Wild American crows use funerals to learn about danger

Kaeli Swift

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Committee:
John Marzluff
Aaron Wirsing
Donna Cross

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Abstract

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Chair of Supervisory Committee:

Dr. John Marzluff

School of Environmental and Forest Sciences

While a growing number of animals demonstrate seemingly ritualistic behaviors around the death or body of a conspecific, the evolutionary basis for this behavior remains unclear. Here we demonstrate that wild American crows (*Corvus brachyrhynchos)* are using funeral gatherings as an opportunity to engage in social learning, inform future resource use, infer novel predators, and that this behavior is not shared by another urban bird: the rock pigeon (*Columba livia).* Novel humans paired with a dead crow, a red-tailed hawk (*Buteo jamaicensis),* and a hawk with a dead crow all evoked mobbing and decreased foraging by crows, while pairing with a dead pigeon did not. These findings suggest that dead conspecifics, but not heterospecifics, represent a salient danger akin to observation of a predator. Mobbing and decreased foraging immediately after stimulus removal were strongest when crows were presented a hawk with a dead crow. Over the next 3 d we found that crows avoided food in areas associated with these dangerous events. However, site avoidance was uniform across stimuli suggesting that crow sensitivity to the identity of the threat dissipates after 24 h. In addition, we demonstrated that crows use proximity to predators, dead conspecifics and predators with conspecific remains as a cue to learn and subsequently scold the associated human after only 1 training event, and that this association could last 6 weeks. Together, these data provide important insights into the nature of crow funeral gatherings and how crows navigate the threatening landscape.

KEYWORDS: American crow, *Corvus brachyrhynchos,* fear extinction, response to dead conspecific, conditioned learning, rock pigeon, *Columba livia,* response to dead heterospecific, animal funeral, necrophobia

INTRODUCTION

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 pica*; Miller and Bringham 1998), chimpanzees (*Pan troglodytes*; Stewart et al. 2012), and bottle-nosed dolphins (*Tursiops aduncus*; Dudzinski et al. 2003) are among those that demonstrate behaviors such as congregating around, or the touching and grooming of dead conspecifics. African elephants (*Loxodonta africana*) show higher levels of interest in conspecific bones and ivory than other large terrestrial mammals (McComb et al. 2005). Given that predators or other environmental threats may generate conspecific remains, it stands to reason that animals may be interested in, and learn from such remains as indications of danger akin to other conspecific alarm cues.

Animals can reduce their risk of predation by being attentive to cues in the environment such as predator odors (Eichholz et al. 2012), observations of predators (Cooper Jr. 2008) and alarm vocalizations from conspecifics (Templeton et al. 2005) and heterospecifics (McKee Shriner 1998). In addition to providing information on immediate risk, responses to these alarms provide arenas where naïve animals learn about novel predators through classical conditioning (Griffin et al. 2000). In classical conditioning, a biologically insignificant stimulus (the conditioned stimulus), such as a novel predator, is paired with a biologically significant stimulus (the unconditioned stimulus), such as conspecific alarm vocalizations, and after a number of paired presentations the conditioned stimulus elicits the same defensive response as the unconditioned stimulus (Pavlov 1927). These stimuli subsequently prompt anti-predator behaviors such as mobbing (Curio et al. 1978) and site avoidance, even at the cost of avoiding high quality or abundant food (Lima and Dill 1990). Fear can be extinguished, however, through repeated exposure to the conditioned stimulus without reinforcing its predictive value of the unconditioned stimulus (Myers and Davis 2007). It remains unclear if conspecific carcasses function as effectively as other alarm cues to indicate danger and induce conditional learning.

Given the intense interest some animals display towards conspecific carcasses, future aversion to areas associated with a body may indicate that animals are using them as a cue of danger. Necrophobic behaviors have been observed in common ravens and house mice (*Corvus corax*, *Mus musculus*; Peterson and Colwell 2014, Prounis and Shields 2013), though neither study looked at continued aversion to the areas following carcass removal. Iglesias et al. (2012) showed that western scrub-jays (*Aphelocoma californica*) avoid areas associated with conspecific death for up to 48 h and that these responses are not the result of neophobia or territory guarding, and that, while similar, are behaviorally unique from typical predator mobbing. It has not been tested, however, if wild animals can use dead conspecifics to infer novel predators in the absence of alarm call playbacks.

Wild American crows are also among the animals that gather and vocalize around dead conspecifics (Marzluff and Angell 2005). It is possible that funeral behaviors observed in crows are opportunities to learn about danger, such as the learning of new, threatening people and, like jays and ravens, areas associated with depredation. It was our aim to test danger learning and avoidance as the evolutionary basis for funeral behaviors in crows.

To test danger learning we conducted 3 experiments on wild crows. In Experiment 1 we asked: (i) Is the sight of a dead conspecific sufficient to elicit alarm calling and recruitment or is the presence of an unconditioned predator also necessary? (ii) Do crows learn the areas associated with these dangers and subsequently avoid them? (iii) Do crows use dead conspecifics to identify novel predators and, if so, how does this process compare to conditioned learning when novel predators are paired with unconditioned stimuli (hawks)? (iv) Can fear extinction be achieved with only 3 additional exposures? For Experiment 2 we determined if a dead conspecific is a more salient source of dangerous information than a similarly sized, dead heterospecific. In Experiment 3, we compared crow responses to dead conspecifics with those of another urban bird species, the rock pigeon.

METHODS

General Information

We conducted all experiments, each of which consisted of 3 phases (Fig. 1), in the greater Seattle, Redmond, Kirkland, Mercer Island and Bellevue, WA areas (47.640560˚N, -122.265912˚W). The observer (KS) 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, unshelled 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 at a distance of 15-25 m away, for up to 2.5 h and measured the time until the first bird approached within 2 m of the food pile (Food Discovery Time, FDT). We terminated the conditioning phase once birds successfully approached the food within the 2.5 h observation period for 3 consecutive days. This criterion was met in most trials in 3 d. However, in *N*=7 tests, birds took up to 10 d to meet the criterion, after which we moved on to the stimulus presentation phase.

During the stimulus presentation phase we provided food as normal after which a volunteer exposed a stimulus 2 m from the food pile. Volunteers wore 1 of 6 realistic facemasks with neutral expressions (to preclude any contaminating effects of facial expression) (see Fig. 1B in Marzluff et al. 2010) and a white sign around their neck that read “UW CROW STUDY” to preclude interruptions by pedestrians or police. During the stimulus presentation, the data collector recorded the number of birds within 25 m and any instances of scolding. Thirty min after the first bird perched within 25 m of the stimuli and was observed gazing toward the experimental set-up (Stimulus Discovery Time, SDT), the volunteer removed the stimuli. Following stimuli removal, for up to 2.5

h, the observer recorded the time before a bird approached within 2 m of the food pile (FDT). After 2.5 h, all but a small amount (5 pieces) of food was removed. If birds approached the pile in the presence of the stimulus, we recorded the FDT as 0 sec. For both the FDT and SDT, we counted only non-hatch year birds.

