



## Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice

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In mixed-species foraging flocks of forest birds, one or a few nuclear species frequently produce alarm calls and are followed by other species in the flock. We tested the hypothesis that similar asymmetries may exist in a second interspecific social context, multispecies mobbing behaviour. We examined mobbing behaviour evoked by an eastern screech-owl, *Megascops asio*, model and playback in two nuclear species, Carolina chickadees, *Poecile carolinensis*, and tufted titmice, *Baeolophus bicolor*, and in a species that follows them, the white-breasted nuthatch, *Sitta carolinensis*. Asymmetries in mobbing were not the same as those in mixed-species flocks. Nuthatches and chickadees mobbed with greater frequency and intensity compared to titmice, which remained at greater distances from the owl model and vocalized less frequently. We also tested for the existence and nature of potential interspecific vocal information flow during mobbing. Chickadee and nuthatch calling rates were positively correlated, as were chickadee and titmouse calling rates. Nuthatches and titmice rarely mobbed simultaneously. These results suggest the existence of positive feedback among species' mobbing intensity during a multispecies mobbing association as opposed to heterospecific vocal interference or a lack of heterospecific influence. However, randomization simulations showed that this positive feedback was not driven by a particular 'nuclear' species during mobbing, suggesting that the correlations may result from a mutually interdependent escalation of mobbing intensity.

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Acoustic alarm signals that function adaptively to communicate with conspecifics and predators are often available in the public domain, allowing other species the opportunity to detect and benefit through adaptive responses to these signals (Shier 2002). Many mammals and birds have learned to associate heterospecific alarm calls with the presence of a predator (Hauser 1988; Shriner 1998; Fichtel 2004; Rainey et al. 2004; Magrath et al. 2007). The nature and directionality of vocal antipredator information flow among species is particularly relevant to species involved in interspecific social foraging groups. The benefits of interspecific sociality may, in fact, be linked to the complementary information provided by heterospecifics about different species of predators (Rasa 1983; Zuberbühler 2000). Avian mixed-species foraging flocks are a complex case of potential vocal information transfer, as they often contain large numbers of species. The diverse antipredator responses of heterospecifics in such flocks may have an additive effect on the information available as a consequence of flock membership (Goodale & Kotagama 2005a).

In mixed-species bird flocks, alarm calls are given by flock members in response to predators that represent immediate and usually extreme risk of predation (Ficken & Witkin 1977). The response to these alarm calls is for all birds in the flock to immediately stop movement and produce vocalizations for several minutes, and the first loud calls by flock members signal a return to activity (Morse 1973; Gaddis 1980; Sullivan 1984). Previous research has identified particular 'leader' and 'follower' species types in most avian mixed-species foraging flocks, termed 'nuclear' and 'satellite' species, respectively (Moynihan 1962; Morse 1977; Greig-Smith 1978; Diamond 1981; Munn 1984; Goodale & Kotagama 2005b). Nuclear species typically give frequent vocalizations, including alarm calls, or occur in large, active conspecific social groups, or both (Greenberg 2000). Satellite species often occur singly or in pairs and follow the nuclear species in the flock (Munn 1985). Vocal information about the presence of aerial predators typically flows from the nuclear species to the satellites (Munn & Terborgh 1979), although vocal information flow between multiple nuclear species also occurs (Goodale & Kotagama 2008).

The typical nuclear-satellite behavioural asymmetry can be observed in the forest flocks of eastern temperate North America where Carolina chickadees, *Poecile carolinensis*, tufted titmice,

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*Baeolophus bicolor*, and white-breasted nuthatches, *Sitta carolinensis*, co-occur in interspecific social-foraging groups during the nonbreeding season. Chickadees and titmice, the nuclear species, are often followed by many satellite species, principally woodpeckers and nuthatches (Morse 1970; Berner & Grubb 1985; Dolby & Grubb 1999). White-breasted nuthatches reduce vigilance and increase foraging rates when chickadees and titmice are present (Dolby & Grubb 1998). Observational and experimental evidence suggests that satellite species respond evasively to the aerial predator alarm calls of chickadees and titmice as described above (Gaddis 1980; Sullivan 1984).

