



Western scrub-jay funerals: cacophonous aggregations in response to dead conspecifics

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All organisms must contend with the risk of injury or death; many animals reduce this danger by assessing environmental cues to avoid areas of elevated risk. However, little is known about how organisms respond to one of the most salient visual cues of risk: a dead conspecific. Here we show that the sight of a dead conspecific is sufficient to induce alarm calling and subsequent risk-reducing behavioural modification in western scrub-jays, *Aphelocoma californica*, and is similar to the response to a predator (a great horned owl, *Bubo virginianus*, model). Discovery of a dead conspecific elicits vocalizations that are effective at attracting conspecifics, which then also vocalize, thereby resulting in a cacophonous aggregation. Presentations of prostrate dead conspecifics and predator mounts elicited aggregations and hundreds of long-range communication vocalizations, while novel objects did not. In contrast to presentations of prostrate dead conspecifics, presentations of a jay skin mounted in an upright, life-like pose elicited aggressive responses, suggesting the mounted scrub-jay was perceived to be alive and the prostrate jay was not. There was a decrease of foraging in the area during presentations of prostrate dead conspecifics and predator mounts, which was still detectable 24 h later. Foraging returned to baseline levels 48 h after presentations. Novel objects and mounted jays did not affect foraging. Our results show that without witnessing the struggle and manner of death, the sight of a dead conspecific is used as public information and that this information is actively shared with conspecifics and used to reduce exposure to risk.

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All organisms must contend with the risk of injury or death; many animals reduce this danger by assessing environmental cues to avoid areas of elevated risk (Lima & Dill 1990) and by producing alarm signals, which can, among other functions, alert and recruit support from conspecifics (Caro 2005). Risk avoidance and alarm signalling have been documented in response to the presence of a predator (Seyfarth et al. 1980), predator state (Gotceitas et al. 1995; Bell et al. 2006; Berger-Tal & Kotler 2010), evidence of the recent presence of a predator (e.g. urine, faeces) (Apfelbach et al. 2005) and to predators holding prey (Barash 1976; Kruuk 1976). Many aquatic organisms and some insects respond to chemical cues from injured, dead or digested conspecifics by fleeing or attacking (Chivers & Smith 1998; Wisenden 2003; Verhaghen et al. 2010; Wagner et al. 2011), and rats avoid an area bearing the scent of a poisoned conspecific (Carr et al. 1981; but see Galef & Stein 1985). Honeybees, *Apis mellifera*, and bumblebees (*Bombus*

Latreille, 1802), behaviourally adjust their exposure to risk as they make foraging decisions based on cues from dead conspecifics encountered in flowers (Dukas 2001; Abbott 2006), and honeybees subsequently decrease their recruitment dances (Abbott & Dukas 2009). These examples suggest that dead or dying conspecifics can be a relevant source of information regarding potential risk in an area.

Such responses are not restricted to the olfactory modality, as a handful of terrestrial species have been described to respond to visual detection of a dead conspecific. Konrad Lorenz was among the first to describe corvids potentially responding to the sight of a dead conspecific. He relates an anecdote wherein he is mobbed by his 'tame' jackdaws, *Corvus monedula*, as he carried a pair of black swim trunks. He concluded the trunks must have resembled a dead jackdaw and he was therefore perceived as a threat by the jackdaws (Lorenz 1997). European magpies, *Pica pica*, have been anecdotally described as having 'ceremonial gatherings' in response to a magpie seen dying apparently in mid-flight (Miller & Brigham 1988). American crows, *Corvus brachyrhynchos*, and ravens, *Corvus corax*, are thus far the only species reported to alarm-call in response to discovering the carcass of a conspecific, potentially

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communicating risk to conspecifics (Heinrich 1999; Marzluff & Angell 2007); however, there have not yet been controlled experiments to determine the impact of this alarm response on subsequent behaviour, nor which stimuli are effective at eliciting such a response in these species. Although there are few reports, responding to dead or dying conspecifics is not particular to corvids. Both wild and captive chimpanzees, *Pan troglodytes*, have been observed to respond when conspecifics die as a result of illness, injury or predation, with reports of alarm calling and social interaction occurring only after the chimpanzees witness an accident or predation event (Anderson et al. 2010). Elephant, *Loxodonta africana*, family groups inspect and handle the bones of dead conspecifics preferentially over the bones of a similarly-sized heterospecific (McComb et al. 2006). While the functions of such behaviours are unknown, there is evidence that taxonomically diverse animals react to situations that include dead conspecifics.

We observed that the western scrub-jay, *Aphelocoma californica*, a nonmigratory corvid that lives in territorial pairs, reacts to encounters with a dead conspecific by hopping from perch to perch and calling loudly; we term this response a 'cacophonous reaction'. The predominant vocalizations used during cacophonous reactions are most similar to the long-range calls termed 'zeeps', 'zeep-scolds' and 'scolds' (Webber 1984). The first individual to discover the dead bird will call, and this usually attracts other individuals, which either join in calling or observe silently from nearby perches (see [Supplementary Video S1](#)). When individuals successfully attract other jays with their calls, we term the response a 'cacophonous aggregation' (CA). To test the hypothesis that western scrub-jays use dead conspecifics as cues of risk and communicate that risk to others, we conducted three experiments in which we presented stimuli near feeders that jays were trained to visit at a specific time, and a fourth experiment where we only played back alarm calls. In experiment 1, we presented jays with novel objects or prostrate dried skins of dead conspecifics to address whether CAs are a response to dead conspecifics specifically, or a more general response to novel objects. In experiment 2, we presented jays with prostrate dried skins of a dead conspecific or a predator mount to compare CAs evoked by dead conspecifics to those evoked by predatory threat. In both experiments, we quantified foraging behaviour during and after experimental presentations to assess whether jays showed risk-reducing behaviours. In experiment 3, we presented prostrate dried skins of a dead conspecific or dried skins of a dead conspecific mounted in a life-like posture to compare how jays would respond to a dead jay and a potential territorial intruder. In experiment 4, we played back scrub-jay vocalizations from CAs evoked during presentations of dead conspecifics and owls, or we played back a recording of ducks quacking as a control, to determine whether conspecific vocalizations alone are effective at attracting other jays. We predicted that, if western scrub-jays use dead conspecifics as cues of risk and communicate this risk to others, risk-reducing behaviours (decrease in foraging in the area) would occur in response to predator (great horned owl, *Bubo virginianus*) mounts and dead conspecifics, but not to novel objects. Furthermore, we predicted that upright, life-like dead conspecifics, but not prostrate dead-like conspecifics, would elicit aggression, and that playbacks of vocalizations from CAs would attract conspecifics, whereas the heterospecific vocalization playback would not.

