BRILL

*Behaviour 151 (2014) 1–22*

**Behaviour**
brill.com/beh

# Dead heterospecifics as cues of risk in the environment: Does size affect response?

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Accepted 1 August 2013; published online 2 October 2013

**Abstract**

Organisms can minimize their exposure to risk of death or injury by assessing their environment and modifying their behavior accordingly. There is evidence that the current or recent presence of a predator introduces cues to the environment that organisms may use in risk assessment. However, we know little about whether terrestrial organisms use the remains of victims of predation as one such cue of elevated predation risk. A previous study showed that western scrub-jays (*Aphelocoma californica*) respond both to dead conspecifics and to encounters with a predator with alarm calling and aggregation (cacophonous aggregations), suggesting that they use dead conspecifics as indirect evidence of predation risk. Here we examine whether western scrub-jays also use dead heterospecifics as an indicator of risk. We find that jays respond with cacophonous aggregations to dead sympatric and allopatric jay-size heterospecifics but react weakly if at all to smaller heterospecifics. This suggests that size may be an important factor in determining whether a dead heterospecific is a relevant cue of risk. To our knowledge this is the first controlled experiment showing an animal using the visual cue provided by a dead heterospecific as an indicator of risk and communicating this risk to other conspecifics.

**Keywords**

*Aphelocoma californica*, bird, cacophonous aggregation, cues of risk, dead conspecific, response to dead, risk assessment, western scrub-jay.

## 1. Introduction

Organisms depend on cues in the environment to assess and minimize the risk of death or injury (Lima & Dill, 1990). Many prey organisms increase

DOI:10.1163/1568539X-00003120

vigilance or minimize the time spent in habitats with certain features because these features indicate a riskier environment (Laundre et al., 2001; Shrader et al., 2008). This 'landscape of fear' can change when new information is encountered, with previously safe locations considered less safe if predator cues are encountered there (Hernandez & Laundre, 2005; Shrader et al., 2008). Some of these cues include the current presence of a predator (Warkentin, 2005; Cooper Jr., 2008; Barrera et al., 2011; Manzur & Navarrete, 2011) or a predator holding prey (Barash, 1976; Kruuk, 1976), or direct evidence left by the recent presence of a predator, such as urine or feces (Apfelbach et al., 2005). Once predators are detected, many animals use specific vocalizations that communicate the type of risk or level of danger, which elicits an appropriate response in receivers (Seyfarth et al., 1980; Evans et al., 1993; Zuberbühler, 2000; Templeton et al., 2005; Griesser, 2008, 2009). However, there is less known about how terrestrial organisms respond to cues of conspecific and heterospecific victims of predation in the absence of a predator.

In addition to direct cues of predator presence, information about potential risk can come from trace evidence of the prey left behind after a predation event. Some predators do not swallow their prey whole, leaving behind feathers, fur, bones or various body parts of their prey where they were attacked or consumed. Therefore, encountering evidence of an attack or remnants of a predator's meal may influence an organism's landscape of fear by increasing the perception of risk in that area (Iglesias et al., 2012). Indeed, many aquatic organisms, some insects, and some post-metamorphic salamanders and anurans attend not just to chemical cues released by predators as indicators of risk (Kats & Dill, 1998), but also by conspecific and heterospecific victims of predation (Chivers et al., 1997, 1999; Chivers & Smith, 1998; Wisenden, 2000; Abbott, 2006; Verheggen et al., 2010), suggesting that cues from victims of predation are relevant indicators of risk in an area. In addition, some terrestrial animals, such as chimpanzees (*Pan troglodytes*) (Anderson et al., 2010) and elephants (*Loxodonta africana*) (McComb et al., 2006) touch and handle dead conspecifics, while crows (*Corvus brachyrhynchos*) (Marzluff & Angell, 2007), ravens (*Corvus corax*) (Heinrich, 1999) and magpies (*Pica pica*) (Miller & Brigham, 1988) respond by vocalizing and aggregating near the body. However, it is unknown whether these terrestrial species glean any information from carcasses or carcass remnants about potential risk and modify their behavior to decrease exposure to such risk, or whether this behavior has a different social function. Further, it is not known whether any terrestrial species respond to carcasses or carcass remnants from heterospecific victims of predation.

We recently showed that western scrub-jays (*Aphelocoma californica*), a long-lived, nonmigratory bird that lives in territorial mated pairs, respond both to dead conspecifics and to predator encounters by alarm calling to incite aggregation; this suggests that jays use dead conspecifics as indirect evidence of predation risk (Iglesias et al., 2012). To examine this behavior, we presented three experimental treatments at feeders frequented by jays: a great-horned owl (*Bubo virginianus*) mounted in an upright position, a dead jay carcass with surrounding feathers to simulate a predator attack, and novel objects similar or different in color, and similar in size, to the dead jay (Iglesias et al., 2012). We found that scrub-jays that encounter a dead conspecific or an owl call loudly and attract other scrub-jays, whereas novel objects never elicited such a response. Most of the time (86%) these alarm calls attracted other jays to the area (4.23 ± 0.30 jays attracted), which joined in the calling (termed a cacophonous aggregation, or CA); responses where alarm calls fail to attract others are termed a cacophonous reaction. In predator trials, aggregating jays often swooped at the predator model. We also found that jays reduced their feeding activity in the area during and after presentations of dead jays and owls, but not novel objects. Taken together, these results suggest that western scrub-jays use both dead conspecifics and predators as indicators of risk in an area, and that they respond by communicating that risk to conspecifics, likely to instigate mobbing of the predator, and subsequently by avoiding the area (Iglesias et al., 2012).

