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Occurrence and variability of tactile interactions between wild American crows and dead conspecifics

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Observations of some mammals and birds touching their dead provoke questions about the motivation and adaptive value of this potentially risky behaviour. Here, we use controlled experiments to determine if tactile interactions are characteristic of wild American crow responses to dead crows, and what the prevalence and nature of tactile interactions suggests about their motivations. In Experiment 1, we test if food or information acquisition motivates contact by presenting crows with taxidermy-prepared dead crows, and two species crows are known to scavenge: dead pigeons and dead squirrels. In Experiment 2, we test if territoriality motivates tactile interactions by presenting crows with taxidermy crows prepared to look either dead or upright and life-like. In Experiment 1, we find that crows are significantly less likely to make contact but more likely to alarm call and recruit other birds in response to dead crows than to dead pigeons and squirrels. In addition, we find that aggressive and sexual encounters with dead crows are seasonally biased. These findings are inconsistent with feeding or information acquisition-based motivation. In Experiment 2, we find that crows rarely dive-bomb and more often alarm call and recruit other crows to dead than to life-like crows, behaviours inconsistent with responses given to live intruders. Consistent with a danger response hypothesis, our results show that alarm calling and neighbour recruitment occur more frequently in response to dead crows than other stimuli, and that touching dead crows is atypical. Occasional contacts, which take a variety of aggressive and sexual forms, may result from an inability to mediate conflicting stimuli.

This article is part of the theme issue 'Evolutionary thanatology: impacts of the dead on the living in humans and other animals'.

Thereupon Allah sent forth a raven who began to scratch the earth to show him how he might cover the corpse of his brother. So seeing, he cried: 'Woe unto me! Was I unable even to be like this raven and find a way to cover the corpse of my brother'? Then he became full of remorse at his doing.

Qur'an Sura 5.31

1. Introduction

Within the field of comparative thanatology, observations of prolonged transport of dead infants, and affiliative, sexual or aggressive contact with dead adults call into question the understanding and motivations behind animal responses to conspecific (members of the same species) death [1,2]. Tactile interactions with conspecific corpses have been widely observed among dolphins, elephants and non-human primates, though whether tactile interactions are a characteristic response of these species is unknown [3–5]. Prolonged contact may even continue over the course of days or weeks in cases involving dead infants [6,7]. Among these mammals, tactile interactions may manifest as

affiliative behaviours such as grooming and gentle touching, aggressive interactions and sexual behaviours [8]. Touching or remaining close to dead conspecifics may expose animals to disease or increase the risk of attack from dangerous scavengers, such as stinging insects or larger predators [9–12]. Therefore, what purpose, if any, these interactions serve remains unclear.

Tactile interactions may aid the assessment of an individual's state or identity, or allow animals to acquire other important information such as cause of death [8,13]. Alternatively, they may be a by-product of adaptive behaviours such as territory defence, mating or caretaking [4]. To date, motivations behind mammalian contact with dead conspecifics remain largely untested. In contrast to large or marine mammals, systematic studies of death responses among birds are more feasible due to the fact that carcasses are smaller and easier to obtain and transport, and limited olfactory abilities enable realistic experiments using taxidermy specimens. Among birds, some corvids demonstrate consistent responses to dead conspecifics, though it remains unknown if they engage in tactile interactions.

Humans have long noted the attendance of corvids near their dead, even incorporating them into their parables, as is evident in the epigraph we chose to start this paper. When confronting a dead conspecific, wild American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*) and California scrub-jays (*Aphelocoma californica*) alarm call and recruit other birds to the area [14–16]. Following these events, jays and crows avoid or show wariness in areas associated with conspecific death, and crows harass people they observed handling dead crows [14,15]. These findings suggest that crows and some other corvids recognize dead conspecifics as cues of danger and use such information to inform future actions and learn novel threats. During studies with California scrub-jays, dead jays were presented in the absence of predators that might otherwise keep observers away, but no episodes of contact akin to those described in some mammals were reported [14]. Studies done on crows and ravens, however, have largely prevented such opportunities for contact due to the manner in which birds were presented (as hanging effigies or paired with predators, [15,16]).

Given the similarities between crows and the mammals for which contact has been repeatedly observed, crows make a viable model for exploring tactile interactions between wild animals and their dead. Like dolphins, elephants and primates, crows share a large relative brain size and a complex social system [17–19]. If interactions with dead conspecifics serve to provide key information to the investigating animal, it is possible that crows would seek the same kinds of information as these mammals. Among crows, interactions may also be simply extensions of typical scavenging behaviours that include interest in dead animals. Alternatively, given that crows defend territory boundaries and female mates, particularly during the period of peak female sexual receptiveness between March and April, it is possible that contact with dead crows is the result of attempts to evict intruders [20,21]. Through two controlled experiments, we seek to determine if tactile interactions between wild crows and dead conspecifics are a defining feature of crows' response repertoire, and if food, information acquisition or territoriality are motivating factors.