During the post-exposure phase on days 5-7 the experiment split into 2 Trial Types: A and B. In Trial Type A, birds were returned to baseline conditions and simply provided food as described above. This was to test for site aversion. In Trial Type B, following food provisioning by the observer, a volunteer wearing the same mask as seen during the stimulus exposure phase would arrive and stand 2 m from the food pile. We matched the experimental procedure during all days for this trial with the stimulus exposure phase (see above). The purpose of this trial type was to test for novel predator leaning and to create a difference in exposure rate between the trial types to evaluate the prevalence of fear extinction. Only Experiment 1 used both trial types. All others only used Trial Type A during the post-exposure phase. All procedures were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC) under protocol number 3077-01.

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

In 2013 and 2014 we selected 17 independent sites and, within each site, identified 7-9 territorial pairs (Fig. 2). In 2014 one of the control stimuli was not tested therefore fewer territories were needed. In April-July we used nesting areas to define the locations for tests and established specific test locations 35-45 m from the nest tree. From August-September we identified test locations by the presence of fledged young and/or consistent presence of an adult pair. Within each site, each adjacent territory received a unique stimulus and masked person and experimental locations were spaced to assure independence. Territories in the urban core are smaller than their suburban counterparts (Marzluff et al. 2001) and the minimum distance between 2 test locations was 90 m, however the median distance between test locations was 430 m. Such spacing was adequate; of 24 previously marked individuals we only observed 1 previously tested bird recruited to mob at a different test site during the stimulus presentation event, though 6 were seen on other days.

We placed 1 of 5 stimuli 2 m from food during the second phase of the experiment (Fig. 1). The stimuli were: 1) taxidermy-mounted "dead" crow being held by masked person 2) a taxidermy-mounted red-tailed hawk (*Buteo jamaicensis)* perched on a branch 2 m from masked person, 3) a taxidermy-mounted red-tailed hawk positioned with a taxidermy-mounted "dead" crow 2 m from a masked person, 4) masked human control and 5) food only control. In 2014, stimulus 4 was not used. We used 3 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 hawks, or hawks and crows, volunteers positioned and uncovered the birds without the mask, before exiting to a hidden location and returning with the mask on. Following the stimulus presentation, volunteers left to remove the mask before returning to collect avian stimuli.

During the post-exposure phase half of all non-food only control treatments (*N* = 57 trials) followed Trial Type A, whereas the other half (*N* = 57) followed Trial Type B (Fig. 1). In Trial Type A, we provided food as during the conditioning phase. In Trial

Type B, after the observer provided food, a colleague would immediately arrive 2 m from the food pile wearing the same mask seen during the stimulus presentation phase. The format of these tests matched that of the stimulus presentation phase. The presentation order of the stimulus treatments under the 2 treatment types was counter balanced between the 17 sites.

Experiment 1

Longevity of Response

Following completion of the conditioning, stimulus presentation, and post-exposure phases, we tested study birds for longevity of response to the masked person. For 11 of the sites (1 each from Redmond and Kirkland and all Seattle sites), up to 5 additional weekly longevity tests were conducted. All territories under Trial Type A were tested beginning a week from the stimulus presentation phase. Birds tested under Trial Type B only received a longevity test if they were still scolding the masked person and/or refusing to approach within 2 m of the food pile for the full 2.5 h after mask departure on the last day of the post-exposure phase (*N* = 36 were still responding). The first 4 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 until 30 min after the arrival and observation of the first bird within 25 m. We discontinued longevity tests when birds did not scold *and* approached food within 2.5 h. 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 specificity of response to the dangerous face. Following the first encounter with an adult bird, the masked volunteer walked around the approximated home range (based on observations by volunteers and primary observer) of the birds 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/or the masked person. The FDT was counted as the first time a bird approached the food pile following the discovery of the masked person. The masked person departed 30 m following the arrival of the first bird within 25 m.

Experiment 2: Crow Response to Dead Heterospecific

We tested the response of crows to the sight of a dead pigeon being held by a masked person in August-September 2014. We established 5 unique sites within the greater Seattle and Bellevue areas (Fig. 2) based on consistent presence of adult crows 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, we presented the crows 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 held by a masked person in December 2013 and August-September of 2014. Since pigeons breed year round, behavioral differences due to breeding did not differ between winter and summer tests. We used 6 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 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 2014 experiments used a taxidermy-mounted “dead” pigeon.

Videography

The stimulus presentation, post exposure phase 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 Pearson’s X^2 analysis for the proportional comparisons of mobbing response and a one-way ANOVA to compare mob size. We analyzed site avoidance by comparing the change in delay of the Food Discovery Time (ΔFDT) with a two-factor repeated-measures ANOVA. The first factor was Pre-Post Stimulation (day 1-3, and day 5-7). The second factor was Day (day 1,2,3,4,5,6, and 7) and the between subject factor was Stimulus Treatment. All reported ANOVA results are of the interaction effect of Pre-Post Stimulation day and Stimulus Treatment. All experimental tests were considered to be independent. Prior to analysis, we log transformed FDTs to increase normality. When comparing only 2 variables with a hypothesized outcome (eg, danger vs control) we used one-tailed repeated-measures ANOVAs. We analyzed proportional comparisons of response to longevity tests with a Pearson's X^2 test and standard z-tests. For the proportional comparisons, we compared 3 dangerous stimuli and trial type (A vs. B, Fig. 1). All ANOVAs and X^2 tests were run using IBM SPSS Statistics version 19.

RESULTS

Experiment 1

Response to Dead Conspecific and/or Predator

Across years, territorial adults scolded during 95% of trials that presented dangerous stimuli ($N = 102$ tests), whereas only 17% scolded during masked-person only control presentations ($N = 12$ tests) and 0% scolded during food only control presentations ($N = 17$ tests). Control tests never resulted in mobbing. Of those crows that did not scold when we presented a danger, 2 observed a dead conspecific, 2 a hawk, and 1 and hawk with a dead crow. Between the 3 dangerous stimuli, hawk with dead conspecific presentations were more likely to result in mobbing than hawk or crow only (Pearson's $X^2_2 = 8.81$ $P = 0.01$; Fig. 3). There was also a difference in mob size (one-way ANOVA: $F_{4,126} = 8.61$, $P < 0.001$; Fig. 4). Crows who saw a hawk with a dead crow recruited the largest number of birds (post HOC Tukey HD, $P < 0.001$).

Immediately following the stimulus presentation event, 17% ($N = 101$ tests) of crows exposed to a dangerous stimulus did not approach the food pile within the next 2.5 h. All crows that received a control treatment ($N = 29$ tests) returned to the food. Birds who saw a hawk with a dead crow were the most likely not to approach the food (Pearson's $X^2_2 = 10.60$, $P = 0.005$; Fig. 5).