METHODS

Sites, Feeders and Presentations: General Information

We conducted experiments in residential back yards, at least 400 m apart to ensure we did not test the same individual birds at

multiple feeders (Carmen 2004). All sites were located in Davis, California, U.S.A. and were selected in response to volunteers solicited through the University of California, Davis community. Feeders used in experiments were constructed out of 1 m tall wrought-iron plant holders with a clear plastic plant saucer and were placed within 2–3 m of a tree or fence to provide perch sites. Assistants placed 10 peanuts (in shells) in the feeders every morning and watched for 30 min at a minimum distance of 5 m. We presented the first stimulus (described below) after approximately 2 weeks, when jays were predictably visiting the feeders at the time of refill. We placed peanuts in the feeder upon arrival and allowed jays to take them as video and audio equipment was set up; more than the usual number of peanuts were placed in the feeder at this time (~25 peanuts) since previous experience had shown that if jays emptied the feeder before we were ready to present stimuli, the jays would not revisit the feeder until the next morning. Observations indicated that the rapid rate of depletion was due to jays rapidly caching rather than eating the peanuts, but we occasionally observed jays eating peanuts. Since one peanut can satisfy a jay's energetic need for at least 1 h (Fleischer 2000) and there was enough time before all presentations for jays to ingest at least one peanut, levels of satiation are not likely to have differed between presentations. Once recording equipment was in place, and after jays had taken at least two peanuts, we placed the stimulus on the ground approximately 1 m from the feeder while the jay was away caching peanuts. Stimuli were covered, then taken to the feeder and left exposed on the ground. In only one of 73 trials did a jay return from caching peanuts before the experimenter returned to the observation location; thus, human disturbance is unlikely to have influenced jay behaviour. Stimuli were covered and removed once CAs ended and jays were no longer in sight of the experimenter.

We recorded the number of peanuts taken during stimulus presentations in experiments 1 and 2. After all stimulus presentations, we left 10 peanuts in the feeders and checked the feeders 24 h and 48 h later. We topped the number of peanuts up to 10 after each check if any were missing. We compared the proportion of peanuts taken 24 h before presentations and 24 h and 48 h after presentations. We assumed jays were responsible for any missing peanuts; no other species were observed to take peanuts during our behavioural observations. Once jays discovered the feeder and learned to anticipate refills (2-week acclimation period), they would be present at refill time and chase away any squirrels that approached the feeder. Squirrel foraging could also be detected by the presence of shells near the feeder, but no such evidence was present during the experimental period.

Experiment 1

Experiment 1 took place 14 June–15 August 2007. Fourteen sites were presented with a novel object ([Fig. 1a](#)) followed 4–10 days later by a dead jay skin ([Fig. 1b](#)). We did not randomize the order of presentations since permanent feeder abandonment in response to the dead jay treatment would make the novel object treatment impossible (see [Supplementary Material](#) for details). Order effects on the qualitative outcome of results were unlikely, however, since novel object stimuli were largely ignored by jays (see [Results](#)); furthermore, CAs occurred in response to dead jay treatments even when not preceded by novel object treatments (see [Results](#), experiment 2). The novel object was a piece of wood (23 × 10 × 2.5 cm) painted blue, pink or yellow surrounded by similarly painted tongue depressors arrayed to resemble scattered feathers (see [Supplementary Fig. S1](#)). We chose to approximate the size, shape and colour (blue) of a dead conspecific with the novel object to determine whether jays were specifically reacting to

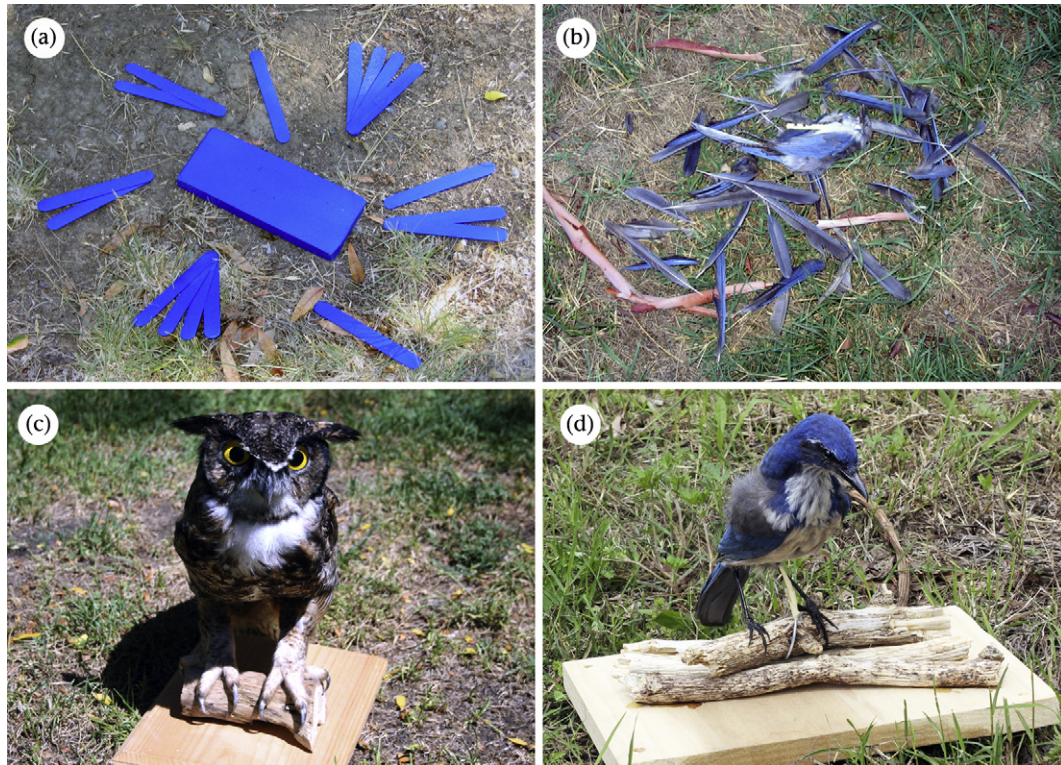


Figure 1. Stimuli used in experiments 1, 2 and 3. (a) Wooden novel object painted blue (yellow and pink objects were also presented) surrounded by tongue depressors glued together to resemble scattered feathers. (b) Dried skin of dead jay surrounded by feathers. (c) Mounted great horned owl. (d) Mounted western scrub-jay. The novel object and dead jay stimuli each provided a visual stimulus roughly 60 cm in diameter.

a dead conspecific or were simply highly reactive to objects with these general characteristics. We also incorporated different colours to determine whether the response, if any, was specific to the colour blue. Colour was semi-randomly assigned by matching an alphabetized list of sites (by site volunteer's name) to an unstructured list of our three colours (each colour appeared at least four times, but blue, being potentially salient to jays, was included a fifth time, and a coin was flipped to choose between pink or yellow to bring the total to 14). For dead jay stimuli, we used four scrub-jay carcasses prepared as skins surrounded by feathers. The novel object and the dead jay stimuli each provided a visual stimulus roughly 60 cm in diameter. Jay carcasses for all experiments were permit-salvaged (federal permit number MB 117665-1, state permit number SC-8508) and tested negative for West Nile virus before use. All procedures were approved by the University of California, Davis Institutional Animal Care and Use Committee (IACUC) under protocol number 15379.

Experiment 2

In experiment 2, we presented dead jays (Fig. 1b) and great horned owl mounts (Fig. 1c) in mixed orders (see below), and presentations were separated in time by 13–35 days. This experiment took place 23 March–10 June 2008. We presented 18 sites with one of four dead jay skins (the same skins used in experiment 1) and one of two owl mounts. Owls were posed in a perched position and prepared by the Museum of Wildlife and Fish Biology at the University of California, Davis. We reused six sites from experiment 1 in experiment 2. We performed three presentations at each site in one of four orders (1: dead jay–owl–dead jay; 2: owl–dead jay–owl; 3: dead jay–owl–owl; 4: owl–dead jay–dead jay). Our goal was to compare the number of calls, duration of calling and the effect of vocal aggregations elicited by predators and by dead conspecifics on foraging. Therefore,

we did not include a novel object experiment and we omitted from all analyses trials where neither calls nor aggregations occurred; in these instances, jays either did not see the stimulus (four dead jay presentations) or quietly inspected the stimulus from a nearby tree without taking a peanut from the feeder (one dead jay, one owl presentation). In experiment 2, we also measured the latency to approach the feeder 24 h and 48 h after dead jay and owl presentations and compared this to the mean latency of the 3 days prior to presentations.