To meet our objectives, we present wild crows four stimuli: a dead adult crow, a dead juvenile crow, a dead feral pigeon and a dead eastern grey squirrel (Experiment 1). Although, in our area, scavenging accounts for a minority of a crow's diet, crows are known to scavenge both pigeons and squirrels ([22]; K.S. personal observation). By contrast, crows are not known to regularly scavenge conspecifics [23]. Given that taxidermy-prepared animals are of no real food value, we expect contact with heterospecifics to lack alarm calling and neighbour recruitment, be exploratory and aggressive in nature, and only last for brief periods until crows determine they are of no value. If interactions with dead crows mirror those with squirrels and pigeons in these ways, it is likely that contact is food motivated. Alternately, efforts to glean information such as the individual's state, identity or signs of depredation may be responsible for observed contact. If such information acquisition motivates tactile interactions, we expect that interactions will be coupled with alarm calling and recruitment, be primarily non-aggressive in nature and occur frequently and uniformly across the study period. Finally, previous studies have suggested that danger learning and avoidance motivate crows' attraction to dead conspecifics [16]. If crows exhibit a danger response, we expect higher rates of alarm calling and recruitment coupled with lower rates of contact in contrast to heterospecifics.

We then determine what role stimulus posture has on the occurrence of interactions (Experiment 2). In contrast to food or information, crows may regularly contact dead crows because they fail to recognize their deceased state and mistake them for an intruder, provoking territoriality and mate guarding. To test this, we present wild crows with a dead adult crow or a life-like upright mounted crow. We expect that the life-like crow will result in scolding and dive-bombing, but infrequent recruitment, and that contact will be primarily aggressive. If crows fail to correctly assess the state of the dead crow, then we expect to see similar behaviours between life-like and dead crows. Lastly, because our initial crow stimulus resembles female copulation posture (wings outstretched with tail exposed), we wondered if any observed sexual responses in Experiment 1 were mediated by stimulus posture. To test this, in addition to evaluating if crows attempt to copulate with the life-like crow, we present crows with a dead adult crow with wings prepared close to the body ('tucked' crow in dead posture). If sexual behaviour is released by stimulus posture, we expect that neither the tucked crow, nor the life-like crow will elicit copulation attempts.

2. Material and methods

(a) General information

We conducted experiments at sites in Washington, USA in the cities of Seattle, Bellevue, Issaquah, Renton and Kent. For these experiments, we selected individual trial sites based on the presence of a territorial adult pair. We identified pairs based on seasonally relevant breeding activity including nest building, nestling provisioning or the presence of a fledgling. In our area, helping behaviour occurs infrequently, so we assumed that no more than two adults occupied a single territory [24]. Each pair only received one stimulus during the course of the study. All trials were spaced at least 300 m apart in an attempt to prevent carry over effects and increase independence.

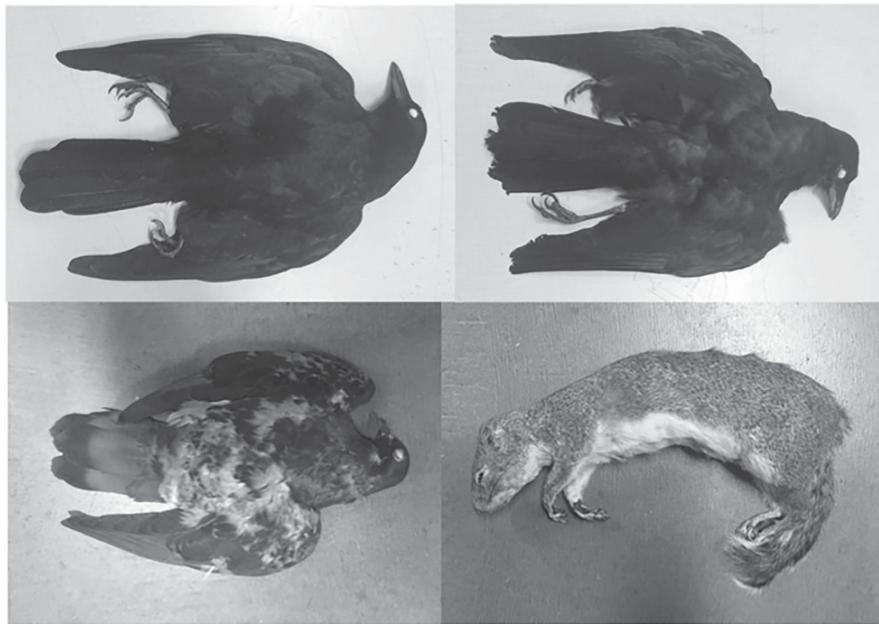


Figure 1. Stimuli used in *Experiment 1*. Clockwise from top left: adult American crow in standard dead posture, juvenile American crow in standard dead posture, feral pigeon in standard dead posture and Eastern grey squirrel in dead posture. (Online version in colour.)

