# Wild American crows gather around their dead to learn about danger

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While a growing number of animals demonstrate avoidance of areas associated with conspecific death, the extent to which wild populations may use these experiences to learn about novel predators remains unclear. Here we demonstrate with experiments that wild American crows, *Corvus brachyrhynchos*, respond to dead conspecifics by mobbing, increasing the time to approach food in areas associated with these events, and learning new predators based on their proximity to dead crows and hawks. Avoidance of either dead conspecifics or areas associated with them is not shared by another urban bird, the rock pigeon, *Columba livia*. Crows mobbed and increased the time to approach food over the next 72 h after observing novel humans paired with a dead crow, a red-tailed hawk, *Buteo jamaicensis*, or a hawk with a dead crow. The sight of a dead pigeon did not elicit these responses. These findings suggest that, for crows, dead conspecifics, but not dead heterospecifics, represent a salient danger akin to the observation of a predator. On the day the stimulus was presented, the number of trials that resulted in mobbing and avoidance of the food was strongest when crows were presented a hawk with a dead crow. In addition, we demonstrate that crows use the proximity of a human to predators, to dead conspecifics and to predators with dead conspecifics as cues to learn to recognize and subsequently scold the associated human after only one training event, and that this association can last 6 weeks. Together, our results support previous findings that crows learn places associated with conspecific death, and further demonstrate that crows can learn and remember people who appear complicit in these events.

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Animals can reduce their risk of predation by attending to cues in the environment such as predator odours (Eichholz, Dassow, Stafford, & Weatherhead, 2012), observations of predators (Cooper, 2005) and observations of predators with prey (Conover & Perito, 1981; Kruuk, 1976). Risk may also be communicated through conspecific and heterospecific alarms such as vocalizations (Shriner, 1998; Templeton, Greene, & Davis, 2005) and olfactory cues (Ferrari, Wisenden, & Chivers, 2010). In fish, these cues trigger area avoidance and increased shelter activity (Lawrence & Smith, 1989). Less is known, however, about the extent to which animals use visual remains of conspecifics as evidence of predation risk.

Humans place substantial significance on conspecific death (Tattersall, 1998), whereas few animals have been reported to show more than a passing interest. Black-billed magpies, *Pica hudsonia* (Miller & Bringham, 1998), western scrub-jays, *Aphelocoma californica* (Iglesias, McElreath, & Patricelli, 2012), chimpanzees, *Pan troglodytes* (Stewart, Piel, & O'Malley, 2012), African elephants, *Loxodonta africana* (Douglas-Hamilton, Bhalla, Wittemyer, &

Vollrath, 2006), and bottlenose dolphins, *Tursiops aduncus* (Dudzinski et al., 2003), are among those that congregate around or touch and groom dead conspecifics. The evolutionary basis for these behaviours in mammals remains unclear (McComb, Baker, & Moss, 2006). Emerging evidence suggests that, for some birds, these interactions are used to assess danger and trigger antipredator behaviours.

Wild common ravens, *Corvus corax*, and American crows, *Corvus brachyrhynchos*, mob in response to distress call playbacks paired with a dead conspecific and avoid areas where they are present (Avery, Tillman, & Humphrey, 2008; Peterson & Colwell, 2014). Western scrub-jays also mob in response to dead conspecifics, and they do so in the absence of artificial distress calls (Iglesias et al., 2012). Furthermore, following carcass removal, scrub-jays show reduced feeding activity in the area for 24 h. A similar effect was seen when scrub-jays were presented an upright-mounted great-horned owl, *Bubo virginianus*, suggesting that dead conspecifics are used as indirect evidence of predators. These behaviours were not observed in response to jay-like, novel objects or upright-mounted scrub-jays. A subsequent study showed that mobbing and area avoidance are also extended to sympatric and allopatric jay-sized heterospecifics (Iglesias, Stetkevitch, & Patricelli, 2014). Together,

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these studies suggest that dead conspecifics, and certain hetero-specifics, can elicit learning and avoidance of places associated with death. What remains unclear, however, is whether the presence of dead conspecifics is an effective trigger to induce conditional learning of a novel predator in wild populations.

Through classical conditioning, naïve animals can learn about novel predators through exposure to an unfamiliar predator in association with conspecific alarm cues, such as odours or vocali-zations, or by watching responses of knowledgeable individuals (Griffin, Blumstein, & Evans, 2000). These stimuli subsequently prompt antipredator behaviours such as mobbing (Curio, Ernst, & Vieth, 1978) and site avoidance, even at the cost of avoiding high-quality or abundant food (Lima & Dill, 1990). Fear can be extin-guished, however, through repeated exposure to the conditioned stimulus without reinforcing its predictive value of the uncondi-tioned stimulus (Myers & Davis, 2007). While brain-imaging studies suggest that captive American crows learn to recognize people associated with dead crows (Cross et al., 2013), it remains untested whether wild animals can use dead conspecifics to infer novel predators in the absence of alarm call playbacks. Under-standing this potential, and its vulnerability to extinction, could inform management for both the reintroduction of naïve in-dividuals, and as a means to create more effective 'scarecrows'.

Here, we add to previous studies by testing whether, as in scrub-jays, wild crows reduce feeding activity after only a brief exposure to a predator, to a dead conspecific or to a dead, similarly sized heterospecifc. Furthermore, we expand by asking whether crows' interest in dead conspecifics facilitates learning of novel, threat-ening people and whether this knowledge is resistant to extinction. Lastly, we also determine whether another urban bird, the rock pigeon, *Columba livia*, uses dead conspecifics to assess risk. To test danger learning, we conducted three experiments on wild crows. In experiment 1, we examined (1) whether the sight of a dead conspecific is sufficient to elicit alarm calling and recruitment, or whether the presence of an unconditioned predator is also neces-sary, (2) whether crows learn areas associated with these dangers and subsequently avoid them, (3) whether crows use dead con-specifics to identify novel predators and, if so, how this process compares to conditioned learning when novel predators are paired with unconditioned stimuli (hawks), and (4) whether fear extinc-tion can be achieved with a minimum of three additional expo-sures. For experiment 2, we determined whether a dead conspecific is a more salient source of dangerous information than a similarly sized, dead heterospecific. In experiment 3, we compared re-sponses of rock pigeons and crows to dead conspecifics.

## METHODS

### General Information

We conducted the three experiments, consisting of three phases each (conditioning, stimulus presentation, post-exposure; Fig. 1), at sites in Washington, U.S.A. (in and around the cities of Seattle, Redmond, Kirkland and Bellevue, and Mercer Island; 47°34′9″–47°49′14″N, 121°33′13″–122°13′56″W). In our study area, crows live on small (25–150 ha) territories as pairs or small families (Marzluff, McGowan, Donnelly, & Knight, 2001). We assumed that no more than two adult birds occupied each terri-tory, as helping behaviour occurs infrequently in crow populations in the northwestern United States (Verbeek & Butler, 1981).

A single observer and data collector (K.N.S.) provided food at a consistent location at roughly the same time daily throughout all phases of each experiment. Crows received a 2:1 mix of raw, un-shelled peanuts and cheese puffs. Pigeons received a 2:1 mix of birdseed and crumbled white bread. After providing food, the observer monitored the food pile from 15–25 m away, for up to 2.5 h, and measured the birds' latency to approach within 2 m of the food pile ('food discovery time').

