γ-rays. Fortunately for all life on Earth, the atmosphere filters, or attenuates, most of the deleterious short- wavelength light (Tett 1990). The long-wavelength part of the sunlight spectrum is also reduced, so that the surface of the Earth is illuminated by light with wavelengths ranging from 290 nm to about 3,000 nm. Our eyes can detect light with wavelengths between 400 and 700 nm, which is why we have labelled this part of the spectrum, somewhat misleadingly, “visible light”. Maybe some of the mistakes in the literature could have been avoided, if we had simply named this spectral range “human visible light”. Wavelengths between 290 and 400 nm belong to ultraviolet radiation, or UVR (UVB 290–315 nm and UVA 315–400 nm as defined by the International Commission on Illumination, or Commission Internationale de L’Eclairage, C.I.E.), and wavelengths between 700 and 3,000 nm belong to infrared light, or IR.

Water also acts as a filter, and as a consequence, the spectrum of light is further reduced (in intensity as well as spectral range) with increasing depth (Jerlov 1976). How exactly the light spectrum changes, depends on the water quality, i.e. the amount and type of dissolved material (Jerlov 1976). A common assumption is that UVR is not transmitted well by water and therefore not relevant to fish. This may be true for tannin-rich lakes or eutrophic waters. In clear waters, however, such as present around coral reefs, or in oligotrophic lakes, both UVA and UVB are transmitted to depths rich in fish life (Siebeck and Marshall 2001; Tedetti and Sempere 2006; Fig. 17.1a), at intensity levels that can negatively affect the health of fish (Sweet et al. 2012).

Short wavelength light is scattered more strongly than longer wavelength light, which is why we go to great lengths in photography, for example, to remove UVR with lens coatings and filters, in order to improve the clarity and contrast in our photographs. On the other hand, long wavelength light is absorbed more strongly than short wavelength light. Put together, this leaves a small spectral band of light that is least attenuated. In clear oceanic waters, the wavelengths best transmitted are

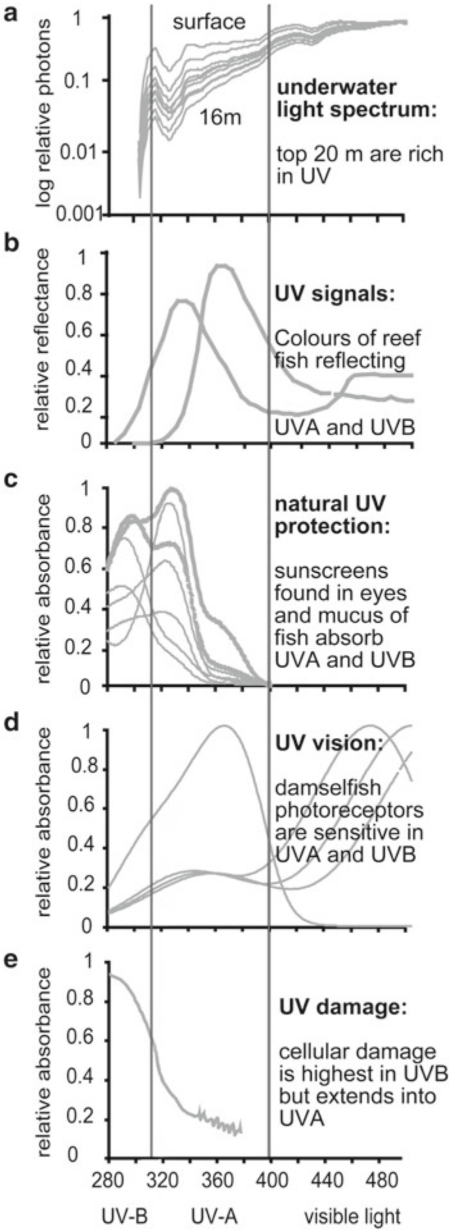

Fig. 17.1 Summary of the various parameters important for a comprehensive analysis of underwater UV communication. (**a**) Light environment on a coral reef. Different curves show light environment at different depth from surface to 16 m, at the Cobia Hole, Lizard Island, Australia. (**b**) UV colours of two reef fish (*P. amboinensis* and *A. leptacanthus*) with near pure UV colours. (**c**) Absorbance spectra of 'natural sunscreens' found in mucus and eyes of many fish. (**d**) Absorbance spectrum of the UV cone as well as beta band absorbance of the other cones of *P. amboinensis*. (**e**) DNA absorbance spectrum. The two lines demarcate three spectral regions, UVB (<315 nm), UVA (315–400 nm) and human visible (>400 nm)

475–480 nm meaning that it is these wavelengths that reach the greatest depths (Jerlov 1976).

The scattering of short wavelength light has implications for the range over which UV signals are suitable for communication. A clear crisp image of a UV signal is only available if the sender and receiver are close together. With distance, UV signals will appear increasingly blurry, thus limiting the amount of detail and hence the information that can be conveyed. On the other hand, there is also an advantage of this effect, namely, that unintended observers in the distance, such as predators for example, are less likely to see and be attracted by the signal exchange.

3 The Vocabulary – UV Colours

When light encounters an object, it is reflected, absorbed and/or transmitted depending on the properties of the object. While the colour of an object is determined by the spectrum of light it reflects, it is important to remember that colour and reflectance are not synonyms. Reflectance describes a physical property of an object while colour is the interpretation of this physical property by the visual system and brain of an observer. The reflectance of an object can be quantified with spectro-radiometric methods (Marshall 2000b) while the perceived colour cannot easily be quantified and varies between different observers. Despite these perceptual differences between observers, we have developed labels for different wavelength spectra so that we can at least talk about our interpretations of reflected light, i.e. colours. Since I anticipate the readership to be largely human I will use those labels (i.e. red, green, blue etc., instead of wavelength ranges) in the remainder of this chapter.

Colour patterns found on fish are created by two different mechanisms that can occur in combination, or isolation of one another. Specialised colour cells, or chromatophores (xanthophores: yellow; melanophores: black; leucophores: white; erythrophores: orange/red, and very rarely also cyanophores: blue) in the dermis of the fish either contain pigment or reflective/refractive structures (iridophores: iridescent colours, most blues and UV) (Cott 1940). Recently, two novel types of chromatophores have been described, erythro-iridophores, which contain both pigment and reflecting platelets (Goda et al. 2011) and chromatophores which contain fluorescent red pigment (Wucherer and Michiels 2012).

Blue and UV colours are generally of structural origin (for detailed review of blue colours see Bagnara et al. 2007). A true blue pigment colour has so far only been found in callionymid fish (e.g. the mandarin fish, *Synchiropus splendidis*; Goda and Fujii 1995). Structural colours are created by interference phenomena, similar to the colours on butterfly wings (e.g. Ghiradella et al. 1972). Stacks of crystals, usually guanine, with a high refractive index are interspersed with cell material of low refractive index and are thought to be responsible for the wavelength specific reflection of light. The distance between the layers determines which wavelengths are reflected, the smaller the distance, the shorter the reflected wavelengths (Land 1972). Some fish are known to be able to control the distance between the layers and can use this mechanism to rapidly change colour from the UV through to purple (damselfish *Pomacentrus amboinensis*, Siebeck unpublished results; Fig. 17.2), to blue-green (damselfish *Chrysiptera cyanea*, Kasukawa et al. 1986 and *Pomacentrus coelestis*, Siebeck unpublished results; Fig. 17.2); or even through most of the spectrum to red (e.g. paradise whiptail, *Pentapodus paradiseus*, Mäthger et al. 2003).

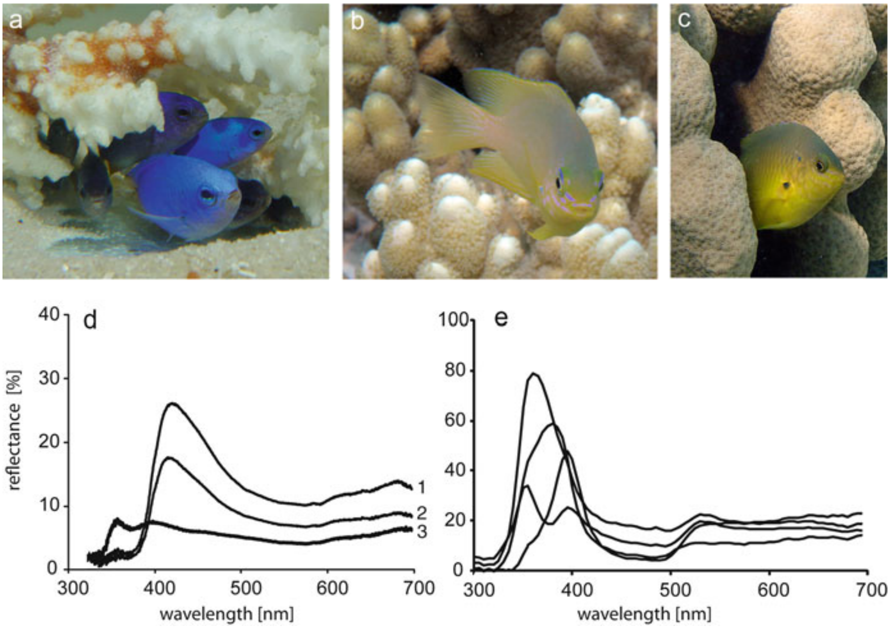

Fig. 17.2 Colour change in damselfish. (**a**) Seven *Pomacentus coelestis* specimens displaying a range of colours from *bright blue* through to *UV-black* (corresponding reflectance is given in **d**). *P. amboinensis* with purple facial patterns (**b**) and (**c**) *P. amboinensis* with UV facial pattern invisible for human eyes (corresponding spectral reflectance is given in **e**). (**d**) Spectral reflectances of three stages during the colour change of *P. coelestis*: 1, *bright blue*; 2, *dark blue*; and 3, *UV black*. Whenever a fish started to leave the shelter it changed colour from *UV black* to *bright blue* in around 2–3 s. It appears that *UV-black* is used for camouflage in this species (personal observations) and (**e**) spectral reflectances of the facial pattern of *P. amboinensis* from purple (peak at 400 nm) to UV peak at 360 nm

Many fish have UV-reflective patterns or patches on their bodies (e.g. Macias Garcia and de Perera 2002; Kodric-Brown and Johnson 2002; White et al. 2003; Siebeck 2004; Leclercq et al. 2010). In most cases, UV reflection is paired with reflection of longer wavelengths, such as a blue, green, yellow or red (Marshall 2000b) so that UV-blind animals can see a pattern/patch but will perceive it to be of a different colour than that seen by UV-sensitive animals (Fig. 17.3). Few fish have been described that have body areas which only reflect UV light and thus, that have patterns that are invisible to UV-blind animals (*Apogon fragilis*, Marshall 2000b; *Pomacentrus amboinensis* and *Apogon leptacanthus*, Figs. 17.1b and 17.3a). As our visual system is not sensitive to UVR we have to use specialised equipment to make these patterns visible. A possible reason of why so few of these pure UV patterns are known is that they are difficult to detect for us UV-blind creatures, and that they may not always be present as some fish can change colours and may switch their UV colours off.

Colour change is a common phenomenon in teleosts fish. Colour changes happen in response to the environment (e.g. a dark fish will pale if placed into a white bucket), as part of behavioural interactions and communication, as response to the

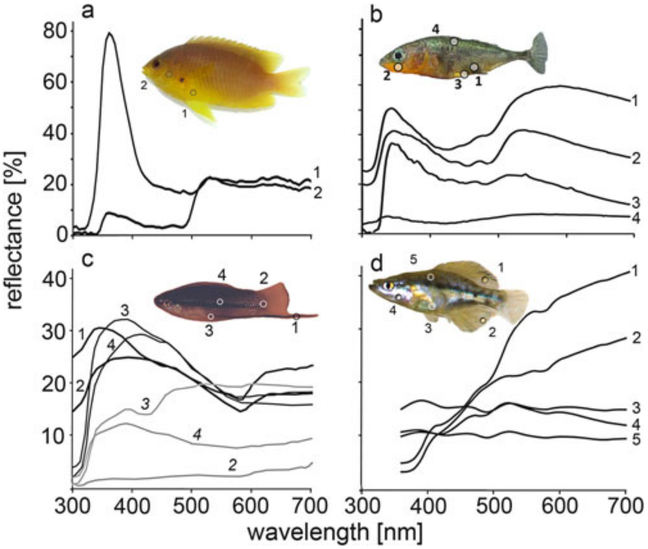

Fig. 17.3 Spectral reflectances of (**a**) Ambon damselfish, (**b**) Three-spined sticklebacks, (**c**) Swordtails and (**d**) Amarillo fish. In each panel, corresponding numbers cross-reference the spectral curve with the location of the measurement on the fish. The two sets of numbers for the Swordtails indicate spectral measurements of male (*black, normal*) and female (*grey, italics*) fish (Data and image for three-spined sticklebacks were kindly provided by Dr. Rick, for swordtails by Dr. Cummings and for Amarillo fish by Dr. Macias Garcia)

illumination (sun tanning) and during ontogenetic development (Leclercq et al. 2010). Some types of colour changes are under the control of the animals, e.g. those during behavioural interactions, while others, such as ontogenetic colour changes, or sun tanning (melanin dispersion in response to UV exposure) are not. Colour changes can be achieved by dispersing or concentrating pigment granules within the chromatophores, or by changing the distance between the crystals in the multilayer stacks within the iridophores. The Ambon damsel, *Pomacentrus amboinensis*, for example, can shift the peak reflectance of its UV patterns from 370 to 400 nm (Fig. 17.2, Siebeck unpublished results). Seen from the perspective of UV-blind animals, these fish can effectively switch their patterns on and off by shifting them from visible to UV colours. The function of this is currently unknown but it is possible that the animals modulate the distance over which their patterns can be seen in this way (violet light is less scattered than UVR and thus useful over larger distances).

While we can make UV-reflective areas visible with the help of technology, what a UV-yellow or UV-blue etc. looks like to a UV-sensitive animal is just about impossible to imagine for UV-blind creatures like us. We are not only missing a colour but a whole colour dimension. Consider the world from the perspective of a human dichromats (people with extreme red/green colour blindness). Dichromats see colours completely differently compared to human trichromats (normal red, green and blue spectral sensitivities) and they would struggle to imagine how striking a poppy field in flower looks like to a trichromat.

4 Signal Detection – UV Sensitivity

4.1 Ocular Media Filters

The light spectrum is further reduced by the various structures in the eyes of an observer. The ocular media (cornea, lens and humors) of fish, often contain UV-absorbing pigments that can heavily filter the light available for vision (Merker 1937; Dunlap et al. 1989; Siebeck et al. 2003). A survey of over 200 species of reef fish showed that around half of the species do not transmit UV through their ocular media and are therefore unlikely to be sensitive to UV light (Siebeck and Marshall 2000, 2001, 2007). The other half, however have ocular media that transmit UV to various degrees through to the retina and therefore have the potential for UV vision. Measuring the ocular media transmission is a useful tool for the assessment of the potential for UV communication in any species, as Merker pointed out as far back as 1937 (Merker 1937; Fig. 17.1c).

Interestingly, the presence of UV-reflective patterns is not indicative of potential UV sensitivity (Marshall et al. 2003). Many fish with UV-reflective patterns have UV-absorbing ocular media and are thus not able to see the full spectrum of their own colours. It is unclear what function, if any, their UV colours might have. One can speculate that UV reflectance might enhance the contrast, and with that the conspicuousness, between colours of their body patterns, which may perhaps be useful to advertise territory ownership or fitness to UV-sensitive competitors.

By the same token, the mere presence of UV-transparent ocular media does not predict the presence of UV-reflective colours in fish. This finding can be explained more easily, as communication is not the sole function of UV vision. UV-sensitivity has been found to be important for prey detection in planktivorous fish (Browman et al. 1994; Flamarique 2013) and may also be important for the detection of polarised light, which in turn may help fish orient during their pelagic larval phase (Leis et al. 2011), and potentially also help them detect and avoid dangerous levels of UV radiation.

4.2 Photoreceptor Spectral Sensitivities and UV Vision

The retina contains light sensitive photoreceptor cells, which are the sensory structures ultimately responsible for vision as they convert quanta (photons) of light into electrical impulses, the language of the nervous system and brain. Like humans, fish have a duplex retina with rods (scotopic, or dim light vision) and cones (photopic, or bright light vision). Unlike humans, fish possess two morphological cone types, double and single cones, which are arranged in regular mosaics (Collin and Pettigrew 1988). Depending on the type of visual pigment they contain, cones can be further classified into different spectral classes. Visual pigments are all based on the same structure of a chromophore attached to an opsin protein. The different sensitivities of visual pigments are due to differences in the amino acid sequence of the opsin protein and the type of chromophore (Hunt et al. 2001). Opsins in the long-wavelength sensitive class (LWS) maximally absorb at wavelengths between 495 and 570 nm, in the middle-wavelength sensitive (MWS/RH2) class between 470 and 530 nm, in the short-wavelengths sensitive (SWS) class between 415 and 480 nm and in the UV/Violet-sensitive (VS/UVS) class between 355 and 435 nm (Bowmaker 2008). Molecular interactions between the chromophore and the opsin are responsible for the fine-tuning of the specific absorption peak of each visual pigment (Kochendoerfer et al. 1999). The photoreceptors sensitivities of teleosts fish are often matched to the light environment of their habitats (Marshall et al. 2006; Shand et al. 2008). This is either achieved by fine-tuning the spectral sensitivities and/or by expressing different combinations and numbers of visual pigment classes (Bowmaker 2008; Hofmann et al. 2009). The number and type of expressed visual pigment classes can change throughout ontogenetic development and often coincides with changes in habitat or lifestyle. Most of these spectral sensitivity changes involve UV cones, which can be lost in juvenile fish (e.g. salmonids, Allison et al. 2003; Cheng et al. 2006) and then sometime regained at a later stage (e.g. rainbow trout, Allison et al. 2006).

UV-sensitive cones (peak absorption: 355–370 nm; Fig. 17.1d) are single cones that, in a square photoreceptor mosaic, are found in the position of corner cones (Allison et al. 2003). In the absence of such UV-sensitive cones, UV light can also be detected via the secondary absorption peak (β-band) of longer wavelength-sensitive cones. While UVR can be detected with both systems, it can only be discriminated from longer wavelengths light if at least two spectral cone types are present, one sensitive to UVR and another one sensitive to longer wavelength light. Since photoreceptors are basically photon counters, UV photons captured via β-band absorption simply contribute to the overall photon capture of a cone principally sensitive to longer wavelengths. In other words, while photoreceptors preferentially absorb light of particular wavelengths, they do not pass on the wavelength information but only the fact that they have absorbed a certain amount of light. It is through visual processing, in the form of comparisons of the output of the different photoreceptors types that wavelengths can be discriminated and the impression of colour can be formed. In the human visual system with its three different spectral sensitivities, the output of all cones is compared in pair-wise, or opponent fashion: red versus green, and yellow (red + green) versus blue. This means that the presence of UV-sensitive photoreceptors or indeed the presence of any type of photoreceptor, does not automatically indicate that these photoreceptors contribute to colour vision. The alternative possibility is that the absorption of light by different cone types triggers some sort of wavelength specific behaviour (see Kelber and Osorio 2010 for discussion of different ‘degrees’ of colour vision).

5 Signal Exchange – UV Communication

In the previous sections, I have discussed the various basic prerequisites for UV communication. The illumination in the habitat of the communicating fish has to contain UV wavelengths, the senders have to have UV-reflective patches/patterns (of fixed or changeable reflectance) and the visual system of the intended observers has to be sensitive to UV light. Another important aspect to consider is that of signal to noise ratio, or conspicuousness.

5.1 Signals

The question of why coral reef fish are colourful has intrigued scientists for a long time and sparked various opposing hypotheses, including a function of colour as bold poster signals on the one hand (Lorenz 1962) and as method for camouflage in the natural environment on the other (Longley 1917). It seems that both were right to some extent, they simply focussed on the extremes of a range of functions that are unique solutions in the trade-off between the need to be camouflaged and to be conspicuous at the same time. One of the problems that I have previously mentioned is that much of this discussion was for a long time purely motivated from the perspective of the human visual system looking at photographs taken with artificial illumination or of fish in daylight outside the water (but see Longley 1917). This approach is flawed for many reasons detailed in Bennett et al. (1994). Colours have evolved in context of the specific visual environment and are designed for the eyes of intended observers rather than our eyes. Colours that appear bright and conspicuous to us may blend into the background and aid camouflage when seen in the natural conditions by a predator visual system etc. So we need to consider not only the correct viewing conditions, but also the visual system of the (intended and unintended) observers to understand which fish colours appear conspicuous.

A colour patch or pattern can only be seen, and thus act as a signal, if there is sufficient contrast (colour and/or luminance) between it and its background (Endler 1990). What constitutes sufficient contrast is dependent on the visual system of the observer and varies between different species. In general, high colour contrast can be achieved in at least two ways. Many colour patches or patterns are surrounded by colours that reflect in a different part of the light spectrum, e.g. blue and yellow (Lythgoe 1979; Marshall 2000b) Fig. 17.4. Alternatively, conspicuousness can be influenced behaviourally, by selecting a position in front of a specific background (Marshall 2000a). The underwater light environment around coral reefs is rich in scattered short wavelengths light, so that any UV-reflective patches or patterns that are not framed by UV-absorbing colours will be hard to detect by UV-sensitive eyes on a fish seen against an open water background. Seen against a mostly UV-absorbing coral reef on the other hand, the same fish would appear far more conspicuous to that same observer. Conversely, irrespective of whether a UV-reflective patch is framed by non-UV colours, or the entire fish is seen against a UV-rich background, will have no impact on the conspicuousness of the same fish to the eyes of a UV-blind observer.

Losey directly investigated this observer-dependent conspicuousness in a system of two species of damselfish (*Dascyllus aruanus* and *D. reticulatus*) that occur in mixed schools and that of their three potential predators *Bodianus bilunulatus*,

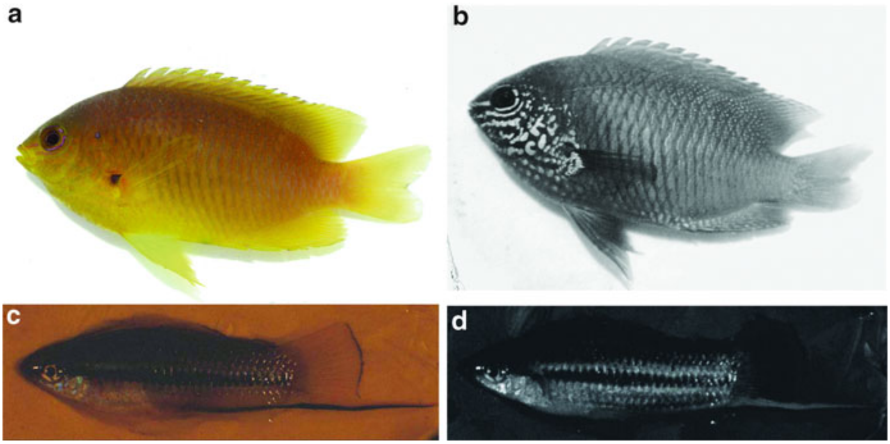

Fig. 17.4 Ambon damselfish (**a, b**) and Swordtail (**c, d**) seen in the human visible (**a, c**) and UV spectral range (**b, d**). It is important to note that the UV images show the level of UV reflectance (*white* is highly UV-reflective and *black* is UV-absorbing) and are not representative of what they might look like to a UV-sensitive fish (Swordtail images were kindly provided by Dr. Cummings)

Sphyraena barracuda and *Cheilinus bifasciatus* (Losey 2003). Using visual modelling, Losey found that *Dascyllus* conspecifics are more conspicuous to each other than they are to their predators. Also, *D. reticulatus* has a highly UV-reflective spot on an otherwise UV-absorbing flag-like dorsal fin, which is not visible to the predators and thought to be useful e.g. as a warning signal in close range communication.

5.2 UV Communication

Despite the strong interest in UV vision over the past 30 years, we still know surprisingly little about how UV signals are used in fish communication. Most groups have concentrated on demonstrating the presence of UV reflectance and/or UV sensitivity through microspectrophotometric analysis of photoreceptor sensitivities (Losey et al. 2003), or ocular media transmission studies (Merker 1937; Douglas and McGuigan 1989; Siebeck and Marshall 2000, 2001, 2007). What we do know about the role of UV signals for communication in fish comes from behavioural studies and falls into four functional categories: mate choice, territorial interactions, species recognition and schooling. In most of these behavioural experiments the light environment is manipulated with the help of UV-opaque (transmission 400–700 nm) and UV-transparent (transmission 300–700 nm) filters. Since the UV-opaque filter reduces overall quantal flux, controls include conditions with UV-transparent neutral density (ND) filters of different strengths. Ideally these are then paired with the UV-opaque filter (but sometimes two ND filters are run in separate trials), which then allows the assessment of whether brightness or wavelength is important for the observed behaviour. Another control with empty filter containers tests for potential bias of the fish towards specific light environments. Only if no bias is found can it be concluded that the fish respond to the changed appearance of a fish seen through the filter rather than to the filter itself.

5.2.1 Mate Choice

Mate choice experiments have been conducted for the largest range of fish species and a role of UV reflectance was found simultaneously in three different studies (Macias Garcia and de Perera 2002; Kodric-Brown and Johnson 2002; Smith et al. 2002). Another comprehensive study looking at mate choice in the context of intended and unintended observers followed a year later (Cummings et al. 2003), and is described in Sect. 5.3.1, below. Many mate choice experiments measure association times between females and selected males and then argue, rather than test (but see Macias Garcia and de Perera 2002), that these association times are a measure of mate choice behaviour. Another, more convincing approach that has been used is to carry out the experiments during courtship times so that the males on display show clear signs of courting (Rick et al. 2006). Ideal would be to assess the number of successful displays; i.e. assess whether a females follows the male into the nest, or shows clear courtship behaviour (Archard et al. 2009). Free interactions between males and females are required for some of these approaches which of course are not possible if we want to manipulate the light environment and control for confounding factors, such as olfactory cues.

Association times were used to investigate mate choice in the guppy by several groups. One study discovered that female guppies preferentially associated with males seen through UV-transparent rather than UV-blocking screens (Smith et al. 2002). The size of the UV-reflective area (Kodric-Brown and Johnson 2002) rather than UV brightness (White et al. 2003) was also found to be important, i.e. positively correlated with female association times. In the natural light conditions in the habitat of the fish, the quality (with respect to short-wavelength light) and quantity of light was found to be negatively correlated with male courtship displays (Archard et al. 2009). This slightly surprising result was attributed to the fact that predators tend to be more active during bright light conditions, which would make it risky for the males to display during those times. The light environment selection by males for courtship displays might explain why these fish have large UV-reflective areas. Complex patterns like those of the Ambon damselfish would be difficult to see and assess in low light conditions (Fig. 17.5). The finding that the brightness of the pattern did not influence female behaviour and the conclusion that the important information is contained in the shape/size of the UV-reflective area is supported by the visual modelling results detailed in Marshall et al. (2006) as well as the results for species discrimination detailed below (Siebeck et al. 2010). Shape and size information are reliable cues underwater, while brightness often varies rapidly due to waves and ripples at the surfaces of the water.