During experimental trials, a single observer, K.S., placed the appropriate stimulus 35–45 m from the nest or fledgling in the absence of any adult birds. We attached all avian stimuli in dead posture to a lead weight via 1.5 m of transparent fishing line to prevent removal by crows. The squirrel was prepared with an internal lead weight and packed with sand. Stimuli were maintained in roughly the same condition and replaced by an identically prepared skin if irreparably damaged. All specimens were collected outside of the study area and presumed to be unfamiliar individuals to the observing crows.

Once the specimen was in place the observer stood and recorded data from 15 to 25 m away. The observer waited for up to 2 h for the first adult bird to come within 25 m of the stimulus and look in its direction (stimulus discovery). Once these criterion were met the observer recorded data for 30 min, after which the stimulus was removed. The distance from the nest, and 25 m radius, was determined using a TruePlus 200 Laser Rangefinder. We recorded all experiments with a tripod mounted JVC Everio camera.

(b) Experiment 1: tactile interaction with conspecifics and heterospecifics

During the breeding season of 2015 (March–August) and 2016 (March–April), we tested the response of wild American crows to the sight of either a taxidermy-prepared adult crow in dead posture ($N = 78$), a taxidermy-prepared fledgling crow in dead posture ($N = 78$), a taxidermy-prepared adult rock pigeon (*Columba livia*) in dead posture ($N = 77$) or a taxidermy-prepared adult Eastern grey squirrel (*Sciurus carolinensis*) in dead posture ($N = 76$; figure 1). We prepared avian skins with their heads turned to the side with wings slightly outstretched and placed ventral side down. The squirrel skin was prepared caudal side down and slightly curled.

Once the stimulus was discovered by the first adult bird, we recorded the number of birds within 2 and 25 m from the stimulus, the number of scolds emitted and whether dive-bombing or contact with the stimulus occurred. We defined scolding as harsh, unstructured calling. We defined mobbing as the presence of three or more adults engaging in scolding. We defined dive-bombing as u-shaped swoops directed at a specific target that

may or may not result in brief physical contact. If tactile interactions occurred, we used the video recordings to count the number of such instances, determine the amount of time spent with one or both feet on the stimulus (stand time) and categorize the nature of each contact into one of the following five categories:

1. *Peck*. We defined a peck as forceful contact by the living bird with its beak delivered to any part of the stimulus.
2. *Touch*. We identified a touch as non-forceful contact made by the living bird with any part of its body (bill or foot) to any part of the stimulus.
3. *Drag*. We considered dragging to be the intentional movement of the stimulus by the living bird via its beak. Dragging could occur up to a metre and could include attempts to pick up and fly off with the stimulus.
4. *Tissue pull/dismember*. We considered tissue pulling any instances where the living bird removed fur or feathers from the stimulus by grabbing the material in its bill and yanking forcefully. Dismemberment included removal of limbs or cotton stuffing from the stimulus.
5. *Sexual behaviour*. We considered sexual behaviour to include: attempted copulation with the stimulus defined as the observation of the living bird mounting the stimulus and positioning the tail while attempting to, or successfully making, cloacal contact; copulation between mates occurring following the discovery of the stimulus and within 25 m of it; and sexual solicitation posturing occurring on or within 25 m of the stimulus, following stimulus discovery.

(c) Experiment 2: effect of stimulus posture on respondent behaviours

During the breeding season of 2016 (July–August) and 2017 (April–June), we tested the response of wild American crows to the sight of either a (i) taxidermy-prepared adult crow in dead posture with wings partially outstretched as in *Experiment 1* ('standard' crow in dead posture, $N = 52$), a (ii) taxidermy-prepared upright life-like crow mount ($N = 45$) or (iii) a taxidermy-prepared adult crow in dead position but with the