### Conditioning phase

Once the birds at each site approached the food within the 2.5 h observation period for 3 consecutive days (in most tests, birds met the criterion in 3 days; in seven tests, birds took up to 10 days to meet the criterion), we began the stimulus presentation phase on the following day (day 4).
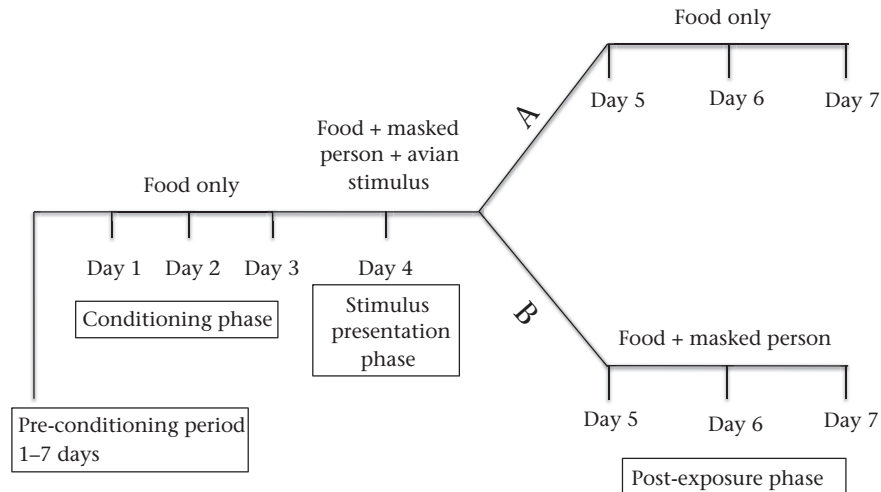
### Stimulus presentation phase

During the stimulus presentation phase, we provided food as normal, after which a volunteer exposed an experimental or a control stimulus 2 m from the food pile (see below). Volunteers wore one of six realistic facemasks with neutral expressions (to preclude contaminating effects of facial expression; see Figure 1b in Marzluff, Walls, Cornell, Withey, & Craig, 2010) and a white sign around their neck that read 'UW CROW STUDY' to limit in-terruptions by pedestrians or police. During stimulus presentation, the data collector recorded instances and durations of scolds and typical crow contact calls, and the number of birds present within 25 m of the stimulus. We define mob formation as the presence of more than two scolding individuals within 25 m of the stimulus. We calculated mob size as the maximum number of individuals present during the stimulus event. Because mobs are highly mobile and most birds were not individually marked, we did not determine whether all individuals within a mob actively scolded beyond the three-bird minimum. The volunteer removed the stimulus 30 min after the first bird perched within 25 m of the stimulus and was observed gazing towards the experimental set-up ('stimulus dis-covery time'). Following stimulus removal, for up to 2.5 h, the observer recorded the birds' latency to approach within 2 m of the food pile ('food discovery time'). We removed all but a small amount (five pieces) of food after 2.5 h. If birds approached the pile in the presence of the stimulus, we recorded the food discovery time as 0 s. The observer used plumage, profile, voice and mouth lining to discriminate between hatch-year and older birds (dos Anjos, Debus, Madge, & Marzluff, 2009; Emlen, 1936). Only birds older than 1 year of age were counted for stimulus discovery time, food discovery time and mob or group size.

### Post-exposure phase

During the post-exposure phase, on days 5–7, we split the experiment into two trial types: A and B. In trial type A, we continued to provide food (as described above) to test for site aversion. In trial type B, following standard feeding by the observer (as during conditioning), a volunteer wearing the same mask as seen during the stimulus exposure phase arrived and stood 2 m from the food pile. The experimental procedure during test trial B otherwise matched that of the stimulus exposure phase, allowing us to test for novel predator learning and to evaluate the influence of varying levels of exposure to danger on fear extinction. Only experiment 1 used both trial types. Experiments 2 and 3 used trial type A during the post-exposure phase.

### Ethical Note

No animals were trapped or handled during the course of this study and any marked individuals were banded 5 years before the onset of the present experiment. Experimental locations were established 35–45 m from nest sites to limit nest disturbance. All procedures were approved by the Institutional Animal Care and Use Committee of the University of Washington (IACUC; protocol number 3077-01).

**Figure 1.** Each experiment consisted of three phases: conditioning, stimulus presentation, post-exposure. Some test locations required extended pre-conditioning (1–7 days) prior to start of the conditioning phase. Stimulus presentations in all experiments occurred on day 4, following 3 days of conditioning. During the post-exposure phase, birds experienced either food provision only (trial type A), or 30 min of exposure to the same masked person they had seen during stimulus presentation (trial type B). Experiment 1 used both trial types. Experiments 2 and 3 used trial type A during the post-exposure phase. The same observer provided food and recorded the crows' responses (up to 2.5 h) each day.

*Experiment 1: Crow Response to a Dead Conspecific and/or a Predator*

In 2013 and 2014, we selected 17 independent sites and, within each site, identified seven to nine territorial pairs (Fig. 2). In April–June, we used nesting areas to define the locations for tests, and established specific test locations 35–45 m from the nest tree. During July–September, we identified test locations by the presence of fledged young or the consistent presence of an adult pair. Within each site, each adjacent territory received a unique stimulus, and test locations were spaced to assure independence. American crow territories in the urban core are smaller than their suburban counterparts (Marzluff et al., 2001), and the minimum

distance between two test locations was 90 m (median distance = 430 m). Such spacing was adequate to ensure independence and preclude carryover effects (see Results).

During the stimulus presentation phase of the experiment, birds received one of five stimuli (three dangerous, two controls). The dangerous stimuli were placed 2 m from the food pile and included (1) a taxidermy-mounted 'dead' crow presented on the outstretched palms of a slowly rotating or turning person who wore a unique mask ('dead crow + mask'), (2) a taxidermy-mounted red-tailed hawk perched on a branch 2 m from a masked person ('hawk + mask') and (3) a taxidermy-mounted red-tailed hawk positioned with a taxidermy-mounted 'dead' crow 2 m from a masked person ('hawk + dead crow + mask'). The control stimuli
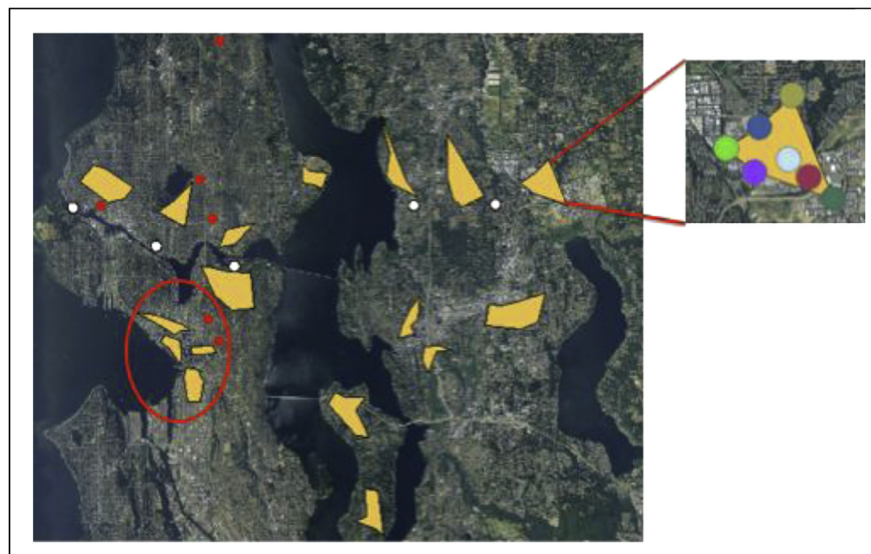