Experiment 1

Site Avoidance Trial Type A: Food Only Post-Exposure

Although there were observable differences in how birds treated the 3 dangerous stimuli during the presentation phase, these differences were not reflected in subsequent avoidance of the area. We found that, regardless of the dangerous stimulus seen during the stimulus presentation phase, crows showed similar changes in delays to approach the food pile (repeated measures ANOVA Pre-Post x Stimulus interaction: $F_{4,69} = 1.29$, $P = 0.28$). As a result, we combined the 3 different dangers and compared these responses to controls. As predicted, birds exposed to dangerous stimuli showed a larger change (relative to the conditioning phase) in latency to approach the food pile than did control treatment birds (one-tailed repeated measures ANOVA, Pre-Post x Stimulus interaction: $F_{1,72} = 3.20$, $P = 0.04$; Fig. 6).

Site Avoidance Trial Type B: Food and Dangerous Human Post-Exposure

Under Trial Type B conditions, 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 Pre-Post x Stimulus interaction: $F_{4,68} = 2.10$ $P = 0.09$). Therefore, we again lumped all dangerous stimuli and compared against controls. We found crows that received a dangerous treatment showed greater changes to their latency to approach the food pile than those that received a control treatment (one-tailed repeated measures ANOVA Pre-Post x Stimulus interaction: $F_{1,71} = 6.30$, $P = 0.0075$;Fig. 7).

Experiment 1

Longevity Tests: Response to Conditioned Human

During the first longevity test (which occurred 1 week after the last mask exposure during the stimulus presentation phase) crows showed little response to masked human controls, but learned the faces of humans associated with dead crows and hawks (one-tailed z-test: $Z = -3.03$, $P = 0.001$). Birds that received a dangerous treatment were equally likely to respond to the masked person regardless of which of the 3 dangers the person was paired with (Pearson's $X^2_2 = 1.95$, $P = 0.38$) or which Trial Type the birds were tested under (Pearson's $X^2_1 = 0.55$, $P = 0.46$; Fig. 8). Even after 6 weeks of additional weekly exposures, birds under Trial Type B showed no significant difference in fear extinction compared to those in Trial Type A, (Pearson's $X^2_1 = 0.16$, $P = 0.69$; Fig. 8) and were no more likely to respond to the person associated with any one of the 3 dangers, (Pearson's $X^2_2 = 0.20$, $P = 0.91$).

Experiment 2: Crow Response to Dead Heterospecific

While 94% of crows scolded the sight of a dead conspecific ($N = 34$ tests), only 40% of crows scolded when encountering a dead pigeon (N=5 tests; Pearson's $X^2_1 = 11.42$, $P = 0.001$). Even in cases where crows scolded in response to the dead pigeon, they did so far fewer times (average ± SE = 7 ± 1.26) than in response to a dead conspecific (60.74 ± 9.89). Crows exposed to a dead pigeon did not recruit any additional birds to the area, unlike the majority of those that saw a dead crow (Pearson's $X^2_1 = 7.42$, $P = 0.006$). Following exposure to a dead conspecific, crows in Trial Type A exhibited a greater change in their latency to approach the food than did crows confronted with a dead pigeon (one-tailed repeated measures ANOVA Pre-Post x Stimulus interaction $F = 2.93_{1,20}$, $P = 0.05$; Fig. 9).

Experiment 3: Pigeon Response to Dead Conspecific

Pigeons flocked to food in the presence of the masked person holding the dead pigeon in 66% of cases ($N = 6$ tests). In contrast, crows never approached the food in the presence of a masked person holding a dead crow ($N = 34$ tests; Pearson's $X^2_1 = 25.19$, $P < 0.001$). This disparity was not explained by a difference in general willingness to approach food near people because mask-only control crows were just as likely to approach food in the presence of a control person as pigeons (Pearson's $X^2_1 = 1.80$, $P = 0.18$). Sight of a dead conspecific had different effects on change in latency to approach the food pile in pigeons relative to crows (Trial Type A; one-tailed repeated measures ANOVA Pre-Post x Stimulus interaction: $F_{1,21} = 8.85$, $P = 0.0035$). Whereas crows increased their delay to the food pile after stimulus exposure, pigeons were faster to reach food during their post-exposure phase as compared to their conditioning phase (Fig. 10).

DISCUSSION

Despite the numerous studies observing animal response to conspecific olfactory and auditory alarm cues, few studies have systematically tested the response of animals to conspecific carcasses. Documentation of spontaneous funerals immediately following conspecific death in dolphins and primates, have captured a variety of behaviors ranging from sexual arousal, aggressive interactions with the body, and increased post mortem grooming (Dudzinski et al. 2003, Buhl et al. 2012, Engh et al. 2010). Furthermore, American bison (*Bison, bison*) and elephants maintain intense interest in conspecific carcasses even after they've been reduced to bones (King 2013, McComb et al. 2005). Given the small number of studies that have evaluated these behaviors, the evolutionary basis for why some non-human animals demonstrate intense interest in dead conspecifics remains unclear (McComb et al. 2005). Although funeral responses may be species or context specific, in our study we demonstrated that wild crows are using the bodies of dead conspecifics as an indication of danger both in terms of the place it was discovered and as a means to learn dangerous people. For corvids, this suggests that the evolutionary basis for this behavior is, at least in part, danger learning and avoidance.

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

In Experiment 1, we demonstrated that wild American crows use the discovery of a dead, unfamiliar conspecific as an opportunity to recruit others to engage in mobbing, inform future resource use, and as a proxy to learn novel human threats. 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 that are consistent with danger learning. However, in their study crows were tested in isolation, where they could not mob and did not vocalize. Our finding that they scolded and mobbed people holding dead crows, without our needing to artificially mimic 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 in response to people with dead conspecifics is neither a typical feeding responses 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. This suggests that, like western scrub-jays, the discovery of a dead conspecific is effective at triggering typical anti-predator behaviors (Iglesias et al. 2012). Certain dangers did, however, evoke stronger immediate anti-predator behaviors than others.

If a predator with a dead crow was observed, crows both mobbed and avoided the food site more aggressively over the next several hours. Crows' ability to tailor their immediate response to the threat is supported by studies that show animals such as breeding wood mice (*Apodemus sylvaticus)* and blue jays (*Cyanocitta cristata*) adjust subsequent foraging decisions in light of predator identity (Navarro-Castilla and Barja 2013, Conover 1979). That crows responded most strongly to a predator with a conspecific prey is consistent with responses by herring and lesser black-backed gulls (*Larus argentatus* and *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 findings support the conclusion that crows are sensitive to predator behavior (with or without prey) and subsequently adjust the aggressiveness of their mobbing response.