Experiment 3

This experiment took place 21 July–4 October 2009. We presented nine sites with the prostrate dead jay (Fig. 1b), followed 16–64 days later by the mounted, life-like jay (Fig. 1d). We did not randomize the order of presentations; instead, we allowed a comparable amount of time between presentations in experiment 3 as was allowed in experiment 2 (in experiment 2, order did not affect variables of interest in experiment 3 in a manner that would affect interpretation of results from experiment 3). We presented the skins in established territories during the breeding season, when territory-holding jays aggressively defend territories. In experiment 3, we recorded whether calls were elicited, whether CAs occurred, whether peanuts were taken during presentations and whether aggressive behaviours (swoops or contact with claws or beak) were directed at either stimulus. T.L.I. prepared the skin for the mounted jay in the same manner as skins presented as prostrate carcasses, except that black porcelain beads were inserted into the eye sockets of the mounted jay.

Experiment 4

Experiment 4 took place 4–9 September 2009. Using a Crate TX15 amplifier, we played back 1 min audio recordings at 12 sites at

approximately 90 dB measured at 4 m distance with a Larson-Davis 824 sound pressure level meter. Audio files consisted only of calls produced by the first jay to vocalize in response to dead jays or owls in CAs during experiment 2; all recordings were collected at different sites than the playback location (separated by at least 400 m), so calls were not from familiar birds. We used four different audio recordings of dead-jay-induced CAs consisting of about 50 calls each and two recordings of owl-induced CAs consisting of about 90 calls each. The control playback was composed of calls we recorded from approximately six captive Peking ducks, *Anas platyrhynchos domestica*, held at the Hopkins Avian Facility at the University of California Davis. The 1 min recording consisted of approximately 175 calls, and only one recording was used for all control playbacks. Each category of calls (CA in response to dead jay, owl or ducks) was played at four sites with only one playback per site. We observed how many jays were attracted by the playback and whether they vocalized.

Equipment and Data Collection

All experimental trials were videorecorded (JVC Everio and Sony HC-1) and audiorecorded (Marantz PMD670) from the time of presentation until no jays were in sight or heard calling. T.L.I. and assistants scored audio and video, and data were used to supplement field observations. We scored the number of peanuts taken during all presentations and the occurrence of swoops (flight within 3.5 m across the top of the stimulus with a discernible dip in flight) from video. We used audio to determine CA duration, which included the time from the first call to the last call before all jays are silent. We counted calls from audio recordings, and Raven Pro 1.3 (<http://www.birds.cornell.edu/raven>) was used to visually categorize the calls to type using descriptions in Webber (1984). We used field observations to determine the maximum number of jays present, the number of peanuts taken daily and, in experiment 2 only, the latency to take peanuts after presentations. Birds were not individually marked. Instead, we used the maximum number of birds visually detected simultaneously in the yard. Following each experiment, we measured the distance between the stimulus and the perches used when calling using a measuring tape or a Bushnell Yardage Pro laser rangefinder.

Statistical Analysis

We used model comparison based on Akaike's Information Criterion for small sample sizes (AICc) and set site as a random intercept to understand the effect of stimuli on cacophonous reactions, CAs and foraging behaviour. Model selection is an alternative to null hypothesis testing that allows simultaneous evaluation of several competing hypotheses based on the observed data, where models within the set being compared are assigned a relative weight that allows competing hypotheses to be evaluated quantitatively (Johnson & Omland 2004; Anderson 2008). All data were analysed with R statistical software (version 2.10.1) (<http://www.R-project.org>) using either linear mixed-effect regression (lmer) or generalized linear modelling (GLM) with the lme4 package, or mixed-effect Cox models (for survival analysis) with the coxme package for latency data. Models contained site as a random intercept except where novel object colour was a predictor and in models sets for experiments 3 and 4.

RESULTS

Vocalization and Aggregation

In experiment 1, cacophonous reactions occurred at all presentations of the dead jay, and 12 of 14 presentations escalated into

CAs, whereas presentations of novel objects never resulted in CAs or cacophonous reactions. Stimulus identity (dead jay versus novel object) was a strong predictor of the total number of calls produced (Fig. 2a, Table 1, set 1) and the maximum number of jays present (Table 1, set 2), but the colour of the novel object had no effect on behaviour (Table 1, sets 3, 4). Results from this experiment show that CAs are not a response to the appearance of an unfamiliar object, but are elicited by the appearance of a dead conspecific.

In experiment 2, 41 of 48 presentations resulted in cacophonous reactions; of these, 86% of dead jay presentations escalated to CAs and 85% of owl presentations escalated to CAs. Subsequent presentations were more likely to elicit a CA (Table 2, set 1) regardless of stimulus identity. Since the total number of calls performed in response to a dead jay was greater in experiment 1 (June–August) than in experiment 2 (March–June) (Fig. 2a, b), we used date as a predictor in a post hoc model for experiment 2. This model is included in Table 2 (set 2) and shows that date was a good predictor of call number. These results suggest there is a seasonal component to the strength of the response to perceived risk, with more calls elicited during fledging than during the nesting season. The sequence of presentations (1: dead jay–owl–dead jay; 2: owl–dead jay–owl; 3: dead jay–owl–owl; 4: owl–dead jay–dead jay) did not affect behaviour, as this explanatory variable did not improve models. However, further exploration revealed that sites encountering an owl first, instead of a dead jay, resulted in more jays being attracted by cacophonous reactions at that site regardless of whether the subsequent eliciting stimulus was an owl or dead jay (Table 2, set 3). Finally, we observed that the three types of vocalizations, 'zeep', 'scold' and 'zeep-scold', performed in response to dead jays were also performed in response to owls.

In addition to the similarities, we found some differences between jay behaviours towards the owl and the dead jay. CAs lasted longer during the owl presentations than during the dead jay presentations (Table 3, Table 2, set 4), and jays called from perches that were closer to the owl than to the dead jay (Table 3, Table 2, set 5). In addition, jays swooped (Supplementary Video S2), a behaviour associated with mobbing (Cully & Ligon 1976), at owl mounts in 77% of presentations, but never did so with a dead jay (Table 2, set 6). Thus, dead jay and owl stimuli evoked similar risk-reduction responses, as determined by decreases in foraging, but the owl stimuli evoked mobbing and approach behaviours, whereas the prostrate dead jay stimuli did not.

In experiment 3, the mounted jay and prostrate jays both elicited vocalizations (Table 4, set 1). However, prostrate jays elicited CAs at all presentations, and the mounted jay elicited CAs at 33% of presentations (Table 4, set 2). Jays in two of the three aggregations swooped at the mounted jay, but never swooped in response to a prostrate jay (Table 4, set 3).