Chickadees, titmice and nuthatches also interact in a context other than that of the mixed-species foraging flock. Small forest birds (chickadee = 10 g, titmouse = 21 g, nuthatch = 21 g) commonly show simultaneous mobbing behaviour towards small owls, such as pygmy-owls in western North America (Nocedal & Ficken 1998; Deppe et al. 2003; Templeton et al. 2005) and eastern screech-owls, *Megascops asio*, in eastern temperate woodlands (McPherson 1981; Gehlbach 1994; Gehlbach & Leverett 1995). The formation of a mobbing group is typically initiated by vocalizations with broadband frequency, rapid onset and high delivery rate (Marler 1955; Curio 1978; Klump & Shalter 1984). Unlike responses to alarm calls in foraging flocks, these mobbing associations are active and relatively noisy interactions with a less extreme threat than is present for the alarm calls described above (Curio 1978). In mobbing associations, the flock tries to drive the predator away from a given area. Eastern screech-owls are sit-and-wait predators of adult birds during the early morning and late evening hours (Gehlbach 1994) and so may be vulnerable to disturbance from mobbing birds during the day.

#### *Directionality of Potential Vocal Information Flow*

Here, we address two previously unexamined aspects of the multispecies mobbing behaviour of small woodland birds. Our first hypothesis was that the directionality of interspecific information flow is consistent across two behavioural contexts, the mixed-species foraging flock and multispecies mobbing association. We analysed the order of species' responses during the onset of a mob and species' vocal contributions during multispecies mobbing. If the foraging flock pattern of vocal antipredator information flow from nuclear flocking species to satellite species is maintained during predator mobbing associations, we predicted that chickadees and titmice would play a central role in maintaining the multispecies mob. In fact, there is some evidence of a 'nuclear' role of chickadees and titmice in mobbing associations. Heterospecifics show mobbing behaviours in response to chickadee and titmouse mobbing calls (Hurd 1996; Turcotte & Desrochers 2002; Sieving et al. 2004; Betts et al. 2005; Templeton & Greene 2007).

#### *Interspecific Interactions during the Mobbing Association*

The dynamics of species' interactions during multispecies mobbing behaviour are unknown. Several experimental studies (Vieth et al. 1980; Hurd 1996; Forsman & Mönkkönen 2001; Templeton & Greene 2007) have shown that mobbing calls stimulate mobbing behaviour in heterospecifics (Altmann 1956; Latimer 1977; Ficken & Popp 1996). However, natural interspecific interactions during mobbing have not been quantified. Our second hypothesis was based on an analysis of natural temporal patterns of these species' mobbing calls within a bout of mobbing. We hypothesized that escalation of mobbing intensity in conjunction with heterospecifics would be favoured over a strategy of independent escalation. Coordination of mobbing intensity among

small prey species would be beneficial if successful interference with a predator's hunting success (Pettifor 1990; Flasskamp 1994; Deppe et al. 2003; Sunde et al. 2003; Hendrichsen et al. 2006) requires large amounts of noise. Chorusing may also mitigate the risk of mobbing itself or the predation risk associated with mobbing calls (Krama & Krams 2005). Ficken (1989) hypothesized that the apparently clumped patterns of conspecific calls in mobbing black-capped chickadees may prevent a predator from localizing individual callers. If escalation of the mob is contingent upon the behaviour of heterospecifics, species' calling rates should be positively correlated. Alternatively, heterospecific calling may interfere with conspecific communication (Brumm 2006; Planque & Slabberkoom 2008). If such interference occurs during mobbing, negative correlations among species' calling rates are expected.

Asymmetries in vocal information flow may also occur within the mobbing chorus. If mobbing behaviours of all species have equal relevance to mobbing heterospecifics, then changes in the calling rate of any given species may result in coincident changes in the calling rate of heterospecifics in an interspecific mobbing chorus. Alternatively, particular species may have greater influence on the mobbing intensity of heterospecifics. In particular, chickadees and titmice may play a 'nuclear species' role in mobbing. If so, then nuthatch mobbing vocalizations and behaviour should be dependent upon chickadee and titmouse mobbing behaviours. Evidence of this asymmetry may exist at the level of individual mobbing calls such that nuthatches would be more likely to call immediately after a chickadee or titmouse call.