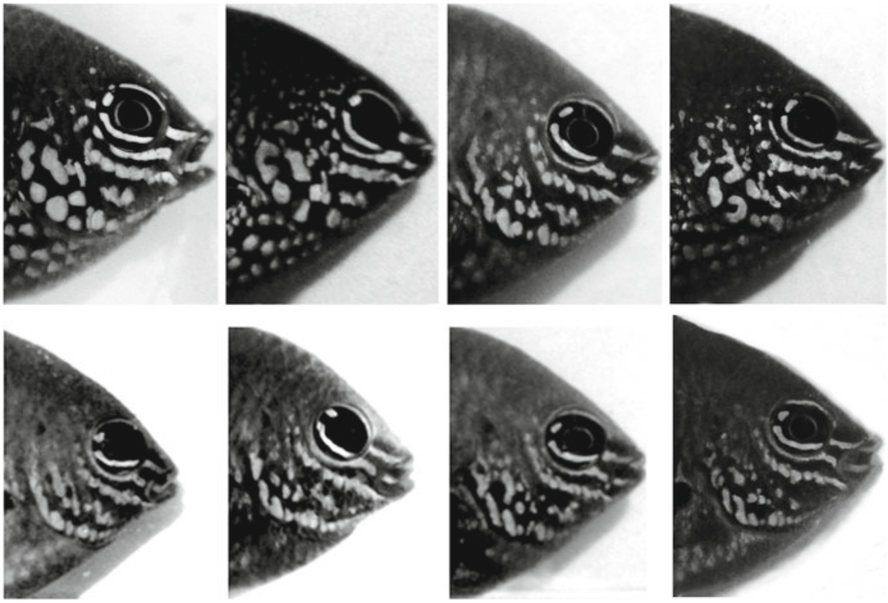

Fig. 17.5 Ambon damselfish UV facial patterns (*top row*) vary between individuals (four different fish are shown) and are different from those of Lemon damselfish (*bottom row*). Our results show that Amon damselfish can use these patterns for species (Siebeck et al. 2010) as well as individual recognition (Parker et al. unpublished results). These images were taken with a digital camera (SONY DSC-F707) and through a UV-pass filter (Oriel filters 51720 and 51124)

Amarillo fish, *Girardinichthys multiradiatus,* females also preferentially associate with males seen through UV-transmitting rather than UV-opaque dividers (Macias Garcia and de Perera 2002). A case for why this should be seen as evidence for a role of UV signals in mate choice can be made as no preference was found for females looking at a choice of males in conditions lacking UV and also for females looking at a choice of females seen through either a UV-transparent or UV-opaque filter (see Fig. 17.3d for colours). Rather than only manipulating the light environment, as was the case in all other studies, the authors also used UV-opaque powder to obscure and change the UV reflective areas. This approach could be useful for future experiments testing the importance of signal shape and/or size information in a number of different behavioural interactions.

The role of UV signals in three-spined stickleback mate choice has also been investigated. These fish represent an interesting case because for a long time it was thought that the red nuptial coloration was the key to female mate choice (for review see Rowland 1994). Similar to the studies on bird sexual selection pointed out by Bennett et al. (1994), these studies solely concentrated on human visible light and assessed stickleback colours from the perspective of the human visual system. More recently, it was discovered that sticklebacks have in fact UV reflective bodies (Rick et al. 2004; Fig. 17.3b) and that this short-wavelength component to the coloration of these fish is important for sexual selection as females prefer courting males seen through UV-transparent dividers (Boulcott et al. 2005; Rick et al. 2006) and vice versa (Rick and Bakker 2008c). The literature on the importance of red colours is not entirely wrong as demonstrated by a study in which female sticklebacks had the choice between four males, each lacking a different band of wavelengths corresponding with the maximum sensitivity of their UV, SWS, MWS and LWS cones (Rick and Bakker 2008a). When empty filters were presented, the fish spent equal amounts of times in front of each filter, however when males were presented behind these filters, females spent relatively more time next to males lacking blue or green wavelengths compared to those lacking UV or red wavelengths. This demonstrates that in these fish, both short and long wavelength components of the male coloration are important for sexual selection. Future studies on coloration need to take the entire spectrum into account when evaluating signal function.

5.2.2 Territorial Interactions

A role of UV signals in territorial interactions in fish was first demonstrated for the Ambon damselfish, *Pomacentrus amboinensis* (Siebeck 2004) and then, also for the three-spined Stickleback, *Gasterosteus aculeatus* (Rick and Bakker 2008b). In both studies, male territory owners were exposed to a choice of two size-matched male intruders either seen through a UV-transparent or UV-opaque filter. In both cases, the intruder in UV+ conditions was preferentially attacked, irrespective of brightness controls. It could be concluded from both studies that the fish were able to see ultraviolet light as they based their decisions of who to attack on the presence of UV signals rather than brightness differences. It could also be concluded that the UV components of their body coloration were important signals during male-male territorial interactions.

5.2.3 Species/Individual Recognition

We wanted to know why the intruders lacking visible UV patterns (in UV- conditions) were treated differently from intruders with UV patterns (in UV+ conditions) and hypothesised that in the absence of UV patterns the intruder would no longer be recognised as a conspecific and therefore attacked as would be a different species (Siebeck et al. 2010). To test this hypothesis we presented size-matched male intruders from two different species of damselfish that differed mostly in UV-reflective patterns to territory owners. In UV+ conditions the territory owners preferentially attacked conspecific intruders demonstrating that they could discriminate between the two species on the basis of visual cues only (the fish were presented in UV-transparent tubes) and that they indeed preferentially attacked conspecific intruders. When both species were presented in conditions lacking UV, this preference no longer existed, demonstrating that UV patterns were indeed necessary for the fish to discriminate between the two species when only visual cues were available. As a second line of evidence for the importance of the patterns for species recognition, we tested whether Ambon damselfish were able to discriminate between conspecifics and heterospecifics (*P. moluccensis*) on the basis of their facial patterns alone (Fig. 17.5). We used standardised images of the UV patterns and trained fish to associate a particular pattern with a food reward. When tested against a pattern belonging to a heterospecific, the fish were able to identify the rewarded stimulus with up to 80 % accuracy thus demonstrating that the patterns alone are sufficient for species discrimination (Siebeck et al. 2010). Recently, we repeated these experiments with conspecifics facial patterns and found that the patterns can also be used to discriminate between conspecific individuals (Parker et al. unpublished data).

5.2.4 Schooling Behaviour

An influence of UV light on schooling decisions was found for three-spined sticklebacks (Modarressie et al. 2006). Individual fish were presented with a choice of two groups of conspecific fish. One group was seen through a UV-absorbing filter and the other was seen through a UV-transparent filter. Test fish preferred to associate with the group seen through the UV-transparent filter. Despite differences in quantal flux between the two treatments, the authors concluded that wavelengths rather than brightness led to the observed behaviour. Support for this conclusion comes from the control condition in which the test fish preferred to associate with the group of fish seen through the darker of two neutral density filters (both UV-transparent).

5.3 Benefits and Costs of UV Communication

5.3.1 Benefits: 'Private' Communication?

Communication involves a sender and one or more intended receivers. In addition, in a densely populated coral reef, there may be a multitude of unintended receivers ready to eavesdrop, such as predators and/or competitors. In order to attract the attention of a potential mate or to advertise fitness and territory ownership, fish have to be conspicuous to intended receivers. However, this may have the negative consequence that a predator may also be attracted to the displaying fish. Using the ultraviolet waveband is thought to solve these opposing pressures of sexual and natural selection as it allows the sender to be conspicuous to other fish only if they are nearby, (due to the rapid attenuation of the signal) and only if they are able to see in the ultraviolet. The first effect applies to all receivers intended or unintended and limits the effective working range of UV signaling. Since courtship interactions as well as territorial interactions usually happen within close proximity, UV attenuation is unlikely to limit communication between the intended receivers. Predators, on the other hand, have to spot their prey from larger distances, at which the UV signals appear blurred and may even make the fish blend into an UV-rich scattering background. Another reason to think that UV communication may be private is that many predators around coral reefs have ocular media that strongly absorb UV light and are thus unlikely to have UV vision (Siebeck and Marshall 2001). This hypothesis of private communication has been discussed for various systems including birds and fish; however it is rarely directly tested.

One early exception was a comprehensive study on swordtails, *Xiphophorus,* which found direct evidence for private communication, (Cummings et al. 2003; Fig. 17.3c). The authors found that UV signals were more conspicuous in males rather than females (as seen by intended receivers), that females preferred males seen through UV-transparent filters, that the amount of UV in the courtship signal was positively correlated with predator density, and that predators showed no preference for fish displayed behind UV-transparent or UV-opaque filters. Put together it demonstrates that in this system UV signals indeed solve the problem of simultaneous conspicuousness and camouflage and that this is driven by predator density.

Interestingly, this is not always the case. In three-spined sticklebacks, UV signals were found to enhance predation risk, at least when a UV-sensitive predator, such as the brown trout, *Salmo trutta*, is concerned (Modarressie et al. 2013). It appears that the scattering alone is not enough to render UV communication private, but that the sensitivity of the predator visual system is the key to potential private communication. More studies are required to fully test predator sensitivity to UV wavelengths.

5.3.2 Costs: DNA Damage

It is well known that exposure to UV causes cell damage, either by direct absorption of UV by DNA (Sutherland and Griffin 1981; Fig. 17.1e), or through the indirect actions of reactive oxygen species such as singlet oxygen generated by photosensitisers (Malloy et al. 1997). UV-induced DNA lesions may cause inhibition of embryonic and larval development, decrease survival by slowing transcription and mitosis, cause cell death or at the very least, lead to energetic costs associated with DNA repair (Malloy et al. 1997).

Fish that communicate with UV signals live in UV-rich habitats. They produce UV signals by allowing UV light to penetrate their skin so that it can be reflected by the specialised structures in their skin. In order to see UV signals, fish have to allow UV light into their eyes so that it can be absorbed by UV-sensitive photoreceptors. In contrast, fish that do not rely on UV communication go to great lengths to protect themselves from UVR. They secrete mucus containing natural sunscreens (mycosporine-like amino acids, or MAAs) to cover their skin, and deposit such MAAs and sometimes also carotenoid pigments into the ocular media of their eyes in order to prevent UVR from penetrating their skin and eyes (Dunlap et al. 1989, 2000; Siebeck and Marshall 2001; Zamzow and Losey 2002; Siebeck et al. 2003). These UV defences are energetically costly, as the water soluble MAAs have to be taken up via the diet and once secreted into the mucus have to be replaced continuously (Zamzow 2004). Despite the presence of such UV defences in the coral trout, *Plectropomus leopardus,* a recent study has concluded that the melanoma found on these iconic reef fish was caused by UVR (Sweet et al. 2012). So how do our UV-communicating fish with reduced external defences deal with these dangers? The answer to this question is currently unknown but there are several possibilities.

A protective mechanism that does not interfere with UV communication is to repair the damage incurred by UV-radiation before cell death occurs. Several DNA repair mechanisms exist in fish and one of the repair mechanisms relies on an enzyme complex (photolyase) that requires UVA to repair UVB-specific DNA damage (for review see Sinha and Hader 2002). It is possible that fish that rely on UV communication have more efficient repair mechanisms to compensate for the reduced amount of protection in their eyes and skin. It is also possible that animals that can see UV light may simply avoid exposure to UV by seeking shelter and thus controlling exposure levels behaviourally. Controlling UV exposure is energetically advantageous as it reduces the need for costly repair of damage. Evidence for UVR avoidance has been found in freshwater fish, such as salmon (Kelly and Bothwell 2002) and yellow perch (Williamson et al. 1997).

6 UV Future

Despite the stabilisation of stratospheric ozone, UV levels are predicted to increase further, partly due to changes in climate patterns (longer droughts lead to less run off, increased number of cloudless days lead to UV increase) and increasing ocean acidification (less dissolved organic carbon leads to increased UV-transparency of the water; Hoegh-Guldberg et al. 2008). While UV is regularly identified as a risk factor (e.g. Halpern et al. 2008), no knowledge exists about the effects of increased UV levels on fish. Recently, melanoma was discovered in the coral trout, *Plectropomus leopardus* (Sweet et al. 2012). If UV radiation was indeed the cause, as suggested, any increases in UV radiation would be predicted to have severe effects on fish living in the relatively shallow coral reef environment. At the same time, the visibility of UV signals would be increased, which may have positive (communication range increase) and negative effects (eavesdropping is possible from a greater distance). It is unclear whether fish that rely on UV communication are more or less vulnerable to changes in UV radiation compared to animals with strong external UV protection and future research needs to address this.

Interestingly, the predicted increase of storm frequency also associated with climate change, as well as eutrophication observed along the coast and in many freshwater systems, could lead to a reduction of UV transmission in water, particularly in summer during the breeding season of many fish. A prolonged decrease in UV levels, such as would be predicted to follow severe storm activity, flooding events or algal blooms, would render signalling with UV colours limited or impossible and thus impede effective communication. The consequences of a reduction in signals important for sexual selection have already been demonstrated in Cichlids. Increased turbidity of their habitat led to a reduction in available colours for signalling which had a negative impact on diversity (Seehausen et al. 1997).

7 Conclusion

Despite the discovery of UV sensitivity over 100 years ago, it is only in the last 30 years that we have started to investigate vision outside of our own visual capabilities. One of the problems with studying UV vision and communication is that these wavelengths are invisible to us. The advancement of UV-sensitive camera systems and the development of small portable spectrometers have made it possible to detect these wavelengths and many laboratories have started to investigate UV communication. Despite these three decades of work, there remain many more questions unresolved than resolved. Where we have resolved questions, we have uncovered answers that have given us a glimpse into the complex language of colour and its role in the ecology of fish.

We have learned that UV signals are important to a range of fish and there are probably many more that we have not discovered yet. With global change and the uncertain future levels of UV radiation more studies of the costs and/or benefits of UV communication are needed. Can fish that make use of UV communication, and that therefore have reduced external natural sunscreens, survive any increases in UV radiation? When seen in the light of the recent discovery of melanoma in the coral trout, which has strong natural sunscreens, this question is of particular concern due to the fact that UV communicators allow UV into their eyes and skin to see and create UV signals. The intuitive expectation would be that UV communicators are at increased risk from UV damage. Alternatively, it is possible that the internal defences (DNA repair) of UV communicators are more efficient compared to the fish that do not communicate in the UV, and that UV communicators may therefore actually be less vulnerable than fish with high levels of sunscreen protection, such as the coral trout. In any case, fish with and without UV communication would be affected in different ways and it is possible if the current balance shifts, that future reefs will be dominated by one or the other group. Future studies are required to find out exactly how vulnerable fish are to UV radiation.

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Chapter 18
Young Squeaker Catfish Can Already Talk and Listen to Their Conspecifics

Walter Lechner

Abstract Numerous fish species are able to produce sounds and communicate acoustically. Nevertheless, hearing and sound production in fishes is poorly understood and the ontogenetic development of acoustic communication has only been studied in a few species. So far the yellow marbled squeaker catfish *Synodontis schoutedeni* is the only species that has been shown to be able to communicate acoustically across generations at all postlarval stages of development. In two further fish species the smallest size groups were not yet able to detect sounds of equal conspecifics. Increasing body size in *S. schoutedeni* correlates with increasing hearing sensitivity for lower frequencies, decreasing hearing sensitivity at higher frequencies, increasing sound pressure level and duration of stridulation sounds, and decreases in stridulation sound dominant frequency. The excellent hearing sensitivities of *S. schoutedeni*, which are characteristic for Otophysi (fish with a Weberian apparatus), is probably the reason for their ability to communicate acoustically in early stages of development.

1 Introduction

The Teleostei, or modern bony fishes, are the most species-rich group of vertebrates. They consist of approximately 30,000 known and extant species (Froese and Pauly 2012), more than of all other vertebrates species combined. Their diversity in matters of morphology and biology exceeds that of all other vertebrates by far and this diversity is also apparent in the different mechanisms for receiving and producing sounds. Fishes have evolved a unique diversity of sound detecting and sound producing mechanisms.

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1.1 Hearing in Fishes

Pliny the Elder in the first century AD was probably the first to write about fish hearing (cited after Popper and Casper 2011). In the nineteenth century Retzius showed that there is probably more anatomical variation in the ears across fish species than in all other vertebrate groups (Retzius 1881), but questions of if and how fishes can hear were not answered until many years later. In an experiment with a blinded catfish von Frisch (1923) was the first to prove, that fishes are able to detect sounds and not only just "feel" vibrations.

In contrast to tetrapods fishes do not possess external or middle ears, and without additional structures are likely only able to detect the particle motion component of sounds. Their inner ears have two main functions, they serve the "vestibular" and "auditory" senses, the first responsible for balance, the second for hearing (Popper et al. 2003). Fishes use their lateral line to detect nearby water motion, and can also feel very low frequencies with this organ (Coombs and Montgomery 1999; Slabbekoorn et al. 2010; Higgs and Radford 2013).

To be able to detect the pressure component of sounds, many fish groups have evolved connections between gas filled chambers and the inner ear which transfer sound pressure to the ear. The so called Weberian apparatus of otophysan fishes is the best known of those structures, named after a German scientist who first described it (Weber 1820). A tiny chain of one to four ossicles ("Weberian ossicles"), connected by ligaments, transfers oscillations of the swimbladder in a sound field to the inner ear and thus makes Otophysi sensitive to sound pressure, increasing their hearing sensitivity and broadening the range of sound frequencies they can detect. With more than 8,000 extant species living mainly in freshwater, the four otophysan orders, Cypriniformes (carps and loaches), Characiformes (tetras), Siluriformes (catfishes) and Gymnotiformes (South American knifefishes) comprise about a quarter of all fish species and are the dominant fish group in freshwater worldwide. About half of all freshwater fish species are Otophysi.

Several further fish groups have evolved different ways of coupling gas filled chambers to the inner ear. For example the Mormyridae (elephantfishes) with their otic bulla, the Anabantoidei (labyrinth fishes) with their suprabranchial chamber, and several species of the Holocentridae (squirrelfishes) along with some Clupeidae (herrings) and further taxa, which possess anterior extensions of the swimbladder to the ear (for overviews see e.g. Braun and Grande 2008; Ladich and Popper 2004).

In general, fishes with additional hearing structures were termed "hearing specialists", in contrast to "hearing generalists" or "hearing nonspecialists" without adaptations related to hearing. These groupings however, are inexact and should not be used (Popper and Fay 2011).

In the second half of the twentieth century scientists tested hearing sensitivities of several fish species using mainly behavioural methods. These methods were extremely time consuming and labor intensive. Towards the end of the last century invasive and non-invasive neurophysiological methods, though their results must be interpreted with care (Fay 2011), increasingly began to replace behavioural methods and made measurements of hearing in fishes more rapid and easier.

Thus, our knowledge of hearing abilities in different fish species has increased enormously in the last decades (Ladich and Fay 2013). Nevertheless, considering the huge number of fish species and their diversity, our ken in fish hearing is still very rudimental.

Fishes without accessory hearing structures are able to detect only lower frequencies up to about 1 or 2 kHz and show high hearing thresholds, while species with accessory hearing structures are able to detect frequencies up to several kHz or even hundreds of kHz in some shads (Mann et al. 1997) and show higher sensitivities; in frequencies below approximately 50 Hz hearing sensitivities converge in all groups, fishes are insensitive to sound pressure in those low frequency ranges and perceive only the particle motion components of sounds (Popper et al. 2003).

1.2 Sound Production in Fishes

Similar to their variety of hearing structures, fishes have evolved a large diversity of sonic organs, and the fact that fishes produce sounds has been well known by humans for ages. Already in the fourth century BC Aristotle described sounds emitted by a number of fish species (cited after the English translation by D'Arcy W. Thompson – Aristotle 1907). Beside accidentally generated sounds produced while swimming, feeding, or breathing, a large number of fish species have evolved different mechanisms to produce sounds for acoustic communication. The most common method of sound production in fishes is oscillating the swimbladder in various ways, either directly by rapid contractions of intrinsic or extrinsic muscles or indirectly with several different bony skeletal elements moved by muscles. The former way of drumming with the swimbladder is well known in many species of the orders Perciformes (perch-like fishes), Gadiformes (cods and relatives), Ophidiiformes, Beryciformes, and Siluriformes (catfishes) (Ladich and Fine 2006; Parmentier and Diogo 2006).

The second widely-used way for sound generation in fishes is the production of stridulatory sounds. Stridulation sounds are produced by rubbing teeth, fin spines or other bony structures against each other (Fine and Ladich 2003), e.g. rubbing the base of the pectoral fin spines within the pectoral girdle or pharyngeal teeth grating.

In some common sound producing groups like gobies and loaches, and also in some cichlids and species of further groups, the sound producing mechanisms are still unidentified (Ladich and Fine 2006; Kasumyan 2008) or have been identified lately as in Pomacentridae, the damselfish family (Parmentier et al. 2007).

1.3 Acoustic Communication

Acoustic communication in fishes has been demonstrated in contexts of agonistic, territorial, courtship and defensive behaviour (Amorim 2006; Ladich and Myrberg 2006; Myrberg and Lugli 2006) and even for species discrimination as shown in nearly related, sympatric elephant fish species (Crawford et al. 1997; Feulner et al. 2009).

Distress calls and disturbance sounds uttered by fishes are well known by fishermen who hear them when handling the catch. Many fish species are able to produce distress sounds when being attacked by predators. The purpose of this kind of fright reaction is not fully understood. No predator has been observed so far releasing its prey because it is uttering distress sounds. It is possible that distress sounds are used to warn conspecifics or even to attract further predators, which could increase the chance for escape (Ladich and Myrberg 2006).

Despite the high variability in sonic organs, the vocal repertoire of fishes is rather limited compared to sounds produced by the larynx or syrinx in tetrapods. Just one to five different types of sounds are normally produced by fishes (Amorim 2006). Nevertheless acoustic communication plays an important role in life of many fish groups.

1.4 Ontogenetic Development of Hearing and Sound Production

Our knowledge of fish hearing is rather scarce, and there are many yet unanswered questions concerning sound production and sound communication in fishes. It is thus not surprising that our understanding of the ontogeny of hearing, sound production and acoustic communication in fishes is even more limited; only few studies have been conducted so far. Concerning the ontogeny of hearing, no consistent trends have been reported. An increase of hearing sensitivities with size has been found in several perciform and batrachoidid species (Kenyon 1996; Iwashita et al. 1999; Wysocki and Ladich 2001; Sisneros and Bass 2005; Vasconcelos and Ladich 2008), but scientists have also discovered no difference in hearing sensitivity between two differently sized groups of goldfish, different size groups of zebrafish and gobies (Popper 1971; Zeddies and Fay 2005; Belanger et al. 2010), a slight decrease of sensitivity at lower frequencies with size in marine perciforms (Egner and Mann 2005; Wright et al. 2011), or only a change in the range of detectable frequencies with varying size in zebrafish (Higgs et al. 2001, 2003). Studies on the ontogeny of hearing in two catfish species of the families Mochokidae and Claroteidae revealed an increase in hearing sensitivity with size in lower frequencies, but a decrease of sensitivity at the highest frequencies tested as soon as the chain of Weberian ossicles was fully developed (Lechner et al. 2010, 2011). A further study showed lower sensitivities at high frequencies in bigger specimens of *Ancistrus ranunculus*, a loricariid catfish species (Lechner and Ladich 2008).

The development of sound production in fishes seems to be more consistent; dominant frequencies of sounds decrease with size. This decrease of sound frequency has been found in several perciform, mormyrid, catfish and toadfish species (e.g. Ladich et al. 1992; Myrberg et al. 1993; Lobel and Mann 1995; Connaughton and Taylor 1996; Crawford 1997; Henglmüller and Ladich 1999; Wysocki and Ladich 2001; Amorim and Hawkins 2005; Vasconcelos and Ladich 2008; Parmentier et al. 2009; Colleye et al. 2009, 2011; Lechner et al. 2010; Bertucci et al. 2012), most studies additionally found increases in sound pressure level, total duration, and pulse periods of sounds with size of test specimens.

Hearing and sound production are the key skills for acoustic communication. The ontogenetic development of acoustic communication has only been studied in three fish species so far. While in the croaking gourami *Trichopsis vittata* and in the toadfish *Halobatrachus didactylus* the smallest size groups tested were not yet able to detect sounds of equally sized conspecifics (Wysocki and Ladich 2001; Vasconcelos and Ladich 2008), young squeaker catfish *Synodontis schoutedeni* are capable of hearing sounds produced by their congeners of all size and age groups (Lechner et al. 2010).

2 Ontogeny of Hearing and Sound Production in a Squeaker Catfish

More than 3,000 extant species of catfish (Otophysi, order Siluriformes), belonging to approximately 36 families, are known (Ferraris 2007). Members of the African catfish family Mochokidae are commonly called "squeakers", because they produce loud stridulation sounds. This is especially true for members of the most species-rich genus, *Synodontis*, which stridulate with their pectoral fin spines. Furthermore, squeaker catfish possess a structure called the "elastic spring apparatus" which enables them to produce drumming sounds with their swimbladder (Sörensen 1895). But drumming sounds in squeakers have been reported rarely; only Abu-Gideiri and Nasr (1973) have reported drumming sounds produced by a mochokid species, *Synodontis schall*.

The yellow marbled squeaker catfish *Synodontis schoutedeni* lives in African Congo river system. It's a small to medium sized mochokid. Due to its pretty colour pattern (Fig. 18.1), maximum size of little more than 15 cm, and peaceful behaviour, it is quite popular amongst aquarists. Nevertheless, squeaker catfish are extremely hard to breed in captivity (without injection of hormones for artificial stimulation) and the authors of the ontogenetic study were lucky to get young squeakers bread successfully without hormone injection (Drescher 2007).

Synodontis schoutedeni shows excellent hearing abilities due to its chain of three Weberian ossicles and its relatively large swimbladder (Lechner and Ladich 2008) (Fig. 18.2). As a representative of the family Mochokidae it is potentially able to produce communication sounds in two ways, with its pectoral fin spine and its swimbladder (Fig. 18.2); however, drumming sounds could not be recorded in this species.