**Figure 2.** Map of study areas in Seattle (left landmass), Mercer Island (central landmass), and Kirkland, Redmond and Bellevue (right landmass, clockwise). Orange polygons show 17 unique sites for experiment 1 (Seattle, $N = 9$ sites; Mercer Island, $N = 2$ sites; Kirkland, $N = 2$ sites; Redmond, $N = 1$ site; Bellevue, $N = 3$ sites). Inset shows an example of the independent test locations (each 250 m in diameter) within each site for experiment 1. White circles indicate the five locations for experiment 2; closed red circles show the six locations for experiment 3. The red open circle indicates urban core.

included (1) a slowly rotating or turning person wearing a mask and standing 2 m from the food pile ('mask-only control') and (2) food only ('food-only control'). Between sites, we varied the sequence of stimulus presentations so that the order of control and dangerous stimuli were counterbalanced. In 2014, the mask-only control was not used, and thus fewer sites were tested in 2014 than in 2013. We used three identically prepared taxidermy mounts of crows (randomized across trials) but only a single, mounted red-tailed hawk. All dead birds were collected outside the study areas. Whenever we used a hawk, or a hawk with a dead crow, the volunteer positioned and uncovered the birds without donning the mask. After placing the stimulus, they moved to a concealed location, donned the mask, and returned to the stimulus location. Because of time constraints, in 43% of cases, birds were present during the stimulus set-up and witnessed the unmasked volunteer interact with the avian stimuli. Given that humans were common at each site and that their presence with or near dangers was already an element of our experimental design, we do not believe witnessing the set-up biased the response. Following the stimulus presentation, volunteers returned to the concealed location to remove the mask before returning to collect the stimulus.

During the post-exposure phase, experiments followed one of two possible trial types (Fig. 1). In trial type A ($N = 74$, which included 17 food-only controls), we provided food as during the conditioning phase. In trial type B ($N = 57$), after the observer provided food, a colleague wearing the same mask used during the stimulus presentation phase immediately arrived and stood 2 m from the food pile. The format of trial type B matched that of the stimulus presentation phase. Order of trial type assignment for each stimulus was counterbalanced between sites.

*Longevity of response*

We tested study birds for longevity of response (scolding, diving or mobbing the masked person, or refusing to approach within 2 m of the food pile for the full 2.5 h after the masked person's departure) for both trial types A and B. We administered up to six weekly tests (longevity tests 1—6), but because of time constraints, only 11 of the 17 sites (one each from Redmond and Kirkland, and all nine Seattle sites; 77 of 114 potential territories) were tested beyond the first longevity test. Tests were discontinued prior to completing all six tests if the birds became unresponsive. Tests in trial type A began 1 week from the stimulus presentation phase provided that the birds had responded during the stimulus presentation phase ($N = 24$ of 74 did not respond: $N = 5$ mask-only controls, $N = 17$ food-only controls). Birds in trial type B were tested 1 week from the last day of the post-exposure phase provided they were still responding at that time ($N = 20$ of 57 stopped responding; of those, $N = 5$ were mask-only controls). The first four longevity tests followed the format of the post-exposure phase in trial type B; birds were provided food and then exposed to the masked volunteer standing 2 m from the food pile until 30 min after the arrival and observation of the first bird within 25 m. If birds remained responsive during the longevity test in week 4, during the fifth longevity test we did not provide food and instead presented either a person wearing the conditioned mask or a novel, unconditioned mask followed approximately 6—9 h later by the opposite mask, to test for recognition of the dangerous mask. Volunteers began from the hidden areas adjacent to the experimental spot where they typically put on and removed the mask. Following the first encounter with an adult bird, the masked volunteer walked around the approximated home range of the birds (based on observations by volunteers and the primary observer) for 30 min, and the observer recorded the number of crows within 25 m and any instances of scolding. If the birds responded during the fifth test, on week 6 we presented birds with the dangerous mask at a distance

of 25, 50 or 75 m from the food pile. This step was to test for context-dependent learning of the masked volunteer. The observer recorded the number of birds within 25 m of the food pile and the masked person. As during other tests, stimulus discovery was considered the time the first bird came within 25 m of the stimulus and was observed gazing towards it. Food discovery was counted as the first time a bird approached the food pile following stimulus discovery. The masked person left the area 30 min following stimulus discovery. In 12 cases during week 6, the primary observer was unable or unlikely to see the masked volunteer and the associated birds. In these cases, the masked volunteer was trained to discriminate between adult and hatch-years birds, provided a camera to record the birds' postures and vocalizations, and provided a range finder with which to calculate the 25 m observer distance.

*Experiment 2: Crow Response to a Dead Heterospecific*

We tested the response of crows to the sight of a dead pigeon being presented on the outstretched palms of a slowly rotating or turning masked person, and their subsequent aversion to the associated area, during August—September 2014. We established five unique sites within the greater Seattle and Bellevue areas (Fig. 2) based on the consistent presence of adult crows with juveniles, and a minimum distance of 400 m from all previous experiments. Sites were 1000 m from each other. This experiment followed trial type A (Fig. 1) except that, after the conditioning phase, the crows were presented with a masked person holding a taxidermy-mounted 'dead' pigeon 2 m from the food pile.

*Experiment 3: Pigeon Response to a Dead Conspecific*

We tested the response of rock pigeons to the sight of a dead pigeon presented on the outstretched palms of a slowly rotating or turning masked person in December 2013 and August—September of 2014. Since pigeons breed year-round, behavioural differences due to breeding did not differ between winter and summer tests. We used six unique sites at least 350 m from previous crow experiments, and 1000 m from each other, within the greater Seattle area (Fig. 2). We selected sites based on consistent presence by pigeon flocks. We used the procedure of trial type A (Fig. 1) except that the stimulus was a masked person holding a dead pigeon 2 m from the food pile. Experiments conducted in 2013 used a fresh pigeon carcass, and experiments in 2014 used a taxidermy-mounted 'dead' pigeon.

*Videography*

The stimulus presentation and the post-exposure phases as well as all longevity tests were filmed on a JVC Everio camera. The camera and tripod were operated by and located near the observer. During the conditioning phase, we did not film, but the tripod was present for acclimation.