## **METHODS**

This research was conducted at Purdue University's 160 acre Ross Biological Reserve and in the adjacent Ross Hills County Park located along the Wabash River in west-central Indiana, U.S.A. Forest type varies from dry oak-hickory ridge-tops, to maple-tulip poplar slopes and bottomland cottonwood-sycamore along the river. The entire reserve is marked with a 40 × 40 m colour-coded grid and covered by an extensive trail system.

The data analysed here were collected during playback experiments conducted between September 2005 and July 2006. Playbacks in September and October 2005 consisted of eastern screech-owl monotonic trills for a period of 10 min. Winter 2006 playback consisted of eastern screech-owl monotonic trills in combination with chickadee, titmouse or nuthatch mobbing calls for a period of 6 min. Otherwise, the 2005 and 2006 playback procedures were identical. A screech-owl model was placed near the trunk of a small tree approximately 2 m from the ground to provide a visual stimulus for mobbing behaviour. Mobbing birds focused attacks towards the model, often swooping towards it and occasionally making physical contact. The use of predator playback in conjunction with a model mimics the natural predator-prey interaction because passerines often mob calling screech-owls. In fact, the playback of screech-owl calls alone will evoke mobbing behaviour (McPherson 1981). The use of predator playback also ensured that all individuals in hearing range had the opportunity to simultaneously become aware of the owl.

This study was approved by the Purdue Animal Care and Use Committee (protocol no. 04-083). Birds resumed normal foraging activity immediately after the end of playback and usually left the area, sometimes before the playback ended. Overall disturbance from the predator playbacks was also minimal because successive playbacks at the same site were separated by at least 7 days to minimize habituation.

Playbacks were conducted using a Saul Mineroff amplified field speaker attached to the tree just below the owl model, a Sony Walkman CD player, and 12 m of speaker cable for remote initiation

of playback. Playback levels were standardized to 85 db at 1 m from the speaker using a digital sound level meter. A Sennheiser ME66 directional microphone, pointed towards the canopy above the model, was attached to a Marantz PDM-690 Professional solid-state recorder (recording at a sampling rate of 44.1 kHz) and placed 5 m behind the speaker.

Mobbing typically had a distinct onset, occurring when one bird flew directly towards the predator and began mobbing vocalizations. Therefore, we defined the onset of mobbing as the onset of mobbing vocalizations at the site of playback. Species were categorized as either first, second or third in joining the mobbing assemblage. Second and third respondents were combined into a single category (secondary respondents). Mobbing occurred in 27 playback trials.

Visual scan samples were taken every minute for two-dimensional positions of each individual. Species identity was noted, but individual birds could not be tracked minute to minute. Position was categorized into distance intervals of 0–5, 6–10, 11–15, 16–20 or 21–30 m from the owl model. Distance estimation was aided by a 40 × 40 m grid of markers at the field site and by the known length of speaker cable. Distance from the owl was analysed by considering the midpoint of each distance category as a continuous variable.

We made audio recordings for 5 min before, during and after each playback ended. Spectrograms were generated using CoolEdit Pro 2.0 (Syntrillium Software, Scottsdale, AZ, U.S.A.). Any chickadee or titmouse call containing at least one D note (Bloomfield et al. 2005; Lucas & Freeberg 2007; Owens & Freeberg 2007) was categorized as a mobbing call. For nuthatches, a single ‘quank’ note or a string of quank notes was considered to be one mobbing call (Grubb & Pravosudov 1993).

We selected 11 playbacks to examine the chickadee–nuthatch vocal interaction and seven playbacks to examine the chickadee–titmouse vocal interaction. Playback trials containing too few of one species’ calls were excluded from analysis of interspecific vocal correlations. Titmouse–nuthatch vocal interactions were not analysed because titmice mobbed intensely with nuthatches on only three occasions. Each co-mobbing period was divided into 5 and 20 s intervals. The numbers of calls by each species in all 5 and 20 s intervals were then counted (calls per 5 s and calls per 20 s). The average span of the co-mobbing periods was relatively large compared to the size of these rate intervals (see [Supplementary Information I: Tables S1, S2](#) for details on the playback trials analysed).