In experiment 4, playback of scrub-jay calls elicited by the owl model attracted jays at all four sites (range 3–7 jays attracted), as did playback of calls elicited by the dead jay (range 2–8 jays attracted); playback of ducks quacking did not attract jays to any of the four sites (Fig. 3). In all cases where jays were attracted, jays also vocalized. The number of jays attracted was not predicted by whether the vocalizations were from CAs evoked by a dead jay or an owl (Table 5). The number of jays attracted was also not predicted by the identity of the audio recording played back (Table 5).

Feeding Behaviours

In experiment 1, the number of peanuts taken was about 90% less during presentation of the dead jay than during presentation of novel objects (Fig. 2c). Jays appeared unconcerned by the novel object stimulus when feeding, and indeed, one jay cached peanuts under it (Supplementary Video S3). In experiment 2, jays took one

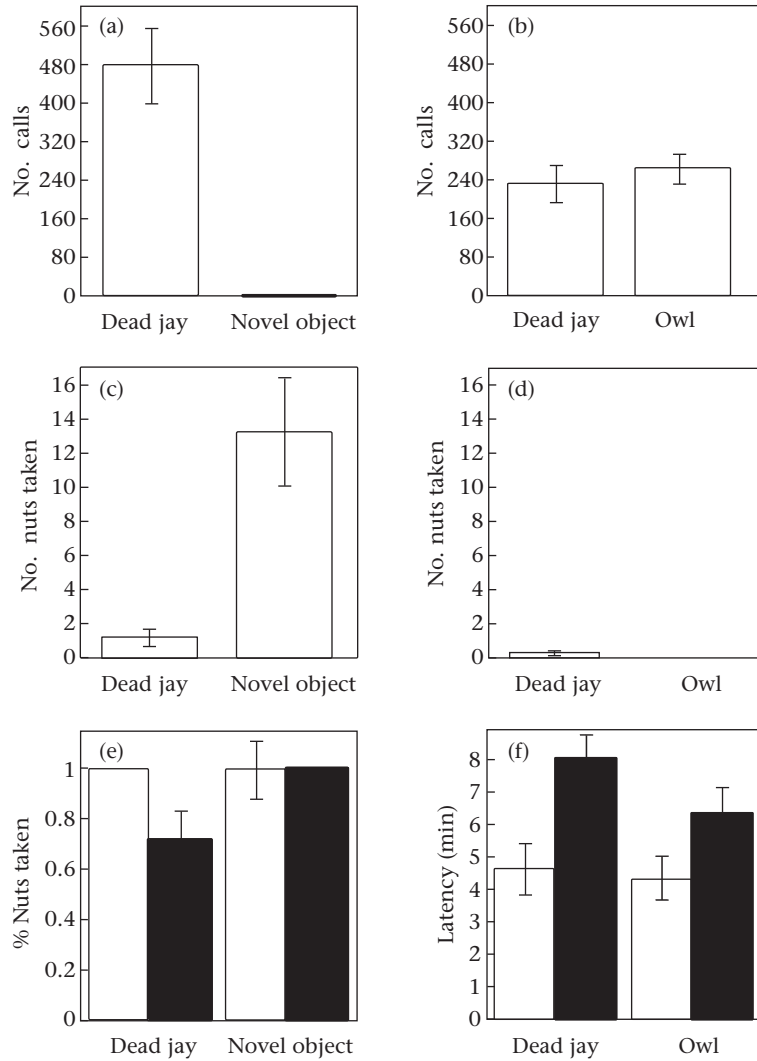


Figure 2. (a, b) Number of calls by scrub-jays in response to stimuli. (c, d) Number of peanuts taken by scrub-jays during stimulus presentation. (e) Proportion of peanuts taken by scrub-jays before (□) and after (■) stimulus presentation. (f) Scrub-jays' latency to approach the feeder before (□) and after (■) stimulus presentation. Error bars show ±1 SE.

Table 1
Results of AICc model selection for experiment 1: dead jay versus novel object showing all models used in each set of comparisons

| Set | Link function | Response variable | Predictor variable | df | ΔAICc | w _i | Coefficient estimate (95% CI) |
|-----|---------------|-------------------|------------------------------------|----|-------|----------------|---|
| 1 | Log | Total calls | Stimulus (dead jay) | 3 | 0 | 1 | 6.16 (5.41, 7.51) |
| | | Total calls | Intercept only | 2 | 8329 | <0.001 | |
| 2 | Identity | Max. jays | Stimulus (dead jay) | 3 | 0 | 0.8 | 1.55 (0.67, 2.35) |
| | | Max. jays | Intercept only | 2 | 2.7 | 0.2 | |
| 3 | Log | Total calls | Intercept only | 1 | 0 | 0.95 | |
| | | Total calls | Novel object colour | 3 | 5.9 | 0.05 | |
| 4 | Log | Max. jays | Intercept only | 1 | 0 | 0.96 | |
| | | Max. jays | Novel object colour | 3 | 6.3 | 0.04 | |
| 5 | Logit | Nuts 24 h | Stimulus (dead jay) + time (after) | 4 | 0 | 1 | -58.21 (-209.19, -11.89) + -30.57 (-111.06, -12.59) |
| | | Nuts 24 h | Intercept only | 2 | 158 | <0.001 | |
| 6 | Logit | Nuts 48 h | Intercept only | 2 | 0 | 0.82 | |
| | | Nuts 48 h | Stimulus (dead jay) + time (after) | 4 | 2.8 | 0.18 | |

AICc: Akaike's Information Criterion corrected for small sample size; ΔAICc: difference in AICc scores between the best model (listed first in each set) and each competing model; w_i: AICc weight (level of support for a model; max. = 1); Total calls: total number of calls elicited during stimulus playback; Max. jays: maximum number of jays present during stimulus playback; Nuts 24 h, 48 h: number of peanuts taken 24 h and 48 h after stimulus presentation; Intercept only: null models; parenthetical descriptors (e.g. '(dead jay)', '(after)') indicate the direction of impact from the perspective of that categorical subset. Coefficient estimates indicate a positive (increase in response variable) or negative (decrease in response variable) effect of predictor variables and are included only when experimental variables were included in the best-supported model. Raw estimates are shown and were calculated using link functions as indicated. For example, for set 1, number of calls in response to stimuli were based on a log link function; therefore, the coefficient estimate is the log of the number of calls and the model predicts that the dead jay stimulus will elicit 473 more calls than the novel object ($e^{6.16} = 473$). A model's ability to predict actual numerical outcomes, however, largely depends on whether it includes the most relevant predictor variables. We do not purport to have captured all relevant explanatory variables and, therefore, the coefficient estimates must be interpreted in that light. Bootstrapping was performed in R to generate all 95% confidence intervals. Code is available from T.L.I. upon request.