In the study of ontogeny of acoustic communication in *S. schoutedeni*, specimens from about 22 mm standard length to about 127 mm SL in six size groups from XXS to XL, were tested for their hearing acuities at 11 sound frequencies from 50 Hz to 6 kHz. Stridulation sounds of corresponding size groups, starting from about 28 mm SL in group XXS up to about 127 mm in group XL have been recorded. Hearing measurements were conducted using the non-invasive AEP- (Auditory Evoked Potential) recording technique (according to Kenyon et al. 1998) (also called ABR- (Auditory Brain response) recording technique). Because study specimens are not harmed using this method, specimens could be tested several times

Fig. 18.1 Medium sized specimen of the yellow marbled squeaker catfish *Synodontis schoutedeni* (Picture: André Werner)

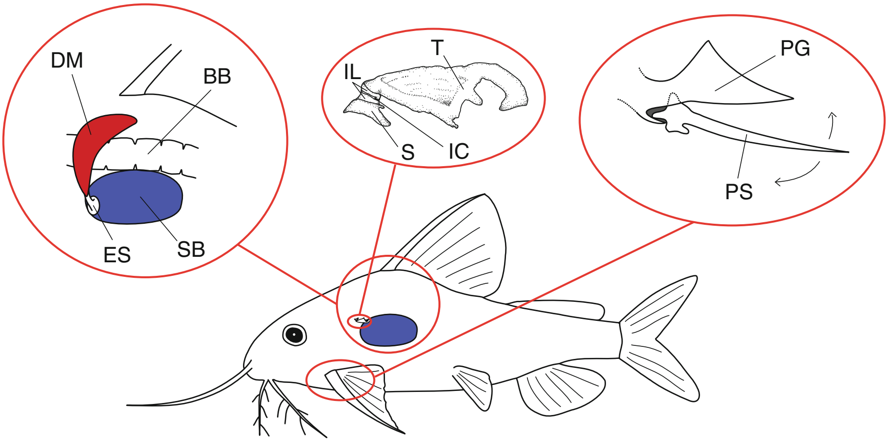

Fig. 18.2 Special adaptations of *Synodontis schoutedeni*. Chain of Weberian ossicles connecting the swimbladder to the inner ear (*center*). Elastic spring apparatus for producing drumming sounds (*left*). Pectoral spine producing stridulation sounds when rubbed in a special groove of the pectoral girdle (*right*). *BB* backbones/vertebrae, *DM* drumming muscle, *ES* elastic spring, *IC* intercalare, *IL* interossicular ligaments, *PG* pectoral girdle, *PS* pectoral spine, *S* scaphium; *SB* swimbladder, *T* tripus

for their hearing acuities during development. The smallest size group XXS consisted of juvenile specimens in postlarval stage. In a study on hearing in the African bullhead catfish *Lophiobagrus cyclurus* (Lechner et al. 2011), even smaller specimens, still in late larval stages with not yet fully developed fins and Weberian ossicles could be tested for hearing. The results in the ontogenetic study of Weberian ossicles and hearing abilities in *L. cyclurus* indicate that a fully developed chain of Weberian ossicles was present in the smallest size group XXS of *S. schoutedeni*, corresponding to the second smallest size group tested in the *Lophiobagrus* study.

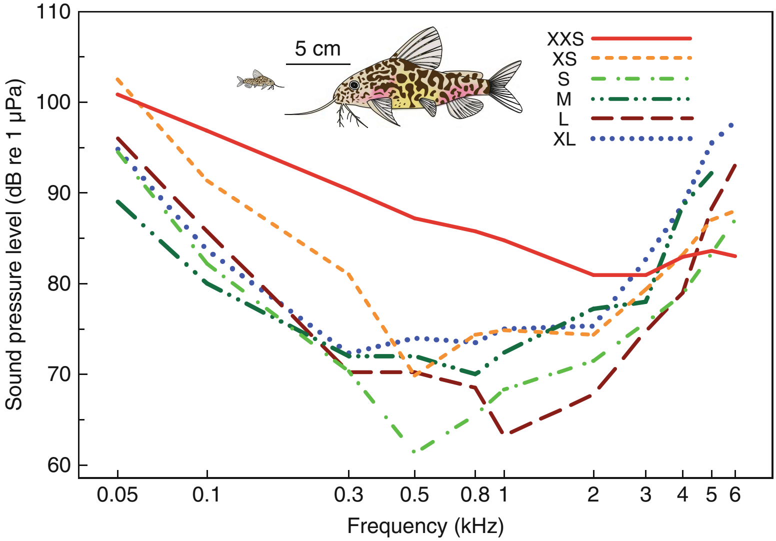

Fig. 18.3 Audiograms (hearing curves) of the six size groups XXS–XL of *Synodontis schoutedeni* tested at 11 frequencies from 50 Hz to 6 kHz. Note the higher hearing thresholds of smaller size groups at lower frequencies and the lower thresholds at the highest frequencies tested. For measures of size groups see text and Lechner et al. 2010 (Modified from Lechner et al. 2010)

All size groups of *S. schoutedeni* showed their best hearing abilities between 300 Hz and 1 kHz, with the exception of the smallest group XXS, which had its best frequency at 2 and 3 kHz. Interestingly, specimens of the small size groups showed lower hearing sensitivities than their congeners of larger groups at the lowest frequencies tested, whereas in the highest frequencies tested the results were reversed, the groups of smaller specimens showed better hearing acuity than the groups of the larger ones (Fig. 18.3). At most frequencies tested significant correlations between size and hearing could be found. From 50 Hz to 2 kHz larger catfish showed significantly better hearing, at the highest frequencies tested (5 and 6 kHz) hearing acuity of larger individuals was significantly lower than that of small individuals. At 3 and 4 kHz no correlation between fish size and hearing abilities was found (Lechner et al. 2010).

Specimens of all size groups of *S. schoutedeni* produced stridulation sounds during ab- and adduction (off and towards the body) movement of their pectoral fins (Fig. 18.4). Sounds produced by individuals in the smallest size groups were of significantly lower sound pressure level, shorter duration and shorter pulse period than sounds produced by individuals in larger size groups. Stridulation sounds of individuals in the smallest size groups were more broad band and had higher dominant frequencies, while bigger sized specimens exhibited dominant frequencies that were more pointed and which decreased significantly with size (Figs. 18.4 and 18.5) (Lechner et al. 2010).

Interestingly, all size groups showed their best frequency of hearing in the frequency range with the most energy (dominant frequency) for stridulation sounds produced by their own size groups (Fig. 18.5). Nevertheless, specimens of all size

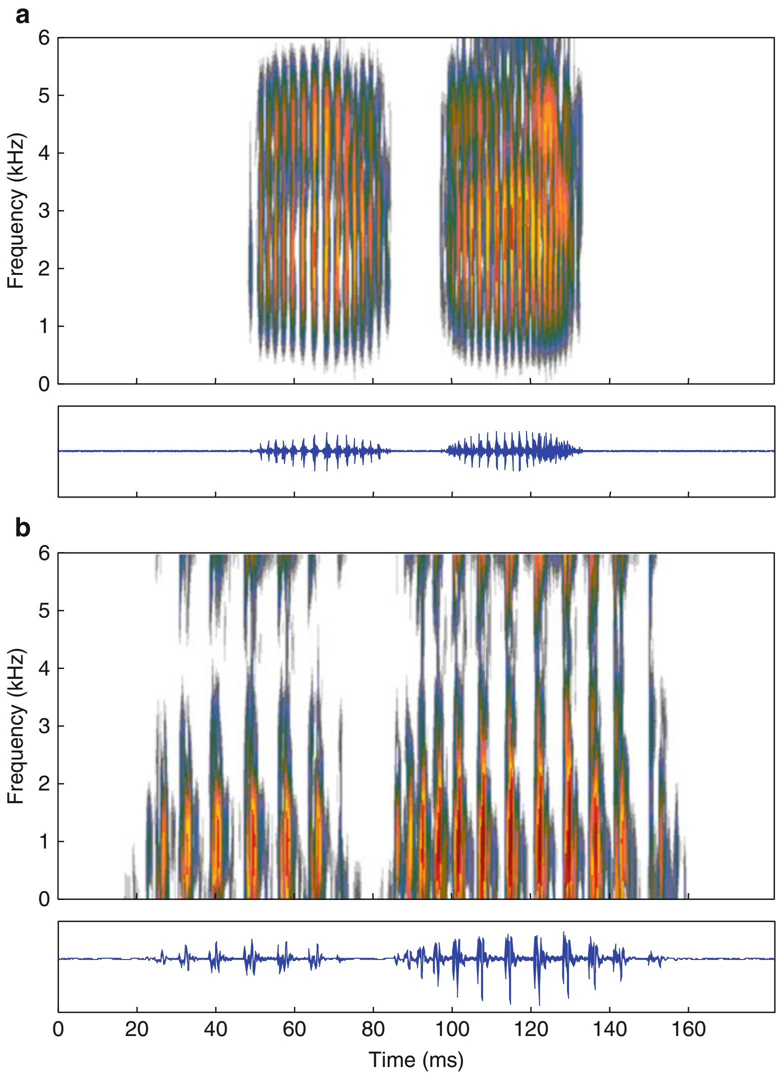

Fig. 18.4 Sonagram (*top*) and oscillogram (*below*) of adduction sounds (*left*) and abduction sounds (*right*) of a specimen of group XXS (**a**) and a specimen of group XL (**b**) of *Synodontis schoutedeni*; 44.1 kHz sampling frequency, 650 Hz (for XXS) and 600 Hz (for XL) filter bandwidth, 75 % overlap, Hanning window (Modified from Lechner et al. 2010)

groups were able to hear the sounds produced by all other size groups. Specimens of group XXS were therefore able to detect sounds produced by their own group as well as the (louder) sounds produced by the bigger groups. In addition, specimens of the largest group XL could not only hear sounds produced by congeners of similar size, but could also hear those produced by catfish of the smallest size group XXS (Fig. 18.6) (Lechner et al. 2010). This means that acoustic communication with stridulation sounds is possible between all generations of *Synodontis schoutedeni*.

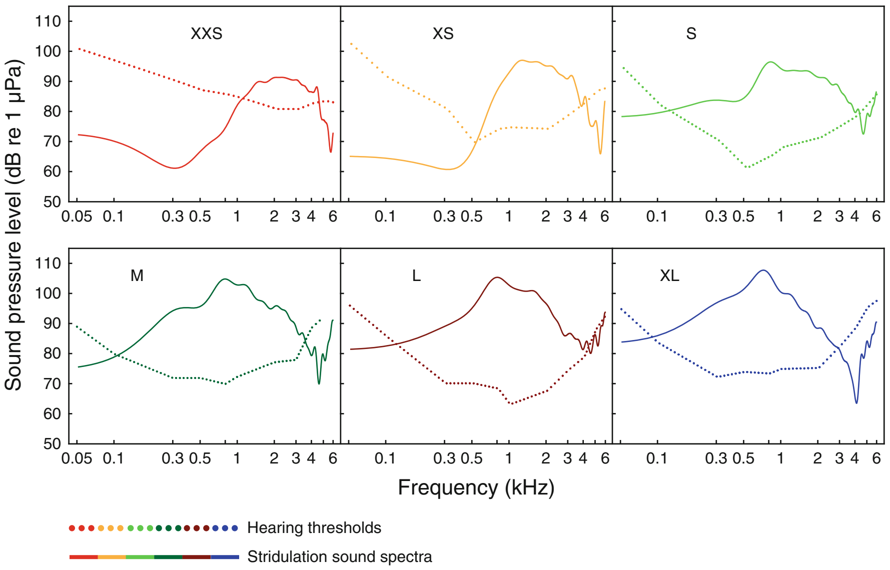

Fig. 18.5 Smoothed sound power spectra of stridulatory sounds (calculated for a distance of 5 cm from the recording hydrophone) of the six size groups compared to their auditory thresholds. For measures of sizegroups see text and Lechner et al. 2010 (Modified from Lechner et al. 2010)

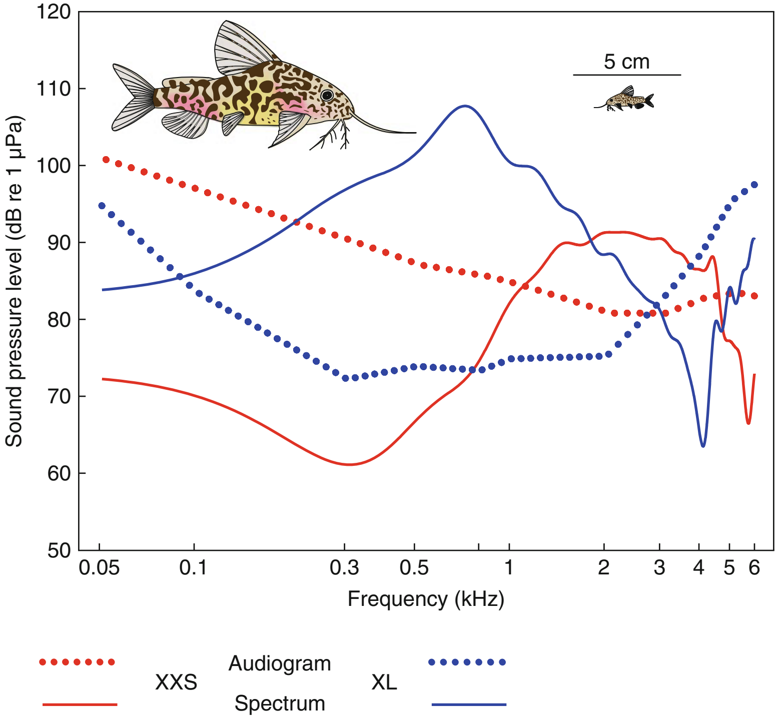

Fig. 18.6 Smoothed sound power spectra of stridulatory sounds of group XXS and group XL (calculated for a distance of 5 cm from the recording hydrophone) compared to their hearing thresholds. Note that both groups are able to detect sounds produced by specimens of their own size group as well as sounds produced by the other sizegroup

3 Conclusions

Different forms of communication are fundamental to animal behaviour. Most vertebrates can interact using visual, acoustical, chemical, and tactile modalities, and some groups can even use electrical signals (Kramer 1990; Moller 2006; Bradbury and Vehrencamp 2011). While acoustic communication is well studied and understood in birds, mammals, frogs, and many sound producing invertebrate species (Gerhardt and Huber 2002; Narins et al. 2007; Bradbury and Vehrencamp 2011), it never grabbed the attention of scientists to a similar extent in fishes. This is probably based on the difficulty for us land living vertebrates to hear underwater sounds (Hawkins 1993). Studies of underwater sounds require greater effort and are more difficult to carry out than similar studies in air (Hopp et al. 1998). Nevertheless, water is full of sounds and noise produced by animals and abiotic sources (Slabbekoorn et al. 2010). The acoustic sceneries of biotopes have considerable influence on their inhabitants, both on land and underwater. To understand and consider these bioacoustics influences, it is necessary to know, what and how participating creatures hear and talk. But our understanding of hearing and acoustic communication in fishes is currently rudimentary.

If an animal produces sounds in a specific context, it is of course of high interest for the sender that receivers are able to hear those acoustic signals. Human generated noise, or “underwater noise pollution”, deriving e.g. from shipping, recreational activities, sonar, or industrial activities (e.g. pile driving, seismic air guns), highly affects fishes and aquatic life (see e.g. Popper and Hastings 2009a, b; Slabbekoorn et al. 2010 for overviews). A very nice example of the influence of anthropogenic noise can be found in toadfish, whose intraspecific acoustic communication is impeded by the noise of ferry boats in their habitat (Vasconcelos et al. 2007).

Because hearing abilities vary greatly between different fish groups and species (Fay 1988; Ladich and Fay 2013), general statements about the effect of different kinds of noise on fishes are nearly impossible. More studies covering a broader range of the variety of hearing abilities in fishes are indispensable to improve our understanding in fish hearing. We know that different fish groups show best hearing in very different frequency ranges and also use sounds of variable frequency ranges for acoustic communication.

The study of the squeaker catfish *Synodontis schoutedeni* is an excellent example of fishes producing sounds in their “best frequencies” of hearing (or showing best hearing abilities in the dominant frequency range of their own sounds?). This is even evident at different developmental stages with stage dependent best hearing frequencies and sound characteristics (Fig. 18.5). At least some fish groups thus seem to adapt their hearing to frequencies of communication sounds (or vice versa), or even adapt communication sound frequencies to their natural habitats. This has been shown in many tetrapod species (e.g. Ryan and Brenowitz 1985; Slabbekoorn and Peet 2003) and also in fishes (e.g. Lugli 2010).

Propagation of low frequency sounds over long distances in shallow waters is rather shallow (Myrberg 1981; Mann 2006), but the majority of acoustically communicating fish species lives in rather shallow waters and many of them utter sounds of low frequencies. Thus acoustic communication is probably used over short distances in those species. The main frequencies of fish stridulation sounds are mostly in the low kHz range. This would allow communication in shallow water over larger distances than with swimbladder drumming sounds. The main frequencies of fish drums are in much lower frequency ranges and thus cannot propagate over longer distances at least in shallow waters (see e.g. Amorim 2006; Ladich and Fine 2006 for reviews and main frequencies of the sounds of vocalizing fish groups). This supports the hypothesis that stridulation sounds in catfishes are being used as alarm calls and drumming sounds are being used for nearby communication.

In contrast to the croaking gourami *Trichopsis vittata* and the Lusitanian toadfish *Halobatrachus didactylus* (Wysocki and Ladich 2001; Vasconcelos and Ladich 2008), the squeaker catfish *Synodontis schoutedeni* is able to detect conspecific sounds in early stages of development (Lechner et al. 2010). Comparing hearing abilities of squeaker catfish, croaking gouramis and Lusitanian toadfish, shows that the catfish has much better hearing acuity at most frequencies (Ladich and Yan 1998; Wysocki and Ladich 2001; Vasconcelos et al. 2007; Vasconcelos and Ladich 2008; Lechner and Ladich 2008; Lechner et al. 2010). This ability to communicate acoustically at very small size stages is probably based on the excellent hearing abilities of *S. schoutedeni* and high sound pressure levels of the stridulation sounds produced by the smallest size groups. But this is the first and so far only evidence showing that the ability to communicate acoustically is present in very young specimens. However, this is probably more a matter of very few studies conducted in this field so far than of exceptional abilities in this species. Similar studies in further vocative fish species with excellent hearing acuities would probably bring similar results. Stridulation sounds of squeaker catfish are fright reactions which are probably used to warn conspecifics of predation. Alarm calls are useful for specimens of all size groups. In contrary toadfish sounds are territorial and advertising calls; croaking gouramis use their sounds in territorial fights which are typical for adults (nevertheless, already small size stages show this territorial behaviour). The meaning of those sounds is different, maybe this is a reason for squeaker catfish to be able to detect their alarm sounds already at very young stages. It is neither necessary nor useful for toadfish and gouramis to detect conspecific agonistic and advertisement calls as very young fish.

But why do smaller specimens of *S. schoutedeni* hear better at higher frequencies than larger congeners? This is a question still to be answered. Significantly better hearing of the smaller specimens at the highest frequencies tested has been shown in *S. schoutedeni* and the African bullhead *Lophiobagrus cyclurus* (Lechner et al. 2010, 2011). Comparing hearing abilities of the pimelodid catfish *Pimelodus pictus* used in three studies (Ladich 1999; Amoser and Ladich 2003; Wysocki et al. 2009) indicates similar trends – the smallest specimens tested by Wysocki et al. (2009) showed lower hearing thresholds at the highest frequencies tested than the largest fish tested by Ladich (1999); and data of hearing in gouramis (Ladich and Yan 1998; Wysocki and Ladich 2001) also show a slight trend of better high frequency hearing in smaller specimens. The biological significance of this fact has still to be found.

Both groups, catfishes and gouramis, use air-filled cavities to aid their hearing, catfish the swimbladder and gouramis their suprabranchial chamber. The physical properties of swimbladder and connective tissues vary over the course of development, and are thus also likely to exhibit variable response properties to sound energy. This could be one reason for those findings. The interestingly congruence of best hearing and sound production frequency in all generations of *S. schoutedeni* maybe is a hint for its biological relevance.

Only one single study so far has shown, that there are fish species which are able to communicate acoustically across all generations. These new and surprising results in the study on ontogeny of sound production and hearing in the mochokid catfish *Synodontis schoutedeni* (Lechner et al. 2010) provide further evidence for many new findings researchers probably will discover in the future in the so far poorly studied field of fish hearing and sound production. The class of bony fishes is highly diverse both in anatomy and biology and so are the capabilities in hearing and sound production of the approximately 30,000 species of teleosts. General statements in fish bioacoustics are nearly impossible. Fishes are an important food source for men in all parts of the world and bioconservation and fisheries management are fields of the highest interest. So far only little attention has been drawn to factors such as "noise pollution" and fish-bioacoustics. But today, authorities and scientists more and more realize their importance. We can expect numerous new studies in these so far poorly understood fields of fish hearing, sound production and communication and probably many of those studies will bring findings as new and surprising as those of the study of the squeaker *Synodontis schoutedeni* did.

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Chapter 19
Cognition and Recognition in the Cephalopod Mollusc *Octopus vulgaris*: Coordinating Interaction with Environment and Conspecifics

Elena Tricarico, Piero Amodio, Giovanna Ponte, and Graziano Fiorito

Abstract Cephalopods provide numerous examples of behavioral and neural plasticity and richness of the behavioral repertoire that has been claimed in favour of cognitive capabilities. Here we revise the most recent knowledge on octopus cognition and recognition processes. The examination of data and observations available provide the basis for asking new stimulating questions about the cognitive abilities of octopuses and their allies and open novel scenarios for future comparative research.

1 Introduction

A rapid glance at the videos posted in YouTube over the last few years provides a large variety of characters inspired by the richness of behavioral repertoire of cephalopod molluscs, and octopods in particular. In many instances, octopus arms appear in medium shots or close-ups. Their manoeuvres assist human beings or appear in the scene to disclose objects and people thus facilitating the glance of the main 'message' to be delivered.

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The interest for cephalopods is not novel for human society. Humans made extensive use of these animals as source of food both in the past and nowadays. This is also witnessed by the very primitive and almost unchanged fishing methods utilized to catch cephalopods (Boyle and Rodhouse 2005). The long-standing tradition to use cephalopods in artistic representations are also key examples. Remarkable are figures from Middle Paleolithic and Minoan or Chiriqui civilizations (see review in Borrelli and Fiorito 2008). What probably attracted (and still attracts) people and science is the natural curiosity of these creatures. Aristotle considered octopuses stupid for the easy way humans are able to catch them by hands (Borrelli and Fiorito 2008). On the other hand, their exploratory drive is recognized as a sign of their intelligence (Mather et al. 2010). For their refined nervous system and complex behavioral machinery, cephalopods (Mollusca, Cephalopoda, Coleoidea) are considered among the smartest invertebrates, attracting the interest of animal behavior students, neurophysiologists and evolutionary biologists (review in Huffard 2013).

Intelligence of (or in) cephalopods is a debated and commonly spread topic, as represented by different web pages available in the Internet including those available in Wikipedia (http://en.wikipedia.org/wiki/Cephalopod_intelligence) or even among facebook pages (https://www.facebook.com/pages/Cephalopod-intelligence/114928831856755?nr). Wikipedia includes a series of examples to provide arguments in favour of the existence of intelligence in this taxon (i.e. predation techniques, dexterity, communication, and tool use). What anyone can learn in these pages is that cephalopod predation techniques maybe very complex as for the cases of octopuses moving between different aquaria to catch their live prey (see anedoctical accounts in Borrelli and Fiorito 2008), or the most recent case of pack-hunting in the squid (Benoit-Bird and Gilly 2012). Cephalopods, but mostly octopuses, are also known for the extreme flexibility of their arms, capable of a wide and diversified range of movements in absence of any skeletal support (e.g. Mather 1998; Sumbre et al. 2006; Margheri et al. 2011; for review see also Borrelli et al. 2006). This capacity is essential in problem solving and while exploring objects and crevices as performed during active foraging (review in: Hanlon and Messenger 1996; Borrelli et al. 2006; Borrelli and Fiorito 2008). Finally, communication via body patterns, i.e. potential signals emitted through skin (Barbato et al. 2007; Mäthger et al. 2009; Wardill et al. 2012; Zylinski et al. 2011), and the capability of tool use (see the reports by Pliny the Elder and Lady Power cited in Borrelli and Fiorito 2008; but see also Finn et al. 2009) are the classic examples of the richness of their behavioral repertoire.

Sophisticated cognitive ability is generally presumed to be derived from the demands of social groups (Humphrey 1976) and linked to a long life span. Recent studies support the hypothesis that these are not prerequisites, and that environmental pressures are also important (e.g. Milton 1988; Heyes 2012; but see also Amodio and Fiorito 2013).

Octopuses are short-living animals and many aspects of their natural habits and lifestyle are still unknown. Contrary to squids forming fish-like schools (Mather and O'Dor 1984; Boal and Gonzalez 1998; Adamo and Weichelt 1999), octopuses are typically solitary living animals (Altman 1967; Kayes 1974, but see Mangold-Wirz 1959 for *Eledone moschata*), although some species may occur in high densities (e.g. *Octopus joubini*: Mather 1980, 1982; *O. briareus*: Aronson 1986, 1989; *O. bimaculoides*: Forsythe and Hanlon 1988; *O. tetricus*: Godfrey-Smith and Lawrence 2012). The paucity and simplicity of their reciprocal interactions, such as avoidance or touches, had led to categorize them as "asocial" (Yarnall 1969; Boyle 1980; Mather 1980), with meetings being rare and sometimes cannibalistic, even in the context of mating (e.g. Hanlon and Forsythe 2008). However, at least at a certain age, individuals of *O. vulgaris* tend to overlap their home range and encounters are not a rare event (see Amodio and Fiorito 2013). In laboratory, octopuses have been described to form and maintain dominance hierarchies (*O. cyanea*: Yarnall 1969; *O. rubescens*: Dorsey 1976; *O. maya*: Van Heukelem 1977; *O. vulgaris*: Boyle 1980; *O. joubini*: Mather 1980; *E. moschata*: Mather 1985; *O. bimaculoides*: Cigliano 1993); hierarchies in this context may be an artifact of the natural territorial behavior. Indeed, crowding may change the social behavior of species (such as cats, canaries or lizards) that are solitary living or territorial in the field and form hierarchies when confined in groups (e.g. Brattstrom 1974; Leyhausen 1979). Thus, octopuses seem thus to alter their social organization from solitary to hierarchical under similar conditions, leading to hypothesize that octopus social attitude and lifestyle could be more 'plastic' than usually assumed (Tricarico et al. 2011; review in Amodio and Fiorito 2013).

Nevertheless, octopuses demonstrate a refined and extraordinary ability to adapt their behavioral repertoire to the environment and circumstances. This may have contributed greatly to their success in the competition with fishes during evolution (Packard 1972; Grasso and Basil 2009). In the wild, octopuses collect and transport, by 'stilt-walking', coconut shell halves on soft sandy bottoms and use them to build dens. They also move bipedally along bottoms using a rolling gait (review in Huffard 2013). However, one of the most outstanding expression of their phenotypic plasticity (*sensu* West-Eberhard 1989) or polyphenism (*sensu* Mayr 1963) is their capability to display several environmentally-cued phenotypes (Barbato et al. 2007; Huffard 2013). To prevent intense predation pressure (mostly from fish competitors), cephalopods evolved an effective and impressive camouflaging ability that exploits features of their surroundings to enable them to 'blend in' (review in: Hanlon and Messenger 1996; Borrelli et al. 2006). Camouflaging does not represent a limitation for communication in cephalopods (Barbato et al. 2007). The diversity of body patterns octopuses may display to disguise and to signal to 'others' (review in: Hanlon and Messenger 1996; Borrelli et al. 2006; but see also Brown et al. 2012).

Each octopus can produce tens of body patterns. Although the total repertoire is genetically endowed, these patterns – with many gradations – can be displayed according to the situation in which the animals stay at a given moment, including both the external surrounding (e.g. the environmental context, the background or the 'social' partner) and motivational state (e.g. defense, aggression, or reproduction). The effective and impressive camouflaging ability achieved through crypsis (*sensu* Endler 1991) and/or mimesis (*sensu* Wickler 1968; Pasteur 1982) is used as the most common primary defense. Visually conspicuous primary defenses appear to be rare in cephalopods (but see Huffard et al. 2010 for exceptions). Finally, exploration, defined as extracting information from the environment (*sensu* Hutt 1967), is a major force in octopus behavior, and these animals show a sequence of exploration-learning-forgetting-relearning that makes learning adaptive (West-Eberhard 2003). As mentioned, octopuses have an intrinsic curiosity and, as solitary hunters, attend to any novel object in their visual field, and forage through chemotactile exploration mostly by using their arms (Mather 1991; review in Borrelli et al. 2006). The diversified variety of receptors present in hundreds of suckers on each arm (a limited knowledge on these receptors is currently available, but see: Young 1971; Hague et al. 2013) allow animals to gather chemical and tactile information of the substrate helping them in finding hidden prey by touch (review in Hanlon and Messenger 1996).