Repeated measures mixed models (SAS, Proc MIXED, SAS Institute, Cary, NC, U.S.A.) were used to model interspecific effects on distance and calling rate as well as differences between species in average distance and mob duration. Repeated measures modelling allows analysis of variation occurring within a subject while accounting for differences between subjects, and it is the recommended method of analysis for time series data, such as calling rates over time. Playback trial was used as the subject in repeated measures analysis (e.g. 11 playback trials for the chickadee–nuthatch analysis). For analysis of spatial correlations, each species’ distance was used as both the dependent and independent variable in reciprocal models. Scan samples during which either species was absent were omitted from analysis. Likewise, for analysis of calling rate correlations, the calling rate of each species was used as both the dependent and independent variables in reciprocal models. When comparing mobbing duration and spatial positions among species, we first report statistics from the overall ANOVA, followed by comparisons of least-squares means and the accompanying Tukey-adjusted *P* values for the *t* statistics (generated using the ‘LSMEANS/diff’ command in Proc MIXED).

We removed any linear or hyperbolic underlying effect of time from the onset of playback on both species’ calling rates and spatial

positions from consideration of the interspecific correlations by adding time within the co-mobbing period (starting at the beginning of the co-mobbing period) and time-squared terms to the models. Time-by-calling rate interactions were added but removed from the models if they did not improve the model fit. To check for a correlated response by both species to the artificial temporal patterns imposed by the timing of individual calls within our playback treatments, we added time since the previous playback call to the models. Because the distribution of nuthatch calling rates was non-normal, ln-transformations of nuthatch rate were used in all models below. Titmouse calling rate (as a dependent variable) was ln-transformed and species’ distances were square-root transformed to normalize model residuals.

Randomization simulations were used to determine whether calls tended to follow those of a heterospecific more closely than expected by chance. This was done by focusing on species pairs (chickadee–nuthatch and chickadee–titmouse). For each pair, we calculated a distribution of the time intervals from the call of one species to the previous calls of the other species in the pair (and the reciprocal of this). We then compared the results of a randomization simulation conducted on the observed distribution to that conducted on two sets of hypothetical distributions. The first was a random distribution in which the observed conspecific intercall intervals for each species were randomly placed in a period with the same time span as the actual co-mobbing period. This random distribution gave us an estimate of how close in time the calls of any individual of a given species would follow those of an individual of a second species if the timing of their calls was uncorrelated. The second hypothetical distribution took the total number of calls of the following species and placed each call an average of 0.5 s (range 0–1 s) after the call of the leading species. This distribution gave us an estimate of the expected distribution of intercall intervals when the onset of calling for a given species closely followed that of a leading species. A sample of 1000 randomized distributions was generated for each species pair and for each distribution (i.e. observed, random, and following). We then calculated the percentage of 1000 comparisons in which the actual distribution (observed, random, or following) differed significantly (based on Kolmogorov–Smirnov tests) from its corresponding randomized distribution for each playback trial. Eleven chickadee–nuthatch mobs and four chickadee–titmouse mobs were used to test for asymmetries in call-to-call patterns. See [Supplementary Information II](#) for a more detailed description of the randomization simulations.

## RESULTS

### *Species’ Relative Contributions to Mobbing Behaviour*

#### *Response order*

Mobbing behaviour began  $226 \pm 29$  s (mean  $\pm$  SE across all species) after the onset of playback. Mobbing onset time was not affected by the species identity of the first mobbing individual (repeated measures ANOVA:  $F_{2,28} = 1.96$ ,  $P = 0.159$ ). The mobbing onset times of nuthatches and chickadees were correlated when nuthatches began mobbing first (Pearson correlation:  $r_9 = 0.69$ ,  $P = 0.019$ ) but not when chickadees began mobbing first (Pearson correlation:  $r_2 = 0.86$ ,  $P = 0.144$ ). The mobbing onset time of chickadees was not correlated with that of titmice (Pearson correlation:  $r_8 = 0.46$ ,  $P = 0.17$ ), nor were the mobbing onset times of titmice and nuthatches correlated (Pearson correlation:  $r_8 = -0.29$ ,  $P = 0.41$ ).

The type of playback treatment (owl only, owl + mobbing call) did not influence the species identity of the first respondent to the playback (chi-square contingency test:  $\chi^2_4 = 5.38$ ,  $P = 0.25$ ).