Table 2

Results of AICc model selection for experiment 2: dead jay versus great horned owl, showing only models comprising approximately the top 90% of AICc weights

| Set | Link function | Response variables | Predictor variables | df | Δ AICc | w_i | Coefficient estimate (95% CI) |
|-----|---------------|--------------------|------------------------------------|-----|---------------|--------|--|
| 1 | Logit | CA occur | Iteration | 3 | 0 | 0.9 | 1.72 (1.08, 25.06) |
| 2 | Log | CA occur | Intercept only | 2 | 5.6 | 0.05 | |
| | | Total calls | Date | 3 | 0 | 1 | 0.008 (0.005, 0.023) |
| 3 | Identity | Total calls | Iteration | 3 | 33.1 | <0.001 | |
| | | Max. jays | First stimulus (owl) | 3 | 0 | 0.48 | 1.54 (0.42, 2.73) |
| 4 | Identity | Max. jays | Intercept only | 2 | 1.1 | 0.28 | |
| | | Max. jays | Stimulus (dead jay) | 3 | 2.6 | 0.13 | |
| | | CA duration | Stimulus (dead jay) | 4 | 0 | 0.87 | -3.63 (-6.07, -1.48) |
| 5 | Identity | CA duration | Iteration | 4 | 4.5 | 0.09 | |
| | | Perch distance | Stimulus (dead jay) | 4 | 0 | 0.8 | 0.37 (0.02, 0.67) |
| 6 | Logit | Perch distance | Intercept only | 3 | 3.9 | 0.11 | |
| | | Swoops | Stimulus (dead jay) | 3 | 0 | 1 | -20.77 (-50.40, -20) |
| 7 | Logit | Swoops | Intercept only | 2 | 34.8 | <0.001 | |
| | | Nuts 24 h | Time (after) | 3 | 0 | 0.98 | -1.08 (-4.42, 1.96) |
| 8 | Logit | Nuts 24 h | Intercept only | 2 | 8.3 | 0.02 | |
| | | Nuts 48 h | Stimulus (dead jay) + time (after) | 4 | 0 | 0.99 | -0.75 (-4.75, 1.46) + -0.56 (-2.54, 1.34) |
| 9 | Log | Nuts 48 h | Intercept only | 2 | 9.9 | 0.01 | |
| | | Latency 24 h | Stimulus (dead jay) + time (after) | 7.9 | 0 | 0.98 | -0.07 (-0.85, 0.72) + -1.32 (-2.22, -0.42) |
| 10 | Log | Latency 24 h | Intercept only | 7.1 | 7.8 | 0.02 | |
| | | Latency 48 h | Intercept only | 2.3 | 0 | 0.87 | |
| | | Latency 48 h | Stimulus (dead jay) + time (after) | 4.2 | 3.7 | 0.13 | |

CA: cacophonous aggregation; Perch distance: distance between stimulus and perches used when calling; Latency: latency to approach feeder; Swoop: flight within 3.5 m across the top of the stimulus with a discernible dip in flight. All other abbreviations as in Table 1. Four models, where predictor variables were stimulus (dead jay or owl), iteration (first, second or third presentation of stimuli), first stimulus (dead jay or owl) and intercept only (null model), were compared in sets 1–5, except where date was also used as a predictor in a post hoc model added to set 2. Estimates indicate a positive (increase in response variable) or negative (decrease in response variable) effect of predictor variables except for latency 24 h and 48 h, where a negative estimate indicates a decrease in likelihood of approaching the feeder. Raw estimates are shown and were calculated using link functions as indicated.

to two peanuts during the dead jay presentations and took no peanuts during owl presentations (Fig. 2d). In experiment 3, jays took peanuts during 12% of presentations of the prostrate dead jay (one site) and during 67% of presentations of the mounted jay (six sites; Table 4, set 4).

In experiment 1, 24 h after novel object presentations, the proportion of peanuts taken was no different from the proportion taken the day before, whereas there was a 29% decline 24 h after encounters with the dead jay (Fig. 2e, Table 1, set 5); there was no effect 48 h after trials with the dead jay (Table 1, set 6). In experiment 2, there was a decline in the number of peanuts taken 24 and 48 h after presentation of both the dead jay and the owl. However, this decline may not be biologically meaningful, as the model coefficients were small and the 95% confidence interval included zero (Table 2, sets 7, 8, Supplementary Fig. S2). In experiment 2, mean latency to approach the feeders was greater 24 h after presentations of the dead jay and the owl than it was for 3 consecutive days prior to presentations (Fig. 2f, Table 2, set 9). There was an increase in latency after 24 h with both stimuli, and although stimulus was included in the best model, indicating that latency after seeing a dead jay was greater than latency after seeing the owl, this difference may not be biologically meaningful as the model coefficient was small and the 95% confidence interval included zero (Table 2, set 9). The effect on latency was no longer detectable after 48 h (Table 2, set 10).

DISCUSSION

Here we show that a dead conspecific in the absence of a predator is sufficient to induce both alarm calling and subsequent risk-reducing behavioural modification in western scrub-jays. Western scrub-jays responded to dead conspecifics with loud calls near the carcass, and playbacks of these calls were effective at attracting conspecifics and inducing them to call. Similarly, ravens, crows and magpies have been described to gather around a dead conspecific (Miller & Brigham 1988; Heinrich 1999; Marzluff & Angell 2007), and ravens and crows have been described as calling and attracting others (Heinrich 1999; Marzluff & Angell 2007), suggesting this may be a shared trait within corvids. In this study, we demonstrate through a series of experiments that western scrub-jays respond similarly to the presence of a dead conspecific and a predator (a great horned owl model), suggesting that these responses are related to antipredator behaviour. The jays showed no response to novel coloured objects of similar size to a jay, suggesting that their response to the other stimuli used in the present study was not a neophobic response to an unexpected object in their territory, or a response to an object with characteristics that superficially resembled a dead conspecific in colour, size and shape. In addition, birds that encountered a dead conspecific altered their foraging behaviour by temporarily avoiding rich food resources, similar to avoidance after exposure to predator models. Our results show that,

Table 3Duration of cacophonous aggregations, CAs (excluding cacophonous reactions), number of jays aggregated (CAs ≥ 2 jays aggregated) and distance between eliciting stimuli and perches used by jays while calling in response to stimuli for experiments 1 and 2

| Experiment | Stimulus | Duration of CA (min) | | No. jays aggregated* | | Perch distance (m) | |
|------------|--------------|----------------------|------------|----------------------|--------|--------------------|-----------|
| | | Mean \pm SE | Range | Mean \pm SE | Range | Mean \pm SE | Range |
| 1 | Dead jay | 9.4 \pm 2.16 | 2.55–25.5 | 4.17 \pm 0.27 | 2–5 | 5.95 \pm 0.56 | 2.93–9.24 |
| | Novel object | No CAs | No CAs | No CAs | No CAs | No CAs | No CAs |
| 2 | Dead jay | 5.25 \pm 0.78 | 0.33–13.32 | 4.63 \pm 0.67 | 2–10 | 1.93 \pm 0.15 | 1.05–3.17 |
| | Owl | 8.71 \pm 1.10 | 0.85–20.9 | 3.91 \pm 0.43 | 2–9 | 1.51 \pm 0.09 | 0.57–2.44 |

* Note: this variable differs from the maximum number of jays observed simultaneously ('Max. jays') used in statistical analyses, which included cacophonous reactions (i.e. ≥ 1 jay).