A comparative analysis of cephalopods' habits reveals that octopus has less feeding specialization and a higher versatility in foraging than other cephalopods (Borrelli 2007; review in Amodio and Fiorito 2013). This behavioral flexibility corresponds to a marked ecological plasticity of the octopus as represented by changes in the lifestyle during development (from larval to post-metamorphosis and juvenile phases) or the horizontal and vertical migrations of individuals at different ages/stages. Dealing with different environments and being exposed to potentially different degrees of complexity increases the behavioral flexibility of these animals. As a consequence octopuses are capable of a rapid learning, as for higher vertebrates, and a sufficiently complex nervous system allows cognitive abilities to drive the evolutionary convergence of this taxon with higher vertebrates (Packard 1972; Borrelli 2007; Grasso and Basil 2009).

Dramatic evolutionary changes in the body plan and in the gross morphology of the nervous system are at the basis of the diversification of the phylum Mollusca. Their nervous system vary greatly in complexity and in the number of neurons among taxa; a complexity that reaches its highest degree with cephalopods. Ganglia becomes fused together forming "brains" whose size (relative to body weight) is comparable to that of vertebrates and positions cephalopods just below higher vertebrates (Packard 1972). In these large brains, for example in the octopus, 200 million of cells are accommodated (Young 1963).

In cephalopods, the ganglia recruited to form the central nervous system are considered homologous to the labial, buccal, cerebral, pedal, pleural, and visceral ganglia of gastropod molluscs. Differently from the typical molluscan design, in the cephalopods brain the ganglia are fused together and clustered around the most anterior part of the esophagus. The agglomeration of the ganglia, which happened by the shortening of the connectives and commissures, forms three almost distinct parts: the supra- and the sub-esophageal masses, and a pair of optic lobes lateral to the supraesophageal mass and positioned just behind the eyes. This provides cephalopods with the highest degree of centralization compared with any other mollusc. Such nervous system continues to have basic invertebrate organization: layers of cell bodies distributed externally around an inner neuropil (Young 1971; Hochner 2012). Gross morphology, neuroanatomy, and organization of the cephalopod brain have been extensively described (Young 1971; for review see also Nixon and Young 2003).

Finally, the brains of cephalopods present a marked diversification of cerebrotypes that appear to be correlated to differences in the habitats occupied within the marine environment (Nixon and Young 2003; Borrelli 2007; Grasso and Basil 2009). For example, octopods and decapods largely differ for their brachial and inferior frontal lobes; these being larger in the octopods as a consequence of their benthic lifestyle and tactile sensorial modality.

2 Neural Modulation and Sensory Modalities

The great detail of knowledge available on the morphological and functional organization of the 'brain' of octopus (review in Young 1971; Borrelli and Fiorito 2008) have been also complemented by ultrastructural studies that provided strong evidence for the existence of chemical synapses in the brain (review in Ponte 2012). The characterization of these chemical synapses is still largely unexplored (Messenger 1996). Only recent efforts increased the knowledge available on the distribution of different modulators in different areas of the brain (see citations in: Ponte 2012; Ponte et al. 2013).

On the other hand, the analysis of hundreds of lesion experiments conducted mainly on octopuses and of several dozen of serial histological sections of the brains of the animals allowed Young and coworkers to describe the functional anatomy of the nervous system and identifying a 'circuitry' leading to their visual and tactile processing (Young 1991; Borrelli and Fiorito 2008). In this circuit learning and memory is achieved by a series of intersecting matrices (Young 1991). As summarized by Young, during tactile processing the decision to grasp or reject an object by an octopus is made on the basis of the interaction of a network made up by eight matrices. The system is tuned to take any object unless pain signals are conveyed. According to Young, the interaction between positive signals and negative ones (localized in different 'modules' or lobes of the brain) plays the major role in decision making by the animal. In addition, memory traces are stored in the inferior frontal system (Young 1991; Borrelli and Fiorito 2008). Like the tactile learning system, also visual stimuli are classified and processed by a network of matrices (four). In this case the optic lobe plays a major role. The visual system is tuned to promote the animal to attack the stimulus unless unpleasant feelings are perceived. The cells from the retina reach the outer plexiform zone (in the optic lobe) where they make contact with a large number of neurons (second-order visual cells) that act as feature detectors. These constitute dendritic fields of various shapes and extensions and allow visual recognition of a stimulus. Axons of the second-order cells are arranged into columns projected toward the centre of the optic lobe where interact with similar inputs (Young 1991). Outputs of the optic lobe reach various areas of the brain with some proceeding directly to lobes controlling direct command for rapid escape reaction (i.e. magnocellular; Young 1971). Other fibres reach other sites in the brain (peduncle and basal lobes) that regulate movements, while others proceed towards other components visual system. The interaction between areas promoting the attack and those providing inhibition regulates the animal's behavior. Memory traces of visual experiences are located within the optic lobes (review in Borrelli and Fiorito 2008).

The idea promoted by Young and colleagues on the existence of multiple matrices in the central nervous system working to control behavioral responses is based on the principle that the information is processed through a series of matrices that allow signals to interact to some extent with each other and to regulate subsequent behavior for attack (visual) and take (tactile), or retreat (visual) and reject (tactile) responses. The system is tuned to facilitate exploratory behavior. According to Young the matrices in the octopus brain are analogous to the hippocampus and neocortical centers of higher vertebrates. However, a complete integration between visual and tactile information is relegated only at the level of the effectors, although limited cross-modality has been shown in few cases (review in Borrelli and Fiorito 2008).

The most recent electrophysiological studies in the octopus confirm the view that convergent evolution has led to the selection of similar networks and synaptic plasticity in remote taxa (i.e. cephalopods and higher vertebrates), contributing to the production of complex behavior and learning capabilities (for review see Hochner et al. 2006). A similar architecture and physiological connectivity of the vertical lobe system of the octopus with the mammalian hippocampus, together with the large number of small neurons acting as interneurons, suggest a typical structure with high redundancy of connections working with en passant innervations. This makes it possible to create large-capacity memory associations (review in Hochner et al. 2006). However, the analogy between the octopus and mammalian systems is not complete, the major differences being in the morphological organization and biophysical characteristics (for review see Hochner et al. 2006).

Sight is the sensory channel highly developed and abundantly used in cephalopods (review in Williamson and Chrachri 2004). Cephalopods have an excellent visual ability, rivaling that of higher vertebrates. This sensory modality provide animals with the ability to respond to many environmental and biological demands such as predation, navigation, discrimination, learning, some forms of proprioception (Mather 1991, 2008; Hochner et al. 2006; Gutnik et al. 2011) and even to communicate with each other, particularly by adopting appropriate dress (i.e. body patterns; Borrelli et al. 2006). Body patterns are produced by a combination of chromatic, textural, postural and locomotor components. Patterns, whose number varies with the species (ranging between 10 and more than 35), are neurally controlled and are produced via neuro-muscular coordination at different levels in the skin. Chromatic patterns are produced by chromatophores (providing pigmentary colors of longer wavelengths), and reflecting cells (producing white or iridescent structural colors of shorter wavelengths, i.e. iridophores, reflector cells, and leucophores). Skin texture is a further component of the animal body pattern, and is produced by contraction of muscles in the dermis, providing extreme variability of the skin ranging along a gradient from smooth, rugose to highly papillate. The graded variety of chromatic, textural and postural components provide the basis of body patterns emitted for long (chronic) or short (acute) time. Acute patterns are those that, being exhibited for seconds or minutes, animals exhibit while interacting with conspecifics or predators; they are involved in secondary defense (when a cephalopod has been detected by a predator) or in signaling (review in: Hanlon and Messenger 1996; Borrelli et al. 2006).

Communication may be public or covert, as occurs also in fish (review in Amodio and Fiorito 2013). Cephalopods have in fact the ability to detect polarized light (Cronin et al. 2003; Boal et al. 2004) that is some circumstances may produce 'hidden' signals to other species. Polarized reflective patterns are produced by animals in intra-specific context (Mäthger et al. 2009) by changing the reflecting properties of iridophores in the skin. This allows 'hidden' or 'private' communication channels since many predators (i.e. fishes) are not able to recognize these polarized patterns (Shashar et al. 1996). Sight is at the basis of social interactions (Tricarico et al. 2011).

Touch, possibly associated with taste (Wells 1963, 1978), has an important role for octopuses such as in foraging and learning, and can be involved also in social interactions. Boyle (1980) suggested that *O. vulgaris* estimates the relative size (and strength) of a conspecific by the tactile information obtained through 'Arm Alignment', and Tricarico et al. (2011) found that the individuals of the same species executed more numerous physical contacts in the presence of conspecifics never seen or met. The importance of touch for octopuses is confirmed by the large dimension of the inferior-frontal lobe, a brain region specialized for tactile learning (Young 1991; Borrelli 2007).

Social interaction is also facilitated by olfaction. Since visibility is often limited in water, chemical cues are reliable sources of information to aquatic animals even regarding the identity of conspecifics (e.g. in crustaceans; see Gherardi et al. 2010). The potential for chemoreception in octopuses is still underestimated (but see Boal 2006); however, literature provides evidence of its importance in the life of this taxon. *O. vulgaris* is capable of detecting chemical substances at a distance (Boyle 1983; Chase and Wells 1986), and – similarly to cuttlefish and squids – uses chemical signals to coordinate its reproductive behavior (Boal 2006) and in some cases also problem solving ability (e.g. *Enteroctopus dofleini*: Anderson and Mather 2010).

According to Amodio and Fiorito (2013), one of the constraint of *O. vulgaris* social learning ability is the lack of cross-modality integration when two sensory systems (i.e., visual and chemotactile) are considered (see above and Borrelli and Fiorito 2008 for a review). However, integration of different sensory channels are clearly shown in foraging activities (Mather 1991; Borrelli and Fiorito 2008) and also for social recognition sight, touch and olfaction could be part of a multimodal system of information transfer (Partan and Marler 2005), as found in other invertebrates (e.g. the stomatopod *Gonodacytlus festai*, the crayfish *Procambarus clarkii*, the American lobster *Homarus americanus* and the wolf spider *Schizocosa ocreata*; reviewed in Aquiloni and Gherardi 2008). The synchronous use of different media (i.e. multimodality *sensu* Rowe and Guilford 1999) has the clear advantage of improving detection, recognition, discrimination and memorability of signals by the receivers (Guilford and Dawkins 1991; Rowe 1999).

3 Cognition

As mentioned above, octopuses posses a well developed central nervous system with intriguing functional analogies with the mammalian brain (Hochner 2008, 2012; Shomrat et al. 2008). The three parts constituting the cephalopod ‘brain’ (i.e. optic lobes and supra- and sub-esophageal masses) represent a hierarchical functional series of units modulating all functions including visceral, sensory-motor modulation of the behavioral responses, and sophisticate learning (review in Borrelli and Fiorito 2008). These masses altogether represent more than one-third of the number of neural cells composing the nervous system of the octopus (Young 1963; Borrelli and Fiorito 2008; Hochner 2012).

This refined neuronal organization is the “hardware” regulating octopus’ vertebrate-like behavioral machinery: an expression of unusual cognitive abilities for an invertebrate. As reviewed by Borrelli and Fiorito (2008), various forms of learning have been tested in cuttlefishes, squids and octopuses. In the octopus sensitization, classical and instrumental conditioning, associative learning, problem solving are all well documented (review in Borrelli and Fiorito 2008). In addition, social learning has been reported in *O. vulgaris* and in the cuttlefish (Fiorito and Scotto 1992; Huang and Chiao 2013; for a critical review see also Amodio and Fiorito 2013). Finally, octopuses are reported to exhibit ‘personalities’ and have the capability to manipulate objects as a form of play (e.g. Mather and Anderson 1993; Kuba et al. 2006; Pronk et al. 2010). A marked inter-individual variability in behavioral performance (e.g. Borrelli 2007; Pronk et al. 2010) is provided as support of the presence of personalities in this taxon, a debated issue of increasing interest in invertebrates (Gherardi et al. 2012).

The richness of the behavioral repertoire, its flexibility, and the special adaptations and working-principle of the neural circuitry underlying behavioral responses are considered crucial elements for supposed presence of primary consciousness (Mather 2008; Seth and Edelman 2009).

4 Recognition

Little experimental data exist on social (and individual) recognition among octopuses and other cephalopods. On the basis of the available knowledge, Boal (2006) concludes that there is no robust experimental evidence for assuming the capability of recognition of species, offspring or kin in cephalopods. However, some examples may provide insights for future studies.

Among octopuses, individuals of *O. bimaculoides* are reported to be able to distinguish same- from opposite-sex on the basis of the odor as suggested by measures of changes in ventilation rate (Boal 2006). On the other hand, males of *Hapalochlaena lunulata* approach and attempt to mate either female or male conspecifics (Cheng and Caldwell 2000).

Several species are known to use body patterning as defense systems (e.g. camouflage) but also as an intra-specific means of communication, mostly in the contexts of fight and mating (Packard and Sanders 1971; Young 1962; Wells and Wells 1972; Packard 1961; Borrelli et al. 2006). Octopuses are territorial: they inhabit home dens that defend from conspecifics (e.g.: *O. briareus*, Aronson 1986; *O. bimaculoides*, Cigliano 1993; *O. cyanea*, Forsythe and Hanlon 1997; *O. vulgaris*, Woods 1965; Guerra 1981). However, neighbors typically show few agonistic interactions between each others (Kayes 1974); this seems to be related to the "dear enemy phenomenon" (i.e. the reduced aggressiveness towards neighbors in territorial animals; Fisher 1954), also reported to occur in birds, mammals, and many other vertebrate and invertebrate species (see Tibbetts and Dale 2007). Recently, Tricarico et al. (2011) showed that *O. vulgaris* can recognize conspecifics and can discriminate (and remember) familiar from unfamiliar individuals. Octopus unfamiliar pairs, i.e. pairs composed of individuals that have had no previous experience of each other, exhibit more numerous physical contacts and show shorter latencies than familiar pairs, being thus more aggressive and prone to interact. This means that this species is able of, at least, class-level or binary individual recognition (Tibbetts and Dale 2007), an ability never found in other cephalopod species. The ability to recognize and remember 'opponents' and conspecifics may have an adaptive value for *O. vulgaris*, being the likely proximate mechanism regulating the "dear enemy phenomenon" and possibly explaining the scarcity of interactions between octopuses, as observed in the field. Despite the needs of more in depth studies needed to clarify whether *O. vulgaris* is able of true individual recognition, the study by Tricarico et al. (2011) is to the best of our knowledge the sole reporting conspecific social recognition in cephalopods (see Boal 2006 for a review).

It is noteworthy to report that Anderson et al. (2010) noted that octopuses are also capable to recognize the caretakers in the laboratory. Recognition of humans among animals is a peculiar capability reported in a few species that, if confirmed in octopus, may further provide evidence of the peculiarity of these animals among other invertebrates.

5 Conclusions

Despite the abundant information we have about the nervous system and the extremely rich behavioral repertoire of octopuses (Borrelli and Fiorito 2008), knowledge about their social capabilities is still scanty. This is mainly due to the difficulties encountered in working with these extremely active animals (particularly in the field) and to the still limited attention devoted to the their social behavior, being always considered solitary. The main future challenges are to disentangle the doubts about the lifestyle of octopuses, the biological significance of social learning and behaviors, and the presence of personality. Finally, the role of the different sensory channels involved in social interactions should be also detailed. New stimulating questions about the cognitive social abilities of this taxon are thus still waiting to be addressed in order to open novel scenarios for future comparative research.

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Chapter 20
How Corals Coordinate and Organize: An Ecosystemic Analysis Based on Biocommunication and Fractal Properties

Pierre Madl and Guenther Witzany

Abstract Tropical coral reefs harbour some of the most diverse biological communities on our planet and as such rival tropical forests communities in species diversity and number of individuals from all domains. The cooperative interplay of prokaryotes, eukaryotes – particularly – the interactions among plantae and animalia shape this delicate balance, which ultimately culminate in the beauty of the coral reef biome. Some algal species but especially scleractinian corals with their interconnected organizational structure precipitate a calcium-carbonate skeleton that, upon generation after generation, form and shape structures that can even be seen from space. Yet this process is limited by light penetrability – either by depth or by visibility – that provides endosymbiotic algae with the energetic flux to convert light quanta into biochemically available energy. As a result, the sheer dominance of coral species somewhat camouflages the delicate balance between reef builders and bioerosive processes. This intrinsically interwoven biocommunicative dynamics is a key issue in order to comprehend how such structures can evolve and stretch out over 1,000s of km. Neglecting the importance of these processes compromises a full understanding of reef-dynamics and in turn promotes accelerated reef degradation due to improper use of reef resources to those who rely on them. Doing so simply increments reef instability and as such its long-term survival. This article attempts to shed light on the crucial role of biocommunicative processes and how these are manifested across taxa. In fact biocommunication is so essential in assigning each organism a specific role in this network of interdependences that the elegance even within organisms themselves – seen from a biomic perspective –attain self-similar properties. In turn and regardless of the taxa involved, self-similarity in coral reef ecosystems is an underlying feature that relies on intact and efficient biocommunicative pathways.

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1 Introduction

Although the coral reef biome seems to be an ecosystem characterized and shaped by coral species, it should not be forgotten that the underlying and thus governing network of relationships is embedded in inter- and intraspecific communication patterns. In fact, tropical coral reefs are embedded in an oligotrophic environment, with productivity so high that almost nothing is exported but recycled within the system (Veron 1995). Seen from this perspective a coral reef is one large organic body that strictly relies on the exchange of signs and signals at the physico-chemical level. As demonstrated by several studies, every coordination within or between organisms-in-populations depends on communication processes (Witzany 2010, 2011, 2012; Witzany and Baluska 2012). Although signalling molecules according their evolutionary origins and variety of adaptation processes differ throughout all kingdoms, domains, families, genera and species, certain biocommunicative patterns are quite conservative and can be found across all hierarchic levels:

- Abiotic parameters such as temperature, light, gravity, etc., affect the local ecosphere of an organism; these are sensed, interpreted (against memorized background information) and subsequently used to organize behavioural responses for optimal adaptation. This is particularly important to attain optimal energy-efficient and thus stable turnover rates.
- Transspecific communication with non-related organisms – a for example found in attack, defence and symbiotic (both microbiota as well as endosymbionts) signalling interactions.
- Species-specific communication between same or related species.
- Intraorganismic communication such as signal mediated coordination within the body of the organism. Specifically it regards cell-to-cell communication as well as intracellular signalling between cellular parts.

This article gives an overview of the manifold levels of coral biocommunicative patterns and thereby not only broadens understanding of these organisms and how they shape their own environment – but in turn are shaped by the developing reef structure themselves. This highlights its importance, without which this ecosystem would not be possible at all.

In general, the context of a given situation determines the meaning of the used signs: (a) growth and (b) development are different modes of behaviour and need other patterns of signalling than (c) defence or (d) reproductive patterns (Fig. 20.1). When dealing with growth and development one also must include the concept of self-similarity – an issue to which an entire sub-chapter (towards the end of this chapter) is dedicated to. Likewise, (e) mutualistic symbioses require different forms of coordination from those of (f) commensalism or (e) parasitism. Thus, this systematic approach of coral communication demonstrates that the meaning (semantics) of physico-chemical signals (photonic interactions and molecules) is context-dependent, and helps to give a better understanding of the full range of sign-mediated interactions of life within the coral community.

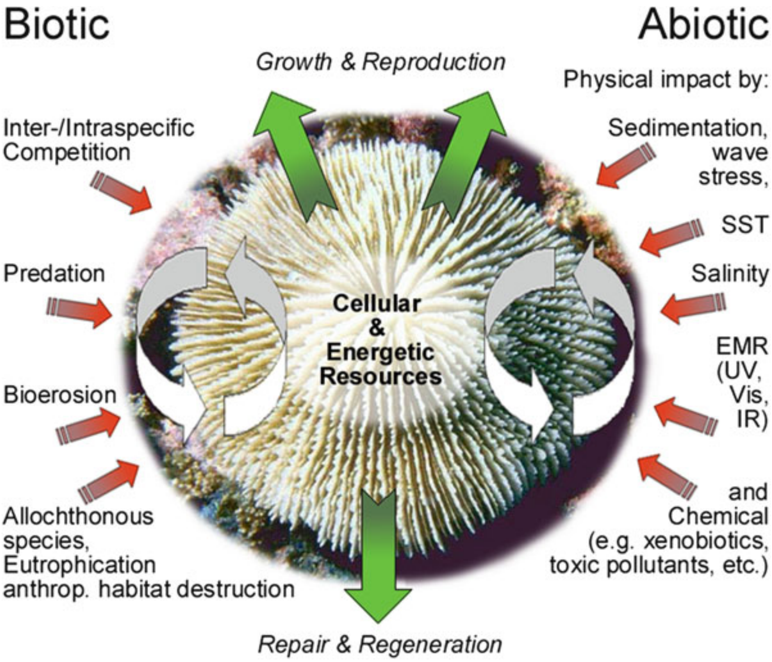

Fig. 20.1 Under optimal environmental conditions, reefs oscillate around suitable climax populations. Thereby all organism (incl. corals) take part in an efficient energy turnover that enables them to attain a quasi-stable position in the web of life and thereby improve their overall chances of survival. This net advantage is used to maintain repair-, regeneration, and growth processes and to further strengthen stress-resisting capabilities. Legend: *EMR* electromagnetic radiation, *SST* sea-surface temperature, *UV* ultraviolet, *IR* infrared (Adapted from Madl et al. 2005)

Hence, coral species diversity must be regarded as the result of these various pathways of interaction, so much so that species characterization change over distance in such a way that morphological distinctions, and therefore species boundaries, merge. Accordingly, speciation in corals is envisaged as a gradual change within lineages, yielding pseudo-species and hybrids – both elements of a reticulate evolutive concept. This concept implies that there is constant mixing of genes in the form of horizontal gene transfer (Krediet et al. 2013), uniformity of biodiversity and equal rates of speciation and extinction that leads to races, subspecies and ecomorphs (Veron 1995). In accordance, the species composition of reefs can be summarized as the outcome of (i) prevailing environmental conditions (ii) community history, (iii) ecological succession, (iv) environmental disturbance, and (v) bioerosion/coral predation (Veron 1995).

Before diving deeper into issues of coral biocommunication, a few words about the supporting framework that makes this cooperative ensemble to that what it is: one of the largest organic structures of the world. In fact, they can reach dimensions that become so huge as to be seen even from outer space.

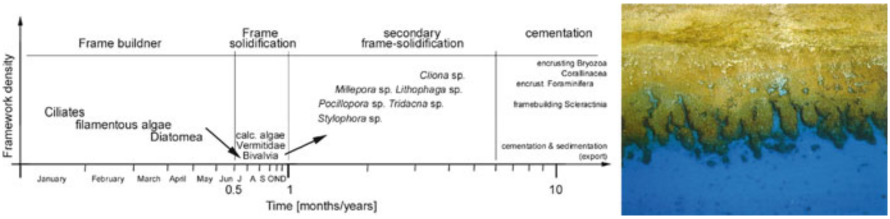

Fig. 20.2 Schematic timeline of framework building activities initiated by calcareous algae (*Porolithon*, *Melobesia*) bryozoa and foraminifera. Degenerative processes (bioerosive activity) pick up once a given substrate density is exceeded (Adapted from Velimirov, personal communication, Nov. 2011). *Insert*: section of a ribbon reef revealing self-similar properties (Spalding et al. 2001)

In order to understand the role of corals as keystone species among this biome, it is essential to comprehend that coral diversity is only possible by the common effort of organisms found among protists, unicellular algae, corallinacea, vermitids, molluscs, just to name a few that form the underlying supportive framework. Figure 20.2 highlights successive events that render the substrate ideal for colonization by scleractinia. The underlying bio-communicative vocabulary must be such as to redirect the unordered activity of a many species (many degrees of freedom) to converge towards the formation of a climax community dominated by corals (which implies a reduction to a single degree of freedom). Intermediate results are embedded in feedback loops that increase the survivability of the underlying biological matrix in such a way as to modify their activity to further strengthen the initiated path of development – just as is the case of a strange attractor in chaotic systems. Thus, sign and symbol-related vocabulary, along with feedback loops are essential elements that shape the phylo-ontogenesis of coral reef evolution. This implies that organismic activity is not random and chaotic but rather mutually enforcing. From ecological observation it is known that environmental tolerance increases with latitude, thus once a coral dominated biome is established, the persistence of long-lived, stress-tolerant species are evolutionary conservative and relative immune from extinction (Veron 1995). Even though organisms are subject to constant epigenetic modulation, this conservative property ensures that coral reefs can endure in an otherwise very dynamic biotic system over space and time.

2 Semio-Physical and -Chemical Vocabulary

Communication patterns within and among corals are rather complex. Depending on the developmental stage or other situational contexts, e.g. growth patterns, reproductive effort and tissue repair require a vocabulary that involves different physico-chemical bits of information that are necessary to perceive, interpret and react to environmental stimuli. Sensing spatial delimitations from neighbouring sessile organisms or microbiotic shifts in mucosal community composition of corals

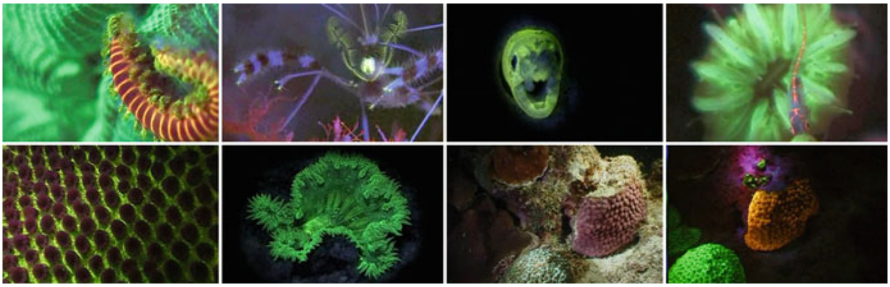

Fig. 20.3 Many reef animals reveal fluorescence when shined upon with an UV-radiation source. The resulting fluorescence pattern in the visible range is species-specific and most likely a biocommunicative tool in an environment predominantly shaded by the bluish hue of ocean water. *Top row* from *left* to *right*: fire bristle worm *Pherecardia striata*, banded coral shrimp *Stenopus hispidus*, tiger snake eel *Myrichtys maculosus* and a gobiid resting on a *Eusmilia fastigiata*. *Bottom row*: *Montastrea cavernosa* and soft coral. *Last pair* shows reef section under normal light and UV-light (Modified after Chaumette and Chaumette 2008)

(quorum sensing), or predation pressure from carnivorous species, often involves a physical set of vocabulary (Golberg et al. 2011). Coping with such challenges requires learning – a real intrinsic property of autopoietic systems. Corals seem to be able to do so as it is known that diurnal polyp and/or tentacle extension, reveal geographic variations (particularly in high-latitude locations) that differ to like-individuals kept in aquaria and as follows is an acquired result of fish predation (Veron 1995). Another coping strategy regards the colourful appearance of the reef community. This is not an accidental by-product, rather the electromagnetic spectrum – particularly within the UV-range via the emission and perception of photonic signals – is an essential tool of communication used to exchange information among species. In this way, the underwater world, and reefs in particular, generate a photonic landscape that serves to exchange bits and pieces of information essential for their survivability. Examples regard coordination of sexual reproduction among mass-spawning corals, schooling behaviour of reef fish, juvenile fish that seek shelter in branching corals us UV-signalling to communicate to each other the arrival of a predator – just to name few examples. As has been shown by Mazel (2004) fluorescence is also applied in hunting rituals by mantis shrimps. The most sticking example of how sign-mediated communication is effectively used for mutual advantage regards cuttlefish and squids during stress and mating rituals. Here utilization of their chromatophores signals their mating partner or rival readiness or rejection. Another example concerns the frequently used “cleaner-blue” – a bluish color used by fish and shrimps to signal their cleaning services to commensal members requesting some “cosmetics” (banded coral shrimp in Fig. 20.3). Hence changes in bodily color patterns not only reflect different growth stages but also altered social functionality amidst the reef community. In this way, information is shared first on a physical level and later transcribed into an array of biochemical substances that are then further used in intraspecific sign- and signal-mediated pathways.