Therefore, the data from different playback treatments containing owl playback were pooled for categorical analysis of response order. Nuthatches were the most frequent first respondent to a playback (chi-square goodness-of-fit test:  $\chi^2_2 = 8.22$ ,  $N = 27$ ,  $P = 0.016$ ; Fig. 1a). However, once the first respondent had arrived, all species were equally likely to join a mob as either the second or third respondent ( $\chi^2_2 = 0.23$ ,  $P = 0.89$ ; Fig. 1b).

Nuthatch-to-chickadee was the most prevalent mob assemblage order (37.0%), relative to the following orders: chickadee alone (3.7%), chickadee–titmouse (11.1%), chickadee–nuthatch (7.4%), titmouse alone (11.1%), titmouse–chickadee (3.7%), titmouse–nuthatch (3.7%), nuthatch alone (14.8%) and nuthatch–titmouse (7.4%) ( $\chi^2_8 = 21.33$ ,  $P = 0.0063$ ).

#### Duration of vocal mobbing

Species differed in average duration of vocal mobbing (repeated measures ANOVA:  $F_{2,29} = 8.40$ ,  $P = 0.0002$ ). Vocal mobbing durations for nuthatches (least-squares mean  $\pm$  SE:  $307 \pm 30.2$  s) and chickadees ( $217 \pm 33.2$  s) were significantly longer than that for titmice ( $93.9 \pm 32.3$  s; Tukey multiple comparison test: nuthatch:  $t_{29} = 4.82$ ,  $P_{\text{adj}} = 0.0001$ ; chickadee  $t_{29} = 2.66$ ,  $P_{\text{adj}} = 0.032$ ), but did not differ from each other ( $t_{29} = 2.01$ ,  $P_{\text{adj}} = 0.128$ ).

#### Spatial proximity to the predator

Species differed in average proximity to the owl during mobbing (repeated measures ANOVA:  $F_{2,18} = 9.23$ ,  $P = 0.0017$ ; nuthatch: least-squares mean  $\pm$  SE =  $9.80 \pm 0.89$  m; chickadee:  $13.20 \pm 0.79$  m; titmouse:  $14.38 \pm 0.97$  m). Nuthatches remained closer to the owl than did chickadees (Tukey multiple comparison test:  $t_{18} = 3.59$ ,  $P_{\text{adj}} = 0.002$ ) and titmice ( $t_{18} = 3.93$ ,  $P_{\text{adj}} = 0.001$ ), which did not differ from each other in average proximity to the owl ( $t_{18} = 1.14$ ,  $P_{\text{adj}} = 0.269$ ; Fig. 2). Chickadees ranged further from the owl during mobbing than did simultaneously mobbing nuthatches. Similarly, titmice ranged further from the owl during mobbing than did simultaneously mobbing chickadees or nuthatches.

#### Interspecific Interactions during Multispecies Mobbing

##### Spatial correlations

Minimal approach distances were positively correlated between each species pair, suggesting some level of interspecific coordination in the mob (reciprocal repeated measures models for each species pair: species1 distance = species2 distance + time after playback onset). The distance from the closest chickadee to the owl decreased in conjunction with the closest nuthatch's distance

(separate repeated measures models:  $F_{1,40} = 10.45$ ,  $N = 10$  playback trials,  $P = 0.0025$ ) and with the closest titmouse's distance ( $F_{1,33} = 7.20$ ,  $N = 11$  playback trials,  $P = 0.011$ ). The distance from the closest nuthatch to the owl decreased in conjunction with the closest chickadee's distance ( $F_{1,40} = 10.98$ ,  $N = 12$  playback trials,  $P = 0.002$ ) and with the closest titmouse's distance ( $F_{1,19} = 9.8$ ,  $N = 11$  playback trials,  $P = 0.006$ ). Likewise, the distance from the closest titmouse to the owl decreased in conjunction with the closest nuthatch's distance ( $F_{1,20} = 7.80$ ,  $N = 11$  playback trials,  $P = 0.011$ ) and with the closest chickadee's distance ( $F_{1,33} = 9.43$ ,  $N = 12$  playback trials,  $P = 0.004$ ). Chickadee distance from the owl model also decreased with increasing time during the playback ( $F_{1,33} = 18.51$ ,  $P = 0.0001$ ); however, no other species' distances were affected by time.