After exposure to a human with a dead crow, hawk, or hawk with crow remains, crows in both Trial Type A and B (Fig. 1) avoided the area more than they had during their conditioning phase. House mice avoid trays containing both food and conspecific cadavers, but whether they make ongoing associations with those trays has not been addressed (Prounis and Shields 2013). Common ravens have also been shown to avoid areas associated with effigies, though in this case not only did they witness a highly stimulating reenactment of the individual's death, but researchers used raven distress playbacks, and effigies remained present for 48 h (Peterson and Colwell 2014). Our findings indicate that crows learn the spatial context associated with a dangerous event and that aversion to this area can continue for 72 hours even 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 et al. 2004). Our results suggest that both predators and dead conspecifics meet this threshold for crows, and underscore the high level of threat crows perceive a dead conspecific to represent. We did not, however, find that there was a difference in site avoidance depending on which danger the crows received. Given that both hawks and humans are highly mobile and that the risk of repeated encounter with a predator decreases with time (Kats and Dill 1998), the finding that crows are more sensitive to the identity of the threat in the hours following exposure, but not days, indicates that crows temporally adjust anti-predator behaviors. This is consistent with other studies that show animals adjust foraging decisions in light of temporal variations in risk (Lima and Bednekoff 1999; Lima and Dill 1990). Danger learning was not limited to site avoidance however, as we also found that crows made associations with the people in close proximity to the dangerous stimuli.

A week following the presentations of a novel human paired with a dangerous stimulus, more than half of birds in each trial type scolded or refused food after exposure to the dangerous human. It was previously known that crows are highly sensitive to human aggression even to the extent that they are attentive to gaze (Clucas et al. 2013) and can learn and recall human faces after being captured by them (Marzluff et al. 2010). The ability to recall their initial captors is mediated by the amygdala (Cross et al. 2013) an area that is critical to fear learning. At the onset of the present study, what remained unclear was whether crows could learn people who were only indirectly associated with danger. Our results indicate that crows associated humans with danger when they were in close proximity to both dead conspecifics and/or predators and, in some cases, scolded and/or refused food for up to 6 weeks. Unlike most mammalian studies or other predator learning studies in birds (Milad et al. 2006; McLean et al 1997), subjects in our experiments only received 1 training event in which to learn the associated person as opposed to 2 or more. This is the first study, to our knowledge, that shows crows are learning human faces based simply on their proximity to known threats after only 1 training session.

The finding that stimulus type had no effect on whether or not crows would respond when seeing the person 1, and up to 6, weeks later suggests that dead crows and predators are equivalent at triggering fear conditioning. Since urban crows interact with a variety of people who can be friendly, neutral or dangerous, it may be adaptive to cast a wide net when learning and responding to even just potentially dangerous people.

We did not find that crows that received 3 additional exposures to the conditioned human (Trial Type B; Fig. 1) differed with respect fear extinction from those that did not (Trial Type A; Fig. 1). This suggests a difference of only 3 additional exposures is not enough to trigger robust 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 2014). Wild birds may be less vulnerable to extinction since errors are more likely to be fatal than for captive rats.

Experiment 2: Crow Response to Dead Pigeon

In Experiment 2 we showed that crows are less attentive to a dead heterospecific than they are to a conspecific. This comes in contrast to a previous study on wild western scrub-jays that showed dead, jay-sized heterospecifcs evoked scold calls by the discovering jay as often as did dead conspecifics (Iglesias et al. 2014). For crows, a dead heterospecifc may be a cue of danger, but it is also a potential food source. Therefore advertisement of its 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 dropped it, or left it behind. Disinterest in pigeon carcasses in contrast to crows may also result from the discrepancy in their average life expectancies. Pigeon typically live for only 2.4-2.9 years (Hetmanski 2007), whereas crows live 13-14 years (Marzluff and Angell 2005). Therefore interest in conspecific carcass may be partly attributed to the rarity of adult crow death in contrast to more frequent pigeon death.

Experiment 3: Pigeon Response to Dead Pigeon

Whereas crows responded strongly to humans with dead crows in nearly all cases, in Experiment 3 we showed that another prolific urban bird, the rock pigeon, takes little notice of dead conspecifics. Although the volunteer held 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 the threat than crows. When shown a predator with a struggling live conspecific, European starlings (*Sturnus vulgaris*) were subsequently more wary of the predator and showed greater latency to feed than if they had seen the predator alone or with a dead conspecific (Conover and 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.

Overall

Although aversion to conspecific carcasses has been shown in a variety of animals, prolonged interest in conspecific remains is currently limited to only a few social, long lived non-human animals. The evolutionary basis for such interest may give insight into the development of the more complex rituals associated with human death. Here we have shown that conspecific carcasses represent a salient danger akin to predators, and that wild crows use funerals as a means to communicate dangerous places and subsequently avoid areas associated with these events. Furthermore, territory holders made memories of the person associated with the dangerous stimulus that could last for up to 6 weeks. These findings support the hypothesis that the evolutionary basis for funeral behaviors in corvids may be danger leaning and avoidance and offer insights for crow management.

Attention and avoidance of areas associated with crow death suggests that using crow effigies and falconry abatement methods may help successfully manage problematic crow populations. Continued presence of a person involved with these presentations will further help identify the area as an ongoing source of danger. Although these results provide insight into one function of crow funerals, it remains to be studied how our results compare with response of crows to the death of a familiar individual. If this distinction exists, it will provide a deeper understanding of crow funeral behavior and allow for a richer comparison with observations of such events in social mammals.

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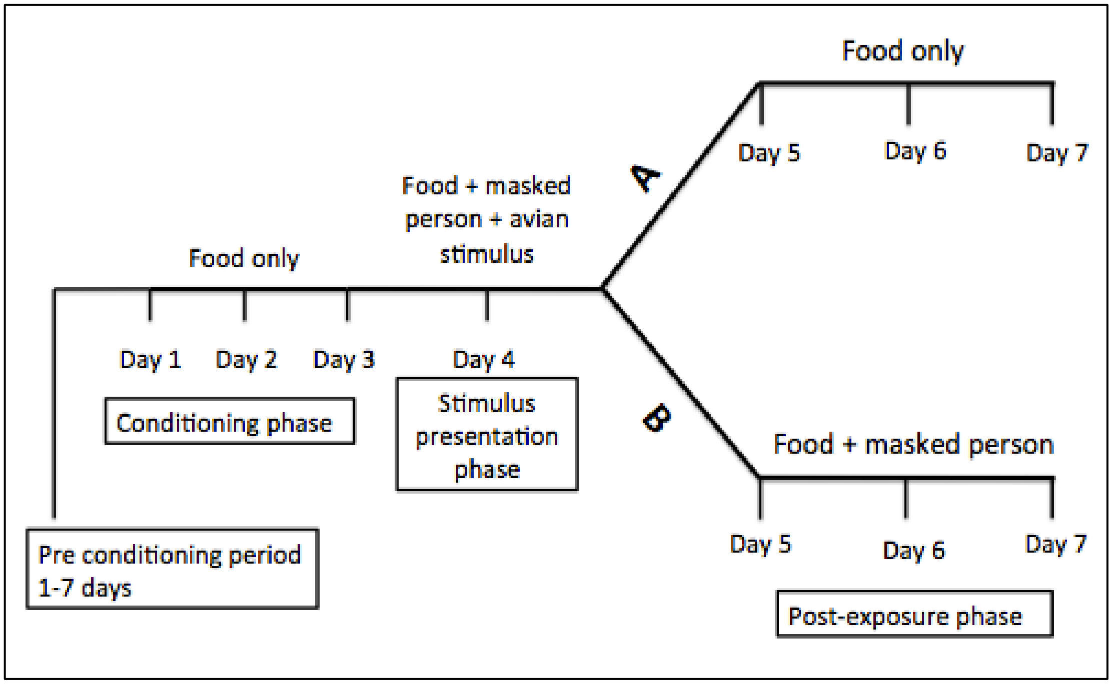