Table 4

Results of AICc model selection for behavioural responses of scrub-jays during presentation of stimuli in experiment 3: mounted jay versus prostrate dead jay

| Set | Response variable | Predictor variable | df | Δ AICc | w_i | Coefficient estimate (95% CI) |
|-----|-------------------|--------------------|----|---------------|-------|-------------------------------|
| 1 | Call | Intercept only | 1 | 0 | 0.65 | |
| | | Stimulus (mount) | 2 | 1.3 | 0.35 | |
| 2 | CA | Stimulus (mount) | 2 | 0 | 0.98 | -20.26 (-51.13, -18.72) |
| | | Intercept only | 1 | 8 | 0.02 | |
| 3 | Swoop | Stimulus (mount) | 2 | 0 | 0.52 | 18.31 (0.00, 20.47) |
| | | Intercept only | 1 | 0.2 | 0.48 | |
| 4 | Take nut | Stimulus (mount) | 2 | 0 | 0.81 | 2.64 (0.47, 22.51) |
| | | Intercept only | 1 | 3.3 | 0.19 | |

Response variables included the occurrence of calls, CAs and peanuts taken during presentations and aggressive behaviours (swoops or contact with claws or beak) directed at either stimulus. All models in each set are shown. Coefficient estimates \pm 95% CI are shown for the best model when it contained an experimental predictor variable (e.g. stimulus). Raw coefficient estimates are shown and were calculated using the binomial link function (logit). See Table 1 for further details and explanation of abbreviations.

without witnessing the struggle and manner of death, a dead conspecific was used as public information about risk, and that this information was actively shared with conspecifics and used to reduce exposure to risk.

CAs elicited with dead jays and owls were similar in that cacophonous reactions escalated to CAs in equal frequencies, and both stimuli elicited similar numbers of vocalizations and attracted a similar number of jays. The similarity extended to include the occurrence of the vocalization types 'zeep', 'scold' and 'zeep-scold' (Webber 1984) in CAs; thus, jays did not appear to use specific call types to denote stimulus type, although further research is needed to determine whether characteristics within each call type vary with the eliciting stimulus. In addition, playback of recorded scrub-jay vocalizations elicited by presentations of owls and jays attracted similar numbers of jays and evoked CA vocalizations. These similarities, taken together with the comparable decrease in foraging, suggest that dead conspecifics and predators may both be used as indicators of risk in the area.

However, there were also some notable differences between CAs elicited by owls and dead jays. Jays perched closer to owls while calling, CAs lasted longer with owls, and jays never swooped at a dead jay but did so in 77% of owl presentations. The observation that jays called from more distant perches when encountering a dead jay than when encountering an owl may indicate greater vigilance and an attempt to locate the predator by using higher

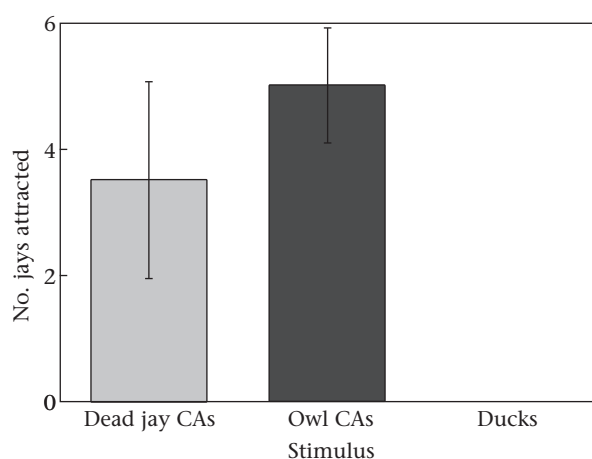


Figure 3. Number of scrub-jays attracted to playbacks of heterospecific (duck) or conspecific vocalizations elicited by presentation of a dead scrub-jay or owl.

Table 5

Results of AICc model selection results for behavioural responses in experiment 4: playback of cacophonous aggregation (CA) calls evoked by a dead jay or an owl

| Response variable | Predictor variable | df | Δ AICc | w_i |
|--------------------|--------------------|----|---------------|--------|
| No. jays attracted | Intercept only | 1 | 0 | 0.718 |
| | Elicitor | 2 | 1.9 | 0.282 |
| | Playback file | 6 | 16.8 | <0.001 |

Elicitor: dead jay or owl; Playback file: recordings of CAs from six sites.

perches with a wider vantage point. A nonmutually exclusive, alternative hypothesis is that the owl provided a target for aggressive behaviour (swoops), which requires closer proximity. CA duration with owls may have been longer because the predator mount was visible but not moving during the experiment (CA duration in natural encounters with owls or other predators is likely to be related to the predator's response). Finally, the lack of swooping during presentations of the dead jay may simply reflect the lack of a threatening target. The jays' responses to presentation of the dead jay and the owl suggest that both stimuli are used as evidence of possible threat, with the owl mount representing direct evidence and the dead jay representing indirect evidence.

CAs were always elicited by prostrate dead jays, but an upright, mounted dead jay elicited few aggregations. When aggregations did occur, aggressive behaviours (swoops) were directed at the mounted jay, but swoops were never directed at the prostrate jay. Since jays swoop when mobbing predators to drive them from the area, swooping at the mounted jays is probably a territorial response to chase away the target from the area (Cully & Ligon 1976). Alternatively, the mounted jay may have elicited aggression since it did not behave as expected; aggressive behaviour towards sick individuals has been observed in jackdaws and rooks, *Corvus frugilegus* (Wilmore 1977). Whether jays perceived the life-like mounted jay as an intruder and/or a sick individual, our results demonstrate that jays did not treat the prostrate dead jay as if it were a live intruder, but rather as an indicator of risk.

Although dead conspecifics and predator models were always effective at eliciting a vocal response in these experiments, the reacting individual was not always effective at attracting other conspecifics into an aggregation. In experiments 1 and 2, 15% of cacophonous reactions failed to attract conspecifics into a cacophonous aggregation. It is unlikely that other jays failed to hear the calls, since territory sizes are small enough that most vocalizations from the interior of a territory would be detectable by neighbours (Carmen 2004). Since we were not working with a banded population and therefore have no information about sex, age or status, we cannot determine whether this failure to recruit an aggregation relates to characteristics of the calling individual.

When we examined results from dead jay presentations in experiments 1 and 2, there was evidence of a seasonal change in the strength of response. The behavioural responses were qualitatively similar in both experiments: CAs were elicited in about 85% of presentations, birds decreased foraging during CAs, aggression between conspecifics was not observed during CAs, and there was an effect on foraging 24 h after presentations (i.e. fewer nuts were taken in experiment 1, and latency to take peanuts increased in experiment 2). However, there was a quantitative difference in the strength of response to dead jay presentations: the number of calls performed (and therefore, duration of aggregations) and the decrease in subsequent foraging was greater in experiment 1 than in experiment 2 (24 h after presentations). Experiment 1 was conducted between mid-June and mid-August when young have fledged but are still in the natal territory being fed occasionally by the parents. This seasonal difference in territory occupancy did not lead to a difference in the number of jays attracted to CAs, since the

mean number of aggregating birds did not differ substantially between the two experiments (Table 3). But the presence of fledglings on territories may have influenced the duration of CAs in other ways, for example, if the benefit to prolonged antipredator behaviour by parents is higher when their fledglings are nearby, or if CAs provide an opportunity for fledglings to learn about dangers and cues of risk, and if this learning is facilitated by a prolonged alarm response (Seyfarth & Cheney 1986; Hauser 1988; Griffin 2004; Hollén & Manser 2006; Hollén & Radford 2009). Carmen (2004) found that many vocal behaviours of scrub-jays decrease during March through early June (when experiment 2 was performed), when parents are busy with nesting, brooding and feeding nestlings, which may further contribute to seasonal differences. The need to provide food for nestlings might also have made parents less likely to forgo the rich food source during experiment 2. Further experiments in a banded population are needed to discriminate between these explanations for seasonal changes in the strength of response to dead conspecifics.