Here we expand upon these results by testing the hypothesis that jays also use dead heterospecifics as indicators of risk and that they similarly communicate this risk to other jays by alarm calling. To do so, we present jays at feeders with either dead conspecifics or dead heterospecifics, and we examine the occurrence of cacophonous reactions and aggregations, variation in vocalizations toward different stimuli, and subsequent risk-reducing changes in foraging behavior (i.e., avoidance of the feeders).

Not all dead heterospecifics may be equally informative as indicators of predation risk, so we also examined whether jay response varied with the characteristics of the heterospecific presented. Dead heterospecific birds similar in size to jays may be more informative, because many predators hunt prey within a restricted size range (Andersson & Norberg, 1981; Gotmark & Post, 1996; Bonnaud et al., 2011). Common predators of jays such as Cooper's hawks (*Accipiter cooperii*), great horned owls (*Bubo virginianus*), prairie falcons (*Falco mexicanus*), goshawks (*Accipiter gentilis*) and domestic cats (*Felis catus*) also target similarly-sized birds such as magpies (*Pica nuttalli* and *Pica pica*), pigeons (*Columba livia*), northern flickers (*Colaptes auratus*), American robins (*Turdus migratorius*) and mockingbirds (*Mimus polyglottos*) (Bielefeldt, 1998; Roth & Lima, 2003; Poole, 2007). Rather than using a size-based rule of thumb, jays may respond using a familiarity based rule, responding to any or only to dead heterospecifics that they have encountered in the same habitat (Ramakrishnan & Coss, 2000; Mirza & Chivers, 2003; Magrath et al., 2009; Magrath & Bennett, 2012). Alternatively, jays may respond differently to each species.

To test alternative hypotheses for the characteristics of dead heterospecifics that may influence jay response (size, sympatry and/or species identity) we presented scrub-jays with sympatric and allopatric jay-size heterospecific carcasses, and smaller, sympatric heterospecific carcasses to jays at feeders. For comparison, we also presented conspecific carcasses. For smaller heterospecifics, we use the house finch (*Carpodacus mexicanus*) and the lesser goldfinch (*Carduelis psaltria*), which are sympatric and locally abundant, and therefore likely familiar to jays. For similarly-sized heterospecifics, we use the rock pigeon (*Columba livia*) as a familiar species, since it is sympatric and abundant, and two similarly-sized allopatric species, which do not resemble any species sympatric with scrub-jays and are therefore considered unfamiliar species, the blue-tailed bee-eater (*Merops philippinus*), found in Africa, Southern Europe and Western Asia, and the black-naped fruit dove (*Ptilinopus melanospila*), found in Indonesia, Malaysia and the Philippines.

## 2. Materials and methods

### 2.1. *Field sites and experimental design*

Methods for the experiment discussed in this paper are similar to those described in Iglesias et al. (2012) and therefore, are summarized here excluding only detailed justification and citations for the procedures. Residential back yards, located at least 400 m apart within Davis, CA, USA served as experimental sites. Every morning, assistants placed 15 peanuts in feeders (1 m tall wrought-iron plant holders with clear plastic plant saucers) and watched for 30 min at a distance of $\geqslant$5 m. We began stimulus presentations when jays were predictably visiting the feeders at the time of refill, which took approximately two weeks on average. On experimental days, we placed about 25 peanuts in the feeder upon arrival; in all trials, jays took several of these peanuts as video and audio equipment was set up. While the jay was away caching peanuts, we placed the stimulus on the ground approximately one meter from the feeder. All stimuli were covered and carried to the feeder then left exposed on the ground. Human presence at the feeder is unlikely to have influenced jay behavior since there were no cases where jays returned to the area and called before the experimenter had returned to the observation location. After cacophonous aggregations (CAs) ended and jays were no longer in sight, stimuli were covered and removed. All bird carcasses were prepared as skins; skins were presented surrounded by feathers at feeders (creating a visual target approximately 60 cm in diameter) to simulate evidence of predation (Figure 1). We used species-specific feathers for all experimental stimuli, except for the two allopatric species, for which we used molted, green parrot feathers since species-specific feathers were unavailable. Carcasses were permit-salvaged (federal permit No. MB 117665-1, state permit No. SC-8508) and tested negative for West Nile virus. All procedures were approved by the University of California, Davis Institutional Animal Care and Use Committee (IACUC) under protocol No. 15379.