*Statistical Analysis*

We used $Z$ tests to determine seasonal effects, Pearson's chi-square analysis for proportional comparisons of scolding or mobbing responses and a one-way ANOVA to compare mob size among stimuli. We analysed changes in latency to approach the food pile by comparing the change in food discovery time with a three-factor repeated measures ANOVA. The within-subjects factors were phase (conditioning, post-exposure) and day within phase (day 1, 2, 3). The between-subjects factor was stimulus type. The main test of interest was the interaction effect of phase and

stimulus type. As described in the methods for experiment 1, we considered experimental sites to be independent. Prior to analysis, we log transformed food discovery times to increase normality. We used one-tailed repeated measures ANOVAs when comparing only two variables with a hypothesized outcome (e.g. danger versus control). We analysed proportional comparisons of response to longevity tests with a Pearson's chi-square test and proportional $Z$ tests. For the proportional comparisons, we compared three dangerous stimuli and trial type (A versus B; Fig. 1). We ran all ANOVAs and chi-square tests using SPSS v.19 (IBM, Armonk, NY, U.S.A.).
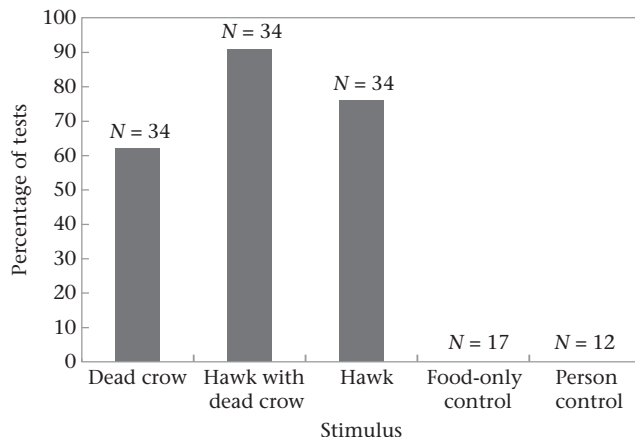
## RESULTS

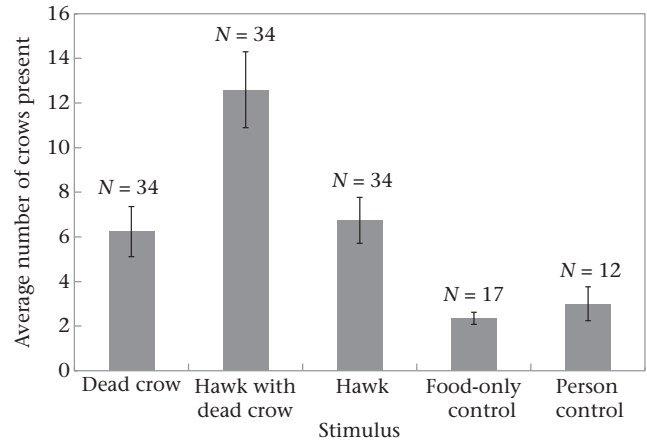### Experiment 1: Response to a Dead Conspecific and/or a Predator

Across years, territorial adults scolded during 96% of trials that presented dangerous stimuli ($N = 102$ tests), whereas only 17% scolded during mask-only control presentations ($N = 12$ tests) and 0% scolded during food-only control presentations ($N = 17$ tests). Of those crows that did not scold when presented with a danger, two observed a dead conspecific, one observed a hawk, and one observed a hawk with a dead crow.

Neither food-only nor mask-only control tests resulted in mobbing. The likelihood of mobbing differed between the three dangerous stimuli (Pearson's chi-square: $\chi_2^2 = 8.17$, $P = 0.02$; Fig. 3). The response of crows that saw a hawk with a dead conspecific primarily drove this result (dead crow versus hawk: $\chi_1^2 = 1.72$, $P = 0.19$; hawk + dead crow versus dead crow only and hawk only: $\chi_1^2 = 6.13$, $P = 0.013$); however, hawk + dead crow versus hawk alone were not significantly different ($\chi_1^2 = 2.71$, $P = 0.10$).

After mob formation, crows spent more time constantly scolding the hawk with a dead crow (mean ± SE = 11.1 ± 1.3 min) than they did the dead crow ($7.5 ± 1.3$ min) or the hawk ($6.1 ± 1.5$ min) alone, but this difference was not significant (one-way ANOVA: $F_{2,75} = 2.83$, $P = 0.065$). The number of birds present during stimulus presentation depended on the type of stimulus ($F_{4,126} = 8.69$, $P < 0.001$; Fig. 4). More birds were present during presentation of the hawk + dead crow than during presentation of the dead crow (mean difference = 6.35; Tukey HD: $P = 0.002$) or the hawk (mean difference = 5.85; Tukey HD: $P = 0.005$). In trials that resulted in mobbing, mob size differed with stimulus type (ANOVA: $F_{2,75} = 3.53$, $P = 0.034$), but this effect was driven solely



**Figure 4.** Mean ± SE number of birds present during the 30 min stimulus presentation phase (day 4) in experiment 1. Number of birds present includes the territorial pair.

by the difference between hawk + dead crow versus hawk (mean difference = 5.25; Tukey HD: $P = 0.043$). There was no significant difference in mob size during presentations of the hawk + dead crow versus the dead crow (mean difference = 4.47; Tukey HD: $P = 0.13$) or the dead crow versus the hawk (mean difference = 0.78; Tukey HD: $P = 0.94$).

During the 2.5 h immediately following presentation of the stimulus, 17% (of $N = 101$ tests) of crows exposed to a dangerous stimulus did not return to the food pile. All crows that received a control treatment ($N = 29$ tests) returned to the food. Crows differed in avoidance of particular stimuli (Pearson chi-square: $\chi_2^2 = 10.60$, $P = 0.005$; Fig. 5). Crows' avoidance of the hawk + dead crow primarily drove this effect (dead crow versus hawk: $\chi_1^2 = 3.06$, $P = 0.08$; hawk + dead crow versus dead crow only combined with hawk only: $\chi_1^2 = 8.82$, $P = 0.003$); however, dead crow versus hawk + dead crow were not different ($\chi_1^2 = 2.73$, $P = 0.10$).

### Site avoidance trial type A: food only post-exposure

During the stimulus presentation phase, 17% of birds avoided the food for the 2.5 h following stimulus removal, whereas during the post-exposure phase, most birds eventually approached the food. Therefore, we analysed the crows' latency to approach food between the conditioning phase and the post-exposure phase. Regardless of the dangerous stimulus seen during the stimulus



**Figure 3.** Percentage of tests for each of the five stimuli where scolding resulted in recruitment of at least two additional adults (mobbing) during the stimulus presentation (day 4) in experiment 1.
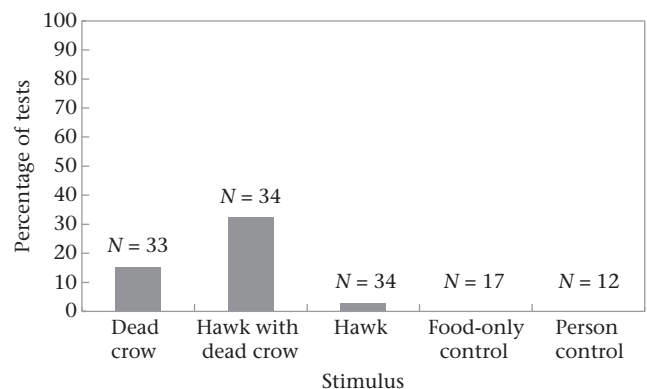


**Figure 5.** Percentage of tests for which crows did not approach the food pile within the 2.5 h time period following stimulus presentation (day 4) of experiment 1.

presentation phase, crows showed similar increases in latencies to approach the food pile during the post-exposure phase relative to the conditioning phase (repeated measures ANOVA: phase∗stimulus interaction: $F_{4,69} = 1.29$, $P = 0.28$). As a result, we combined the three danger stimuli into a single 'danger' treatment and the two controls into a single 'control' treatment. As predicted, birds exposed to dangerous stimuli showed a larger change in latency to approach the food pile (relative to the conditioning phase) than did birds in the control treatment (one-tailed repeated measures ANOVA: phase∗stimulus interaction: $F_{1,72} = 3.20$, $P = 0.04$; Fig. 6). Comparing only the post-exposure phase, birds exposed to danger took longer to approach food than did control birds (one-tailed repeated measures ANOVA: between-subjects: $F_{1,72} = 3.11$, $P = 0.041$).