Benefits and Costs of Cacophonous Aggregations

Since all organisms must cope with the risk of injury or death, assessing and minimizing this risk without dangerous, direct experience can be advantageous (Berejikian et al. 1999; Chivers et al. 2002; Mirza & Chivers 2002; Shier & Owings 2007). Individual animals that can associate a dead conspecific with previously unfamiliar or unrecognized threats may benefit from reduced risk of injury or mortality, particularly in human-altered environments where changes can occur rapidly and frequently, potentially introducing novel threats. Western scrub-jays may benefit by attending to dead conspecifics to reduce their own threat of predation, but it is less clear why they should instigate a cacophonous aggregation that alerts others. Some potential benefits or functions of CAs may be to gather a mob to locate and drive the predator away (Curio 1978), to warn mates and offspring of danger, to help calling birds form a 'landscape of fear' (Laundre et al. 2001), to form location memories of risky areas (Griffin et al. 2010) or to enable mates or offspring to do so (Griffin 2004).

Most of the aggregations observed in this study involved more than just the territorial pair; since birds were not banded, we do not know the relationships among the participants in the CAs. Unlike Florida scrub-jays (Woolfenden & Fitzpatrick 1984), western scrub-jays do not live in large social groups; the mated pair defends a territory year round against neighbouring territory holders (Carmen 2004). Our experiments took place during the breeding season (from late March through mid-August), when pairs may have fledglings and are less likely to tolerate floaters and unrelated juveniles on their territory (Carmen 2004). In experiment 1, some of the extrapair birds observed at sites were probably the current season's offspring, because they were not chased and adults were occasionally observed to feed them. However, in experiments 1 and 2, when there were more than two jays (presumably the mated pair) visiting the feeder, we commonly observed aggression (chases) before and after CAs, but not during CAs (T. L. Iglesias, personal observation). This temporary reduction in aggression during CAs suggests that neighbouring or nearby floater jays were attracted to the alarm calls and tolerated by territorial birds. Mobbing is more effective at driving away predators when the mob of attacking birds is larger (Robinson 1985; Flasskamp 1994), so territory owners may benefit from tolerating unrelated individuals that join the mob. A larger group may also dilute the threat of attack on any one individual (Hamilton 1971).

What benefit might unrelated neighbours or floaters gain by joining a cacophonous aggregation? Responding to mobbing calls from a neighbouring territory may be beneficial if it reduces

predation risk on surrounding territories as well. In addition, gaining information about the identity of a dead conspecific could provide an opportunity to renegotiate territorial boundaries or take over a recently occupied territory, as described in magpies (Birkhead & Clarkson 1985). Floaters may also benefit from such information, if it provides an opportunity to gain a mate and a territory; Carmen (2004) found that 69% of observed male and female individuals in central California paired with an established breeder that retained its territory after losing its mate.

While there may be benefits to aggregating around a dead conspecific, this behaviour may also be costly in some cases. For example, if the cause of mortality is a contagious disease rather than predation, then CAs may increase the probability of infection from dead or infected living conspecifics (Dhondt et al. 2007). For example, West Nile virus can be transmitted via direct or indirect contact between living infected individuals as well as via the mosquito vector (Komar et al. 2003; Dawson et al. 2007), and higher population densities and communal roosting in corvids contributes to amplification of West Nile virus (Reisen et al. 2006). Western scrub-jays do not roost communally or nest at high density, but cacophonous aggregations could potentially contribute to the high transmission rates in scrub-jays as these aggregations bring together birds that are not normally in close proximity. Contact with the carcass was rarely observed (T. L. Iglesias, personal observation); therefore, contagion of any disease from the carcass may be less likely than transmission between aggregating individuals. Incorporating dead conspecifics as environmental cues and instigating aggregations can have benefits and costs, but regardless of the valence of the effect, this behaviour may have impacts at the individual and population level in western scrub-jays and in other species that perform similar behavioural reactions to dead conspecifics.

Response to cues of dead conspecifics has been described in many invertebrate and vertebrate species, and most of these are reported to modify behaviour to reduce exposure to risk (Chivers & Smith 1998; Wisenden 2003; Verheggen et al. 2010; Wagner et al. 2011). However, in many species, responses to dead conspecifics may serve other functions. For example, dead conspecifics may indicate an opportunity for marine crabs (Rittschof et al. 1992) and land hermit crabs (Small & Thacker 1994) to find a better shell. Some descriptions of responses are related to attachment and the maternal instinct, particularly in chimpanzees (Cronin et al. 2011). These accounts suggest that there are potentially multiple functions to responding to dead conspecifics, which are not necessarily mutually exclusive. Given the potentially critical environmental information that a dead conspecific presents, it is surprising that communicative social gatherings around dead conspecifics are either rare, or if present, rarely described.