Between 3 November and 22 December 2008, 24 sites were each presented with a dead bird once. We presented the following: conspecifics (western scrub-jay: 4 different carcasses), two species that were sympatric but smaller than jays (house finch: 4 carcasses; lesser goldfinch: 4 carcasses), one species that is sympatric and similar in size to jays (rock pigeon: 3 carcasses) and two species that are allopatric and of similar size and do not resemble any co-occurring species (blue-tailed bee-eater: 1 carcass; black-naped fruit-dove: 1 carcass). We presented western scrub-jays, rock pigeons and lesser goldfinches each at five sites ($N = 15$ sites), the house finch at four sites ($N = 4$ sites) and the allopatric species, Black-naped fruit dove, at two sites and the Blue-tailed bee-eater at three sites ($N = 5$ sites).

### 2.2. *Data collection and measurements*

All experimental trials were video recorded (JVC Everio and Sony HC-1) and audio recorded (Marantz PMD670, at 44.1 kHz, 16 bit) from the time of presentation until no jays were in sight or heard calling. Audio and video

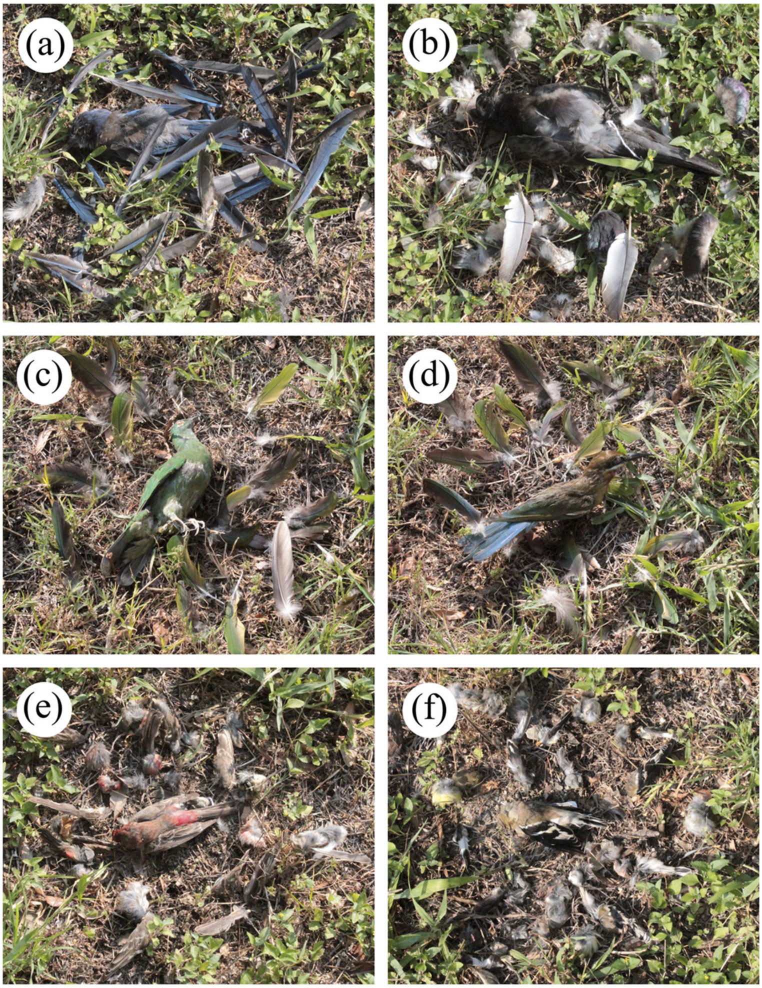

**Figure 1.** Carcasses used as stimuli surrounded by feathers presented on the ground near the feeder. (a) Western scrub-jay, (b) rock pigeon, (c) black-naped fruit dove, (d) blue-tailed bee-eater, (e) lesser goldfinch and (f) house finch. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/1568539x.

were scored by TLI and assistants. The number of peanuts taken during presentations was scored from video. Audio was used to determine CA duration, which includes the time from the first call to the last call before all jays are silent. Field observations were used to determine the number of jays present. Birds were not individually marked; instead, we used the maximum number of birds visually detected simultaneously in the yard for analyses; since territories are smaller than the minimum distance between experimental locations, it is unlikely that any birds were tested in multiple trials (Carmen, 2004; Iglesias et al., 2012).

Raven Pro 1.3 (available online at http://www.birds.cornell.edu/raven) was used to visualize the recorded calls as spectrograms (user-specified program settings: DFT size 512, overlap 0.5, HANN window) in order to count them, categorize them to type and measure call characteristics. The calls performed and measured are most similar to the long-range vocalizations termed ‘zeep’, ‘scold’ and ‘zeepscold’ described by Webber (1984). Scolds and zeepscolds tend to be used in close-range mobbing of predators while zeeps are used in a variety of contexts including mobbing predators, long-distance contact calling, and inter-pair interactions according to Webber (1984). For all elicited vocalizations of all three call types (zeep, scold and zeepscold) not obscured by other sounds or concurrent calls, we measured the following nine variables: maximum frequency, center frequency, 1st quartile frequency, 3rd quartile frequency, maximum time, center time, 1st quartile time, 3rd quartile time, and duration. The first four measurements are frequency characteristics of the calls. Maximum frequency is the frequency at which maximum power (dB) occurs, center frequency is the frequency that divides the call into two frequency intervals of equal energy, and 1st quartile and 3rd quartile frequency are the frequencies that divide the call into two frequency intervals containing 25% and 75% and 75% and 25% of the energy in the selection, respectively. The next four measures indicate the time when the above four frequency measures occurred in the call. The final measure is a measure of each call’s duration in seconds.