*Site avoidance trial type B: food and dangerous human post-exposure*

In trial type B, crows' change in latency to approach the food pile during the post-exposure phase did not vary with the type of dangerous stimulus (repeated measures ANOVA: phase∗stimulus interaction: $F_{4,68} = 2.10$ $P = 0.09$). Therefore, we lumped all dangerous stimuli into a single 'danger' treatment and lumped the two controls into a single 'control' treatment. The difference in latency to approach the food pile during the conditioning phase and the post-exposure phase was greater for crows that saw a dangerous stimulus than for crows that saw a control stimulus (one-tailed repeated measures ANOVA: phase∗stimulus interaction: $F_{1,71} = 6.30$, $P = 0.008$; Fig. 7). Comparing only the post-exposure phase, birds exposed to danger took longer to approach food than did control birds (one-tailed repeated measures ANOVA: between-subjects: $F_{1,71} = 8.25$, $P = 0.003$).

*Longevity tests: response to conditioned human*

Crows that viewed a dangerous stimulus were equally likely to respond in the first longevity test to the previously conditioned masked person regardless of the type of unconditioned stimulus (Pearson chi-square: $\chi_2^2 = 2.67$, $N = 84$, $P = 0.26$) or the trial type (A or B; $\chi_1^2 = 2.33$, $N = 84$, $P = 0.13$; Fig. 8). Even after 6 weeks of additional weekly exposures, birds in trial type B showed no

significant difference in fear extinction compared to those in trial type A ($\chi_1^2 = 0.68$, $N = 31$, $P = 0.41$; Fig. 8), and they were no more likely to respond to the person associated with any one of the three dangers ($\chi_2^2 = 2.46$, $N = 31$, $P = 0.29$). During the fifth longevity test (where crows saw a dangerous stimulus or a person wearing a neutral mask, then a dangerous mask), birds were more likely to scold the dangerous mask than the neutral mask (proportional $Z$ test: $Z = 3.45$, $N = 31$, $P = 0.0006$). During the sixth longevity test, where crows saw the masked person previously associated with danger either 25 m ($N = 13$), 50 m ($N = 10$) or 75 m ($N = 8$) from the food pile, the crows were no more likely to stop responding than they had been during week 4 (proportional $Z$ test: $Z = 0.12$, $P = 0.90$). In addition, crows' failure to respond to the masked person did not differ with distance to the food pile (Pearson chi-square: $\chi_2^2 = 1.07$, $P = 0.90$; birds on two territories at each distance did not respond to the masked person).

*Comparisons between seasons and tests of carryover effects*

The season (April–June, $N = 65$; July–September, $N = 37$) in which birds were tested did not influence the likelihood of scolding the dangerous stimuli (proportional $Z$ test: $Z = -0.18$, $P = 0.91$). The proportion of birds that mobbed during April–June tests ($N = 47$ of 65) was slightly lower than those tested during July–September ($N = 31$ of 37), however, this difference was not significant ($Z = -1.31$, $P = 0.19$). The same trend could be seen with respect to changes in latency to approach food in both type A (repeated measures ANOVA: $F_{1,49} = 1.48$, $P = 0.23$) and type B ($F_{1,48} = 0.59$, $P = 0.45$) tests.

Of 24 marked individuals, only one previously tested bird was recruited to mob at a different test site during stimulus presentation, although six marked birds were seen on other days. The proportion of birds that mobbed the dangerous stimulus during the first week of testing ($N = 7$ of 12 birds) and the last week of testing ($N = 9$ of 13 birds) did not differ across sites ($Z = -0.57$, $P = 0.57$). Crows tested first within a site tended to take longer to approach food after exposure to danger than those tested last, but this difference was not significant (repeated measures ANOVA: $F_{1,22} = 0.80$, $P = 0.38$). Furthermore, crows in control territories that were either greater than ($N = 8$) or less than ($N = 8$) 400 m from a
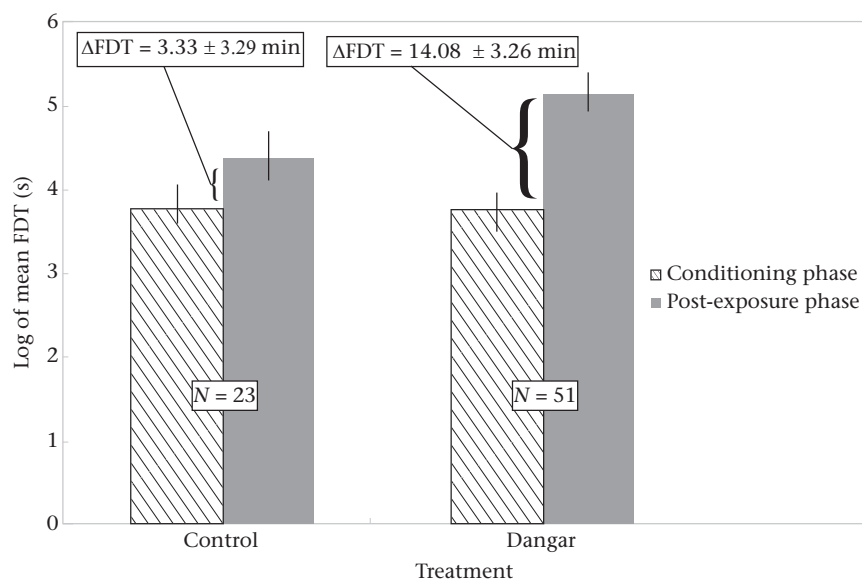