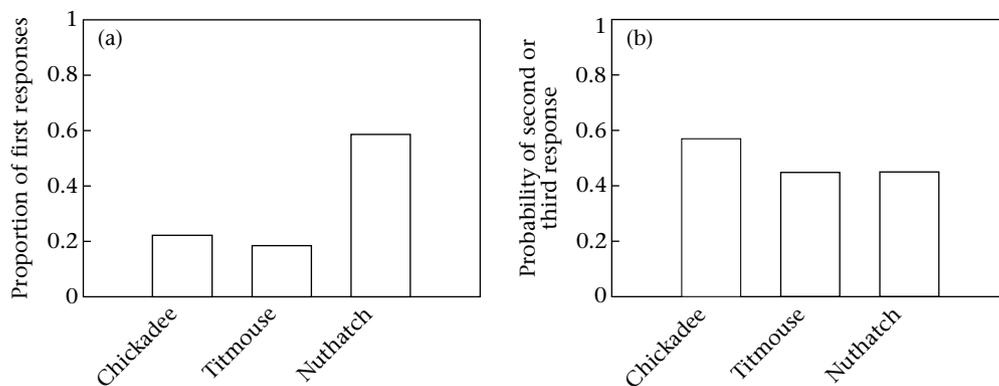
##### Correlations between species' calling rates during mobbing

Two of the seven co-mobbing periods for chickadees and titmice contained playback of mobbing calls and the remaining five had owl calls only. However, because playback type and the time since a single playback call (owl or mobbing call) had no effect on either species' calling rate, these variables were dropped from the models (Supplementary Information I: Table S3).

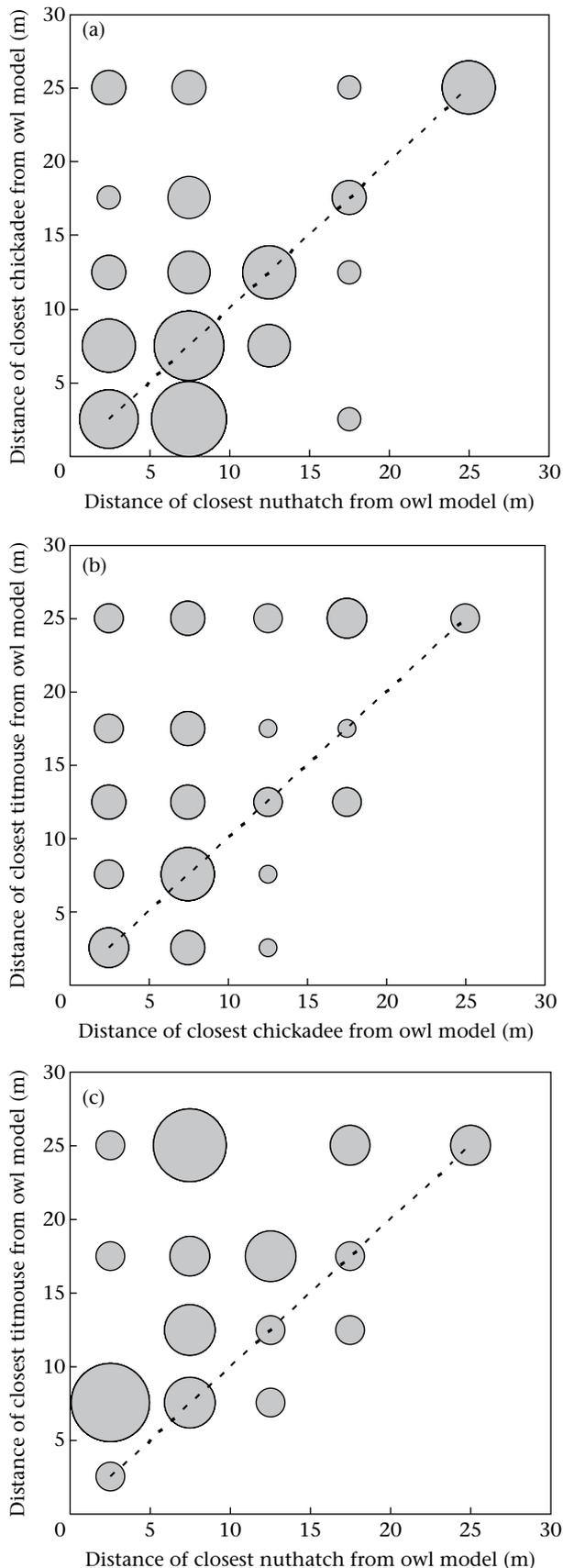
Titmice calling rates increased with an increase in chickadee calling rates when measured over short (5 s) intervals (Fig. 3), but the relationship was not significant when rates were measured over longer (20 s) intervals (separate repeated measures models for each time scale; model: titmouse calling rate = chickadee calling rate + time + time<sup>2</sup>; 5 s:  $F_{1,102} = 5.32$ ,  $P = 0.023$ ; 20 s:  $F_{1,31} = 0.53$ ,  $P = 0.47$ ). Titmouse calling rate also increased with time from the onset of mobbing (5 s:  $F_{1,102} = 8.04$ ,  $P = 0.006$ ; 20 s:  $F_{1,30} = 10.32$ ,  $P = 0.003$ ) and decreased towards the end of the mobbing period (with time<sup>2</sup>; 5 s:  $F_{1,102} = 5.40$ ,  $P = 0.022$ ; 20 s:  $F_{1,30} = 5.06$ ,  $P = 0.032$ ).