### *2.3. Statistical analyses*

All data were analyzed with R statistical software (version 2.13.2, available online at http://www.R-project.org) using linear mixed-effect regression (lmer) modeling with the lme4 package, and generalized linear models (glm) using AICc for all model comparisons (Johnson & Omland, 2004; Anderson, 2008). Principal components analysis was performed using the prcomp function in R. All models, except those evaluating measurements of call characteristics (analyzed with glm), contained site of presentation as a random intercept. Site was used as a predictor variable in model sets evaluating call measurements to test whether variation in call characteristics can be better explained based on individual differences in sound characteristics (since there are different individuals at each site) rather than stimuli presented. Bootstrapping was performed in R to generate all 95% confidence intervals. Code is available from TLI upon request.

To examine what makes an effective elicitor of CAs, we used model-selection to test six non-mutually exclusive hypotheses. Models (hypotheses) were built using different combinations of four variables: conspecific vs. heterospecific, allopatric vs. sympatric, species identity, and size. The model with the most support, from within the set of all models compared, is the one that best explains variation in jay behavioral and vocal response to experimental presentations of bird carcasses. The models/hypotheses are as follows: (1) response varies based on whether the carcass is that of a conspecific or a heterospecific; this hypothesis would be supported by the model that includes heterospecific-conspecific (denoted by the variable ‘hetero’); (2) jays respond based on familiarity of the species; this hypothesis would be supported by the model that includes sympatry-allopatry as a predictor variable (denoted by the variable ‘sympatric’); (3) jay response depends on the size of the bird; this hypothesis would be supported by the model that includes size (denoted by the variable ‘size’); (4) jay response depends on the size of the carcass and whether it is a heterospecific or a conspecific; this hypothesis would be supported by the model that includes the variables ‘size’ and ‘hetero’; (5) jay responses differ according to the species of the carcass; this hypothesis would be supported by the model that includes species identity as a predictor variable (denoted by the variable ‘species’); and (6) jays respond to all species equally; this hypothesis would be supported by the intercept-only model. We used lmer, with ‘site’ as the random intercept, to compare these hypotheses using the following response variables: (i) total number of calls produced in response to seeing a dead bird; (ii) the occurrence of a CA; and (iii) number of nuts taken during a presentation once the dead bird was detected.

Two additional explanatory variables were used to analyze vocalizations given in response to bird carcasses: site and whether CAs occurred. Therefore, two more hypotheses were added to the set of six described above (8 in total) to analyze vocalizations given in response to bird carcasses. Continuing from the numbering scheme above, additional hypotheses included: (7) vocalization characteristics differ between sites, or individual bird vocal characteristics at that site; this hypothesis would be supported by the model that includes site identity as a predictor variable (denoted by the predictor variable ‘site’); and (8) vocal characteristics differ based on whether calls were effective or not at attracting conspecifics and resulting in a CA; this hypothesis would be supported by the model that includes the occurrence of CA as a predictor variable (denoted by the predictor variable ‘CA’).

We compared these eight hypotheses in two separate analyses. In one analysis we examined spectral and temporal characteristics for each of the three call types. In the other analysis we examined the rate of call production using only the first bird to call. In the first analysis, the response variables were principal components derived from nine call measures (described above) for each of the three different call types (zeep, zeepscold and scold). We used the prcomp function in R to extract principal components and performed an additional varimax rotation using the varimax function in R. The Kaiser criterion was used to determine how many components to retain for analysis; we retained the first two principal components for each call type and each component was treated as a separate response variable. Calls for allopatric species were pooled, as there were no models supporting a difference in call characteristics between them. For all three types of calls, center frequency, center time and maximum frequency were ln transformed to normality. Additional measurements were ln transformed in some call types but not others (see Table 2).

In the second analysis of vocalizations, we determined the rate of vocalizing by taking the first 5–10 calls performed by the first scrub-jay to encounter the stimulus and dividing the number of calls by the number of seconds spent calling. We used glm in R to compare the eight hypotheses listed above.

After determining which carcasses were effective at eliciting a CA, we examined these CAs to determine whether the response differed based on the remaining categories of effective stimuli. Small heterospecifics were not effective elicitors; therefore, size was not included as a predictor variable in any model sets evaluating response variables when CAs occurred. We used lmer and set ‘site’ as a random factor. The hypotheses compared included: CAs differ based on (1) the eliciting species’ identity; (2) whether it was a conspecific vs. heterospecific; (3) whether allopatric vs. sympatric and (4) intercept-only. The response variables evaluated included: (i) number of birds that aggregated; (ii) duration of calling; (iii) the number of zeeps; (iv) number of scolds; and (v) number of zeepscolds performed by all birds present. All means are presented ±SE.