**Figure 6.** Change in latency to approach the food pile (change in food discovery time, ΔFDT) between the conditioning phase and the post-exposure phase for control and danger treatments in trial type A tests (food-only, post-exposure phase). ΔFDT values indicated by brackets show untransformed means ± SE change in latency.
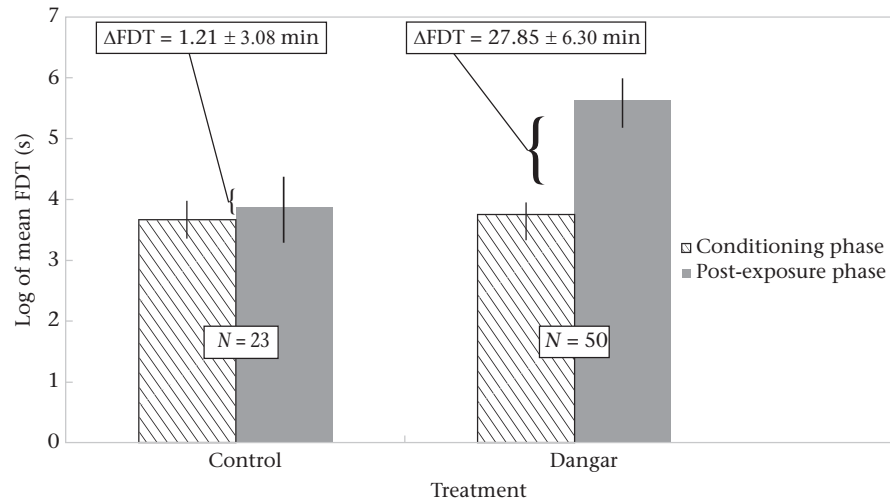
**Figure 7.** Change in latency to approach the food pile (change in food discovery time, ΔFDT) between the conditioning phase and the post-exposure phase for control and danger treatments in trial type B tests (food + human, post-exposure phase). ΔFDT values indicated by brackets show untransformed means ± SE change in latency.
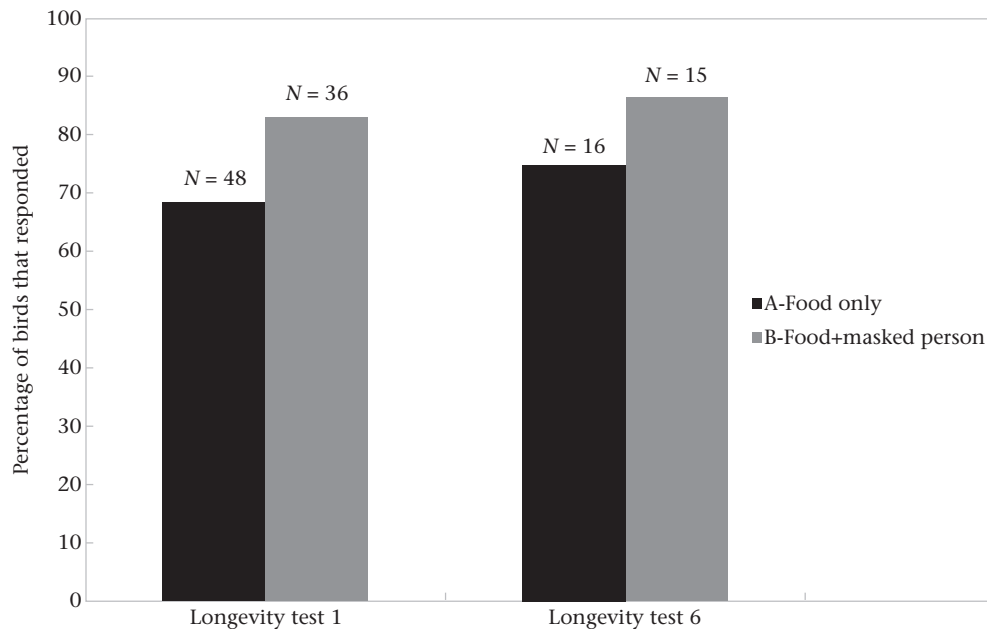


**Figure 8.** Percentage of birds that responded to a masked person by scolding or mobbing the stimulus, or by subsequently avoiding the area for 2.5 h during the first and sixth longevity test for birds in trial type A (food only) and B (food + masked person).

territory where a dangerous stimulus had previously been deployed did not differ in their change in latency to approach food between the conditioning phase and the post-exposure phase (repeated measures ANOVA: $F_{1,14} = 1.20$, $P = 0.29$).

### Experiment 2: Crow Response to Dead Heterospecific

While 94% of the crows scolded when they saw a dead conspecific ($N = 34$ tests), only 40% of the crows scolded in response to a dead pigeon (Pearson chi-square: $\chi_1^2 = 11.42$, $N = 5$ tests, $P = 0.001$). Even in cases where crows scolded in response to the dead pigeon, they did so far fewer times (mean ± SE = $7 \pm 1.26$) than in response to a dead conspecific ($63.74 \pm 9.89$). Crows exposed to a dead pigeon did not mob, unlike the majority of those

that saw a dead crow ($\chi_1^2 = 6.69$, $P = 0.01$). Following exposure to a dead conspecific, crows in trial type A took longer to approach the food during the post-exposure phase relative to the conditioning phase, more than did crows confronted with a dead pigeon (one-tailed repeated measures ANOVA: phase∗stimulus interaction: $F_{1,20} = 2.93$, $P = 0.05$; Fig. 9). During the post-exposure phase, crows that saw a dead conspecific took longer to approach food than crows that saw a dead pigeon (one-tailed repeated measures ANOVA: between-subjects: $F_{1,20} = 6.69$, $P = 0.009$).

### Experiment 3: Pigeon Response to Dead Conspecific

Pigeons flocked to food in the presence of a masked person holding the dead pigeon in 66% of cases ($N = 6$ tests). In contrast,
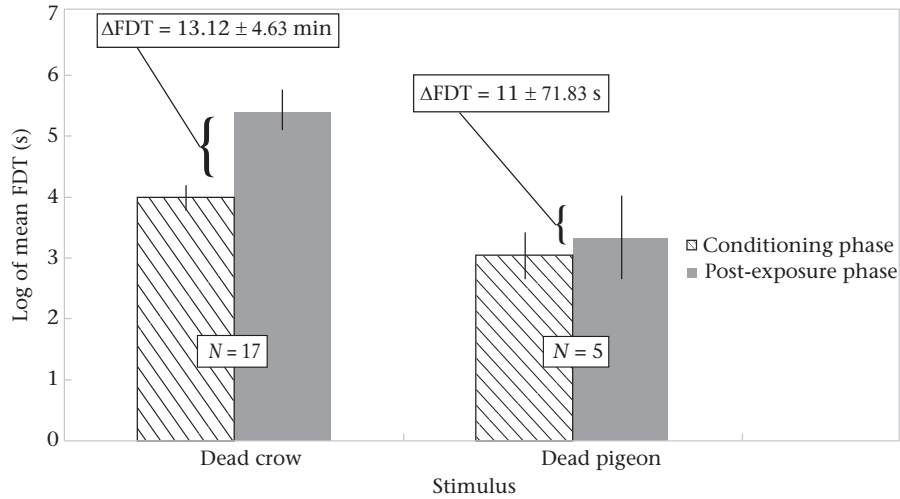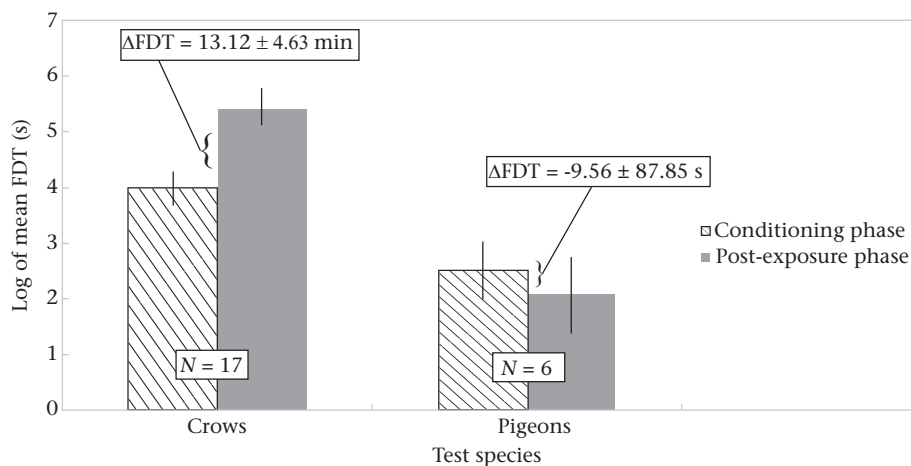
**Figure 9.** Change in latency for crows to approach the food pile (change in food discovery time, ΔFDT) between the conditioning phase and the post-exposure phase after seeing a dead crow (trial type A, experiment 1) or a dead pigeon (experiment 2) during stimulus presentation. ΔFDT values indicated by brackets show untransformed means ± SE change in time.