Figure 1. Each experiment consisted of three phases: the conditioning phase, stimulus presentation phase and post exposure phase. Prior to the conditioning phase, some test locations required an extended conditioning period in order to meet the criteria for conditioning completion. All experiments proceeded through the same first 4 d, but differed (Type A vs Type B) in their post-exposure treatment. The post-exposure phase under Trial Type A consisted of food provision only. Trial Type B included a 30 min exposure period to the same masked person seen on the stimulus presentation day. On all days the observer provided food and recorded the crow responses (up to 2.5 h).

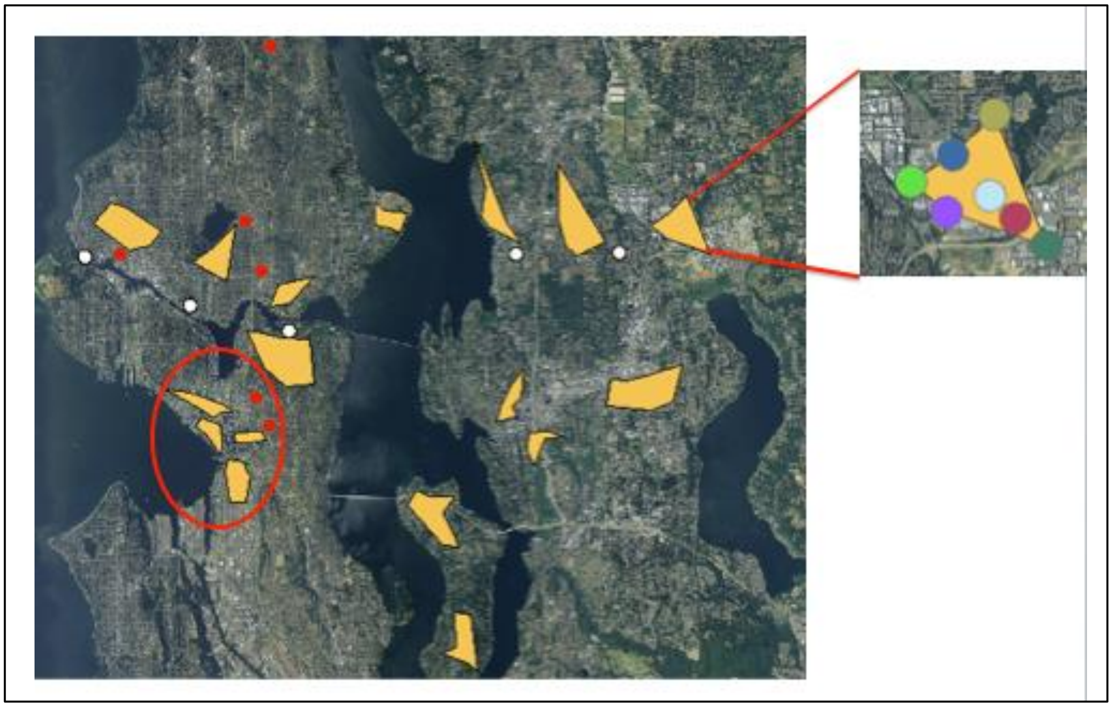

Figure 2. Map of study area in Seattle (left landmass), Mercer Island (central landmass) and Bellevue (right landmass). Orange polygons show 17 unique sites for Experiment 1. Window shows example of the independent test locations contained within each of Experiment 1's sites. White circles indicate the five locations for Experiment 2 and closed red circles show the six locations for Experiment 3. Red open circle indicates urban core. All closed circle are 250 m in diameter.

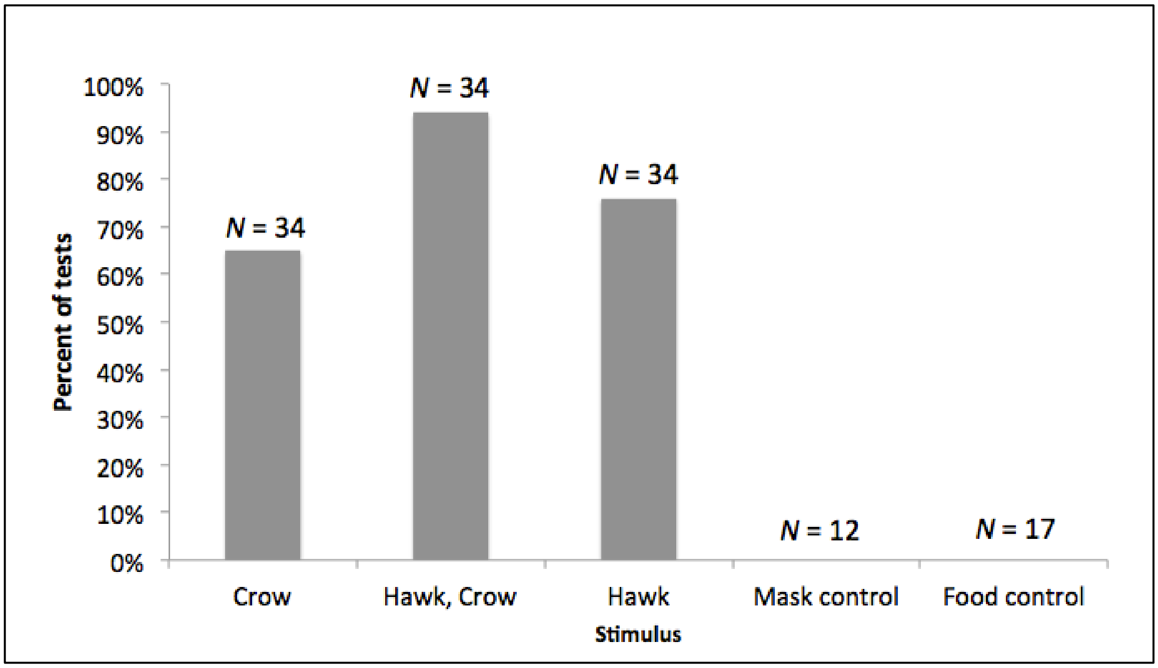

Figure 3. Percent of tests for each of the 5 stimuli that resulted in recruitment of at least 1 additional adult by the territorial pair (mobbing) during the stimulus presentation (day 4) in Experiment 1. Hawk with crows resulted in mobs significantly more than other 2 dangerous stimuli. Controls never resulted in mobs.