## 3. Results

We found that cacophonous reactions and aggregations were elicited by dead heterospecifics as well as conspecifics. Cacophonous reactions, where calls are emitted by the first jay that encounters the stimulus, occurred at all presentations of dead jay ($N = 5$), pigeon ($N = 5$) and both allopatric species (bee-eater and fruit dove, $N = 5$) and in three out of five goldfinch and three out of four house finch presentations (Figure 2a). In all presentations of dead jay, these cacophonous reactions became aggregations (CAs) as additional jays arrived and began calling. The pigeon and both allopatric species elicited CAs in 4 out of 5 presentations; goldfinches elicited CAs in one site of five and house finches elicited no CAs (Figure 2b).

We used the model-selection approach to determine how the occurrence of CAs varied with the type of stimulus. We found that the model including size as a predictor (conspecifics and jay-size heterospecifics vs. smaller-than-

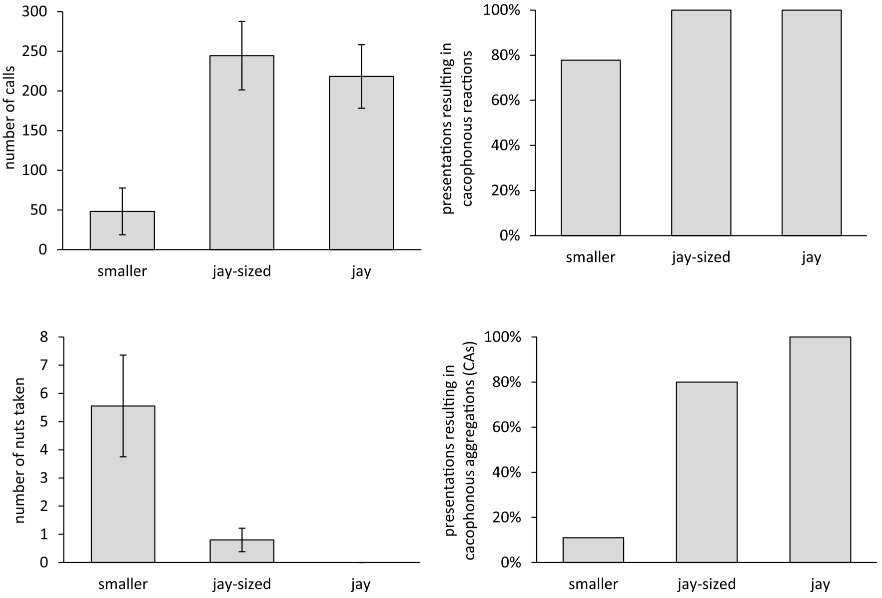

**Figure 2.** Behavioral responses to dead conspecifics, dead jay-sized heterospecifics and dead heterospecifics smaller than a jay. (a and b) The occurrence of cacophonous reactions and cacophonous aggregations (CAs) in response to presentations of dead birds. (c and d) The number of calls elicited and effect on peanut take during presentations of dead birds. All data shown as three categories of elicitors for comparative purposes. Note that separation into these categories does not necessarily indicate where differences occur statistically.

jay heterospecifics) received the strongest support (Table 1, set 1). Similarly, we used the model-selection approach to determine how the total number of calls produced in response to all presentations varied with the type of stimulus. Again, the model including size received the strongest support (Table 1, set 2). Dead conspecifics elicited 218 ± 40 calls and, similarly, jay-size heterospecifics elicited on average 244 ± 43.1 calls, whereas small heterospecifics elicited 48 ± 29 calls (Figure 2c).

We examined spectral and temporal features of the vocalizations produced in response to all experimental presentations, including calls from CAs and cacophonous reactions when no other jays were attracted. We used measurements for each type of call to derive two principal components, which were used as response variables in models; the first principal component for each of the three types of calls was composed of the temporal features measured, while the second was composed of the spectral measurements (Table 2). We did not find support that vocalization characteristics differed based on stimulus size, species identity, whether conspecific or heterospecific, sympatric or allopatric, or whether conspecifics were attracted (CA occurred); rather, we found that site was the best predictor for all three types of calls (Table 1, sets 3–8).

We examined the rate at which the first jay emitted the first 5–10 calls in response to presentations by dividing the number of calls by the elapsed number of seconds. We included calls from cacophonous reactions as well as CAs. We found no support that rate differed based on any predictor variables we considered, resulting in the null model (intercept-only) being the best supported model (Table 1, set 9).

Finally, we looked at whether the number of calls performed by the first jay to encounter the stimulus was related to whether or not cacophonous reactions escalated into CAs. When CAs occurred, the variation in the number of calls emitted before a second jay arrived ranged from 2 to 119 calls (34 ± 9.9). However, we used model selection to test the hypothesis that fewer calls are performed during cacophonous reactions against the null, or intercept-only, hypothesis of no difference. We found that the intercept-only model was best supported (Table 1, set 10), i.e. the number of calls performed by the first bird did not correlate with whether the response was a cacophonous reaction or a CA.