In contrast, chickadee calling rate did not change significantly with titmouse calling rate at either time scale (separate repeated measures models for each time scale; model: chickadee calling rate = titmouse calling rate + time + time<sup>2</sup>; 5 s:  $F_{1,171} = 0.04$ ,  $P = 0.84$ ; 20 s:  $F_{1,36} = 0.86$ ,  $P = 0.36$ ), although chickadee calling rate initially increased with time (5 s:  $F_{1,171} = 11.63$ ,  $P = 0.0008$ ; 20 s:  $F_{1,36} = 16.78$ ,  $P = 0.0002$ ), then decreased towards the end of the mobbing period (with time<sup>2</sup>; 5 s:  $F_{1,171} = 0.41$ ,  $P = 0.52$ ; 20 s:  $F_{1,36} = 5.25$ ,  $P = 0.027$ ).

For the periods of nuthatch–chickadee mobbing, three of the 11 playbacks contained only screech-owl monotonic trills, seven contained mobbing calls in combination with monotonic trills, and one contained only mobbing calls. Because playback type and time



**Figure 1.** (a) Proportion of mobs initiated by each species ( $N = 27$  playbacks). (b) Proportion of mobs in which each species was present but not the initiator compared to all playbacks for which each species was not the initiator (i.e. present or not). For example, chickadees were not the first to arrive in 21 of the 27 playbacks. In 12 of those playbacks, they arrived after another species began mobbing and did not arrive in 9 playbacks (proportion of response to mobs already initiated = 0.57).



**Figure 2.** Pairwise scatter plots of simultaneous distance from the owl model for the closest individual of each species. (a) Chickadee distance as a function of nuthatch distance; (b) titmouse distance as a function of chickadee distance; (c) titmouse

since a playback call (owl or mobbing call) did not affect calling rates, these variables were dropped from the models of nuthatch–chickadee calling rate (Supplementary Information I: Table S4).

Nuthatch calling rate increased with chickadee calling rate during the playback at both timescales (separate repeated measures models for each time scale; model: nuthatch calling rate = chickadee calling rate + time + time<sup>2</sup>: 5 s:  $F_{1,372} = 7.71$ ,  $P = 0.006$ ; 20 s:  $F_{1,89} = 9.65$ ,  $P = 0.003$ ) and decreased towards the end of the mobbing period when calling rate was measured at larger scales (with time<sup>2</sup>; 20 s:  $F_{1,373} = 4.60$ ,  $P < 0.0001$ ; Fig. 4).

Similarly, chickadee calling rate increased with nuthatch calling rate at both timescales (separate repeated measures models for each time scale; model: chickadee calling rate = nuthatch calling rate + time + time<sup>2</sup>: 5 s:  $F_{1,372} = 5.08$ ,  $P = 0.025$ ; 20 s:  $F_{1,89} = 6.75$ ,  $P = 0.01$ ; Fig. 5). Chickadee calling rate also increased with time at both scales (5 s:  $F_{1,372} = 33.07$ ,  $P < 0.0001$ ; 20 s:  $F_{1,89} = 23.56$ ,  $P < 0.0001$ ) and decreased towards the end of the mobbing period (with time<sup>2</sup>; 5 s:  $F_{1,372} = 33.44$ ,  $P < 0.0001$ ; 20 s:  $F_{1,89} = 20.61$ ,  $P < 0.0001$ ).