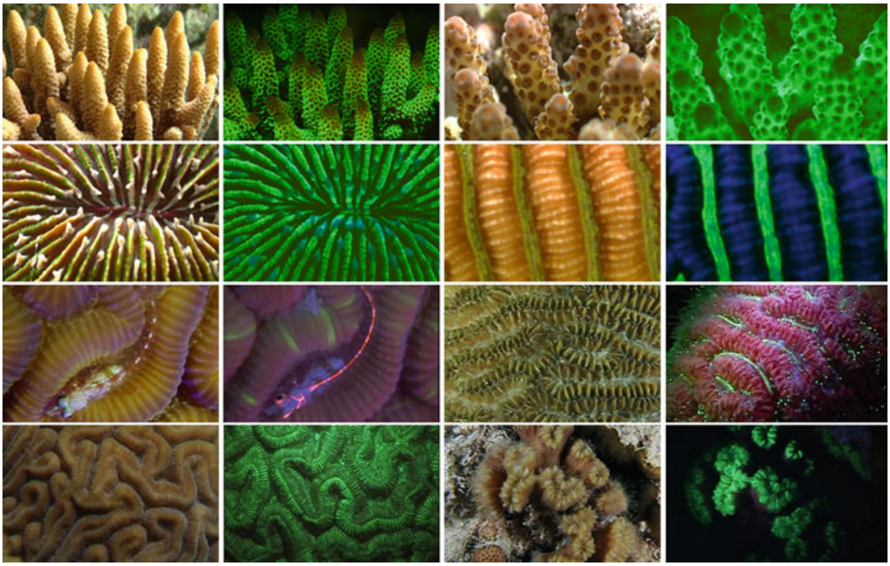

Fig. 20.4 Fluorescence images of some coral species under normal and UV-light. *Top row*: *Acropora* sp. *Second row*: *Fungia fungites* (*left*) and *Platygyra lamellina* (*right*). *Third row*: *Diplora strigosa* with resting gobiid (*left*) and brain coral *Meandrina meandrites* (*right*). *Bottom row*: *Diploria labyrinthiformis* (*left*) and *Eusmilia fastigiata* (*right*) (Adapted from Madl et al. 2005; Chaumette and Chaumette 2008)

With regards to corals, fluorescence proteins (FPs) are not only species-specific but also modulated in their use and as such are adjusted to the state of health and predation pressure in reef ecology (Matz et al. 2006) (Fig. 20.4). FPs play a major role in coral-environment interaction and include endosymbiont masking to cope with herbivorous feeding pressure all the way to dinoflagellate shielding strategies during extreme abiotic conditions (Alieva et al. 2008). Hence, the functional importance of FPs are highlighted by their upregulation in response to light or injury and in reverse by their down-regulation due to heat stress (Kenkel et al. 2011). In addition, coral FPs feature a crucial role in planulae, in that apart from chemotaxis, FPs are also involved during settlement response patterns on crustose coralline algae and are thus a direct indicator of how well recruits colonize a new substrate. The same authors also state that FPs are involved in the modulation of photosynthetic activity of their endosymbionts and during acquisition of free-living "zooxanthellae" into coral tissue (see also Fig. 20.7).

Among corals, most fluorescent emissions concentrate at polyp centers and decline by 70–90 % in regions between polyps. Such a distribution of the host-based FPs is consistent with the hypothesis that these compounds may provide some measure of photoprotection to the coral's reproductive organs (Zawada and Jaffe 2003). Already Salih et al. (2000) postulated that FPs may reduce susceptibility to photoinhibition of fluorescent corals by filtering out damaging UVA and excessive photosynthetically active radiation (PAR). Hence, it is not that far fetched to consider some photoprotection also for endosymbionts and regulation of their photosynthetic activity – especially when thinking about the deactivating role of radical oxygen species (ROS) and proton pumping. As the upregulation of FPs occurs in injured or compromised coral tissue, it yields a scavenging (antioxidative) effect of hydrogen peroxide (H_2O_2), thus describes a fundamental biochemical characteristic of these proteins (Palmer et al. 2009). This is particularly important as corals host highly hyperoxic endosymbionts and as such produce a large quantity of ROS (Bou-Abdallah et al. 2006). However, species specificity variations of this phenomenon rather point toward selection pressure related to some essential functions in parallel evolution, particularly as different colors translate into different metabolic properties (Alieva et al. 2008). In terms of energetic requirements, to produce and maintain fluorescence, FPs have half-lives amounting to 20 days, thus are extremely long-lived and energetically inexpensive for the coral host to maintain (Leutenegger et al. 2007). Thus, FPs are among those crucial clues that aid in the convergence of a multidirective successive gradient to a monodirective one that, when successful, ultimately converge to a quasi-stable coral biome – compare also with Fig. 20.2.

Apart from FPs, several other classes of molecules, which serve as signs in communicative processes have been identified – and regard e.g. secondary metabolites, neurotransmitter, hormones and obligate RNAs such as microRNAs and RNAi. Varying behavioural patterns lead to the production of different signals with different functions: antimicrobials, antifungals, corresponding secondary metabolites, and hormones (Kim 1994; Slattery et al. 1995, 1999; Ramesh and Venkateswarlu 1999; Iwashima et al. 2000; Yasumoto et al. 2000; Roussis et al. 2001; Twan et al. 2003; Watanabe et al. 2003; Iguchi et al. 2004; Kelman et al. 2006; Zhang et al. 2005; Krediet et al. 2013).

As will be demonstrated later, corals also possess a broad variety of hormonal substances for different behavioural purposes, e.g. reproduction cycles and defence patterns against opportunistic microbes, carnivores, herbivores and fungal infections (Hay et al. 1987; Slattery et al. 1999).

3 Interpretation of External Influences

The physical environment is more important than biological mechanisms in driving evolution. Biological factors are hierarchically somewhat lower in that these limit coral biodiversity and hence the rate of evolution (Veron 1995). That is, corals are particularly affected by abiotic stimuli, such as temperature/latitude, light/depth, tides/wave surge, gravity, and only to a lesser extent by symbiosis and nutrients (Bak et al. 1982; Veron 1995; McClanahan and Maina 2003). Natural disturbances such as earthquakes, cyclones and tsunamis change and thereby shape the reef ecosystem. Under natural conditions such interferences result in change of species composition, favouring pioneering and faster-growing species and initiating a new cycle of coral succession. For chronic exposure to abiotic stressors, corals react via morphogenetic

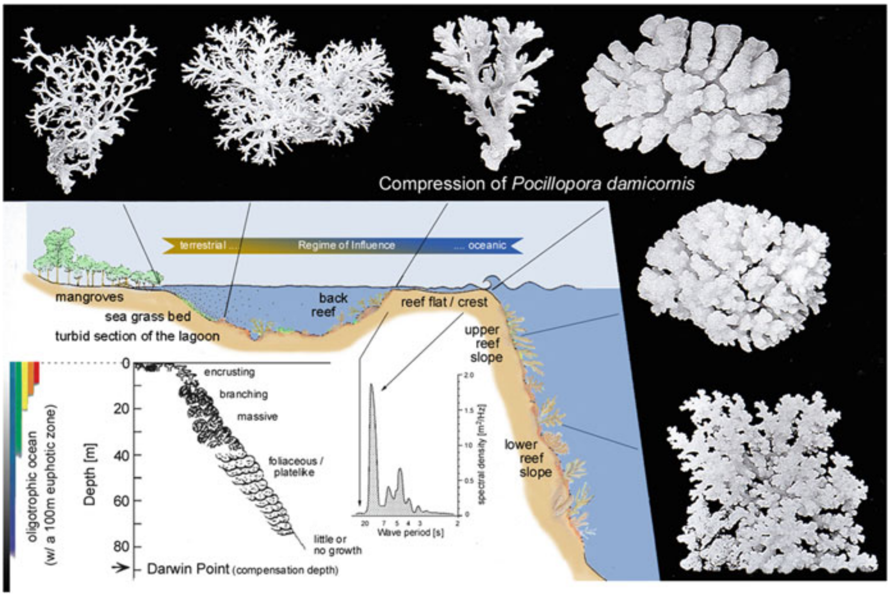

Fig. 20.5 Morphological compression gradient of *Pocillopora damicornis* due to environmental influences. The *left/bottom inlet* idealizes the preferred growth distributions among coral species under gradually altered abiotic conditions. The *right/top* series of inlets displays the attenuation of wave energy by the reef crest (Modified after Veron 1995 and adapted from Madl et al. 2005)

adaptations (Fig. 20.5), i.e. light intensity, swell and surge patterns, and oceanic currents (Geistner 1977; Horiguchi et al. 1999; Gleason et al. 2005; Stambler and Dubinsky 2005; Vargas-Angel et al. 2006; Veron and Stafford-Smith 2000). As a result, the combined input of environmental parameters and their sensing capabilities of the coral organism result in a phenotype that is epigenetically controlled and thus expressed as various morphotypes (growth form, color patterns) even within same species.

In the context of anthropogenic influences, eutrophication owing to land-based intensive farming or off-shore based mariculture, excessive fishing practices, and other man-made activities also interfere with the reefs delicate biocommunicative structures. These influences can be so intense that they easily tip the balance from a coral dominated reef towards a filter-feeding (Hatcher 1997; Elmqvist et al. 2003; Hoegh-Guldberg et al. 2007) or algal-dominated community (Hughes 1994). Closely associated with eutrophication and coastal degradation is the global trend in the decline of mangrove forest cover. Mangroves are an essential part of the wider tropical reef ecosystem, as their numerous prop roots account for a very rich and diverse habitat ranging from algae, sponges, and marine invertebrates to nurseries for young shrimp and coral fishes. Habitat degradation for shrimp farms and other coastal utilisation not only increases coastal erosion, but likewise interferes with the delicate communication patterns of the wider reef ecosystem, thereby detrimentally feeding back onto the adjacent reef (Mumby et al. 2004).

4 Transorganismic Communication

Both mechanical and chemical sign-mediated interactions of corals with other genera, families, and phyla, as well as with members of other kingdoms, are not only essential for their survival, but are the basis of coordination and organisation. These interactions cover the entire range – from the mutually supporting over to neutral or even harmful behavioural patterns. The varieties of symbiotic communications, for example, require very different behaviours from the partners involved (Weis et al. 2001).

Direct and indirect defence mechanisms are manifold and complement each other. Corals possess a 'non-self' warning system, especially when confronted with opportunistic microbes (Rohwer and Kelley 2004). Such microbes include single-celled autotrophic and heterotrophic prokaryotes, autotrophic and heterotrophic eukaryotes, as well as viruses.

Corals interact with non-related species predominantly through their mucopolysaccharide layer (MPSL). This layer forms a boundary through which dissolved nutrients and gases diffuse (Fig. 20.6). Hence, the mucus is a barrier against opportunistic pathogens and can be considered the primary immune organ of corals. Beneficial prokaryotic residents living on and within the MPSL are yet another shield against opportunistic settlers (Shnit-Orland and Kushmaro 2009) and act as an host-associated microbial community (Krediet et al. 2013). Even specific viruses take part in this protective cocktail and thus sustain coral health (Sharon and Rosenberg 2008; Van Oppen et al. 2009). Here in particular, the quorum-sensing network of the various *Vibrio* species inhabiting the MPSL, stress the importance of this communication system (Golberg et al. 2011). Intrinsically coupled to viruses is the microbial community as the former is mostly comprised of bacteriophages (Leruste et al. 2012)

As can be deduced from Fig. 20.6, any shift away from a protective microbial community to a pathogenic mix is reflected by a corresponding shift in prokaryotic species composition. There are large numbers of mucus-adapted microbes, such as phosphate and nitrogen fixers. Studies report that even cold-water corals actively 'harvest' the surface layer to obtain additional nutrients (Neulinger et al. 2008). In order to do so, corals encourage growth of specific microbes by the secretion of specialised mucus (Kushmaro and Kramarsky-Winter 2004). This in turn provides specialised microbiota as the ideal substrate to protect the coral animal from opportunistic settlers by occupying entry niches and through the formation of inhibition zones, e.g. prokaryotically-mediated production of antibiotics (Geffen and Rosenberg 2005) and according to the Hologenome Theory in turn leads to epigenetically modulated microbial species composition (Golberg et al. 2011; Krediet et al. 2013). Any disruption of the highly diversified microbial density on the MPSL will render corals more susceptible to opportunistic pathogens. This pushes the seemingly stable but actually very labile equilibrium of a healthy coral towards one where diseases become established, and ultimately may result in the decline of the whole colony (Rohwer and Kelley 2004).

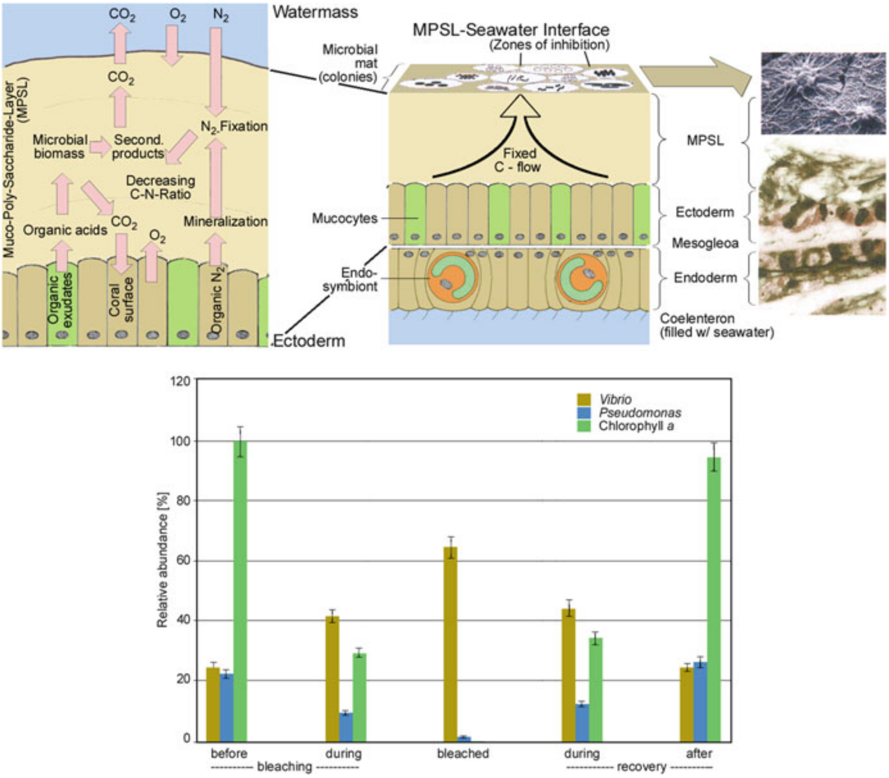

Fig. 20.6 Mucus-microbial interaction: Proposed model of the microbial contribution to coral nourishment. This includes contribution by symbiotic algae, the endolithic community, suspension and detritious feeding and coral mucus microbial community. In addition to particulate and dissolved exchanges of inorganic and organic matter, these processes complement the nutrient requirements of the colony. *Bar chart*: Microbial changes of the MPSL during bleaching and recovery. The percentage of *Vibrio* metabolic groups, *Pseudomonas* and chlorophyll are presented at each phase (Modified after Kushmaro & Kramarsky-Winter 2004 and adapted from Madl et al. 2005)

4.1 Coordination of Defence and Regeneration

Being predominantly sessile in lifestyle, corals are equipped with additional defence mechanisms against mechanically-induced damage and microbes (Gunthorpe and Cameron 1990; Kramarsky-Winter 2004). In this context, it appears that corals can differentiate between the various modes of inflicted tissue damage, i.e. triggered by (a) viruses, (b) bacteria, (c) fungi and (d) invertebrates as well as (e) damage induced by vertebrates. According to the type of damage, corals secrete different combinations of substances that serve to deal with such lesions (Geffen and Rosenberg 2005).

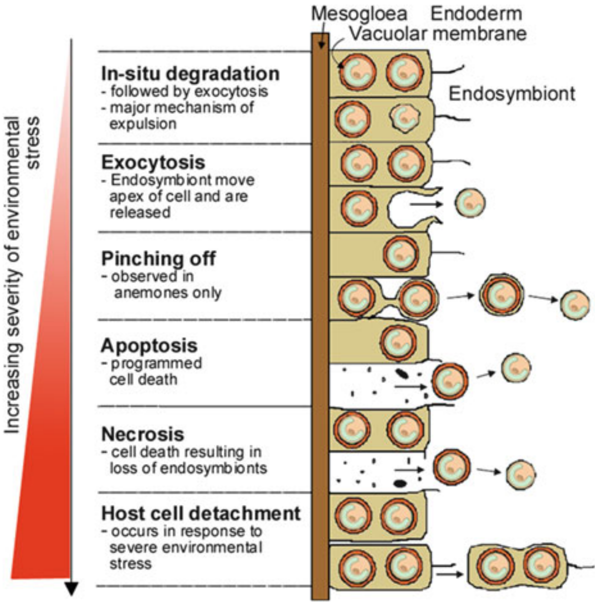

Fig. 20.7 Endosymbiont expulsion increases with the severity of environmental stress exposure (Modified after Lesser 2004 and adapted from Lesser 2004; Madl et al. 2005)

A localised wound response leads not only to the production of mobile signal molecules, but requires a systematic reaction involving the entire organism whereas a mature colony has more reserves than a juvenile recruit (Alker et al. 2004). Reactions to lesions stimulate the transmigration of specific amoeboid wound cells toward the site of injury where they clean up cellular debris. In this way, necrotic tissue can be sloughed off. Only then will the surrounding tissues stretch to cover as much of the wound as possible. If lesions are too large to be covered by stretching tissues, a much slower process takes over: tissue regrowth over the denuded area. This does not take place, however, when corals are affected by disease (e.g. shifted microbial species composition of the MPSL) as these are characterized by a significant reduction of amoebocytes engaged in tissue repair (Kramarsky-Winter 2004). This is of crucial importance as amoebocytes are also involved in coral responses to pathogenic and temperature stress (Mydlarz et al. 2008) – compare with Fig. 20.7.

According to the intensity of damage inflicted by opportunistic species, corals are able to coordinate directly and indirectly their complementing protective measures to varying degrees (Chadwick-Furman and Rinkevich 1994; Koh 1997; Rinkevich 2004). The exposure to parasites or pathogens stimulates the coral organism to produce a specific array of immune substances (Bigger and Olano 1993; Rinkevich et al. 1994; Golberg et al. 2011; Krediet et al. 2013).

In addition, corals also produce enzymes that render their tissues unpalatable to certain predators (Lindquist and Hay 1996; Kelman et al. 1999). Contrary to the predictable succession of developmental phases of individual organisms, modular organisms can proliferate at one end while at the other tissues may be already in the phase of senescence. Death in such organisms often results from becoming too big or succumbing to disease rather than from programmed senescence. Thus, the body of a coral has an age structure – it is composed of young and developing, actively functioning, as well as senescent, parts (Begon et al. 1996; Vytopil and Willis 2001). As will be discussed more in details further below. the modular structure enables corals to respond adequately to spatial limitations, predators, and unfavourable environmental conditions. Their morphology, in particular branching species, not only provides shelter for juvenile fish species and other invertebrates, but actively benefits the survivorship of the coral.

4.2 Communicative Coordination of Symbioses

As outlined above, the coral holobiont hosts unicellular algae, fungi, protists, bacteria, archea, and viruses. Indeed, corals are part of this symbiotic relationship that comprises many different species (Marhaver et al. 2008). The above makes it obvious that there are multiple symbiotic interactions at work in a coral colony, which can be clearly differentiated into mutualistic, aggressive and defensive properties (Van Veghel et al. 1996; Hay 1997). How fragile acute stressors in this delicate interconnected balance can be is briefly demonstrated by relating to the coral's endosymbionts. Owing to the gradual increase in global sea-surface temperatures, communication processes between endosymbionts and coral hosts are increasingly disturbed (Baird et al. 2009; Rosenberg et al. 2009). In fact, the combined effects of thermal stress and excessive sunlight damage the endosymbiont's photosynthetic capabilities (Salih et al. 2000). In such cases, the coral's ability to neutralise endosymbiotic production of radicals is compromised (Lesser 2004). Hence, thermal stress combined with high irradiance – in which even the buffering capacity of FPs are overstretched – pushes the host into the distress phase which leads to degradation of the dinoflagellates or ever more frequent to the expulsion of the endosymbiotic algae (Fig. 20.7), particularly when temperature extremes exceed thermal threshold levels (Hoegh-Guldberg 1999, 2004).

During extended bleaching events coral communities of entire reef sections loose their ability to regenerate and ultimately fade out, giving rise to a completely altered ecosystem (Edmunds and Gates 2003; Rowan 2004; Jones et al. 2008). There are however, and as known from examples in the Red Sea, some clades of *Symbiodinum* that are better adapted to the higher temperatures and therefore develop different symbiotic interactions seem capable to act as a rescue (Stat et al. 2008). Under certain circumstances corals are able to swap less temperature-tolerant clades for better-adapted ones (Buddemeier et al. 2004; Sampayo et al. 2008), thereby enabling corals to partly regain their vitality (Rowan 2004). The most marked differences among clades of *Symbiodinium* can be found between corals of the Caribbean and those in the Indo-Pacific region, while lesser differences exist among clades along a depth gradient within a given region (Toller et al. 2001).

5 Interorganismic Communication

Species-specific and species-related sign-mediated interactions are termed interorganismic communication. Hermatypic reef corals are social organisms and with few exceptions, such as some members of Fungiidae, they are predominantly colonial and modular in appearance. This social capacity implies a competence for species-specific sign-mediated interaction process, which enables corals of the same or a similar species, as well as distantly related relatives, to coordinate their behaviour. This coordination is most obvious during sexual reproduction.

While some corals reproduce sexually, which requires synchronisation of opposite sexes (e.g. mass spawning), others do so asexually via budding or fragmentation. Most corals employ both modes of reproduction (Miller and Ayre 2004). About ¾ of all endosymbiotic coral species spawn eggs and sperm rather than brood larvae. Spawning is associated with higher fecundity, while brooding results in fewer, larger and better developed larvae (Veron 1995). Those species involved in mass spawning expel their gametes at precisely different time-windows that are coupled to the mesoscopic triggers such as the lunar cycle, solar insulation, and/or sea-surface temperatures (Harrison et al. 1984; Penland et al. 2004; Twan et al. 2006) – see Fig. 20.8. Another ¾ of endosymbiotic coral species are hermaphrodites and these include both spawners and brooders. Hermaphroditic corals may have simultaneous or sequential gonad development and/or gamete release, giving varying potentials for self-fertilization (Veron 1995). One may ask why these various modes of reproduction are enforced in favor for one rather than the other. Yet, as briefly mentioned above, these are the results of the various modes of interaction among the individual organism with their environment and as such are most likely also epigenetically modulated.

Evolutionary processes are also induced via hybridisation (Márquez et al. 2002; Miller and Van Oppen 2003). In situ observations along the GBR revealed that in a single night up to 150 species of the highly cross-fertile genus *Acropora* spawn within hours of each other. High cross-fertilisation rates were documented in vivo, while molecular tree topologies confirmed non-monophyletic patterns. This bears little similarity to cladistic analysis based on skeletal morphology or to the fossil record leading to the conclusion that hybridisation is essential for the enormous success among members of this family (Ryan 2006; Van Oppen et al. 2001).

Corals at a mature stage possess more refined capability to differentiate between ‘self’ and ‘non-self’ (Rinkevich et al. 1994; Rinkevich and Sakai 2001). In order to protect their own growth range against proliferating opportunists, corals take defensive measures against ‘non-self’ tissues. Allelopathic reactions, such as the production of chemicals to signal the presence and to limit excessive proliferation of neighbouring coral species, occur in very complex ways and in various combinations and gradations (Yamazato and Yeemin 1986). There are some completely different and complementary defence mechanisms, e.g. escape by growth, aggressive behavior, allelochemicals and aggregation (Bruno and Witman 1996). Aggressive and defensive behavioral patterns reciprocally depend on the extent of physical contact (Bak et al. 1982; Ferriz-Dominguez and Horta-Puga 2001). Such responses can be quite broad, in that they can involve complete rejection of neighboring coral colonies

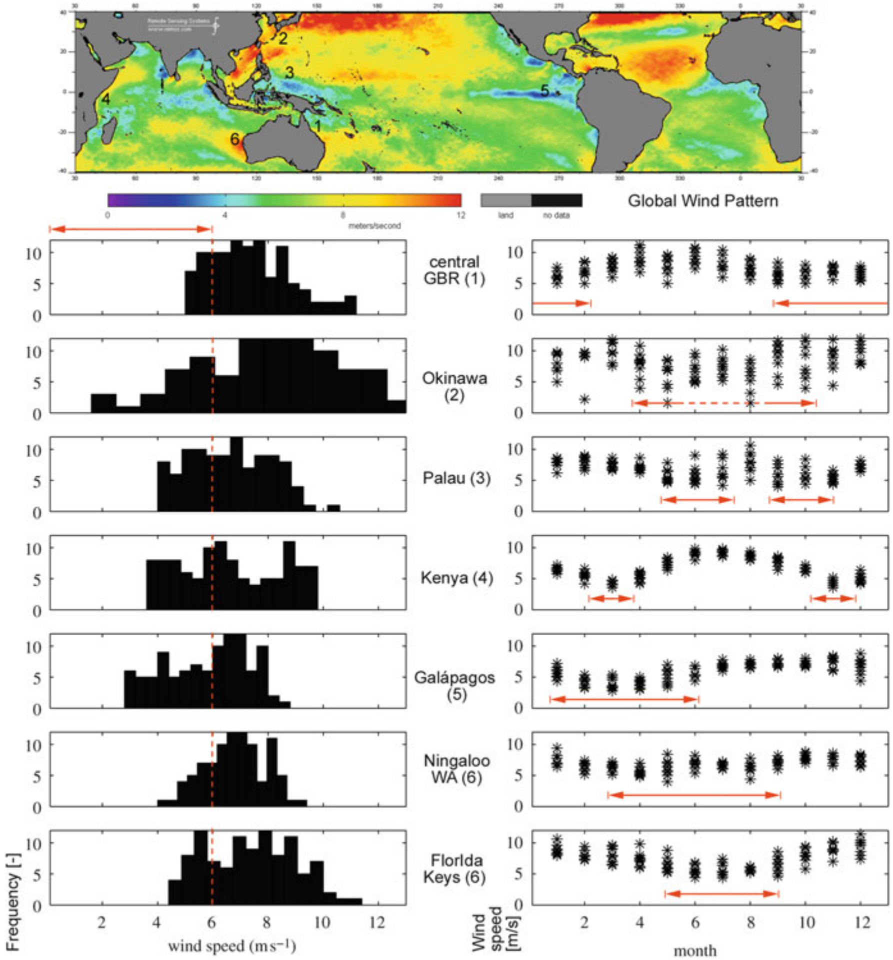

Fig. 20.8 *Top*: Triggers to mass spawning. Global wind fields ($m \cdot s^{-1}$) obtained from remote sensing data, for January 2009, where *blue* is on average less than 5 $m \cdot s^{-1}$. *Bottom*: Wind-speed frequency distributions and monthly averaged wind-speed data ($m \cdot s^{-1}$) extracted from 1996 to 2006. Usually, *white caps* form when winds reach or exceed 6 $m \cdot s^{-1}$ (*red arrows* indicate potential spawning windows) (Modified after van Woesik 2009 and adapted from Madl et al. 2005)

by use of sweeper and or stinging tentacles (Fig. 20.9) – the former literally digest competitors away (Barnes and Hughes 1999). In the opposite case, and among closely related species, it can result in complete merger of both colonies (Connell 1976; Cope 1982; Chadwick-Furman and Rinkevich 1994). Research employing various juvenile coral species showed that there are three kinds of response patterns: fusion, non-fusion and incompatible fusion. In the case of incompatible fusion, the junction of merging tissues lacks endosymbiotic algae. Slow-growing polyps characterize such an interfacial region. Over prolonged periods of time and as a result of this incompatibility, a skeletal barrier forms (Veron 1986; Hidaka et al. 1997).