crows never approached the food in the presence of a masked person holding a dead crow (Pearson chi-square: $\chi^2_1 = 25.19$, $N = 34$ tests, $P < 0.001$). This disparity was not explained by a difference in general willingness to approach food near people because crows that were exposed to a masked person without a dangerous stimulus were just as likely to approach food as were pigeons ($\chi^2_1 = 1.80$, $P = 0.18$). Sight of a dead conspecific had different effects on the change in latency to approach the food pile in pigeons relative to crows (one-tailed repeated measures ANOVA: phase*stimulus interaction: $F_{1,21} = 8.85$, $P = 0.004$). Whereas crows delayed their approach to the food pile after stimulus exposure, pigeons approached the food pile faster during the post-exposure phase than during the conditioning phase (Fig. 10).

## DISCUSSION

Despite the numerous studies observing animal responses to conspecific olfactory and auditory alarm cues, few studies have systematically tested the response of animals to conspecific carcasses. Documentation of spontaneous gatherings immediately following conspecific death in dolphins and primates have captured a variety of behaviours ranging from sexual arousal, aggressive interactions with the body and increased postmortem grooming (Buhl et al., 2012; Dudzinski et al., 2003; Engh et al., 2006). Furthermore, American bison, *Bison bison*, and elephants maintain intense interest in conspecific carcasses even after the carcasses have been reduced to bones (King, 2013; McComb et al., 2006). Given the small number of studies that have evaluated these behaviours, the full extent to which information can be gleaned from these experiences remains unclear. In the present study we demonstrated that, consistent with other corvids, wild crows use the bodies of dead conspecifics as an indication that an area is dangerous. Furthermore, we show that crows make inferences about novel predators based on a novel predator's proximity to dead conspecifics and to hawks. In some cases, these memories last for up to 6 weeks. For crows, this suggests that the



**Figure 10.** Change in latency to approach the food pile (change in food discovery time, ΔFDT) between the conditioning phase and the post-exposure phase for crows (trial type A, experiment 1) and pigeons (experiment 3) that saw a dead conspecific during stimulus presentation. ΔFDT values indicated by brackets show untransformed means ± SE change in time.

interest in dead conspecifics is used to assess both dangerous areas and new threats.

*Experiment 1: Crow Response to a Dead Conspecific and/or a Predator*

In experiment 1 we demonstrated that wild American crows scold in response to the discovery of a dead, unfamiliar conspecific and often recruit nearby adults to engage in mobbing. In this context, mobbing may serve one or more purposes, including chastising the predator (Curio et al., 1978), displaying dominance (Moholt & Trost, 1989), or social learning of the dangerous person (Cornell, Marzluff, & Pecoraro, 2012) or place (Iglesias et al., 2012). Our finding that crows scolded and mobbed people holding dead crows, without playback of conspecific alarm vocalizations, supports the assessment that dead crows represent a salient danger. In contrast, control presentations of people or food rarely elicited scolding by individual crows and never escalated to mobbing, showing that aggregations of crows forming in response to people associated with dead conspecifics is neither a typical feeding response nor a neophobic response to a masked person. This response was also observed in the presence of both a predator and a predator with conspecific remains, suggesting that, like western scrub-jays, the discovery of a dead conspecific is effective at triggering typical antipredator behaviours (Iglesias et al., 2012). Certain dangers did, however, evoke stronger immediate antipredator behaviours than others.

Crows were more likely to mob and to avoid the food pile more consistently over the next 2.5 h in response to a hawk with a dead crow than in response to either a hawk or a dead crow alone. Crows' ability to tailor their immediate response to the identity of the threat is supported by studies showing that animals such as breeding wood mice, *Apodemus sylvaticus*, and blue jays, *Cyanocitta cristata*, adjust subsequent foraging decisions to predator identity (Conover, 1979; Navarro-Castilla & Barja, 2013). That crows responded most strongly to a predator with a conspecific prey is consistent with a previous study on crows (Barash, 1976) and with responses by herring gulls, *Larus argentatus*, and lesser black-backed gulls, *Larus fuscus* (Kruuk, 1976). In crows, exposure to a hawk results in activation of the caudal nidopallium (Cross et al., 2013), a region of the brain proposed to be important in decision making such as fleeing or mobbing (Güntürkün, 2005). Our finding that crows were less likely to mob if a hawk was observed without conspecific prey supports the conclusion that crows are sensitive to predator behaviour (with or without prey) and subsequently adjust the aggressiveness of their mobbing response.

After exposure to a human with a dead crow, or a hawk, or a hawk with crow remains, the crows in both trial types A and B took longer to approach food in the locations associated with these events than they did during the conditioning phase. When we compared differences only in the post-exposure phase between control stimuli and dangerous stimuli, we again found that crows exposed to danger look longer to approach food locations associated with the event, although this difference was more highly significant in trial type B, suggesting that the ongoing presence of the 'conditioned person' may have exaggerated the fear response to the place. House mice, *Mus musculus*, avoid trays containing both food and conspecific cadavers, but whether they make ongoing associations with those trays has not been addressed (Prounis & Shields, 2013). Common ravens have also been shown to avoid areas associated with effigies, although in this case, not only did they witness a highly stimulating re-enactment of the individual's death, but researchers used raven distress playbacks, and effigies remained present for 48 h (Peterson & Colwell, 2014). Our findings indicate that crows learn the spatial context associated with a brief (30 min) dangerous event and that changes in latency to approach food in these areas can last for up to 72 h after the cadaver and/or predator is removed. In rats, a minimum shock threshold is required to stimulate learning of the spatial context in addition to the conditioned stimulus (Baldi, Lorenzini, & Bucherelli, 2004). Our results suggest that both predators and dead conspecifics meet this threshold for crows, and that crows perceive a dead conspecific to represent a high level of threat. However, crows' change in latency to approach food before and after stimulus presentation did not differ with the type of danger stimulus. Given that both hawks and humans are highly mobile and that the risk of repeated encounters with a predator decreases with time (Kats & Dill, 1998), the finding that crows are more sensitive to the identity of the threat in the hours, but not in the days, following exposure indicates that crows temporally adjust antipredator behaviours. This is consistent with other studies showing that animals adjust foraging decisions to temporal variations in risk (Lima & Bednekoff, 1999; Lima & Dill, 1990). Danger learning was not limited to spatial learning, however, as we also found that crows made associations with the people in close proximity to the dangerous stimuli.