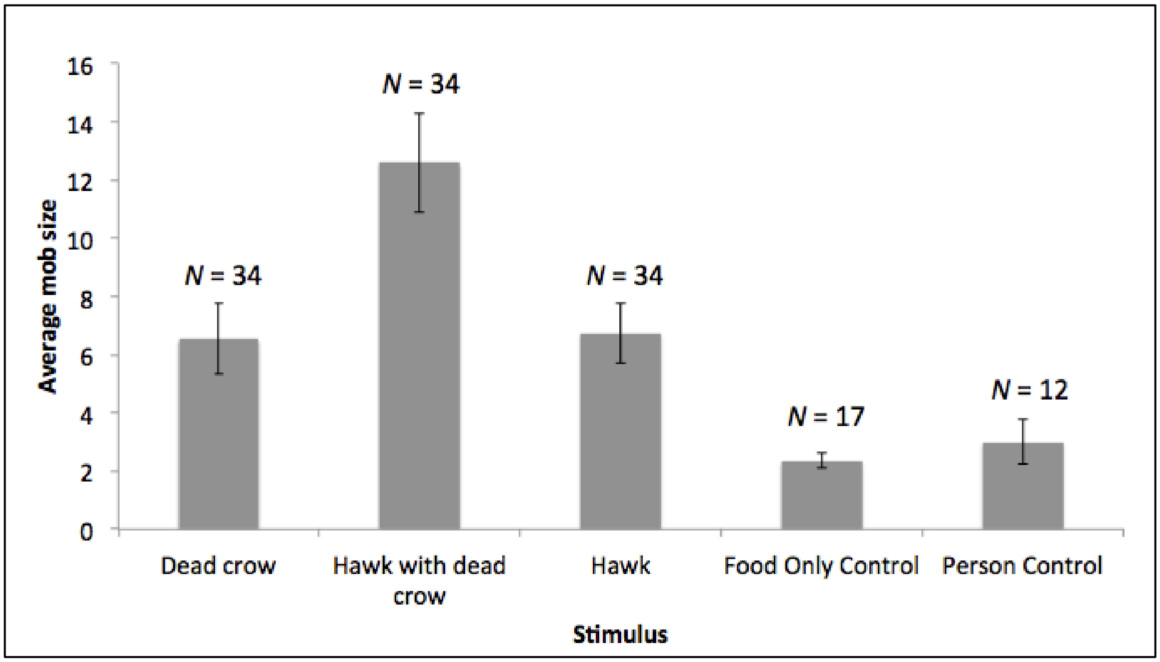

Figure 4. Comparison of average ± SE mob size during stimulus presentation phase (day 4) in Experiment 1. Average mob size includes territorial pair. Hawk with dead crow resulted in significantly larger mobs than other dangerous stimuli. All dangerous stimuli resulted in significantly larger mobs than controls.

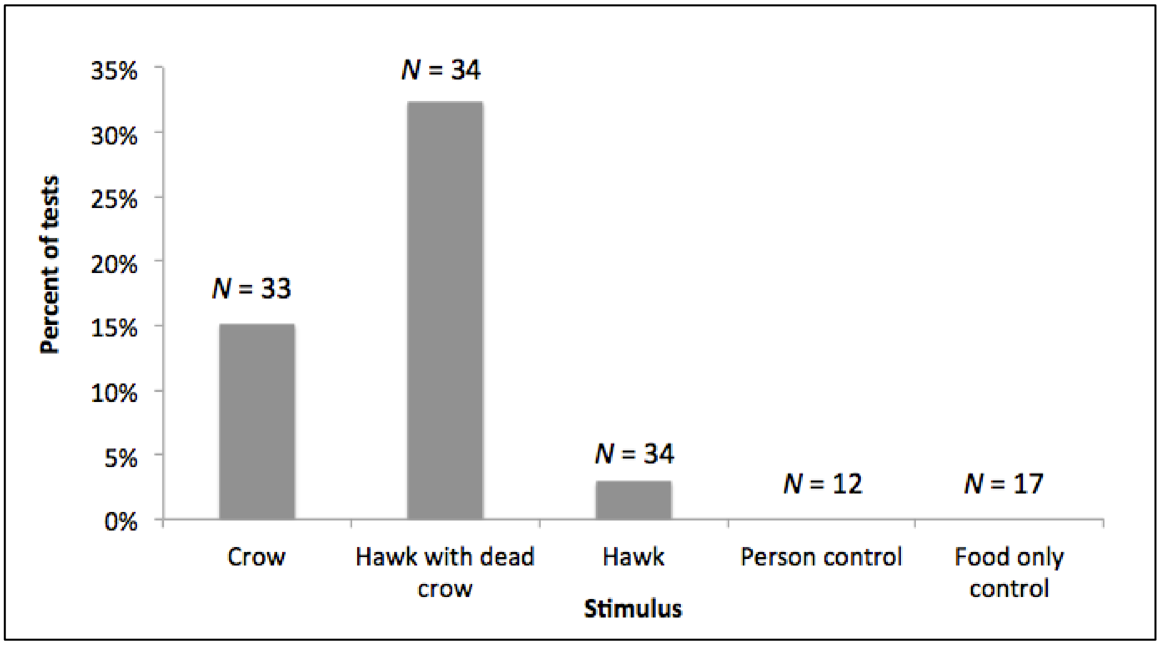

Figure 5. Percent of tests that resulted in crows never approached the food pile within the 2.5 h time period after stimulus departure during the stimulus presentation phase (day 4) of Experiment 1. Hawk with dead crow was significantly more likely to result in complete avoidance of food for full 2.5 h than other dangers.