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Supplementary Material

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References

- Abbott, K. R. 2006. Bumblebees avoid flowers containing evidence of past predation events. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **84**, 1240–1247.
- Abbott, K. R. & Dukas, R. 2009. Honeybees consider flower danger in their waggle dance. *Animal Behaviour*, **78**, 633–635.
- Anderson, D. R. 2008. *Model-based Inference in the Life Sciences: a Primer on Evidence*. 2nd edn. New York: Springer.
- Anderson, J. R., Gillies, A. & Lock, L. C. 2010. Pan thanatology. *Current Biology*, **20**, R349–R351.
- Apfelbach, R., Blanchard, C. D., Blanchard, R. J., Hayes, R. A. & McGregor, I. S. 2005. The effects of predator odors in mammalian prey species: a review of field and laboratory studies. *Neuroscience & Biobehavioral Reviews*, **29**, 1123–1144.
- Barash, D. P. 1976. Mobbing behavior by crows: the effects of the 'crow-in-distress' model. *Condor*, **78**, 120.
- Bell, R. D., Rypstra, A. L. & Persons, M. H. 2006. The effect of predator hunger on chemically mediated antipredator responses and survival in the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *Ethology*, **112**, 903–910.
- Berejikian, B. A., Smith, R. J. F., Tezak, E. P., Schroder, S. L. & Knudsen, C. M. 1999. Chemical alarm signals and complex hatchery rearing habitats affect anti-predator behavior and survival of chinook salmon (*Oncorhynchus tshawytscha*) juveniles. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 830–838.
- Berger-Tal, O. & Kotler, B. P. 2010. State of emergency: behavior of gerbils is affected by the hunger state of their predators. *Ecology*, **91**, 593–600.
- Birkhead, T. R. & Clarkson, K. 1985. Ceremonial gatherings of the magpie (*Pica pica*): territory probing and acquisition. *Behaviour*, **94**, 324–332.
- Carmen, W. J. 2004. Noncooperative breeding in the California scrub-jay. *Studies in Avian Biology*, **28**, 1–100.
- Caro, T. 2005. *Antipredator Defenses in Birds and Mammals*. Chicago: University of Chicago Press.
- Carr, W. J., Landauer, M. R. & Sonsino, R. 1981. Responses by rats to odors from living versus dead conspecifics. *Behavioral and Neural Biology*, **31**, 67–72.
- Chivers, D. P. & Smith, R. J. F. 1998. Chemical alarm signalling in aquatic predator–prey systems: a review and prospectus. *Ecoscience*, **5**, 338–352.
- Chivers, D. P., Mirza, R. S. & Johnston, J. G. 2002. Learned recognition of hetero-specific alarm cues enhances survival during encounters with predators. *Behaviour*, **139**, 929–938.
- Cronin, K. A., van Leeuwen, E. J. C., Mulenga, I. C. & Bodamer, M. D. 2011. Behavioral response of a chimpanzee mother toward her dead infant. *American Journal of Primatology*, **73**, 415–421.
- Cully, J. F. & Ligon, J. D. 1976. Comparative mobbing behavior of scrub and Mexican jays. *Auk*, **93**, 116–125.
- Curio, E. 1978. Adaptive significance of avian mobbing. 1. Teleonomic hypotheses and predictions. *Zeitschrift für Tierpsychologie*, **48**, 175–183.
- Dawson, J. R., Stone, W. B., Ebel, G. D., Young, D. S., Galinski, D. S., Pensabene, J. P., Franke, M. A., Eidson, M. & Kramer, L. D. 2007. Crow deaths caused by West Nile virus during winter. *Emerging Infectious Diseases*, **13**, 1912–1914.
- Dhondt, A. A., Dhondt, K. V., Hawley, D. M. & Jennelle, C. S. 2007. Experimental evidence for transmission of *Mycoplasma gallisepticum* in house finches by fomites. *Avian Pathology*, **36**, 205–208.
- Dukas, R. 2001. Effects of perceived danger on flower choice by bees. *Ecology Letters*, **4**, 327–333.
- Flasskamp, A. 1994. The adaptive significance of avian mobbing. V. An experimental test of the 'move on' hypothesis. *Ethology*, **96**, 322–333.
- Fleischer, A. L. 2000. The influence of time budget and rate of food handling and consumption on the time of breeding of female Florida scrub-jays (*Aphelocoma coerulescens*): a comparison between populations in natural and suburban habitats. M.Sc. thesis, University of South Florida.
- Galef, B. G. & Stein, M. 1985. Demonstrator influence on observer diet preference: analyses of critical social interactions and olfactory signals. *Animal Learning & Behavior*, **13**, 31–38.
- Gotceitas, V., Fraser, S. & Brown, J. A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. *Marine Biology*, **123**, 421–430.
- Griffin, A. S. 2004. Social learning about predators: a review and prospectus. *Learning & Behavior*, **32**, 131–140.
- Griffin, A. S., Boyce, H. M. & MacFarlane, G. R. 2010. Social learning about places: observers may need to detect both social alarm and its cause to learn. *Animal Behaviour*, **79**, 459–465.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Hauser, M. D. 1988. How infant vervet monkeys learn to recognize startling alarm calls: the role of experience. *Behaviour*, **105**, 187–201.
- Heinrich, B. 1999. *Mind of the Raven: Investigations and Adventures with Wolf–Birds*. New York: Cliff Street.
- Hollén, L. I. & Manser, M. B. 2006. Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: the roles of age, sex and nearby conspecifics. *Animal Behaviour*, **72**, 1345–1353.
- Hollén, L. I. & Radford, A. N. 2009. The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, **78**, 791–800.
- Johnson, J. B. & Omland, K. S. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution*, **19**, 101–108.
- Komar, N., Langevin, S., Hinten, S., Nemeth, N., Edwards, E., Hettler, D., Davis, B., Bowen, R. & Bunning, M. 2003. Experimental infection of North American birds with the New York 1999 strain of West Nile virus. *Emerging Infectious Diseases*, **9**, 311–322.
- Kruuk, H. 1976. The biological function of gulls' attraction towards predators. *Animal Behaviour*, **24**, 146–153.
- Laundre, J. W., Hernandez, L. & Altendorf, K. B. 2001. Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **79**, 1401–1409.
- Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology-Revue Canadienne de Zoologie*, **68**, 619–640.
- Lorenz, K. 1997. *The Natural Science of the Human Species: an Introduction to Comparative Behavioral Research*. Cambridge, Massachusetts: MIT Press.
- McComb, K., Baker, L. & Moss, C. 2006. African elephants show high levels of interest in the skulls and ivory of their own species. *Biology Letters*, **2**, 26–28.
- Marzluff, J. M. & Angell, T. 2007. *In the Company of Crows and Ravens*. New Haven, Connecticut: Yale University Press.
- Miller, W. R. & Brigham, R. M. 1988. 'Ceremonial' gathering of black-billed magpies (*Pica pica*) after the sudden death of a conspecific. *Murrelet*, **69**, 78–79.
- Mirza, R. S. & Chivers, D. P. 2002. Behavioural responses to conspecific disturbance chemicals enhance survival of juvenile brook charr, *Salvelinus fontinalis*, during encounters with predators. *Behaviour*, **139**, 1099–1109.
- Reisen, W. K., Barker, C. M., Carney, R., Lothrop, H. D., Wheeler, S. S., Wilson, J. L., Madon, M. B., Takahashi, R., Carroll, B., Garcia, S., et al. 2006. Role of corvids in epidemiology of West Nile virus in southern California. *Journal of Medical Entomology*, **43**, 356–367.
- Rittschof, D., Tsai, D. W., Massey, P. G., Blanco, L., Kueber, G. L. & Haas, R. J. 1992. Chemical mediation of behavior in hermit-crabs: alarm and aggregation cues. *Journal of Chemical Ecology*, **18**, 959–984.
- Robinson, S. K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. *Auk*, **102**, 506–519.
- Seyfarth, R. M. & Cheney, D. L. 1986. Vocal development in vervet monkeys. *Animal Behaviour*, **34**, 1640–1658.
- Seyfarth, R. M., Cheney, D. L. & Marler, P. 1980. Vervet monkey alarm calls: semantic communication in a free-ranging primate. *Animal Behaviour*, **28**, 1070–1094.
- Shier, D. M. & Owings, D. H. 2007. Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*. *Animal Behaviour*, **73**, 567–577.
- Small, M. P. & Thacker, R. W. 1994. Land hermit crabs use odors of dead conspecifics to locate shells. *Journal of Experimental Marine Biology and Ecology*, **182**, 169–182.
- Verheggen, F. J., Haubruge, E. & Mescher, M. C. 2010. Alarm pheromones: chemical signaling in response to danger. In: *Vitamins & Hormones: Pheromones*. Vol. 83 (Ed. by G. Litwack), pp. 215–239. Amsterdam: Elsevier.
- Wagner, C. M., Stroud, E. M. & Meckley, T. D. 2011. A deadly odor suggests a new sustainable tool for controlling a costly invasive species. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1157–1160.
- Webber, T. 1984. Form and function of the long-range calls of scrub jays, *Aphelocoma coerulescens obscura*. Ph.D. thesis, University of Florida.
- Wilmore, S. B. 1977. *Crows, Jays, Ravens and Their Relatives*. London: David & Charles.
- Wisenden, B. D. 2003. Chemically mediated strategies to counter predation. In: *Sensory Processing in Aquatic Environments* (Ed. by S. P. Collin & N. J. Marshall), pp. 236–251. New York: Springer-Verlag.
- Woolfenden, G. E. & Fitzpatrick, J. W. 1984. *The Florida Scrub Jay: Demography of a Cooperative-breeding Bird*. Monographs in Population Biology. Vol. 20. Princeton, New Jersey: Princeton University Press.