One week following presentation of a novel human paired with a dangerous stimulus, more than half of birds in each trial type scolded or dove towards the person or refused to approach food for 2.5 h after the person had left. Crows are highly sensitive to human aggression even to the extent that they are attentive to gaze (Clucas, Marzluff, Mackovjak, & Palmquist, 2013) and can learn and recall human faces after being captured by them (Marzluff et al., 2010). Cross et al. (2013) found that the sight of a novel person holding a dead crow stimulated activation of the dorsomedial portion of the hippocampus and part of the cerebellum, areas consistent with danger learning. However, in Cross et al.'s study, crows were tested in isolation, where they could not mob and did not vocalize. At the onset of the present study, what remained untested was whether wild birds would respond to the sight of a human holding a dead crow with typical antipredator behaviours (scolding, diving, mobbing, etc.) and whether activation of the aforementioned brain areas would indeed result in the learning and aggression towards these people in the future.

Our results indicate that crows learned and remembered humans that were associated with danger when those humans were in close proximity to dead conspecifics and/or predators and, in 38% of cases, the crows in sites eligible for all longevity tests continued to respond for up to 6 weeks. Our finding that the type of dangerous stimulus associated with a person did not influence the crows' response to the person 1 week later, or up to 6 weeks later, suggests that dead crows and predators are equivalent at triggering fear conditioning. Furthermore, unlike most mammalian studies or other predator-learning studies in birds (McLean, Holzer, & Studholme, 1999; Milad, Rauch, Pitman, & Quirk, 2006), subjects in our experiments only received one training event to learn the associated person. That they could later discriminate between the dangerous masked person and a novel-masked person during the fifth week of testing demonstrates that crows are capable of learning the specific identity of the threatening human in this context. This may be key to navigating the urban landscape where humans can be either threatening, helpful (i.e. provide food) or neutral, and thus the extrapolation of danger to all people may result in the loss of food resources.

Fear extinction of crows that received three additional exposures to the conditioned human stimulus without the unconditioned stimulus (trial type B) did not differ from that of crows that received no additional exposure (trial type A). This suggests that subsequent exposures to conditioned stimuli alone do not immediately lead to fear habituation in wild crows. In rats, a single session of exposure to the unreinforced conditioned stimulus can be

enough to extinguish fear response from 70% to near zero (Quirk, 2002). Furthermore, in the present study, a dangerous person positioned 25, 50 or 75 m from the food during week 6 did not result in a higher number of extinctions than was observed during week 4, when the food and the person were last paired together. Nor did we find that there was a difference in extinction between the different distances. This suggests that the decoupling of person and place is not sufficient to disrupt the memory of the person, even if they are far from the dangerous place. Wild birds may be resilient to fear extinction because errors can be deadly. Although it is possible that the use of the masks enhanced the crows' ability recognize the dangerous person and muted potential fear extinction, these results nevertheless demonstrate crows' potential to learn and remember novel predators.

*Experiment 2: Crow Response to a Dead Pigeon*

In experiment 2, crows were less attentive to a dead, similarly sized heterospecific than they were to a dead conspecific. This finding cannot be not explained by the difference in season in which the two experiments were carried out, because we found that season had no effect on the likelihood of scolding or mobbing during the course of experiment 1. This is in contrast to wild western scrub-jays, who scold dead, jay-sized heterospecifics as often as they do dead conspecifics (Iglesias et al., 2014). Given that the crows and pigeons (heterospecific stimulus) in our study area are similar in size (pigeons: 340–369 g; crows, on average, 387 g; dos Anjos et al., 2009; Johnston & Lowther, 2014) and susceptible to some of the same predators, such as red-tailed hawks and Cooper's hawks, *Accipiter cooperii* (Lamberski, Hull, Fish, Beckmen, & Morishita, 2003; McGowan, 2001; Murrey & Tseng, 2008), pigeon carcasses could serve as a relevant indication of predation risk to crows. Pigeon carcasses may be scavenged by crows (J. M. Marzluff, personal observation), therefore advertisement of carcass discovery could come at the cost of access to a food item. Crows that did not scold the person holding the pigeon may have kept their discovery quiet in an effort to gain access to a potential source of food (the carcass) if the person left it behind. In addition, crows are territorial and expel conspecific, but not pigeon, intruders; thus, the discovery of a dead, unfamiliar crow within a territory may be a more salient indication of an undetected predator than a pigeon is.

*Experiment 3: Pigeon Response to Dead Pigeon*

Whereas crows responded strongly to humans with dead crows in nearly all cases, the rock pigeon took little notice of dead conspecifics. Although we presented the pigeon at such an angle that birds on the ground were not shielded from the carcass, pigeons may still need a stronger stimulus to recognize a threat than crows. When shown a predator with a struggling live conspecific, European starlings, *Sturnus vulgaris*, are subsequently more wary of the predator and show greater latency to feed than when they have seen the predator alone or with a dead conspecific (Conover & Perito, 1981). It is possible that, like starlings, pigeons need the enhanced visual stimulation of a struggling bird, or that predators with remains are ignored since they could be scavengers. In any case, it suggests that attention to dead conspecifics by crows is not shared among all urban bird species.

*Applications and Future Directions*

Our research findings are applicable both to the average homeowner and to the development of nonlethal corvid management techniques. The finding that crows learn and remember humans seen handling crow carcasses, suggests that removal of

such bodies should be done with care, either by concealing one's identity or by ensuring there are no visible crows present. Such steps may reduce aggression and conflicts between crows and humans, especially in urban and suburban settings where crows can be more aggressive towards people (Knight, Grout, & Temple, 1987).

By conditioning problematic corvids to dangers associated with specific places, people or foods, the health risk to humans (Oravcova et al., 2014) and to endangered species (Boarman, 2003) may be reduced. Crows have previously been shown to avoid favoured roosting areas following the hanging of crow carcasses for at least 7 days (Avery et al., 2008). In our experiments, 38% of crows remained wary of the person or the place associated with death of a conspecific for 6 weeks. We expand upon this finding by demonstrating that crows were most wary of the conditioned place when repeatedly exposed to the conditioned person (as in trial type B). Conditioning corvids to associate specific people with danger may be a useful augmentation to this technique, as specific people, or their likeness, could function as effective scarecrows that keep offending corvids from valued resources. Crows remember threatening people for years, after only a single transgression, and spread this information through social learning (Cornell et al., 2012; Marzluff et al., 2010). Taking advantage of the ability of corvids to quickly learn but slowly forget dangerous people would be an effective component of an integrated management plan that includes other nonlethal control methods such aversive taste conditioning (Nicolaus & Cassel, 1983), as well removal of anthropogenic attractants and supplements that bolster local corvid populations (Boarman, 2003).

Although these data provide a rich starting place to being understanding the full extent to which crows are responding and learning from these experiences, there is still much to be addressed. Spectral analysis of scold calls may determine whether crows are communicating nuanced details about the nature of the dangers in question. A more thorough understanding of the social relationships between individuals (kin, nonkin, dominant, subordinate, etc.) in adjacent territories may also help reveal underlying causes for differences in mob size with respect to each danger. Aspects of a dead conspecific (sex, age, relationship to territory owners) may also affect response intensity, mob size and call structure. Further testing with a wider variety of heterospecifics may indicate whether larger birds are more sensitive to differences in size, and thus less likely to respond to even slightly smaller birds. Lastly, measurements of activity at variable distances from the dangerous event will help reveal the spatial limitations of effigy management techniques.

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