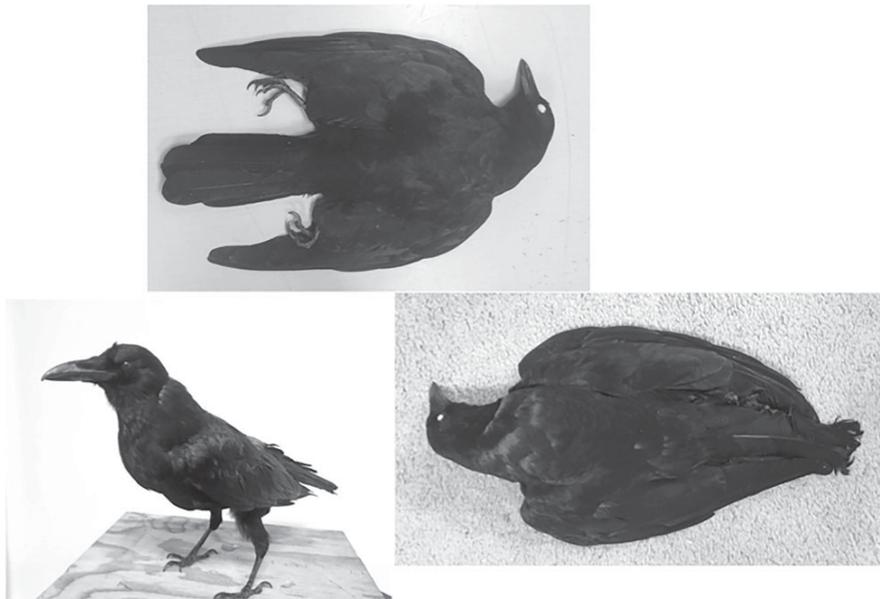


Figure 2. Stimuli used in Experiment 2. Clockwise from top: adult crow in 'standard' dead posture, upright, life-like adult crow and adult crow in 'tucked' dead posture. (Online version in colour.)

wings tucked close to the body ('tucked' crow in dead posture $N = 26$; figure 2). We presented the third stimulus only during March–May of 2017. We prepared the upright crow mount with glass eyes and assuming a standing posture typical of a live American crow. To aid with stability, we attached the specimen to a 36×36 cm piece of plywood via hidden screws in the feet. Site selection, stimulus presentation data collection and contact analysis procedures matched that of Experiment 1.

(d) Statistical analysis

We conducted tests in SPSS v.19 (IBM, Armonk, NY, USA) and RStudio 1.1.383 using the MASS package [25]. Apart from determining the likelihood of contact overall, all tests regarding contact omitted trials where no contact occurred, to control for zero-inflated data. In cases where there were only two stimuli such as heterospecifics and conspecific or life-like versus dead, we used Pearson's χ^2 tests to determine likelihood differences among binomial measurements such as scolding, mobbing or contact. To evaluate differences in binomial responses among three or more stimuli, we used negative binomial regression. In Experiment 1, we used logistic regression to determine if there were interaction effects between date and stimulus types. This test excluded data taken in 2016, because data collection in 2016 was limited to the months of March and April, and its inclusion may have biased the test's outcome. We used negative binomial regression to evaluate means among contact count data (ex: number of pecks) and one-way ANOVAs to compare all other means. In $n = 1$ case, a crow was able to remove the pigeon stimulus to a nearby rooftop. Because the bird was visible and audible for the duration of the trial, we included this point in binomial scolding, mobbing and contact tests, but not in tests of specific interaction types because the observer was unable to film them.

3. Results

(a) Experiment 1: tactile interaction with conspecifics and heterospecifics

The majority of trials (70%) resulted in no contact between wild birds and the stimulus. With respect to conspecifics,

the most typical reaction by wild birds was scolding (94% of 156 trials) often followed by mobbing (54% of trials). Among heterospecifics, scolding occurred less often than in response to crows (41% of 153 trials; Pearson's $\chi^2 = 96.94$, $p < 0.001$) and mobbing was only observed in a small number of cases (7% of trials).

Crows only made contact with conspecifics in 24% of trials. Contact occurred more frequently with heterospecifics than with conspecifics (36% of heterospecific trials; Pearson's $\chi^2 = 4.93$, $p = 0.026$). Of the $n = 55$ that contacted heterospecifics, 82% ($n = 45$) engaged in pecking. During these encounters, birds would often target eyes or other weak spots including ventral areas.

The contacting crow was more likely to scold during contact with a conspecific than a heterospecific (Pearson's $\chi^2 = 38.97$, $p < 0.001$). This finding was not driven only by a lack of a scolding response towards the squirrel, because crows were still more likely to scold during contact with conspecifics than with pigeons (partial χ^2 conspecifics versus pigeons = 14.33, $p < 0.001$). Crows were no more likely to scold during contact episodes with adult versus juvenile crows (partial $\chi^2 = 0.89$, $p = 0.34$). In addition, among trials where contact occurred, mobs were significantly more likely to form in response to conspecifics (60% of $n = 38$ contact trials) than to heterospecifics (7% of $n = 55$ contact trials; Pearson's $\chi^2 = 30.93$, $p < 0.001$). Wild crows contacted adult crows in dead posture in 25% of the 79 trials, juvenile crows in dead posture in 23% of the 77 trials, pigeons in dead posture in 34% of 77 trials and squirrels in dead posture in 38% of 76 trials (table 1). We observed crows engaging in all five categories of interaction with each stimulus, with the exception of sexual behaviours following presentations of the squirrel, which were never observed. Among the touch, peck, drag and tissue pull categories, we observed no difference in responses between the four stimuli (touches: Wald $\chi^2 = 2.28$, $p = 0.52$; drags: Wald $\chi^2 = 4.50$, $p = 0.21$; tissue pulls: Wald $\chi^2 = 5.67$, $p = 0.13$). We found no interaction effect of date and stimulus type on the occurrence of contact (Wald $\chi^2 = 3.20$, $p = 0.36$).