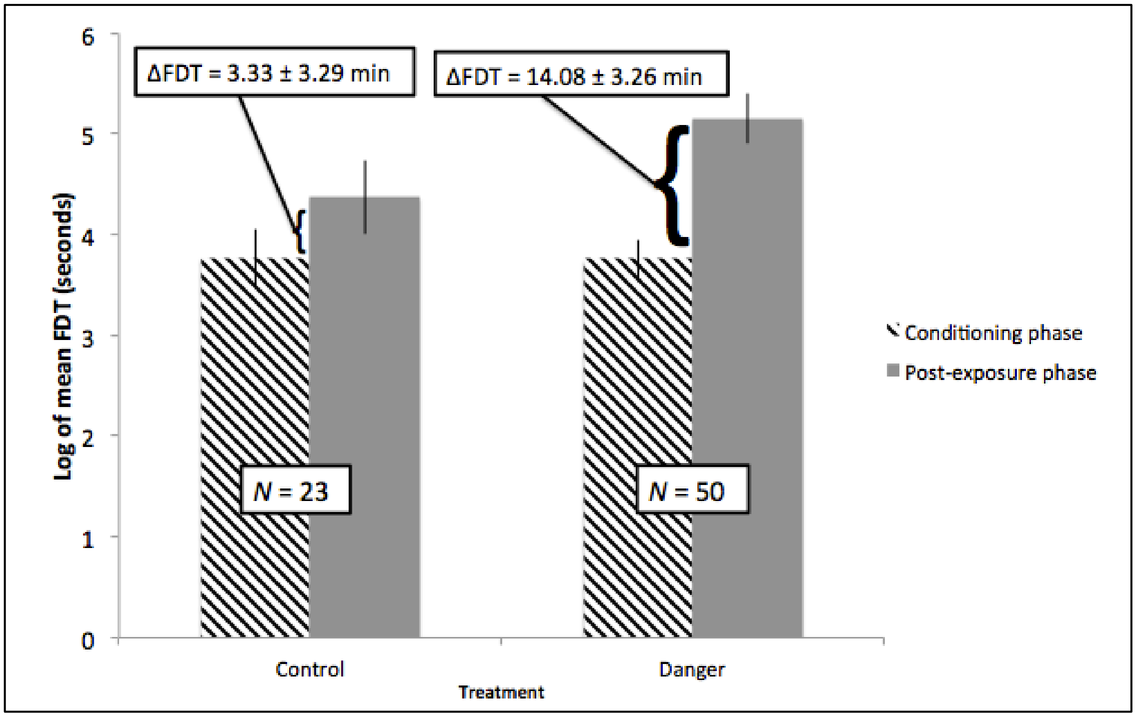

Figure 6. Comparison of change in latency to approach the food pile (ΔFDT) between control and danger treatments in Trial Type A tests (food only post-exposure phase). ΔFDT values indicated by brackets show untransformed average ± SE change in latency. Crows that received a dangerous treatment took significantly longer to arrive at food pile during post exposure phase then they had during the conditioning phase.

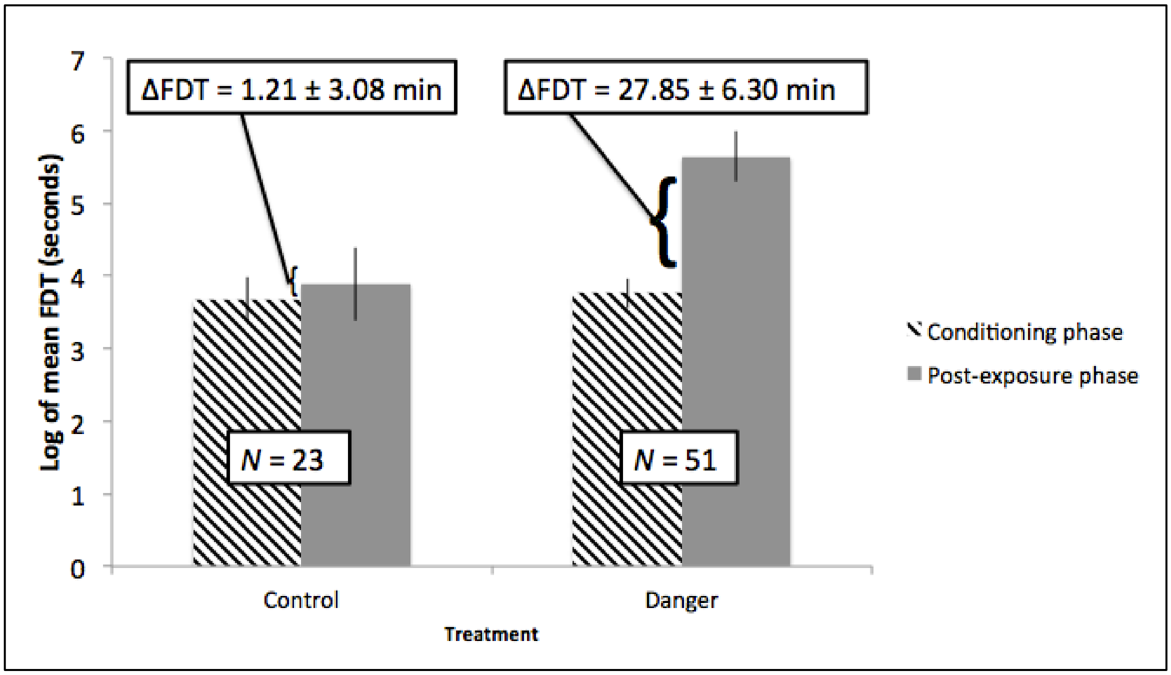

Figure 7. Comparison of change in latency to approach the food pile (ΔFDT) between control and danger treatments in Trial Type B tests (food+human post-exposure phase). ΔFDT values indicated by brackets show untransformed average ± SE change in latency. Crows that received a dangerous treatment took significantly longer to arrive at food pile during post exposure phase then they had during the conditioning phase.