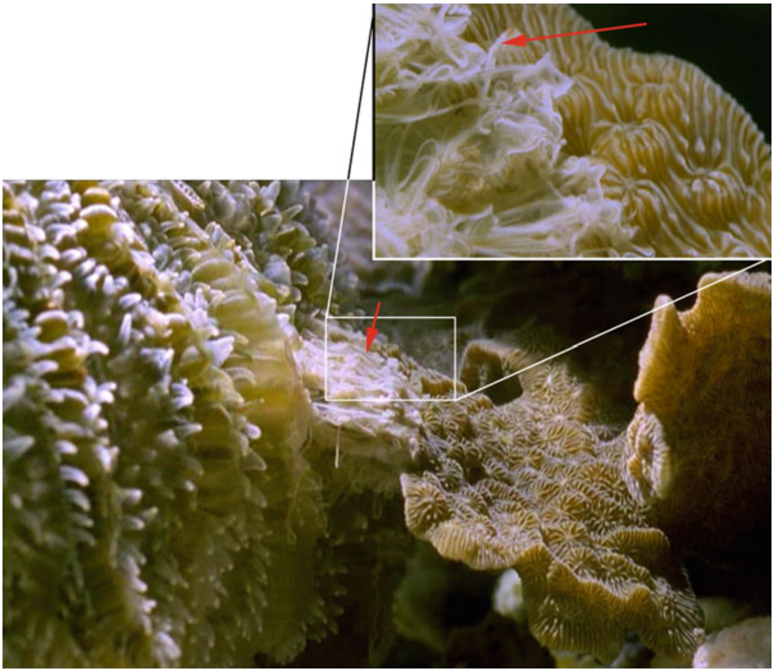

Fig. 20.9 *Physogyra lichtensteini* (*left*) utilizes its sweeper tentacles (Modified mesenterial filaments of the gut, *arrow*) to digest *Pavona explanulata* (*right*) (Adapted from Madl et al. 2005)

Encounters of different coral species quite often result in subduing of the succumbing species by a more dominant species. Overgrowth – by coral, sponges or other community member – is simply one strategy to overcome spatial restriction or to outcompete members that reveal suppressed fitness (Veron 1986; Frank and Rinkevich 2001).

Spatial and nutritional competition among corals and the concomitant stress factor do affect their fitness (Tanner 1997; Idjadi and Karlson 2007). Once resource limitations and habitat constraints are encountered, additional pressure to already stressed individuals can be fatal (Fig. 20.10). In addition, some corals generate considerable amounts of mucus loaded with nematocysts, which spreads out and over into the nearby environment to harm neighbouring colonies. Prolonged mucus production can significantly damage and even kill affected areas of a colony. Other corals kill via the excretion of chemical poisons into the adjacent water body, while others again secrete substances, which render larval settlement of potential competitors unfavourable (Lang 1970, 1971, 1973; Logan 1986; Lang and Chornesky 1990; Geffen and Rosenberg 2005).

Once a coral detects the presence of a nearby species with its ability for non-self recognition, it reacts with the production of finely gradated cytotoxic substances that will be used against potential intruders, or even against related coral species. Corals are able to learn, in that they compare a given stimulation pattern with bodily "memorized" stimulation patterns of the past (Hildemann et al. 1977; Rinkevich 2004).

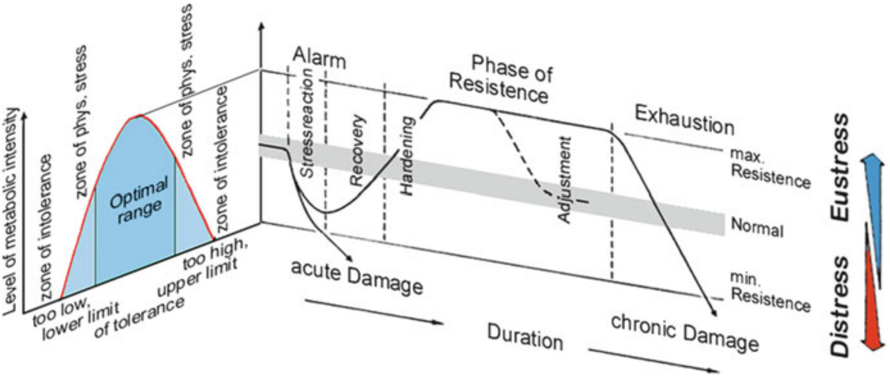

Fig. 20.10 Phase model of stress-responses. According to the dynamic concept of stress, the coral animal passes through a succession of characteristic phases. *Alarm*: the onset of disturbance is followed by stabilization of the structural and functional conditions. If the negative stress event (distress) is taking place faster than the coral is capable to respond, the immediate impairment results in acute collapse (acute damage). If the intensity of the stimulus is not destructive, restitution in the form of "repair" process is quickly initiated. *Resistance*: restitution initiates the resistance phase, in which the resistance "solidifies" (hardening). Despite continued stress, the resulting improvement in stability brings about normalization (adaptation). *Exhaustion*: if the state of stress lasts for extended periods of time, increases in intensity, or acts synergistically with another distressing factor, a state of exhaustion may set in, weakening the organism's host defences, and leading to premature collapse (Modified after Madl 2005)

Hence, corals are capable of differentiating between tissues and chemicals of kin species and those of 'non-related' species. This is essential in order to avoid repercussions that negatively affect the survival rate of nearby individuals of the same species. Fitted with such tools of discrimination, corals are even able to differentiate the sex of their opponents (Ates 1989).

Along with their symbiotic partners, each colony must have some kind of sphere of individuality in order to survive and prosper. Once intruders compromise these preconditions, substances are produced and released into the water body that hamper growth and proliferation of nearby competitors (Kim 1994; Wilsanand et al. 1999; Roussis et al. 2001; Slattery et al. 1995). For the same purpose, even sturdy coral species can produce and release fast-acting antibacterial agents into the environment (Geffen and Rosenberg 2005).

6 Intraorganismic Communication

Intraorganismic communication processes are sign-mediated interactions within cells (intracellular) and between other cells of the same organisms (intercellular). Both communication processes are of crucial importance for the coordination of growth and development.

6.1 Intercellular Communication

Intercellular communication serves to communicate events within coral tissues or compartments to remotely located cells or tissues. Injured corals organise an integrated molecular, biochemical and cell-biological response. This also includes immunological reactions (Bigger and Olano 1993; Hildemann et al. 1977; Rinkevich 2004) and the exchange of ultraweak photon emissions (Madl and Egot-Lemaire 2013).

As such a coral's current state is constantly monitored. This kind of information is to some extent suppressed, especially when the organism undergoes periods of growth. Doing so enables expression of the pre-processed intermediate steps necessary to accommodate such phase transitions. Embryonic development in particular and its subsequent transition into the larval stage as well as the metamorphosis to a juvenile polyp require finely tuned coordination of growth and development (Okubo et al. 2007). Special signalling pathways initiate these steps. Neuropeptides, for example, are hormone-like substances that coordinate metamorphosis even in corals (Iwao et al. 2002), whereas ultraweak photonic interactions relies solely on physical properties of the electromagnetic spectrum (Madl and Egot-Lemaire 2013).

6.2 Intracellular Communication

Intracellular merger of symbiotic dinoflagellates with marine cnidarians is the most important prerequisite to ensure a highly productive and diverse reef ecosystem (Santos et al. 2002; Takabayashia et al. 2004). To assert that the effects of symbiosis are long-lasting, this endocytotic process is coordinated by a gene termed ApRab5. If, however, expression of this gene is disturbed, it leads to sudden separation and expulsion of the symbionts (Chen et al. 2004, 2005).

Therefore, successful intracellular communication between the symbiogenetically assimilated unicellular eukaryotes must take place. It makes sure that external information is transformed and forwarded to endsoymbionts. This information epigenetically influences gene expression of algal DNA. This in turn triggers a particular genetic reply, which leads to the production of signal molecules and generates an adequate response behaviour (Chen et al. 2000). If these modes of communications are recurring frequently it ultimately will be epigenetically memorized.

Viroids, viruses – still the least studied biological entities in coral mucus (Leruste et al. 2012) – and bacteria interfere via various pathways in intracellular communication. So it does not come as a surprise that under extreme circumstances, this interference can disturb or even trigger collapse of the entire coral holobiont – as is the case of induced tissue bleaching by *Vibrio shiloi* in *Oculina patagonica* or *Vibrio coralliilyticus* in *Pocillopora damicornis* (Rosenberg 2004; Rozenblat and Rosenberg 2004). Indeed most *Symbiodinium* species are infected with icosahedral double-stranded DNA-containing viruses. Under normal conditions, they replicate without harming the host. Nonetheless, their latent virulence turns lytic (lethal to *Symbiodinium*) once water temperatures rise, thereby forcing the coral to expel their decaying endosymbionts, which – as in the case of abiotically induced bleaching – likewise leads to tissue bleaching (Villarreal 2005). The modes of elimination of the endosymbiont from the host varies and can range from exocytosis, host cell detachment and host cell apoptosis (Weis 2008) – compare with Fig. 20.7.

Microbial interactions on the other hand are reciprocal; this enables incorporation of specific genetic features into the intruder's genome as well as the export of microbial datasets into those of the host organism (Rohwer 2010). It is very likely that the ability to incorporate different traits in each other is a key principle of symbiogenetic processes (Shackelton and Holmes 2004).

On a macroscopic scale, corals possess a decentralised neural network (Westfall and Sayyar 1997). Alignment of this network is never static, but implies neuronal-like plasticity. Here the faculty of learning and epigenetic flexibility becomes manifest by the animal's past experiences, as it is the capacity to modify (increase or decrease) the magnitude of their connections. Both memory-functions and long-lasting neuronal plasticity require new RNAs for the appropriate protein synthesis (Netea et al. 2011). Such neuronal plasticity implies that signals are relayed via the synapse to the nucleus. Therein, these signals are converted in order to evoke a change in gene transcription. Only then, can the resulting changes (RNAs, proteins) be converted and sent back to the synapse to enable long-lasting change (Moccia et al. 2003; Martin 2004; Thompson et al. 2004).

As demonstrated with the FPs, variation in colour pigmentation of corals is primarily the result of a few genes and their associated proteins within the endosymbionts. It is worth noting that the various colour patterns are the result of phenotypic plasticity rather than species diversity, as previously thought (Kelmanson and Matz 2003) that are subject to epigenetic modulation.

The simple organismic structure of the phylum Cnidaria, groups them close to the 'archaic' section of the animal lineage as they share most characteristics with a common ancestor as well as those of modern animals of higher taxa, i.e. large-scale coral-algal-sponge bioherms emerged some 450 Ma ago (Hallock 1997). It is worth mentioning that evolution, growth and development of the most important coral endosymbionts, i.e. members of the dinoflagellate genus *Symbiodinium*, assign them a similar age. In this respect and based on the emergence of the first cnidarian precursors, the coral animal can be regarded as a 'window into the past' (Margulis and Schwartz 1988). Indeed the failure of symbiosis through lack of light may have played a central role in mass extinctions – particularly the one some $70{\cdot}E^6$ years BP, towards the end of Cretaceous (Veron 1995).

7 Growth and Stability in Coral Reef Communities

Coral reefs are complex ecosystems and in order to understand the various biocommunicative pathways involves comprehension of their complexity. In order to bridge the line of arguments in a way that encompasses this complexity – from the framework-builders to the coral reef itself – requires a simplified approach that so far poses still an intractable challenge. Bradbury and Reichelt (1983) were among the first to investigate the applicability of a fractal approach. While their investigation used coral reef topography stretched only over four orders of magnitude (0.1–100 m) they could identify a trend in maximization of fragmentation, i.e. maximizing surface contact with the surrounding environment. Yet still this approach did not unveil its general applicability as mechanistic connections between organismic processes and their ecological consequences could not be established. Purkis et al. (2006) upscaled this attempt by involving remote sensing technology and merged it with fractal statistics. Therein, the study provides clues to the dynamic nature of fractal properties, namely the competing spatial requirements among corals and algal communities on one side and disturbances of anthropogenic and bioerosive origin on the other. The former is particularly sensitive as reef degradation is commonly indicated by a shift either towards a filter-feeding community (Hatcher 1997; Elmqvist et al. 2003; Hoegh-Guldberg et al. 2007) or an algal-dominated state and a loss in landscape heterogeneity (Hughes 1994).

Besides these dynamics, they summarize that there exists an intense non-linear spatio-temporal instability on the decimeter to meter level on timescales of months to years – a conclusion well in line with Bradbury and Reichelt (1983). Yet there is more to that as this complex meta-stability is known to extend at scales over kilometers to megameters for timescales that extent to decades or even centuries. Nonetheless, the governing principles inducing these properties are still scarcely understood and hard to come by when looking at the molecular level only. There is still no general all-encompassing theory to this fractal dependence as proper understanding of key issues in ecosystem stability is largely absent (Enquist et al. 1998).

With biological diversity being a matter of body size (Enquist et al. 1998; West et al. 1997) that covers at least 15 orders of magnitude – from viruses in the nanometer-range via the prevailing megafauna in the meter-range and the actual dimensions of the coral-reef biome in the megameter-range. In fact, a promising approach in solving the connections among important reference points of ecological communities across diverse ecosystems that interrelate organismic, community and ecosystem properties is to focus on size-dependent (allometric) relationships (Mora et al. 2011b) (Fig. 20.11). This is done not only among members of the same species but even across phyletically distant species (Enquist and Niklas 2001).

Sizes of biological structures such as growth patterns of branching corals occur according to following relation: $m^{3/4}$ – with “m” denoting body mass (Enquist et al. 1998). Nonetheless, West et al. (1997) and Basillais (1998) proposed a quantitative model that at least explains the origin and ubiquity of this quarter-power scaling. In their model, they use several unifying principles of which a space-filling fractal-like branching pattern is most striking. These patterns are characterized by a gradual decrease in branching diameter. Figure 20.12 reveals the self-similar properties of an acroporid coral species and the methodology for its determination.

Fractals have two intrinsic properties, scale-invariance and self-similarity. While the former implies that an object looks the same on all scales, the latter assigns any part of the system – appropriately enlarged – a similar appearance as the whole (Purkis et al. 2006). This self-similar property becomes especially visible among modular organisms across most phyla and – as has been demonstrated above by referring to satellite images – is even observable at the megascopic level. Indeed the

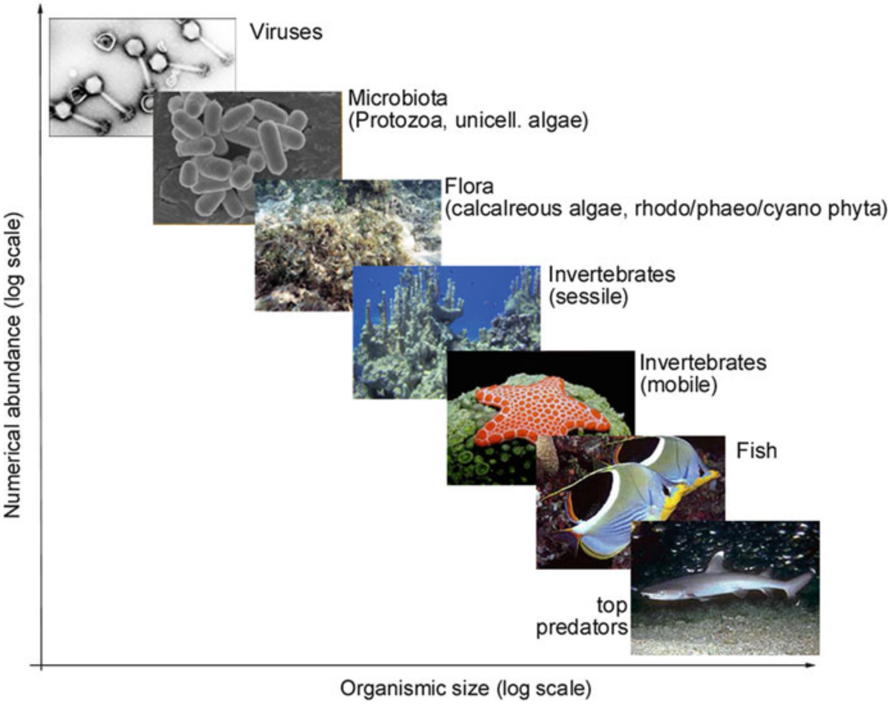

Fig. 20.11 Organismic diversity relative to body size of a reef. As outlined by the log-log-scales the body sizes compromising most of this biomass are small. It implies that the biomass of top-predators cannot exceed the total biomass of the reef ecosystem. Yet at the same time it visualizes a balanced species composition. Any deviation from the linear trend is an indicator of a disturbed ecosystem (Adapted from Madl et al. 2005)

intrinsic fractal property indicates that all members constituting a coral reef biome must be subject to this underlying principle. This includes viral aggregations and prokaryotic ensembles revealing group behavior and the obvious modular organized eukaryotic representatives among porifera and cnidaria. Interestingly, some 19 phyla – apart from hard and soft corals, also sponges, hydroids, bryozoans, colonial ascidians, many protists, fungi and most plants – reveal modular organization (Begon et al. 1996). Fractality among higher invertebrates is most often encountered as group aggregations or local abundances that relate to the topographic features. Examples regard the wall of mouths at outer reefs and reef crests (that constitute the deliminating fractal perimeter) or sea-urchin aggregations at reef flats and within lagoons. Self-similarity among more mobile species such as fish communities are most evidently seen in the collective behavior of swarms and schools.

With regards to corals, the basic unit is made of the corallite and associated tissues that reveal species-specific characteristics, yet neither timing nor form is predictable for the resulting colony. Thus, individual colonies are composed of a highly variable number of such modules in which growth morphologies are subject to environmental influences (compare with Fig. 20.5). Modularity in this regard

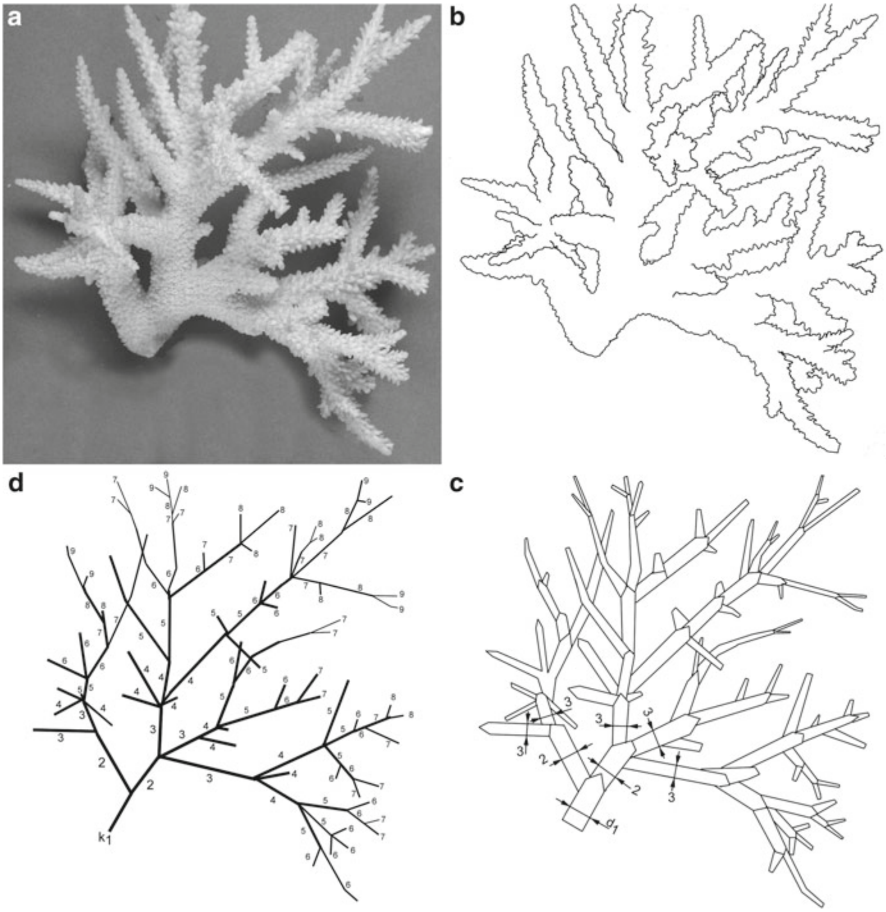

Fig. 20.12 Superposition of schematic and actual branching patterns in an (**a**) *Acropora formosa*. The contour-image (**b**) renders growth pattern more visible, with "k" denoting the generation of the branching structure (**d**) and "d" indicating the diameter of a given generation (**c**) – the latter shows only the first three generations

enables a colony to exist as a physiologically integrated whole – all part of one individual but physiologically independent – or when broken into fragments into a number of individual colonies. The peculiar feature distinguishing corals from other phyla (or domains) is the connecting system linking modules together. Most of the structure in corals is dead (precipitated aragonite matrix) with only a thin layer of living tissue in-between the water-aragonite interface (compare with Fig. 20.6). Growth in corals is obtained by the accumulation of these modules. On the other hand decay is induced either from excess accumulation of calcified sections, from becoming too big, from bioerosive processes or succumbing to disease rather than from predetermined senescence. In any case, growth in a modular organism reveals an age structure that is visible by the presence of young and developing and senescent parts (Begon et al. 1996).

Modular organisms are broadly divided into those that concentrate on vertical growth (most species among Acroporidae, Poccilpopoidae, Poritidae, etc.) and those that spread their modules laterally over a substrate (some species of Oculinidae, Meandrinidae, Mussidae, Faviidae, etc.). The most straightforward approach to determine a coral's fractal pattern – as with many biological geometries relating to a self-similar pattern – necessitates a numerical determination of key parameters, such as corallite diameter, spacing-dimensions of septo-costae, fronds/branch diameters or lengths, etc. Due to simplicity and to keep morphometric data census within reasonable limits, only branching corals have been used in this study. Fungoid, flabellate cerioid meandroid thamnasterioid and hydnophoroid growth forms have been omitted, as efforts to determine their fractal-properties have not been worked out at that stage. Yet it was possible to confirm self-similarity in the neo-cortex of the human brain (Kiselev et al. 2003), thus it is more than likely that fractality is an intrinsic feature also in massive brain corals particularly among members of Meandinidae, Mussidae and Faviidae. As with other modular organisms or organ structures revealing vertical growth, it is more appropriate to use branching diameters rather than internodal length (Madl et al. 2010; Koblinger and Hofmann 1985, 1988; West et al. 1997). Diameters conserve far better the fractal dimension than does inter-nodal distance or length.

By pooling species among four major coral groups, amounting to 77 individual data sets, the morphometrically evaluated parameters – generation-number "k" and the corresponding generation diameter "d", the below graph is obtained (Fig. 20.13). As can be deduced from the trend lines, branching patterns across coral families follow self-similarity properties, thus reveal their true fractal nature.

It follows that, across the broad sampling of diverse coral taxa, biocommunication-mediated biomass production can likewise be described by a single allometric relationship. Coral morphology suggests that their evolution is profoundly influenced by optimization processes of trade-offs enforced by performing growth, survival and reproductive success simultaneously. Obviously, these trade-offs are confined by phenotypic expression to a finite number of coral morphologies. This kind of evidence suggests that communities dominated by corals behave similarly by virtue of shared organizing principles operating at species-level – an observation that has been already confirmed in tropical plant ecosystems (Enquist and Niklas 2001).

Extrapolation of this general allometric framework and incorporation into a model reveal how several prominent organismic community and ecosystem properties emerge from relatively few allometric – so to speak biocommunicative – rules. The constraints of resource transport through 'fractal-like' networks ultimately govern how corals allocate biomass and ultimately fill space. As outlined previously by a number of bionic examples, such constraints are reflected in scaling relationships. These allometric rules determine how metabolic activity and biomass are partitioned among different parts of a coral colony. As done by Enquist and Niklas (2001) for plant communities, such rules provide a quantitative basis for drawing mechanistic connections between numerous features of reef biology, ecology, ecosystem studies and evolutionary biology (Veron 1995).