Table 1. Occurrence of tactile responses during Experiment 1. With the exception of 'Occurrence of contact', all other percentages are representative of the occurrence of the contact category out of the total trials in which contact occurred for each stimulus.

		exploratory behaviours				
	total trials (<i>N</i>)	occurrence of contact	occurrence of touching	average touches (\pm s.d.)	occurrence of dragging	average drags (\pm s.d.)
adult crow	78	<i>n</i> = 20, 25%	<i>n</i> = 12, 60%	4.75 \pm 6.00	<i>n</i> = 17, 85%	5.00 \pm 6.52
juvenile crow	78	<i>n</i> = 18, 23%	<i>n</i> = 9, 50%	11.00 \pm 11.45	<i>n</i> = 16, 89%	6.25 \pm 4.89
pigeon	77	<i>n</i> = 26, 34%	<i>n</i> = 12, 46%	5.92 \pm 8.37	<i>n</i> = 19, 73%	4.53 \pm 3.86
squirrel	76	<i>n</i> = 29, 38%	<i>n</i> = 23, 79%	3.78 \pm 2.61	<i>n</i> = 14, 48%	5.29 \pm 4.46
		aggressive behaviours				
	occurrence of pecking	average pecks (\pm s.d.)	occurrence of tissue pulling	average tissue pull (\pm s.d.)	occurrence of sitting	average stand time (<i>s</i> \pm s.d.)
adult crow	<i>n</i> = 9, 45%	228.89 \pm 292.46	<i>n</i> = 7, 35%	13.71 \pm 20.94	<i>n</i> = 7, 35%	349.57 \pm 326.20
juvenile crow	<i>n</i> = 12, 67%	67.08 \pm 99.38	<i>n</i> = 6, 33%	11.33 \pm 8.64	<i>n</i> = 10, 55%	102.30 \pm 100.99
pigeon	<i>n</i> = 19, 73%	28.61 \pm 37.49	<i>n</i> = 10, 38%	11.30 \pm 22.94	<i>n</i> = 14, 54%	59.79 \pm 72.69
squirrel	<i>n</i> = 26, 90%	49.12 \pm 56.14	<i>n</i> = 11, 38%	2.82 \pm 2.60	<i>n</i> = 12, 41%	47.58 \pm 54.72
		sexual behaviours				
	total sexual events (<i>n</i>)	attempted copulation with stimulus (<i>n</i>)	copulation between stimulus and greater than 1 bird (<i>n</i>)	copulation with mate ^a (<i>n</i>)	solicitation posturing ^b (<i>n</i>)	
adult crow	4	4	1	0	0	
juvenile crow	2	2	1	0	0	
pigeon	4	1	0	2	1	
squirrel	0	0	0	0	0	

^aDefined as copulation occurring following stimulus discovery and within 25 m of the stimulus. Identification of mated pair is based on nesting activity immediately before or after copulation event.

^bDefined as drooped vibrating wings and erect tail.

Crows were less likely to peck the adult crow in dead posture than the other three stimuli (Pearson's $\chi^2_1 = 8.34$, $p = 0.004$); however, when they did, they administered more pecks to adults (table 1; mean \pm s.d. = 228.89 ± 292.46 ; Z-score -2.03 , $p = 0.042$). There was a significant interaction between date and stimulus on the likelihood of pecking (Date \times Stimulus: Wald $\chi^2_3 = 8.13$, $p = 0.043$). This finding appears to be driven by an early season (March–May) bias towards pecking conspecifics (Date \times Con/Hetero-specific: Wald $\chi^2_1 = 4.63$, $p = 0.031$; figure 3). Among cases where birds stood on the stimulus, there was a difference in stand time on each stimulus ($F_{3,39} = 7.56$, $p < 0.001$). This was driven by responses to adult crows presented in dead posture, which were stood upon for the greatest length of time (Tukey's post hoc: Adult–Juvenile mean difference \pm s.e. = 247.27 ± 71.97 s, Adult–Pigeon mean difference \pm s.e. = 298.79 ± 67.60 s, Adult–Squirrel mean difference \pm s.e. = 301.99 ± 69.46 s).

We observed sexual behaviour in $n = 10$ trials: $n = 4$ adult crows in dead posture, $n = 2$ juvenile crows in dead posture and $n = 4$ pigeons in dead posture (table 1). In two of these cases ($n = 1$ adult crow in dead posture and $n = 1$ juvenile crow in dead posture), a second live bird mounted and attempted to copulate during the initial bird's copulation event with the stimulus (see video footage in electronic supplementary material). It was not clear in these cases if the second bird was attempting to mate with the live bird or if it was also attempting to mate with the stimulus. Based on our knowledge of the territorial pair's whereabouts at the onset of the trial, in both these cases, we believed that the second bird was mated to the first bird (however, the study birds were not marked). In cases where copulation occurred, in $n = 3$ for adult crows in dead posture and $n = 2$ for juvenile crows in dead posture, the copulating bird(s) scolded immediately before or after the event and pecked the stimulus aggressively during or after the event. Among sexual events during the presentation of the dead pigeon, $n = 1$ was an attempted copulation with the stimulus and did not include scolding before, during or after the event, $n = 2$ were copulations between the presumed mated pair following stimulus discovery and $n = 1$ was a bird-making solicitation postures while on top of the pigeon (table 1). The observation of copulation behaviour was biased towards the first half of the breeding season (March–May). Only one event was observed after the end of May, and the observation of the bird soliciting from on top of the pigeon occurred 18 June 2015.