In order to examine whether there is specificity to the CA response, we compared CAs that occurred in response to conspecifics, pigeons and al-

**Table 1.**
AICc results showing models describing behavioral response to all species presentations (sets 1, 2 and 16), characteristics of all calls emitted to dead birds (sets 3–10) and characteristics of cacophonous aggregations (CAs) (sets 11–15).

| Set | Response variable | Predictor variable | df | $\Delta$AICc | AICc weight | Coefficient estimate | Coefficient 95% CI |
|---|---|---|---|---|---|---|---|
| 1 | Occurrence of CA | Size (smaller) | 3 | 0.0 | 0.99 | −24.97 | [−51.13, −24.61] |
| | | Species | 6 | 9.6 | 0.01 | | |
| 2 | Number of calls | Size (smaller) | 3 | 0.0 | 0.98 | −2.78 | [−3.95, −1.74] |
| | | Species | 6 | 7.9 | 0.02 | | |
| 3 | Zeep prin.comp1 (freq) | Site | 23 | 0.0 | 1 | | |
| | | Species | 6 | 493.9 | <0.001 | | |
| 4 | Zeep prin.comp2 (time) | Site | 23 | 0.0 | 1 | | |
| | | Species | 6 | 782.4 | <0.001 | | |
| 5 | Scold prin.comp1 (time) | Site | 14 | 0.0 | 1 | | |
| | | Species | 6 | 72.0 | <0.001 | | |
| 6 | Scold prin.comp2 (freq) | Site | 14 | 0.0 | 1 | | |
| | | Species | 6 | 71.8 | <0.001 | | |
| 7 | Zeepscold prin.comp1 (freq) | Site | 17 | 0.0 | 1 | | |
| | | Species | 6 | 726.9 | <0.001 | | |
| 8 | Zeepscold prin.comp2 (time) | Site | 17 | 0.0 | 1 | | |
| | | CA | 3 | 309.3 | <0.001 | | |
| 9 | Call rate | Intercept only | 2 | 0.0 | 0.42 | | |
| | | CA | 3 | 1.8 | 0.17 | | |

**Table 1.**
(Continued.)

| Set | Response variable | Predictor variable | df | ΔAICc | AICc weight | Coefficient estimate | Coefficient 95% CI |
|---|---|---|---|---|---|---|---|
| 10 | Number of calls by first jay | Intercept only | 2 | 0.0 | 0.73 | | |
| | | CA | 3 | 2.0 | 0.27 | | |
| 11 | Number of jays at CA | Intercept only | 2 | 0.0 | 0.59 | | |
| | | Hetero | 3 | 1.8 | 0.24 | | |
| 12 | Duration of CA | Intercept only | 2 | 0.0 | 0.52 | | |
| | | Hetero | 3 | 1.1 | 0.30 | | |
| 13 | Number zeeps | Intercept only | 2 | 0.0 | 0.68 | | |
| | | Sympatric | 3 | 2.7 | 0.17 | | |
| 14 | Number scolds | Intercept only | 2 | 0.0 | 0.72 | | |
| | | Hetero | 3 | 3.4 | 0.13 | | |
| 15 | Number zeepscolds | Intercept only | 2 | 0.0 | 0.65 | | |
| | | Sympatric | 3 | 2.5 | 0.18 | | |
| 16 | Number of nuts taken | Hetero | 4 | 0.0 | 0.66 | 17.07 | [0, 18.90] |
| | | Size (smaller) | | | | 2.01 | [1.79, 20.58] |
| | | Size (smaller) | 3 | 1.8 | 0.27 | | |

Only the top two models are shown and coefficient estimates ±95% CI are shown for the best model when it contains an experimental predictor variable (e.g., size (size of species), species (specific species), hetero (heterospecific vs. conspecific)), except in the case of site (each site would have a coefficient estimate, and $N = 24$). The level of support for a model is indicated by a higher AICc weight (max = 1). ΔAICc is the difference in AICc score between the best model (listed first in each set) and the next competing model. Coefficient estimates in the table indicate the positive (increase in response variable) or negative (decrease in response variable) impact of predictor variables. Predictor variables are followed by a descriptor in parentheses (e.g., size (smaller)) to indicate the direction of impact is from the perspective of that categorical subset.

**Table 2.**
Principal component loadings for all measures for three types of calls: zeep, scold and zeepscold.

| Measure | Zeep | | | Scold | | | Zeepscold | | |
|---|---|---|---|---|---|---|---|---|---|
| | ln | PC1 | PC2 | ln | PC1 | PC2 | ln | PC1 | PC2 |
| 1st quartile time | x | 0.01 | −0.37 | | 0.38 | 0.004 | | 0.09 | −0.35 |
| 3rd quartile time | | −0.01 | −0.50 | | 0.49 | 0.005 | | −0.01 | −0.48 |
| Center time | x | −0.03 | −0.54 | x | 0.52 | −0.002 | x | −0.004 | −0.55 |
| Maximum time | | 0.06 | −0.43 | x | 0.33 | 0.02 | x | 0.09 | −0.39 |
| Duration | x | −0.01 | −0.36 | | 0.47 | −0.01 | x | −0.18 | −0.43 |
| 1st quartile frequency | x | 0.51 | 0.02 | x | −0.02 | −0.52 | | −0.50 | 0.06 |
| 3rd quartile frequency | x | 0.48 | −0.003 | | 0.05 | −0.45 | | −0.47 | −0.03 |
| Center frequency | x | 0.53 | 0.001 | x | 0.03 | −0.54 | x | −0.55 | −0.02 |
| Maximum frequency | x | 0.48 | −0.001 | x | −0.05 | −0.48 | x | −0.42 | 0.03 |