Although the above assumptions have been originally made with a tropical forest ecosystem, it is very likely that similar governing rules act on behalf of the reef ecosystem (Figs. 20.14 and 20.15). Such a model enables usage of a simplified

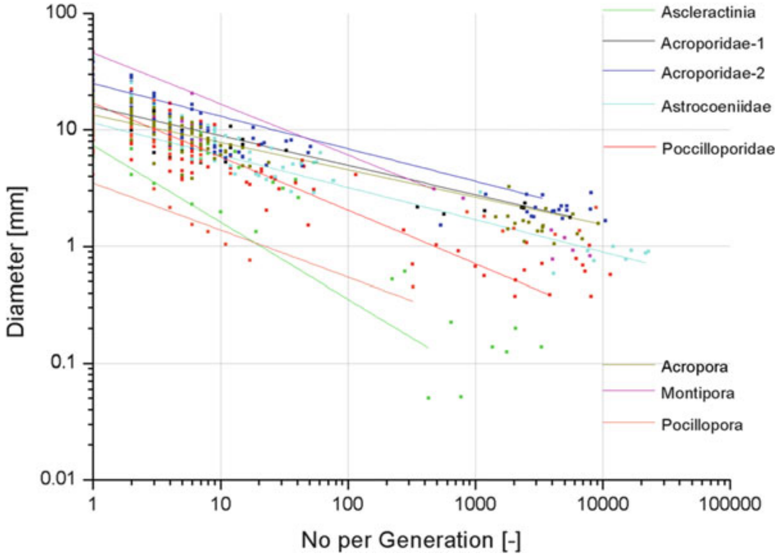

Fig. 20.13 Trends in branching patterns among 92 coral species across various families including Acroporidae, Pocilloporidae, Poritidae and some Ascleractinia (Milleporidae and Stylasteridae). Species used for Fig. 20.13:

A. abrolhosensis
A. abrotanoides
A. anthocercis
A. anthoceris
A. arabensis
A. austera
A. austera
A. awi
A. brueggemanni
A. cerealis
A. digitifera
A. divaricata
A. donei
A. elseyi
A. formosa
A. gomezi
A. grandis
A. granulosa
A. granulosa
A. hemprichii
A. humilis
A. humilis
A. hyacinthus
A. maryae
A. nobilis
A. secale
A. secale
A. selago
A. sp no01
A. sp no02
A. sp no03
A. sp no04
A. sp no05
A. sp no06
A. sp no07
A. sp no08
A. sp no09
A. sp no10
A. sp no11
A. sp no12
A. sp no17
A. sp no20
A. sp no21
A. sp no24
A. squarrosa
A. squarrosa
A. valenciennesi
A. variolosa
Alveopora sp.
Alveopora viridis
Distichopora sp. *no*
Madracis mirabilis
Millepora dichotoma no1
Millepora dichotoma no2
Millepora dichotoma no3
Millepora sp. no3
Millepora sp. no4
Montopora altasepta
Montipora australiensis
Palauastrea ramosa
Paulastrea ramosa
Pavona maldivensis
Pocillopora damicornis
Pocillopora verrucosa
Porites cumulatus
Porites cylindrica
Porites sp.
Seriatopora aculeata
Seriatopora guttatus no1
Seriatopora guttatus no2
Seriatopora guttatus no3
Seriatopora hystrix no1
Seriatopora hystrix no2
Stylaster sp.
Stylocoeniella guentheri
Stylocoeniella sp no1
Stylocoeniella sp no2
Stylophora kuehlmanni no1
Stylophora kuehlmanni no2
Stylophora kuehlmanni no3
Stylophora subseriata no1
Stylophora subseriata no2
Stylophora subseriata no3
Stylophora pistillata no1
Stylophora pistillata no2
Stylophora sp.
Stylophora subseriata no4
Stylophora subseriata no5
Stylophora subseriata no6
Stylophora subseriata no7
Stylophora subseriata no8
Unknown staghorn sp.

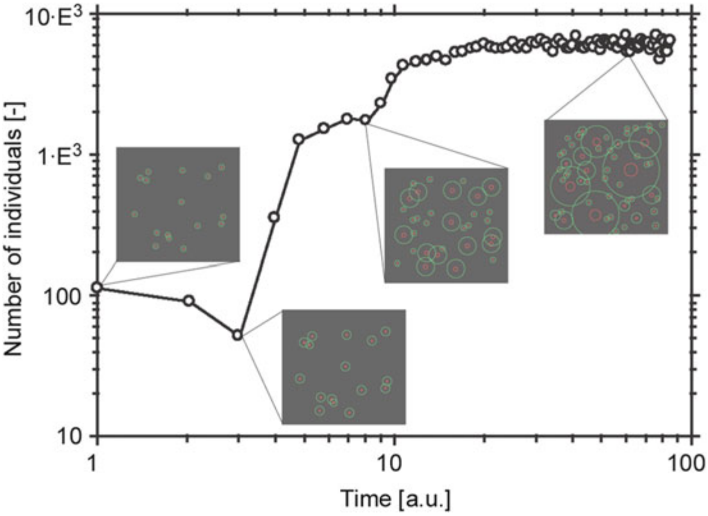

Fig. 20.14 Probable number of individuals plotted against time during a simulated community ontogeny. *Inlets*: polar views of four distinct stages, from the initial random "coral recruits" to the appearance of a mature community consisting of a more or less constant number of individuals – for legend see Fig. 20.14 (Modified after Enquist and Niklas 2001)

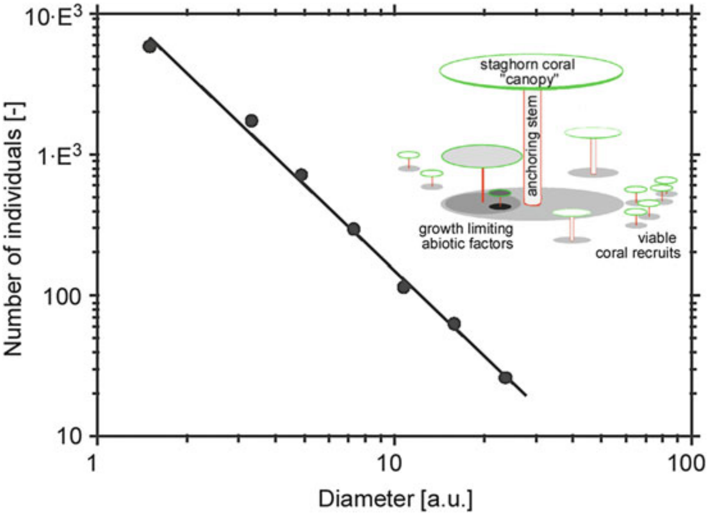

Fig. 20.15 Frequency distribution of a simulated community as the number of individuals plotted against colony diameter of the anchoring stem (*red parts*). Regression corresponds to y prop $x^{-2.0}$. Large *green circles* denote coral canopy radius, *grayish* and *black circles* the shaded areas of the dominating colonies (Modified after Enquist and Niklas 2001)

biocommunicative approach in which dispersal and mortality assumptions shape the dynamics of succession; i.e. recruits are dispersed randomly to a maximum distance d defined by height of the parent colony and the predominant orientation of water currents. Obviously, offspring initiating growth under or near the parent colony must receive less light and nutrients. Thus, depending on the amount of resource attenuation it either induces premature death or less vigorous growth (see initial dynamics and the related die-off in Fig. 20.14). Ecological communities have a phylogenetic structure that is reflected in the biocommunicative fact that general taxonomic and biomass partitioning is directly related to species richness (Enquist et al. 2002). Thus, by extending the model to include anthropogenic distress factors such as eutrophication, decreased visibility and ecosystemic pressure via excess predation, it would make modeling of reef dynamics and their potential effects in efforts to manage such an ecosystem a lot easier. It would also help to identify the general features maintaining the diversity of species assemblages (Enquist et al. 2002).

In conclusion, we can say that besides the non-saturating relationship between biodiversity and function, as documented by Mora et al. (2011a) ignoring biocommunication issues demonstrate that negative interaction between human density and biodiversity are programmed. Using the fractal property of a log-log relationship of species diversity versus species geometry (here diameter), it is definitely possible to clearly deduct the weak or missing biocommunicative links and how potentially devastating human interference at a given trophic level may result – particularly on highly diverse reef ecosystems. Thus, ignoring the biocommunicative features of reefs revealing highly diverse species composition that are subject to biomass reduction by excessive utilization are extremely vulnerable to any further expansion and intensified human activities.

8 Conclusion

There is compelling evidence that evolution, growth and development of scleractinian corals largely depend on successful trans-, inter- and intra-organismic communication processes. Indeed, it is not the individual coral organism that accounts for prosperous long-term establishment within the wider coral reef ecosystem, but rather the active and dynamic sign-mediated interactions with its surrounding that enables the coral to survive in the long run. Only once these processes are successfully established can coordination and organisation within the coral animal and among corals take place in a controlled manner. These processes enable corals to proliferate along with other organisms within the tropical reef ecosystem.

Proliferation of corals depends on successful communication, which means the communication processes may also fail. Such a response of a particular interaction can be misleading, e.g. interaction between the coral and its endo- and exosymbionts pretends to be mutualistic, only to draw a temporary advantage from a given interaction and/or even to damage the exploited organism substantially once a shift in environmental conditions takes place. It is obvious that this cannot be the general form of communication. If all symbionts were to behave in this way, no individual species could survive in the long run. In the majority of cases, there must be efficient and successful interactions that are beneficial or at least not harmful for all the participants involved.

Biocommunication and self-similarity are intrinsically coupled. As has been demonstrated this network of interrelationships is visible among the members of an entire phylum – the cnidaria. However, the biocommunicative network among other taxa cannot be denied as the entire biome reveals a fractal nature. Thus both on the ecosystem levels, across taxa and particularly among anthozoa, self-similarity is an intrinsic property without which, the entire ecosystem cannot attain any other appearance than it actually has. Exceptions to this assumption are only possible once this web of interdependencies flips from a coral-dominated to an algal-dominated ecosystem – an occurrence that has been already observed in the Caribbeans (Hughes 1994). Such dynamic alterations of the web of life imply that all related biotic entities – from viruses all the way up to the larger megafauna and ultimately the entire biome itself undergoes a sudden change into a new dynamic equilibrium that is governed by a new fractal order. In this regard, restoration of the original state and conversion back into a flourishing reef biodiversity is only possible by considering the underlying relationships among the various hierarchical structures that are necessary to maintain a coral-dominated equilibrium. Without taking into consideration the biocommunicative aspects of that relationship, any restorative attempts are most likely condemned to failure.

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Chapter 21
Nematode Communication

Yen-Ping Hsueh, Daniel H.W. Leighton, and Paul W. Sternberg

Abstract Nematodes, a diverse animal phylum that comprises an estimated million species, inhabit very broad ranges of ecological niches throughout earth. These animals, ranging from microscopic to a meter in size, are extremely successful in adapting different environments and have different lifestyles as free-living or parasitic to plants, animals and humans. As a result, nematodes have evolved to communicate with a wide variety of organisms that they live and interact with, including microbes, plants, insects, other animals, and nematodes of the same and different species. These communications play a key role in the mutualism, parasitism, predatory and prey, host and pathogen relationships between nematodes and other organisms and are critical to the ecological fitness of nematodes. In this chapter, we highlight examples of different types of communication among the nematodes and between nematodes and their natural trophic partners, and discuss their implications in nematode evolution.

1 Introduction

Nematodes are a diverse and widespread animal phylum. The phylum comprises an estimated million species, most unknown, that inhabit essentially every niche, from benthic environment to mushroom compost to porcine muscle. As such, they communicate with a wide variety of other groups of organisms including themselves. Adult nematodes range in size from less than a millimeter to greater than a meter, depending in part on whether they are free-living (small) or parasitic on

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large mammals (large). The small size of many nematodes makes them less obvious than larger invertebrates and all vertebrates. We thus pay less attention to their communication.

Nematodes are important parasite of plants, animals and humans and are studied to help control and eradicate their infections. A few nematodes have been the subject of intensive molecular genetic analysis in the past 50 years, notably *Caenorhabditis elegans*. *C. elegans* was deliberately chosen to be a laboratory model of an easily studied animal. A host of studies have been carried out. *C. elegans* was the first animal for which we know a complete sequence of the its genome. This genomic data, along with useful features for laboratory experimentation, such as small size, transparency, stereotyped development and facile genetics including RNA-mediated interference, has led to extensive detailed information about the function of a substantial number of its ~20,000 protein-coding genes. Much of this information is compiled in www.WormBase.org, a biological database about *C. elegans* and increasingly other nematodes. An extensive set of reviews is available at www.WormBook.org, and detailed description of *C. elegans* anatomy at www.WormAtlas.org.

The functions of approximately 70 % of *C. elegans* genes are still unknown. Part of this ignorance is due to lack of systematic analysis of subtle phenotypes and genetic interactions, but part is due to our ignorance about the natural ecology of this species. Recently, researchers have focused more attention on the ecology and evolution of *C. elegans* and related worms. The most exciting aspects of these studies bear on communication, defined broadly, of nematodes with other organisms. Studies of biocommunication are not only fascinating in their own right, but also have great potential to help us understand the selective forces that shape animal genomes and the function of genes. In this chapter we highlight what we consider the most pertinent or developed of these aspects of communication. We do not claim to be comprehensive.

2 Nematode-Nematode Communication

2.1 Overview

Nematodes modulate a variety of behaviors in response to other nematodes and nematode-derived metabolites. These behaviors include chemotaxis, the attraction or repulsion of individuals from another worm or metabolite (Lee 2002); aggregation (also referred to as clumping, swarming and social feeding), the gathering of individuals in a confined region of their environment (Bargmann 2006); leaving, the innate tendency of some worms to abandon a food source (Lipton et al. 2004); mating (Lee 2002); and holding, in which individuals remain at the location of another individual or a metabolite, independently of visible chemotactic behavior (Simon and Sternberg 2002). In some species, nematodes can also undergo radical alterations in physiological development in response to secreted metabolites (Hu 2007). Observed means of communication in nematodes are limited to chemical and mechanical sensation (Lee 2002). Some species of nematode are able to detect the incidence and direction of light, but observed functions of this limited form of vision have not included communication (Jones 2002; Lee 2002). Auditory sensory structures have not been described in nematodes (Jones 2002).

The earliest study of communication between nematodes was motivated by the question of how mating pairs locate one another. Greet (1964) sought to test the hypothesis that opposite genders of the free-living nematode *Panagrolaimus rigidus* (Schneider) attract one another from a distance in order to mate, rather than relying on chance encounters. Two populations of *rigidus* were permitted to roam on an agar surface, separated by a cellophane barrier that permitted the passage of small molecules but not worms. Greet (1964) found that if the segregated populations were of opposite gender, the worms would gather near the cellophane barrier – a behavior that same-gender populations did not exhibit (Greet 1964).

2.2 Communication and Mating

Since 1964, sex pheromones were shown to exist in at least 37 additional species with widely divergent lifestyles. These species include free-living nematodes such as *rigidus*, as well as plant- and animal-parasitic species (Green 1980; MacKinnon 1987). The chemical nature of sex pheromones remains unknown in most species for which they are known to exist. One of the first identified sex pheromones was vanillic acid, produced as a male attractant in the plant parasite *Heterodera glycines* (Jaffe et al. 1989). Recently, activity guided fractionation has been used to isolate sex pheromones in the free-living species *Caenorhabditis elegans* and *Panagrellus redivivus*, which were found to be members of the ascaroside family of small molecules (Srinivasan et al. 2008; Choe et al. 2012a). Same-gender repulsive ascaroside pheromones have also been identified in *C. elegans* (Srinivasan et al. 2012). Reception and production of mating pheromones are most well studied in *elegans*. The receptors are suspected to be G-protein coupled receptors in the anterior amphid sensory neurons, and the intestine is suspected as a major source of ascaroside synthesis (Ludewig and Schroeder 2013).

While chemosensory mechanisms govern nematode attraction from a distance, mechanosensation is critical for actual mating to occur in many species (Lee 2002). Mechanosensation in general is disproportionately studied in *C. elegans* (Jones 2002) – since even a completely mating-incompetent strain of *C. elegans* can still reproduce through the action of self-fertilizing hermaphrodites, this species is especially well suited to the study of mechanosensory communication (Hodgkin 1983). Nematodes possess up to 16 mechanoreceptors in the anterior cuticle, and a number of internal mechanoreceptors that varies between species. Mechanoreception along the length of the nematode is carried out by dendritic processes embedded beneath the cuticle. Additional mechanoreceptors are also found in the external reproductive organs of male nematodes (Jones 2002). These receptors have been found to be critical for successful mating in *C. elegans*, whose males contain four neurons in the mating spicule and an additional 18 neurons in the sensory rays that assist in locating the vulva (Lee 2002). These neurons serve a variety of purposes, with some participating in positioning the male for mating, while others assist with locating the vulva (Liu and Sternberg 1995). Two genes are known to be essential for male mating behavior in *C. elegans*, *lov-1* and *pkd-2*, which are expressed in the ray neurons and located at the cell surface. These two genes are homologous to human genes that form membrane cation channels, although their purpose in the worm is unclear. In the absence of either *lov-1* or *pkd-2*, males will chemotax normally toward hermaphrodites, but fail to locate the vulva (Barr and Sternberg 1999; Barr et al. 2001). Curiously, both *lov-1* and *pkd-2* males are able to mate normally with *elegans* hermaphrodites that have been feminized by mutation, or have aged to the point that they have exhausted their supply of self-sperm. The mechanism for this rescue remains unknown (Morsci et al. 2011).

Lipton et al. (2004) looked at the influence of worm communication and other factors on “leaving” – the innate tendency of some worms to abandon a food source. In the studied species (the androdioecious species *C. elegans*, *C. briggsae*, and *P. pacificus*; and the gonochoristic species *Caenorhabditis remanei*), leaving behavior was most pronounced amongst fertile adults that were not actively bearing offspring, suggesting that innate leaving behavior is a mate-finding strategy. Self-fertile hermaphrodites tended not to leave food under any circumstances, although both males and females were less likely to leave in the presence of the opposite gender. In *C. elegans* specifically, male leaving was only inhibited by the immediate presence of hermaphrodites, and did not persist after their removal of the hermaphrodites. It was concluded that the signal which inhibits leaving is either a labile pheromone, or a cue presented on the surface of the hermaphrodite (Lipton et al. 2004).

2.3 Dauer Pheromones

In addition to behaviors related to mating, there has also been current and historical interest in the physiological changes that occur in response to pheromone signaling. Free-living nematodes such as *C. elegans* normally progress through four larval stages after hatching, and before developing into fertile adults. In an alternate developmental process triggered by a lack of food or a high concentration of nematode pheromone, the non-feeding “dauer” larva occurs in place of the third larval stage (Golden and Riddle 1982). Dauer larvae are resistant to harsh environmental conditions (Cassada and Russell 1975), and are long-lived compared to non-dauer worms (Klass and Hirsh 1976). Upon sensing a more favorable environment, a worm may leave the dauer stage and resume normal development (Cassada and Russell 1975). Similar developmental pathways are found in nematodes with widely varying life styles, including necromenic, animal parasitic and plant parasitic species (Dieterich and Sommer 2009). Outside of *C. elegans*, the dauer-like stage may be referred to as the infective or dispersive juvenile stage. The identity of the dauer pheromone(s) has been determined in both *C. elegans* and the entomopathogen *Heterorhabditis bacteriophora*. In both cases, the pheromone consists of one or more members of the ascaroside family (Jeong et al. 2005; Noguez et al. 2012).

The dauer pathway is most well studied in the model organism *C. elegans* on a both physiological and genetic basis. Through the ablation of individual cells through laser microbeam irradiation, it has been found that at least four chemosensory neurons (ADF, ASI, ASG and ASJ) (Schackwitz et al. 1996) and two neuroendocrine cells (called XXX) (Schaedel et al. 2012) are involved in promoting or suppressing dauer formation. Genetic screens have identified numerous genes required for the dauer formation pathway, including genes involved in signal transduction in chemosensory neurons, and pheromone synthesis (Hu 2007).

Even within a single species, there are strain-strain variations in both the levels of different dauer pheromones produced, and the response profile to the same pheromones. In 13 of 16 studied strains of *Pristionchus pacificus*, the dauer pheromone induces more robust dauer formation in individuals from other strains. It has been speculated this may be an effort to trigger distantly related worms to prematurely enter the non-feeding dauer phase, so as to increase the food supply available to a worm's own strain (Mayer and Sommer 2011). Thus, communication between nematodes, even of the same species, may be for competitive as well as mutually beneficial purposes.

2.4 Ascarosides

The class of small molecule that contains the *C. elegans* dauer and mating pheromones, the ascarosides, are widely found throughout *Nematoda* (Choe et al. 2012b). The term "ascaroside" is defined a glycoside of the dideoxysugar ascarylose. The first ascarosides were found in the mammalian parasitic nematodes *Parascaris equorum* (Fouquey et al. 1957) and *Ascaris lumbricoides* (Jezky and Fairbairn 1967), where they serve structural roles in the germline rather than pheromone roles. Since then, ascarosides have been identified as secreted pheromones in three species (Jeong et al. 2005; Choe et al. 2012a; Noguez et al. 2012), and shown to be secreted by an additional 12 species that are widely divergent in both habitat and phylogeny (Choe et al. 2012b). All known ascarosides have been found exclusively in nematodes (Ludewig and Schroeder 2013), although ascarylose itself is produced by some gram-negative bacteria (Thorson et al. 1994). Thus, the ascarosides appear to be a highly conserved and ancient, but nematode-specific, class of small-molecules that serve multiple roles. Although the number of ascarosides with clearly defined functions is small, so far over 140 ascarosides and ascaroside-related metabolites have been identified from *C. elegans* alone (von Reuss et al. 2012).

The first identified ascaroside, "daumone," from *C. elegans* was originally hypothesized to function alone as a dauer-inducing pheromone (Jeong et al. 2005).

However, subsequent studies showed that the single isolated pheromone could not recapitulate the activity of the original, unpurified secretions (Butcher et al. 2007a; Gallo and Riddle 2009), and numerous other ascarosides were found to have dauer-inducing activity, including one pheromone whose activity decreases past a critical concentration (Butcher et al. 2009; Pungaliya et al. 2009). The rate of dauer pheromone release also varies with environmental conditions, such as ambient temperature (Ludewig and Schroeder 2013). Altogether, these data suggest that *C. elegans* utilizes multiple synergistically acting pheromones that may be processed in different ways (Butcher et al. 2008; Ludewig and Schroeder 2013). Daumone is a potent male attractant in *Panagrellus redivivus* (Choe et al. 2012a).

Ascaroside signaling in *C. elegans* is believed to be received by G-protein coupled receptors (GPCRs) in the anterior chemosensory neurons (Ludewig and Schroeder 2013). Evidence of the involvement of G-proteins began with the finding that mutants for two G-protein alpha subunits, *gpa-2* and *gpa-3*, are defective at entering dauer (Zwaal et al. 1997). Mutants for *odr-1*, encoding a putative guanylyl cyclase, are also insensitive to dauer pheromone (Lans and Jansen 2007). Subsequent research has identified six putative ascaroside receptors, all of them GPCRs: *srg-36*, *srg-37*, *srbc-64*, *srbc-66*, *daf-37* and *daf-38* (Kim et al. 2009; McGrath et al. 2011; Park et al. 2012). All six of these receptors are responsive to specific components of the dauer pheromone, and may function as heterodimers. A putative ascaroside receptor has also been identified in *Caenorhabditis briggsae* that is paralogous to both *srg-36* and *srg-37* (McGrath et al. 2011). Overexpression of *srg-36* and *srg-37* enhances avoidance responses in *C. elegans* unrelated to dauer formation, suggesting that some ascarosides and receptors may mediate multiple functions (McGrath et al. 2011). The growing number of known ascarosides and receptors just to regulate dauer formation has been interpreted as indicating “a highly sophisticated signaling system” (Ludewig and Schroeder 2013).

2.5 Other Behaviors

In addition to chemotaxis and dauer formation, nematode pheromones may elicit more subtle behaviors, such as holding and aggregation. Holding behavior has been identified in assays as the appearance of nematodes to prefer the region of their environment near a source of pheromone, but without any apparent attraction to that region from a distance (Simon and Sternberg 2002). Nematode pheromones may also mediate behavioral changes irrespective of the distribution of the pheromone. Srinivasan et al. (2012) showed that exposure to certain naturally occurring ascarosides triggered *C. elegans* to aggregate, even in the absence of any pheromone gradient (Srinivasan et al. 2012). Although aggregation has been described in many species, and its neurological and genetic regulation partially uncovered, its purpose remains unclear (de Bono and Bargmann 1998).

3 Communication Between Nematodes and Microbes

Microbes and nematodes are both very successful in adapting to different environments. They can be found in almost all ecological niches and have evolved to coexist in a variety of environments. Here we briefly reviewed the roles of microbes as food, pathogens, symbionts or predators for nematodes.

3.1 Microbes as Food Source

Food strongly influences nematode behavior. For *C. elegans* and other bacterivorous soil nematodes, the main food source is bacteria and feeding is mediated by the pharynx, a neuromuscular pump that transports food from the mouth to the intestine (Avery and You 2012). In the lab, *C. elegans* are readily grown on a culture of *E. coli*; however, relatively little is known about the major bacteria species that they consume in nature and whether they have any food preference. Studies in the laboratory showed that when a variety of different bacterial species isolated from soil were individually provided as the sole food source for *C. elegans*, some species supported better growth of the *C. elegans* than the others (Avery and Shtonda 2003). Bacterial species such as *Pseudomonas* sp., *Comamonas* sp., *Acinetobacter junii*, *Pantoea* sp., and *E. coli* strain HB101 are high quality food that better support the growth of *C. elegans* whereas *Bacillus cereus and Bacillus megaterium* that are bigger in size are poor quality food. When given the choice between high-quality food and bacteria that are hard to eat, *C. elegans* showed obvious preference towards high quality food (Shtonda and Avery 2006). This dietary choice was not due to preferential chemotaxis to high quality food; instead, the food preference develops with time, suggesting that the choice was established after both types of food had been consumed (Shtonda and Avery 2006).

3.2 Microbes as Pathogens

Apart from being a major food source, microbes can be pathogenic to nematodes. For example, the soil bacterium *Pseudomonas aeruginosa* which is a cause of human disease, can kill *C. elegans* when provided as food and this pathogenic interaction has established them as a model to study microbial pathogenesis and host-pathogen interactions in *C. elegans* (Tan et al. 1999a). Genetic screens for mutants both in the pathogenic microbes and in the host nematodes have identified novel virulence factors important for *P. aeruginosa* pathogenesis, as well as host mutants with altered immune response to *P. aeruginosa* infection (Mahajan-Miklos et al. 1999; Tan et al. 1999b; Tan and Ausubel 2000). Upon infection, an antibacterial defense system is induced in *C. elegans*; several signaling pathways including the

DBL-1 TGF-β signaling pathway, the DAF-2 and DAF-16 insulin and stress-response pathway, and the PMK-1 MAPK pathway are involved in the defense response (Mallo et al. 2002; Garsin et al. 2003; Ewbank 2006).