(b) Experiment 2: effect of stimulus posture on respondent behaviours

Crows did not appear to distinguish the adult crows in tucked dead posture ($N = 26$) from those in standard dead posture ($N = 52$). There were no differences in their response with respect to scolding (all trials resulted in scolding), mobbing (Pearson's $\chi^2_1 = 0.44$, $p = 0.51$), overall contact (Pearson's $\chi^2_1 = 0.029$, $p = 0.87$) or copulation attempts with the stimulus ($n = 1$ tucked dead crow; $n = 4$ with standard dead crow). As a result, we collapsed these stimuli into a single 'dead posture' category ($N = 78$) for all subsequent analyses.

Crows distinguished between the adult stimulus in dead posture ($N = 78$) and the life-like crow ($N = 45$). Crows scolded in response to the dead crow in all cases, but only scolded the life-like crow in 71% of cases (Pearson's

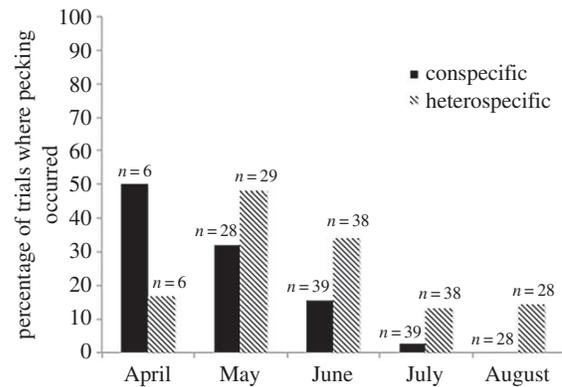


Figure 3. Pecking as a proportion of carcass directed contact in Experiment 1. Graph shows what percentages (Percentage is calculated as the number of trials that resulted in pecking out of the total number of trials where contact occurred for each stimulus type.) of trials resulted in pecking over each month of the 2015 field season. Black bars indicate trials using adult and juvenile crows presented in dead posture. Lined bars indicate trials using pigeons and squirrels in dead posture. The sample size per month for each stimulus is provided above the corresponding bar.

$\chi^2_1 = 25.20$, $p < 0.001$). If scolding occurred, birds scolded more quickly after discovering the crow in dead posture (mean \pm s.d. = 39.94 ± 118.03 s) than they did when they encountered the life-like stimulus (mean \pm s.d. = 241.72 ± 477.77 s; $F_{1,108} = 12.24$, $p = 0.001$). Mobbing also occurred more frequently in response to a conspecific presented in dead posture (63% of trials) than to a life-like crow (31% of trials; Pearson's $\chi^2_1 = 11.49$, $p = 0.001$). By contrast, dive-bombing occurred most often in response to presentations of the life-like crow (Pearson's $\chi^2_1 = 15.08$, $p < 0.001$). Crows dive-bombed the dead crow in 9% of trials and the life-like crow in 38% of trials.

Although crows more often made contact with the life-like crow (49% of trials) than with crows presented in dead posture (33% of trials), this difference was non-significant (Pearson's $\chi^2_1 = 2.90$, $p = 0.088$). If contact occurred, there was no observed difference with respect to pecking (Wald $\chi^2_1 = 0.07$, $p = 0.79$) or touching (Wald $\chi^2_1 = 0.22$, $p = 0.65$). Crows did, however, engage in more feather pulling/dismemberment with the upright stimulus than the dead stimulus (Wald $\chi^2_1 = 4.59$, $p = 0.033$).

We observed $n = 8$ sexual events in response to crows presented in dead posture and $n = 4$ sexual events in response to life-like crows (table 2). Of the $n = 3$ attempted copulations with the upright mount, none of them were preceded or followed by scolding or pecking by the mating bird, whereas all $n = 5$ attempted copulations with the crow in dead posture were. All copulation events were observed before the end of May, with the latest event occurring on 25 May 2017.