The x in the ln columns indicate that measures were ln-transformed for that call type before PCA was performed. For zeep and zeepscold call types, frequency measures load onto PC1 and temporal measures load onto PC2. For scold call types, temporal measures load onto PC1 and frequency measures load onto PC2.

lopatric species since these groups elicited several CAs (only one CA occurred in response to small heterospecifics). We found no support that the number of jays attracted to calls (Table 1, set 11) or the duration of CAs (Table 1, set 12) differed based on species identity, whether it was sympatric or allopatric, or whether it was heterospecific or conspecific. We also examined the number of zeep, scold and zeepscold calls performed by all birds aggregated to determine if different stimuli affected how these calls were used. We found that no type of call was used disproportionately in response to any category of stimuli. We found that the null model had the most support (Table 1, sets 13–15) for all three types of calls; therefore, call type use is not predicted by the identity of the elicitor species, whether it is sympatric vs. allopatric or conspecific vs. heterospecific.

Finally, we examined how our experimental presentations affected jay foraging behavior. We found that the model including the variables ‘hetero’ and ‘size’ was the best at describing peanut-take during presentations (i.e., response differed between conspecifics and heterospecifics and between the two sizes) (Table 1, set 16) (Figure 2d).

## 4. Discussion

Previously, we found that western scrub-jays respond to the sight of dead conspecifics with alarm calls that attract other jays, and with reduced foraging in the area where dead conspecifics were encountered (Iglesias et al., 2012). Here we show that jays respond to dead heterospecifics in a similar manner, but that not all dead heterospecifics are equally effective. Jays respond most strongly to dead heterospecifics similar in size to themselves — whether sympatric or allopatric — with more cacophonous reactions and aggregations, more vocalizations and a greater decrease in foraging than in response to smaller dead heterospecifics. Even though CAs occurred more often with dead jays (100% of presentations) than with similarly-sized dead heterospecifics (80% of presentations), and only once with small heterospecifics, CAs did not appear to differ in the number of jays attracted, the number of calls elicited, or the duration of the aggregation. This suggests that, once elicited, behaviors during CAs are not related to the characteristics of the eliciting species. However, given $\Delta$AICc and AICc weights for these models (Table 1, sets 9–15), a larger sample size may reveal subtle differences.

Heterospecifics can be an important source of information about risk if they are similar in size, natural history, habitat preference and/or behavior, making them vulnerable to similar predators. The size of avian predators in particular is known to affect their optimal prey size, since their swiftness and maneuverability are affected by their weight and wingspan (Howland, 1974; Andersson & Norberg, 1981). Gut content studies lend empirical support to size specialization, showing that raptors predominantly capture adult avian prey of similar sizes (Roth & Lima, 2003). However, other common predators of birds, including the domestic cat and some species of foxes, take jay-sized birds as well as smaller and larger species (Hockman & Chapman, 1983; Golightly et al., 1994; Pearre & Maass, 1998; Bonnaud et al., 2011). Therefore, the size-based behavioral rule we found in this study may be ineffective against predation by house cats and foxes.

Our results suggest that jays use dead conspecifics as a cue of risk and generalize their response to similar-sized heterospecifics that are unfamiliar. However, since we used a limited assortment of dead heterospecifics as stimuli in this study, further work is needed to learn how broadly scrub-jays generalize. During the course of the experiments conducted here, we conducted opportunistic presentations of carcasses of other similarly-sized heterospecifics — including the northern flicker (*Colaptes auratus*), varied thrush (*Ixoreus naevius*) and the yellow-billed magpie (*Pica nuttalli*) (T.L.I., pers. obs.). All of these presentations elicited CAs, suggesting that the response to similarly-sized species is not limited to those species tested here (T.L.I., pers. obs.). It also suggests that heterospecific color is not a major determinant of response since the allopatric species in this study are primarily green and differ markedly from scrub jays in color and pattern yet are still strong elicitors. Further, jays have responded to carcasses that were primarily one color or a combination of colors (e.g., green, blue, red, black, yellow, orange, brown, gray, white, purple, iridescent) (T.L.I., pers. obs.) yet the small heterospecifics in this study bearing some of these colors (red, black, yellow, brown, gray, white) were not effective elicitors. Iglesias et al. (2012) found that jay-size novel objects presented to jays at feeders do not elicit CAs, suggesting that CAs are not simply a response to any novel, unexpected, jay-sized object. It is also unlikely that the CAs are a generalized response to a dead bird of any size, as we found that jays respond less to heterospecific dead birds smaller than themselves. Further experiments are needed to determine whether jays would respond to smaller species that are allopatric, which would indicate an interaction between size and familiarity. Further experiments are also needed to determine whether jays would respond to larger species either allopatric or sympatric. In opportunistic tests, we found that jays respond with CAs to the carcasses of American crows (*Corvus brachyrhynchos*) and great-horned owls (*Bubo virginianus*) (T.L.I., pers. obs.), which can weigh 3–7 times and 12–30 times as much as an adult jay, respectively. This suggests that in addition to similarly-sized heterospecifics, jays may generalize their response to heterospecifics larger than themselves. However, since these larger species can be predators on nests or adults, jays may also respond to them as direct evidence of live predators in the area. While further research is needed to map the elicitors of this behavior along size, familiarity and experience axes, these results suggest that size is an important determinant of this response.