Many other bacterial species were also found to be pathogenic to *C. elegnas*. These include the human pathogens *Enterococcus faecalis*, *Enterococcus faecium*, *Streptococcus pneumoniae*, and *Staphylococcus aureus*; the plant pathogens *Erwinia chrysanthemi* and *Agrobacterium tumefaciens*; and a novel species *Microbacterium nematophilum* first isolated in the laboratory on the basis of its ability to cause substantial local swelling in *C. elegnas* (<u>d</u>eformed <u>a</u>nal <u>r</u>egion; Dar phenotype) (Hodgkin et al. 2000; Garsin et al. 2001; Couillault and Ewbank 2002). When challenged by different pathogens, *C. elegans* activates both broadly acting innate immunity and pathogen-specific immune responses (Pukkila-Worley and Ausubel 2012). Transcriptomic studies revealed that distinct sets of genes were induced by *P. aeruginosa* infection, by *S. aureus* infection and by *M. nematophilum* infection (O'Rourke et al. 2006; Troemel et al. 2006; Irazoqui et al. 2010). This distinction is not totally surprising as the cytopathology of intestinal epithelium is drastically different between nematodes infected by different pathogens. For example, *P. aeruginosa* infection involves intestinal distention, extracellular material accumulation, intracellular invasion, outer membrane vesicles, and abnormal autophagy whereas *S. aureus* infection causes anal deformation, intestinal distention, enterocyte effacement, and cell lysis. Furthermore, it has been observed that a subset of genes is regulated inversely by fungal compared to its regulation by bacterial infection (Engelmann et al. 2011; Pukkila-Worley et al. 2011). For example, antibacterial immune effectors were selectively repressed during infection with the pathogenic yeast *Candida albicans*. *C. elegans* genes repressed by *S. marcescens*, *E. faecalis* and *P. luminescens* infection are over-representated among genes induced by infection with either of two nematode-parasitic fungi, *Drechmeria coniospora* and *Harposporium* sp. (Engelmann et al. 2011; Pukkila-Worley et al. 2011). Nonetheless, the conserved PMK-1 MAPK required for defense response to bacterial infection, is also required for resistance to fungal infections (Pujol et al. 2008a; Pukkila-Worley et al. 2011). Upon fungal infection, the expression of multiple genes encoding antimicrobial peptides was dramatically up-regulated, including the gene cluster containing *nlp-29* and five other *nlp-* genes (Pujol et al. 2008b). Overexpression of these genes confer increased resistance to infection, suggesting an *in vivo* anti-microbial activity (Pujol et al. 2008b).

How does *C. elegans* recognize pathogens? The recognition of the pathogens through microbial-associated or pathogen-associated molecular patterns (MAMPs/PAMPs) is an evolutionarily ancient mechanism (Janeway and Medzhitov 2002; Boller and Felix 2009). Heat-killed, avirulent *C. albicans* and *S. aureus* can still elicit transcriptional responses seen in host defense against pathogens demonstrating that the detection of these two pathogens by *C. elegans* could be mediated through the recognition of PAMPs, although no direct evidence has been shown (Janeway and Medzhitov 2002; Irazoqui et al. 2010; Pukkila-Worley et al. 2011). On the other hand, heat-killed *P. aeruginosa* does not induce an immune response of *C. elegans* and virulence factors are critical for the induction of the defense genes (Irazoqui et al. 2010). This suggests that the recognition of *P. aeruginosa* might involve monitoring the "patterns of pathogenesis" such as the growth of the pathogens, the ability of the pathogen to deliver microbial products into the host cell, or the integrity of the host cytoskeleton during the infection (Vance et al. 2009) and *C. elegans* may employ distinct pathogen-recognition mechanisms for different pathogens.

Although *C. elegans* has been established as a pathogenesis model in the laboratory, little is known about pathogens they encounter in nature. Recently, two studies have found that *C. elegans* is a natural host for microsporidia and for RNA viruses (Troemel et al. 2008; Felix et al. 2011). A novel microsporidia species (*Nematocida parisii*) and novel viruses (Orsay virus, a relative of Nodovirus) have been discovered causing infection in wild *C. elegans* isolates (Troemel et al. 2008; Felix et al. 2011). These recent findings make *C. elegans* a promising model to study the host response to microsporidia and viral infection, and to study the coevolution between the host and their natural pathogens.

3.3 Microbes as Nematode Symbionts

Another type of interaction between nematodes is the mutualistic relationship between nematodes and their symbiotic bacteria. Nematode-bacteria symbiosis is most prominently observed in the entomopathogenic nematodes (EPN) and is essential for the virulence of the parasitic nematodes (Dillman and Sternberg 2012). After seeking and entering the host, the EPNs regurgitate or defecates their bacterial symbiont. The bacteria then infect the insect prey, reproducing rapidly and producing insect-toxic secondary metabolites, quickly leading to the death of the insects. The nematodes consume the nutrient-rich cadaver, reproduce and when resources are depleted the nematodes produce dauer-like progeny (infective juveniles; IJs) adapted for dispersal and survival, which then seek out new hosts (Kaya and Gaugler 1993). Each EPN species is thought to only have one symbiotic bacteria species while each bacteria species may establish symbiosis with multiple nematode species. For example, *Xenorhabdus bovenii* is the symbiontic bacteria of the nematodes *Steinernema affinis*, *S. feltiae*, and *S. intermedia* (Kaya and Gaugler 1993).

The mutualistic relationship of EPNs with pathogenic bacteria has been extensively studied in the relationship between the nematode *Heterorhabditis bacteriophora* and its bioluminescent symbiotic bacteria *Photorhabdus luminescens*. When introduced into the insect host by the nematode *H. bacteriophora*, *P. luminescens* releases potent insecticidal ABC-type toxin complexes (Tcs) and the McF toxin, as well as hydroxystilbene antibiotics that protects it from other microbial competition (Richardson et al. 1988; ffrench-Constant and Bowen 2000; Daborn et al. 2002). Recently, the structures of the Tcs was determined using cryoelectron microscopy, leading to a proposed novel syringe-like mechanism for the membrane insertion and protein translocation of the Tcs (Gatsogiannis et al. 2013). Furthermore, *P. luminescens* exists in two states, the pathogenic state (P-form) and the small-cell, mutualistic state (M-form). The P-form cells are only transiently present inside the nematode intestine and are non-adherent while the M-form cells express maternal adhesion (Mad) fimbriae and are able to adhere and colonize in the nematode intestine to initiate the mutualistic interaction (Somvanshi et al. 2012). Recent studies have found that this phenotypic switching is caused by a stochastic promoter inversion event gene at the Mad locus and an invertase, MadO, is required to flip the Mad switch from OFF to ON (Somvanshi et al. 2012). M-form cells initiate mutualism during the initial step of colonizing early IJs; however, these cells switch to P-form in the fully colonized, late IJ, enabling these nematodes for the next cycle of infection (Somvanshi et al. 2012).

Much remains to be explored regarding the molecular mechanisms of symbiosis in EPNs. The recent advances in the genomic and genetic analyses in some EPNs have provided valuable tools, making EPNs attractive models to study the mechanism of symbiosis (Bai et al. 2007; Ciche 2007; Adhikari et al. 2009; Schwartz et al. 2011; Dillman et al. 2012c).

3.4 Microbial Predators of Nematodes

Nematodes also face constant threat posed by their predators; common predators of the soil dwelling nematodes include insects, mites, tardigrades, predatory nematodes and nematophagous fungi (Small and Grootaert 1983; Nordbringhertz 1988; Martikainen and Huhta 1990; Felix and Braendle 2010). Predation plays a key role in suppressing the population of nematodes in the environment and in theory some of these natural antagonists have the potential to be developed as biological control agents for parasitic nematodes (Kerry 2002). Among the nematode predators, the nematophagous fungi have caught scientists' attention since its first discovery in late 1880s (Pramer 1964; Barron 1977). These predatory fungi can be found in various habitats and a couple hundreds of such species belonging to different fungal Phyla (Ascomycota, Basidiomycota and Zygomycota) have been described (Liou and Tzean 1997; Yang et al. 2007). The wide distribution of the nematophagous fungi in taxonomy suggests that this predacious lifestyle have arisen independently multiple times during evolution. Distinct trapping structures have evolved among different species. These include adhesive columns, adhesive knobs and adhesive networks that trap nematode prey via extracellular adhesive polymers and proteins such as lectin that cover the trapping structure (Rosen et al. 1992; Tunlid et al. 1992) and constricting rings and non-constricting rings rely on mechanical force to trap nematodes (Higgins and Pramer 1967). The constricting ring is formed by three cells; when a nematode enters the ring, the ring cells rapidly swell inward and tightly pinch the nematodes, making them the only type of trap that can actively capture a nematode (Higgins and Pramer 1967; Liu et al. 2012). This sophisticated trapping mechanism nonetheless is not the most efficient one compared to adhesive traps as nematodes can withdraw themselves from the rings before its complete closure (Barron 1977). Recently, it has been shown that the *C. elegans* touch response might have evolved in order to escape from the constricting rings (Maguire et al. 2011).

One remarkable feature of the nematode-trapping fungi is their ability to sense the presence of prey. In general, traps are induced in response to nematodes and do not form constitutively (Pramer 1964). Early studies demonstrated that a morphogenic substance, termed nemin, is secreted from the nematodes to induce trap-formation (Pramer and Stoll 1959). Followup studies showed that purified nematode proteins, valine, and oligopeptide Phe-Val had trap-inducing activities (Wootton and Pramer 1966; Nordbrin 1973). The trap-inducing compounds secreted by nematodes significantly increase the risk of predation by the predatory fungi and therefore, are disadvantageous to nematodes. However, nematodes have not lost the secretion of these compounds during evolution despite of this selective pressure. This suggests that these compounds are likely to have important biological functions that promote the fitness of nematodes to a greater degree than they imperil the nematodes by putting them at a greater risk of predation. As discussed above in the nematode-nematode communication section, in recent years, a group of small molecules called ascarosides has been identified in *C. elegans* and other nematode species that serve as pheromones to regulate behavior and development (Jeong et al. 2005; Butcher et al. 2007b; Srinivasan et al. 2008, 2012; Choe et al. 2012b). Because such broad aspects of nematode biology including dauer formation, mate attraction, social aggregation and chemotaxis are regulated by ascarosides, they have very important roles in communication among nematodes, which make them favorable candidates to be among the trap-inducing factors. Indeed, when ascarosides were tested for trap-inducing activity on several species of nematophagous fungi, strong activity was observed for some of the ascarosides (Hsueh et al. 2013). Different nematophagous fungal species displayed differing ascaroside-responsiveness, suggesting that in nature, different fungal species might prefer nematode species over others as prey or might be adapted to respond to those species they more frequently encounter (Hsueh et al. 2013). Ascaroside-triggered trap morphogenesis in nematophagous fungi demonstrates that in this case, the predators have coevolved with their prey to eavesdrop on their essential communication. Therefore, ascarosides could also serve as a nematode-associated molecular pattern recognized by other organisms that interact with nematodes. The large diversity of ascaroside molecules observed in Nematoda might represent the continual development of new ascaroside signals in the nematodes, in an arms race to develop signals that cannot yet be eavesdropped upon by their predators.

4 Communication Between Plants and Plant Parasitic Nematodes

Plant parasitic nematodes (PPNs) exploit plant tissues and causes significant crop losses. Three major groups of PPN, the root-knot, soybean cyst, and lesion nematodes, are the most economically damaging PPNs. The root-knot nematodes (RKN) alone cause ~$60 billion in crop loss worldwide annually (Bird and DiGennaro 2012). Like all parasites, the interaction between the plant hosts and their PPN parasites is complicated and plays a key role in the parasitic relationship. Here, we discuss examples of direct interactions between PPNs and host plants, as well as examples of indirect interactions that often involve another type of organisms in communication.

4.1 Chemotaxis Behavior of Plant Parasitic Nematodes

For many PPNs, locating the host is the first step before they can initiate an infection. It is known that the infective juveniles (IJs; the J2 juvenile stage) of PPNs are attracted to growing roots (Bird 1959). For example, the RKN *Meloidogyne incognita* and the cyst nematodes (CN) of the genus *Heterodera* are attracted to vapor of host root, including carbon dioxide (Mccallum and Dusenbery 1992; Rasmann et al. 2012). The RKN *Meloidogyne hapla* has also been reported to be attracted to pH gradients and aggregates between pH 4.5 and 5.4 (Wang et al. 2009). It is suggested that the local acidification in the root system due to dissolved CO_2, instead of CO_2 itself, actually attracts the RKN (Wang et al. 2009). The RKNs have a broad host range, so being attracted by a general, nonspecific cue such as CO_2 may increase their chance of finding a host. On the other hand, the CNs have much narrower host range and it seems implausible that attraction to CO_2 is sufficient for them to identify a suitable host. However, one remarkable feature of CNs is that they only hatches very close to the root of the host; this host-specific induced hatching ensures that the freshly hatched IJs may locate the host easily (Rasmann et al. 2012). The hatching stimuli from the root of the host-plant consist of complex root diffusates. Glycinoeclepins A and the tetranortriterpene solanoeclepin A were identified as an active components secreted by the roots of the kidney bean and of the potato, respectively; and *in vitro*, both compounds were shown to be able to trigger CN hatching at very low concentration (10^{-12} g/ml) (Masamune et al. 1982; Schenk et al. 1999).

In addition to CO_2, PPN are also attracted or repelled by plant-derived volatile organic compounds and root exudates (Diez and Dusenbery 1989; Ali et al. 2011). For example, the IJs of the potato cyst nematode *G. rostochiensis* are attracted to potato root diffusates and the plant- produced chemical sesquiterpene and other terpene compounds were found to attract phylogenetically diverse plant parasitic nematodes (Ali et al. 2011). It has also been shown that volatile compounds secreted by cucumber roots attracted RKN, although the identity of the chemicals is unclear (Castro et al. 1989). The molecular mechanism of chemotaxis in plant parasitic nematodes is largely unknown. Recent studies have shown that the CO_2 response is governed by the BAG neurons in the soil nematode *C. elegans* and the EPNs *S. carpocapsae* and *H. bacteriophora* (Hallem et al. 2011). It will be interesting to learn whether the neuronal circuit and the molecular pathways that regulate chemosensation are conserved in PPN.

4.2 Interactions Between Nematode Effectors and Host Machinery

For the RKN and CN, after locating the host, the IJs (J2 stage of the juveniles) penetrate the roots and initiate a series of complicated interactions with the plants to establish permanent feeding sites where they become sedentary. These plant cells at the permanent feeding sites become dramatically transformed in their morphology and physiology to support nematode growth and reproduction (Gheysen and Mitchum 2011). After penetrating the roots, RKNs migrate into vasculature and secrete effectors from the esophageal gland cells through their stylets into host vascular cells. These effectors then manipulate the host cells to undergo several rounds of nuclear division without cell division, resulting in "giant cells", which feed and support the growth and the reproduction of the RKN (Bird and DiGennaro 2012). Similarly, when CN penetrate the roots, they migrate through the host tissues and induce coalescence of numerous adjacent cells by partial cell wall degradation to form syncytia that act as permanent feeding sites (Gheysen and Mitchum 2011).

What are the effectors secreted from nematodes that act on the host plant cells? Several studies attempted to isolate the effector proteins from *Meloidogyne incognita* (RKN) and the soybean cyst nematode *Heterodera glycines* and direct evidence has shown that the nematodes secret mimics of plant peptide hormones (Gao et al. 2001; Huang et al. 2003; Olsen and Skriver 2003; Wang et al. 2010). SYV-46, a protein secreted from the stylet of *H. glycines* was found to mimic the plant CLAVATA3/ESR (CLE)-like proteins that function as plant peptide hormones (Olsen and Skriver 2003). In plants, proteins of the CLE family are involved in the regulation of several physiological and developmental processes such as meristem maintenance and promoting stem cell differentiation in shoot (Fiers et al. 2007). In addition to sharing sequence similarity to the CLE proteins of plants, SYV-46 was able to bind a CLE receptor, CLV2, and could suppress the phenotype of the *Arabidopsis thaliana* mutants lacking *clv3-1* (Wang et al. 2005). These results suggest that the nematode CLE mimics may have a potential to directly regulate the development of the host, which may be correlated to the observation that syncytium development resembles xylem differentiation (Gheysen and Mitchum 2011). The CLE-like gene family has expanded and diversified in the potato cyst nematode *Globodera rostochiensis* (Lu et al. 2009), and similar gene families have been identified in the genomes of the RKNs *M. incognita* and *M. hapla* (Bird and DiGennaro 2012), implying that they could be broadly used by the sedentary parasitic nematodes to manipulate host cell development. One potential CLE-like protein, 16D10 of *M. incognita* was found to be a ligand for scarecrow-like proteins that are transcriptional regulators for rhizobial nodulation and meristem specification (Huang et al. 2003, 2006).

During the early stage of the syncytia and root-knot formation, it was observed that the infection sites showed an enhanced auxin response whereas the auxin transporter and signaling mutants had significantly decreased infection caused by the cyst nematode *H. schachtii* (Hutangura et al. 1999; Goverse et al. 2000; Grunewald et al. 2008). Several studies have suggested that infecting nematodes achieved the elevated auxin response by manipulating the expression of the auxin transporters (Gheysen and Mitchum 2011). In the developing syncytia, the transcription of the auxin influx pump *AUX1* was up-regulated and the auxin efflux pump *PIN-1* was down-regulated, resulting the accumulation of auxin (Mazarei et al. 2003; Grunewald et al. 2009a). The localization of another auxin exporter, PIN3, is redirected from the basal to the lateral plasma membrane in the syncytia (Grunewald et al. 2009a). This redirects the transportation of auxin to adjacent cells and therefore, facilitates the expansion of the syncytia (Grunewald et al. 2009b). More recently, the novel effector protein Hs19C07 from the cyst nematode *H. schachtii* has been shown to interact with the auxin transporter LAX3 and increase the activity of LAX3 (Lee et al. 2011). These evidences again, illustrate how nematodes manipulate the host machinery directly or indirectly to establish the permanent feeding sites.

Ethylene, another plant hormone, has also been associated with nematode infection. Overexpression of ethylene lead to hypersusceptibility and the ethylene insensitive mutants were less susceptible (Wubben et al. 2001). It is thought that the hypersusceptibility of the ethylene overexpression mutants is caused by the increased attraction of IJs to the roots of these plants (Wubben et al. 2001).

4.3 Multitrophic Interactions Involving Plants, Nematodes and Other Organisms

Soil is a complex environment. It is a major niche occupied by a wide variety of plants, nematodes, bacteria, fungi, amoeba, and arthropods. It is not surprising that the interaction between PPN and plants may involve a third player, developing a multitrophic relationship. For example, root symbiotic fungi and bacteria can stimulate root respiration, leading to increased production of CO_2 and exudations that attract nematodes (Rasmann et al. 2012). Plants infected with the fungal pathogen *Fusarium oxysporum* were found to be more attractive to nematodes (Edmunds and Mai 1967) and it has been observed that *Fusarium* wilt of cotton was more severe when the RKNs were present (Mai and Abawi 1987).

Another example of multitrophic interaction involves plants, beetle larvae, and EPNs. Plant leaves attacked by arthropod herbivores are known to emit volatile compounds that attract the natural enemies of the herbivores. When the plant roots are attacked by the beetle larvae, the roots increase their production of (E)-β-caryophyllene, a compound that is highly attractive to EPNs (Rasmann et al. 2005). Recruitment of EPNs to the sites of wounded plant roots illustrates a sophisticated mechanism that contributes to indirect plant defense. Dissecting the mechanism of multitrophic interaction is challenging as it is difficult to set up an experimental system in the laboratory that involves multiple players to mimic the complex interactions in the natural environments. However, such studies are more likely to discover novel mechanisms used by different organisms for interspecies communication.

5 Nematode-Insect Interactions

Nematode interactions with insects can be broadly classified as phoresy, the use of insects to migrate to new environments; necromeny, the eating of dead insects; parasitism, the use of the insect host for nutrition to detrimental effect; and entomopathogeny, the rapid killing of the host insect (Sudhaus 2008; Dillman et al. 2012a). Nematodes have evolved a variety of methods for detecting and distinguishing nearby insects. Just as nematode sexual encounters are guided by communication, rather than chance (Greet 1964), nematode-insect interactions are often deliberate – many nematode species of varying lifestyles will seek out specific hosts in a complex environment, rather than embark upon the first insect it encounters (Hong and Sommer 2006).

In a phoretic relationship, nematodes attach to a larger animal, typically an invertebrate, to traverse greater distances than they would otherwise be able to. In the Nematode orders *Rhabditidae* and *Displogasterida*, phoresy is carried out exclusively by dauer larvae (Sudhaus 2008). Dauers exhibit a behavior called “nictation,” in which the worm stands on its tail and waves its body about. This behavior is believed to facilitate being picked up by a passing insect (Burr and Robinson 2004). Some nematodes seem to exhibit no specific preference for carrier hosts. Phoretic larvae of *Caenorhabditis elegans*, for instance, have been found on a wide range of hosts, including millipedes, flies, snails and slugs (Sudhaus and Kiontke 1996; Barrière and Félix 2005).

Other phoretic nematodes have far more specific associations. *Caenorhabditis drosophilae*, for instance, is believed to specifically associate with the fly *Drosophila nigrospiracula* (Kiontke 1997). *Caenorhabditis remanei* is found to have preferential association with the woodlouse *Trachelipus rathkii* and related species. *C. remanei*, however, is not found associated with the woodlouse *Porcellio spinicornis*, even though this isopod is found in the same environment as *C. remanei* and its phoretic hosts. These preferential associations have been observed in both the wild and controlled laboratory experiments, suggesting that preferential associations do not arise merely from contact with a limited range of hosts (Baird 1999). *Caenorhabditis japonica* has also been found to have a species-specific phoretic association – in the wild, *C. japonica* is found exclusively on the shieldbug *Parastrachia japonensis* (Kiontke et al. 2002).

Few papers have investigated the mechanism by which phoretic nematodes maintain associations with specific hosts, but those that exist support a model in which nematodes sense secreted and surface-bound cues to distinguish potential hosts. In laboratory experiments, *C. japonica* retains a strong preference for its wild host, rarely boarding other insects. Chemoattraction assays have shown *C. japonica* to be specifically attracted to cues presented on the body surface of its preferred host (Okumura et al. 2013). The fig nematode *Ficus racemosa* is able to distinguish not only the species but also the gender of its potential hosts. In its natural environment, *F. racemosa* is presented with many potential wasp hosts, but only the females of certain species are likely to travel to a new fig at which the nematode may disembark.

F. racemosa larvae are able to achieve specific association through the sensation of volatile odors and surface-bound hydrocarbons on the female wasps (Krishnan et al. 2010).

Necromenic nematodes follow a lifestyle initially similar to that of phoretic nematodes described in the previous section. However, once a dauer larva of a necromenic species has found a carrier host, it rarely or never disembarks. Upon the death of the host, the larva feeds on bacteria growing within the carcass (Schulte 1989; Sudhaus and Schulte 1989; Kiontke and Sudhaus 2006). Several phoretic nematodes have been observed to follow a necromenic lifestyle in the laboratory only, which has been referred to as "facultative necromeny" (Kiontke and Sudhaus 2006). As with phoretic nematodes, many necromenic species are found to exhibit species-specific associations. Some of the most comprehensive studies on the host-preference of necromenic nematodes have been performed on the genus *Pristionchus*. *Pristionchus pacificus* exhibits strong species preference, but this preference differs between locations. In Japan, *P. pacificus* is almost exclusively found associated with the beetle *Exomala orientalis* (Herrmann et al. 2007), while in Western Europe it is generally found on the European cockchafer (genus *Melolontha*) (Hong and Sommer 2006). Other species in this genus have similarly strong preferences, with *P. maupasi* also associating with cockchafers, *P. entomophagus* generally associating with dung beetles, and *P. uniformis* preferring the Colorado potato beetle (Herrmann et al. 2006). Laboratory studies of *Pristionchus* chemotaxis have found the various species to be attracted to insect odors, including sex pheromones, as well as plant odors that may indicate insect presence. Chemoattractive profiles differ significantly even between relatively close relatives in *Pristionchus*, which may explain the extreme specificity of their associations (Hong and Sommer 2006; Herrmann et al. 2007; Hong et al. 2008).

Nematodes that cause harm to insect hosts are generally divided into two broad groups: Parasitic nematodes infest and carry out their life cycle within a living host; while entomopathogenic nematodes rely on endosymbiotic bacteria to rapidly kill the host, after which the nematode feeds on the reproducing bacteria (Kiontke and Sudhaus 2006). Invasion by nematodes typically evokes immune responses from the insect host, which are often fatal to the parasite. Parasitic and pathogenic nematodes are therefore under substantial evolutionary pressure to selectively invade only suitable hosts. (Insect immune reactions to parasitic and pathogenic nematodes have long been a subject of intensive study due to interest in such nematodes as pest-control agents. The subject has been previously reviewed by Salt (1963), Poinar (1969), and Dunphy and Thurston (1990).)

As with previous examples for phoretic and necromenic nematodes, parasitic and pathogenic nematodes are capable of infesting specific hosts within a complex environment. *Howardula aoronymphium* and *Parasitylenchus diplogenus* are nematode parasites of various mushroom feeding members of the *Drosophila* genus of flies. Despite at least a dozen species of *Drosophila* being found in the same environment, these two nematode species are only found to parasitize five species, and some at a high rate. The range of preferred hosts seems to be related to phylogenetic similarity, rather than to behavioral similarity (Welch 1959). The means by which parasitic and pathogenic nematodes locate their hosts are quite varied, including compounds in host feces (Grewal et al. 1993), expired carbon dioxide (Hallem et al. 2011), insect volatile odors (Dillman et al. 2012b), and the vibrations induced by passing insects (Torr et al. 2004). Even closely related nematodes show complex and divergent response profiles to insect odors, which may explain the specificity and divergence of host-seeking behaviors. Broad distinctions in responses to insect odors are found to correlate with host-seeking strategy, however (Dillman et al. 2012b). Entomopathogenic nematodes generally follow two different strategies, or a mix of the two: Ambushing, wherein the nematode nictates on a soil surface and jumps toward potential hosts; and cruising, wherein the nematode moves underneath the soil surface to seek out and invade a host (Sudhaus 2008). Ambusher nematodes are found to be generally attracted (jump in response) to anything that produces carbon dioxide. Cruiser nematodes, on the other hand, more specifically chemotax toward potential hosts (Dillman et al. 2012b).

After invading a host, it is necessary for a parasitic or pathogenic nematode to avoid, suppress, or survive the host immune response. Li et al. (2007) showed that pathogenic nematodes most often trigger host immune responses when infecting an insect other than its preferred host. However, evasion of the immune system did not fully correlate with the ability to kill a host; some nematodes, such as *Steinernema glaseri* and *Heterorhabditis bacteriophora* were capable of killing their host after surviving an immune reaction (Li et al. 2007). Suppression of the immune system can occur at multiple levels and may be carried out by the nematode or, in the case of entomopathogenic nematodes, its bacterial symbiont. The cuticle of the entomopathogen *Steinernema feltiae* is capable on its own of suppressing the proPO protease cascade that triggers insect immune responses, which may allow it to evade the immune system entirely (Brivio et al. 2002). This capacity is not sufficient for all nematodes in all hosts; however, Li et al. (2007) also co-injected *S. glaseri* coat proteins during infections to suppress the insect immune system. The susceptibility of the host was only increased to some pathogens, and not others (Li et al. 2007). The influence of nematode cuticles and coats on immune evasion was reviewed by Blaxter et al. (1992). Active immune responses may also be subverted. Both *Steinernema carpocapsae* and its bacterial symbiont, *Xenorhabdus nematophilus*, are capable of both killing the hemocytes that carry out the immune response and suppressing hemocyte sticking, which assists in the killing of parasites (Dunphy and Webster 1984; Ribeiro et al. 1999).

6 Conclusion and Prospects

We have highlighted a few areas of exceptional interest to us as well as areas where the analyses have started to shed bright light on mechanisms of communication. The most striking general conclusion from these studies is that we have only seen glimpses of the extent of communication among nematodes and with their predators, prey, hosts and trophic partners. In the many cases in this book where we see differences in biocommunication of nematodes with that of other groups, we expect that many are simply due to our ignorance. We believe that much progress can be made by straightforward observation and experiment but that the sheer number of nematode species is a distraction as well as being a delight.

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