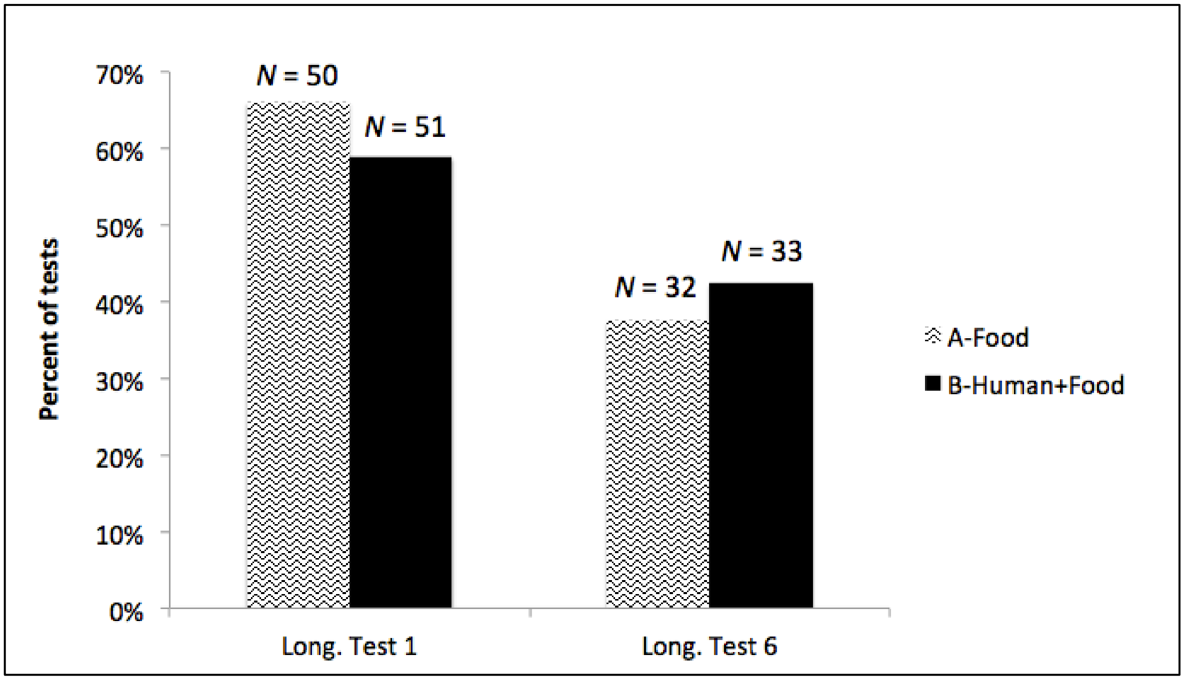

Figure 8. Comparison of continued response (scolded/dive bombed and/or avoided area for 2.5 h post mask departure) to masked person after 1 (A-Food) and 6 weeks (B-Human+Food) of continued weekly exposure in both trial types. Differences in fear extinction are non-significant.

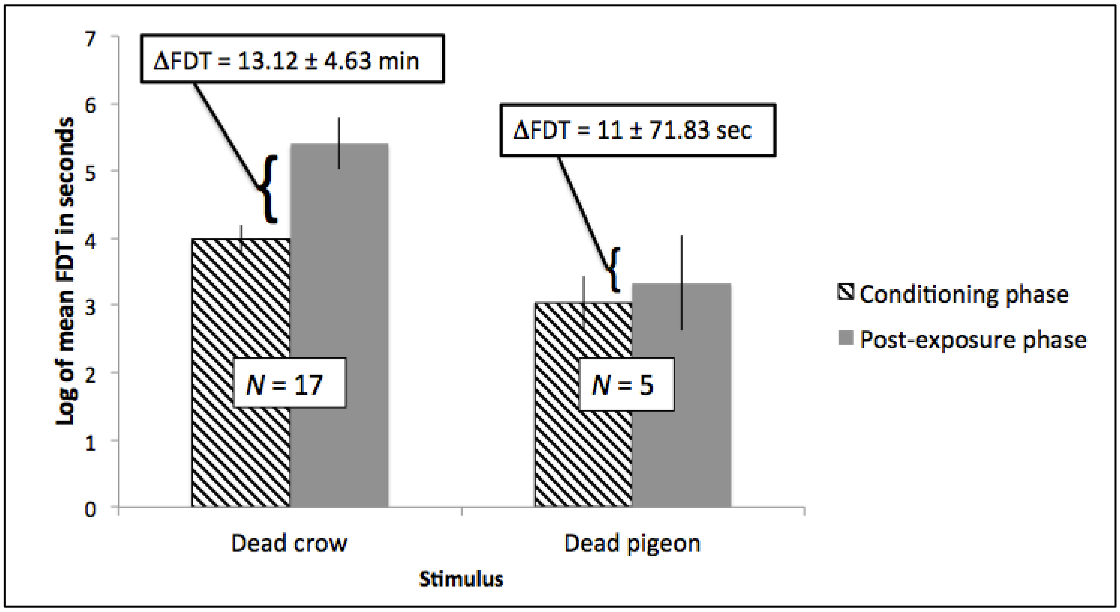

Figure 9. Comparison of change in latency to approach the food pile (ΔFDT) between crows that saw a dead conspecific in Trial Type A, Experiment 1 and crows that saw a dead heterospecific in Experiment 2. ΔFDT values indicated by brackets show untransformed average ± SE change in latency. Crows that saw a dead crow took significantly longer to approach the food pile during post exposure phase as compared to the conditioning phase, than crows that saw a dead pigeon.

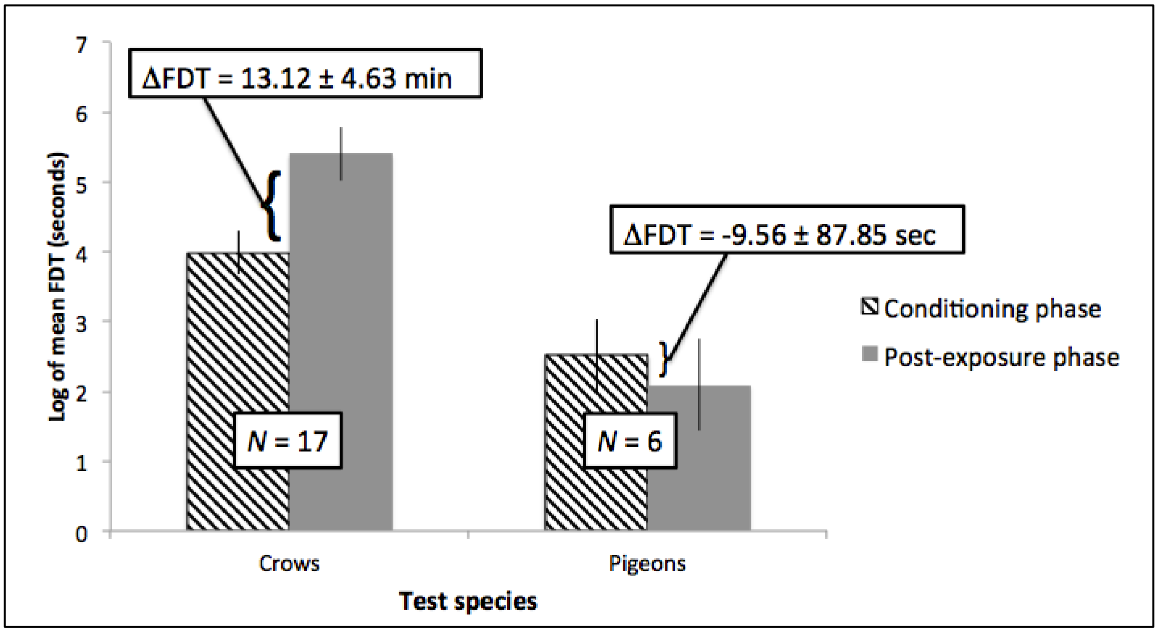

Figure 10. Comparison of change in latency to approach the food pile (ΔFDT) between crows that saw a dead conspecific in Trial Type A, Experiment 1 and pigeons that saw a dead conspecific in Experiment 3. ΔFDT values indicated by brackets show untransformed average ± SE change in latency. Pigeons were faster to arrive at the food following exposure to a dead conspecific, whereas crows showed avoidance of the area.

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