We found that neither call rate nor the measured characteristics of the calls (CAs and cacophonous reactions) elicited by our experimental stimuli differed based on species identity, size, sympatry, whether the species was conspecific or heterospecific, or whether the calls successfully resulted in a CA. When a CA did occur, the use of the different call types was also not affected by any of these variables, including site (size was not considered when analyzing calls performed in CAs, since small heterospecifics only elicited one CA). Therefore, there is no evidence that characteristics of the vocalizations during cacophonous reactions or aggregations encode information about the eliciting stimulus. This is consistent with the hypothesis that these heterospecifics are effective elicitors because they indicate a similar type or level of risk as a dead conspecific. Behavioral modification that reduces exposure to risk in these cases may be similar, if not identical, and therefore communication regarding characteristics of the dead bird may not be necessary or useful. Or calls may simply serve to attract others, leaving decisions about how to cope with risk in the area to the specific cues and context of the situation.

All species we tested elicited at least some calls, however some of these cacophonous reactions, even in response to jay-sized heterospecifics, did not successfully attract conspecifics and result in a CA. As stated above, these calls did not differ based on the nine measurements or on the call rate of the first 5–10 calls. However, calls in response to small heterospecifics were more than 6 times less likely to attract conspecifics, suggesting that the calls differ in some way that we did not measure or a larger sample size is necessary to detect relevant differences. Far fewer calls were elicited by small heterospecifics, which suggests that conspecifics may not be attracted when few calls are performed. However, when CAs did occur, we found a wide variation in the number of calls performed before a conspecific arrived (range 2–119 calls), and our analysis shows that the number of calls was not correlated with whether or not a cacophonous reaction escalated into a CA. Therefore, large numbers of calls are not needed to attract conspecifics. It is unlikely that proximity of conspecifics explains this difference, since order of presentation was randomized, such that there is no reason to expect conspecifics would be farther away in the smaller-sized heterospecific presentations. Potential areas of relevant variation may include other spectral and temporal characteristics of the calls, as well as variation in the performance of such calls, such as inter-call intervals, clustering or evenness of calls or calling bouts, and the duration of silences between calling bouts (Richards & Thompson, 1978; Ellis, 2008; Yorzinski & Vehrencamp, 2009).

While animals can benefit directly by using cues in the environment to mediate risk (Chivers et al., 2002; Mirza & Chivers, 2002; Shier & Owings, 2007), it is less clear why a territorial species such as the western scrub-jay would attract and tolerate others in its territory by inciting cacophonous aggregations (Iglesias et al., 2012). A potential benefit of CAs may be gathering a mob to locate and drive predators away (Curio, 1978); since mobbing is more effective when the group of attacking birds is larger (Robinson, 1985; Flasskamp, 1994), 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). CAs may function to warn mates and offspring of danger, to help form location memories of risky areas (Griffin et al., 2010) or to enable mates or offspring to do so (Griffin, 2004). Territorial neighbors may benefit by responding to mobbing calls if it reduces predation risk on surrounding territories as well.

Navigating a risky environment is a necessary part of staying alive, and using the most relevant information available to assess and manage risk exposure may help in this navigation. Our results show that the western scrub-jay uses the sight of both dead conspecifics and some heterospecifics as cues of risk. Since jays are not restricting their response to familiar heterospecifics, they may be using a size-based rule in determining which indicators of predation risk are relevant. It is well established that some animals take advantage of information gleaned from heterospecifics, e.g., by eavesdropping on heterospecific communication (Chivers et al., 2002; Templeton & Greene, 2007; Fallow & Magrath, 2010; Magrath & Bennett, 2012). However, to our knowledge this is the first controlled experiment showing an animal using the visual cue provided by a dead heterospecific as an indicator of risk and communicating this risk to other conspecifics.

## Acknowledgements

Thanks to all homeowners who assisted in provisioning feeders and recording observations and for allowing access to their yards and to the many undergraduate field assistants. Thanks to D. Warren, the Patricelli lab and the Sih lab for comments on experimental design. Thanks to A. Sih and R. McElreath for helpful comments on early drafts of this manuscript. This work was supported by the University of California (UC) Davis Jastro-Shields research award, UC Davis Center for Population Biology Student Research Funding, UC Davis Animal Behavior Graduate Group Student Fellowships, UC Davis Eugene Cota-Robles Scholarship and the Gates Millennium Graduate Scholarship. We also thank anonymous referees for their thoughtful and helpful comments.

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