4. Discussion

Among some mammals including dolphins, elephants and non-human primates, there are dozens of accounts detailing tactile interactions between living individuals and a dead conspecific, but to date no systematic studies have been done to determine how typical this response is. Our experimental study demonstrates that among one group of

Table 2. Occurrence of sexual behaviours in Experiment 2.

	total sexual events (<i>n</i>)	attempted copulation with the stimulus (<i>n</i>)	copulations with greater than 1 bird (<i>n</i>)	copulations with mate (<i>n</i>) ^a
dead adult crow	8	5	0	3
life-like adult crow	4	3	0	1

^aDefined as copulation occurring following stimulus discovery and within 25 m of the stimulus. Identification of mated pair is based on nesting activity immediately before or after copulation event.

animals, wild American crows, contact with dead conspecifics is not characteristic of their response in that it only occurs in roughly one quarter of encounters, but when it occurs it is extremely varied. During these encounters, we found that crows are much more likely to scold and mob, something we observed significantly less often in response to dead heterospecifics or mounted, life-like crows. In addition, tactile interactions with crows were more often conflicting in nature (i.e. aggressive and sexual) in contrast to other stimuli. Although infrequent, we found that inappropriate contact like prolonged pecking or copulation generally occurred in the first half of the breeding season. Given these findings, we suggest that tactile interactions with dead conspecifics do not represent attempts to assess key information, typical scavenging or territorial behaviours. Our results suggest that costs associated with contact preclude most individuals from touching dead crows but that, in some birds, breeding season-induced changes may be responsible for overcoming more typical necrophobic responses.

Touching conspecific corpses may expose animals to disease or increase the risk of attack from dangerous scavengers, such as stinging insects or larger predators [5]. To avoid these risks, social insects such as ants, termites and bees have special undertaking procedures to efficiently dispose of conspecific corpses [26–28]. Rats (*Rattus norvegicus*) likewise bury cagemates that have been dead for more than 40 h [29]. For these colony living animals, any contact that occurs is therefore associated with body removal and the ultimate driver is maintaining colony health. Why some animals are motivated to engage with dead conspecifics in contexts outside of body disposal remains less clear, but some have suggested that they do it as a means to glean information from the body including attempts to identify the individual or assess its state [5,13]. Our observation that crows primarily responded to dead crows by scolding and mobbing in the absence of contact supports previous studies that crows and other corvids recognize dead conspecifics as indications of danger [14,16]. The finding that contact was uncommon may suggest that crows do not collect information via tactile interactions, tactile interactions are not necessary to collect such information or that the benefits of collecting such information are not outweighed by potential costs.

Although uncommon, we repeatedly observed that wild crows make contact with dead conspecific stimuli including juveniles and adults in varying positions. Contact could be exploratory, aggressive or sexual in nature. To our knowledge, this behaviour has not been previously reported in wild American crows. By contrast, California scrub-jays are not known to touch dead jays [14]. Further study is needed to determine if this behaviour is unique to crows among other corvids.

Our finding that interactions by wild crows with heterospecifics differed from interactions with conspecifics with respect to scolding, mobbing and the prevalence of aggressive and sexual behaviours suggests that interactions with dead crows are not food motivated. Specifically, that crows were significantly more likely to scold and mob in response to dead conspecifics both overall and during trials where contact occurred demonstrates a consistent danger response that was not observed in response to dead heterospecifics. This finding is supported by other observations that cannibalism (consumption of conspecifics) is rare among passerines [30]. To our knowledge, only one documented case of adult–adult cannibalism has ever been reported in crows [23]. Although most birds did not approach heterospecifics, this is not necessarily surprising given that in our area, predation and scavenging account for less than 25% of a crow's diet [22]. Furthermore, crows prefer open carcasses; therefore, carcass integrity may have kept some individuals away [31]. Those that did make contact appeared to be assessing and quickly determining that the specimens were of little food value.

Instead of foraging attempts, interactions with dead adults included behaviours more akin to territory defence such as intense physical aggression and scolding. In Experiment 2, however, we found that crows differed in their response to crows in a life-like versus dead posture in several key ways. In contrast to presentations of life-like crows, when crows encountered dead crows, they scolded more quickly and more often, were more likely to mob and were less likely to dive-bomb. These behaviours are consistent with the danger response hypothesis and suggest that the crows correctly identified the state of the dead bird. These findings are supported by a study on California scrub-jays that showed jays responded with alarm to a dead jay, but aggressively towards an upright jay [14]. Given that crows will attack intruders, and males appear to force extra pair copulations on non-receptive females, the finding that crows physically attacked or attempted to mate with the live mount is not unexpected [21]. With respect to interactions with the dead crows, it remains unclear what might account for the inappropriate and often conflicting nature of tactile responses including carcass destruction or attempts to mate, but we can begin to speculate as to their cause.

Observations of post-mortem contact that can be described as aggressive or sexual have been observed in a variety of animals. Following the death of a Rhesus macaque (*Macaca mulatta*), Buhl *et al.* [32] observed dominant group members interacting aggressively with the body including beating and biting for 50 min. Stewart *et al.* [33] described rough-handling and beating of a deceased female by young male chimpanzees after her death. Dolphins also sometimes direct aggressive and agitated behaviours towards dead conspecifics [4]. Such behaviours have been proposed as

manifestations of frustration or confusion at being unable to elicit a response [33]. This would not account for the early breeding season bias when this behaviour occurred, however. Rather, social theatre or displacement behaviours that arise out of the heightened state of arousal experienced during the breeding season may better explain such observations [8].

Across both experiments, we observed $n = 11$ attempts to mate with a crow in dead posture (4.7% of $N = 234$ trials), 90% of which were coupled with scolding and all of which took place before the end of May. Sexual behaviours around dead conspecifics are rare, but not unique to crows. Hetero and homosexual necrophilia have been observed across a wide variety of taxa. Sexual arousal in response to dead conspecifics has been documented in bottle nosed dolphins [4] and humpback whales (*Magaptera novaeangliae*; [34]). Mating attempts with dead conspecifics have been observed in Richardson's ground squirrel (*Citellus richardsoni*), mallards (*Anas platyrhynchos*), sand martins (*Riparia riparia*) cururu toads (*Rhinella steuax*) and great ameivas (*Ameiva ameiva*; [35–39]). The copulation posture typical of dead birds has been proposed as the releasing factor for such inappropriate attempts to mate, particularly among monomorphic birds [37]. In Experiment 2, however, we show that crows attempted to mate both with a life-like crow in neutral standing posture and a dead crow with the wings tucked close to the body. These observations call into question the validity of posture as the primary releasing factor for copulation events between crows and dead crows, and warrant further investigation.

Given the prevalence of scolding before, during or immediately following copulation events with dead, but not life-like, crows, alarm induced arousal, rather than reproductive attempts, might better explain copulation with dead crows. Increased sexual behaviour following alarm or excitement has been observed in the zebra finch (*Taeniopygia guttata*; [40]), vermilion flycatcher (*Pyrocephalus rubinus*, [41]) and pied avocet (*Recurvirostra avosetta*; [42]). Following the death of a group member, sexual behaviour occurring outside the breeding season was observed in rhesus macaques [32]. Likewise, we observed mating attempts between presumed pairs following discovery of a dead crow. It is possible in this context that distress induces arousal resulting in copulation attempts between mates if possible, but in the immediate absence of the mate results in displacement-mounting. In rooks (*Corvus frugilegus*), sexual displays by males sometimes stimulate reverse mounting by females [43]. In our study, females witnessing male precopulatory behaviour prior to mounting the stimulus may be responsible for the two possible instances of reverse mounting.

In addition to the multiple mating attempts with the dead and life-like crows, we also observed one attempted copulation with the dead pigeon. Attempts to mate with live heterospecifics have been observed in a variety of species including seals and non-human primates [44,45]. Although these events are rare enough that determining causal factors remains difficult, restricted access to conspecific females has been commonly observed in these cases. Such information about the crow involved in this case is not known.

Given that sexual and aggressive behaviours were often expressed simultaneously, it may be that breeding-related endocrine changes downregulate the ability of some birds to process conflicting information. Among primates, ambiguous or conflicting stimuli are processed in the anterior cingulate cortex (ACC). In humans, it has been shown that individuals

with high anxiety show reduced ACC recruitment during tasks involving threat-related stimuli [46]. It is not yet known what area in birds may act as the functional homologue to the ACC, but the corticoidea dorsolateralis has been proposed as a possibility, given its similar pathways as the mammalian cingulate cortex [47]. Further study is needed to determine if the CDL is responsible for processing such information in birds, and if some individuals show reduced activation and lower suppression of inappropriate responses during periods of high excitement such as the breeding season or when exposed to threats. In addition, exploring endocrine differences with respect to adrenocorticosteroid hormone, testosterone and corticosterone between birds that do and do not engage in contact will further elucidate breeding season-induced changes on the release of inappropriate behaviours. Studies examining the change in rates and nature of contact within individuals across the breeding season will help verify that such behaviours wane in correlation to decreased reproductive activity.

This study is the first to demonstrate that American crows occasionally make contact with dead conspecifics. The nature of contact in crows can be exploratory, aggressive or sexual. We show that such behaviours are both atypical and, with respect to sexual and aggressive behaviours, seasonally biased. We suggest that rather than information acquisition, food or territoriality, contact with crows is attributable to an inability among some birds to process conflicting stimuli resulting in inappropriate or conflicting displacement activities. Similar aggressive and sexual behaviours have been anecdotally observed among cetaceans, non-human primates and elephants. It remains unknown, however, whether our findings apply to these animals. A crucial distinction between our study and the vast majority of observations among mammals is that most interactions involving mammals were between familiar individuals. The potential myriad ways this may affect the response of either mammals or birds are unknown. Given that crows maintain permanent pair bonds that can span over a decade, it is possible that responses to familiar individuals contrast with our findings, particularly with respect to affiliative behaviours. Understanding whether these differences exist and what form they take (which may be investigated in experiments employing sedation) will help us better elucidate the significance of death on group members and partners, and help guide best practices when we are confronted with animal death in captive settings.

Data accessibility. The raw data associated with this manuscript can be found within the University of Washington's ResearchWorks archive at <https://digital.lib.washington.edu/researchworks/handle/1773/40753>.

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