#### *Interspecific asymmetries in individual call delivery patterns*

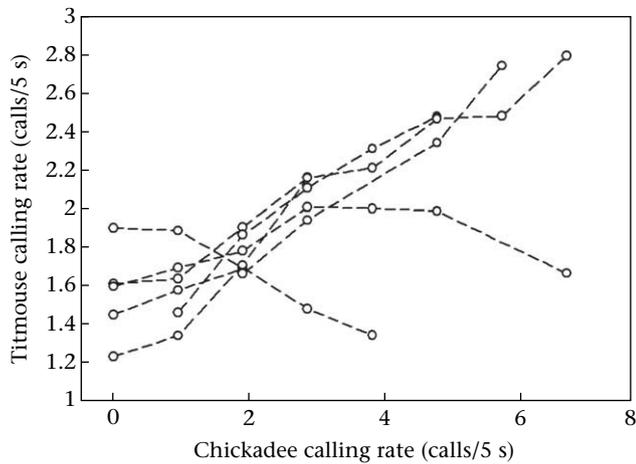
Mobbing calls were not followed more closely than expected by chance by calls of a heterospecific. The randomization simulations detected an overall difference between the three patterns tested for each reciprocal species pair: observed, random, and following (overall ANOVA for each species pair and following order: chickadee following nuthatch:  $F_{3,39} = 49.30$ ,  $P < 0.0001$ ; nuthatch following chickadee:  $F_{3,39} = 19.76$ ,  $P < 0.0001$ ; chickadee following titmouse:  $F_{3,15} = 4.29$ ,  $P = 0.023$ ; titmouse following chickadee:  $F_{3,15} = 4.39$ ,  $P = 0.021$ ). However, for both reciprocal species pairs, the observed percentages of significant Kolmogorov–Smirnov tests did not differ from those of the random calling pattern (Tukey multiple comparison test: chickadee following nuthatch:  $t_{39} = 0.16$ ,  $P_{\text{adj}} = 0.87$ ; nuthatch following chickadee:  $t_{39} = 1.45$ ,  $P_{\text{adj}} = 0.155$ ; chickadee following titmouse:  $t_{15} = 0.01$ ,  $P_{\text{adj}} = 0.99$ ; titmouse following chickadee:  $t_{15} = 0.09$ ,  $P_{\text{adj}} = 0.93$ ) and were significantly less than the percentages that were significant based on the respective hypothetical following pattern (chickadee following nuthatch:  $t_{39} = 10.35$ ,  $P_{\text{adj}} < 0.0001$ ; nuthatch following chickadee:  $t_{39} = 5.66$ ,  $P_{\text{adj}} < 0.0001$ ; chickadee following titmouse:  $t_{15} = 2.91$ ,  $P_{\text{adj}} = 0.012$ ; titmouse following chickadee:  $t_{15} = 2.99$ ,  $P_{\text{adj}} = 0.009$ ; Fig. 6).

## DISCUSSION

### *Directionality of Potential Vocal Information Flow in Multispecies Mobbing*

Our results suggest that the potential vocal information flow among species during mobbing differs substantially from when the same species are in a mixed-species foraging flock. Nuthatches' unexpected role in the facilitation of multispecies mobbing may result in a highly multidirectional vocal interaction among these three species. Nuthatches responded first to the greatest percentage of playbacks, nuthatch mobbing onset times were correlated with those of chickadees, nuthatches called at high rates during mobbing and remained closest to the owl. The strong mobbing behaviour consistently shown by both nuthatches and

distance as a function of nuthatch distance. Each circle represents the position of each species at a single point in time after the start of playback. The size of the circle represents the number of observations in that category (pooled across all playbacks). The dashed line is a reference line assuming equal distances for each species to the owl model.



**Figure 3.** Effect of chickadee calling rate on titmouse calling rate (per 5 s interval). Each dashed line represents the least-squares means for a single playback ( $N = 7$  playbacks) from the full repeated measures mixed model (model:  $\ln(\text{titmouse rate}) = \text{chickadee rate} + \text{time} + \text{time}^2 + \text{chickadee rate} \times \text{time} + \text{time}$  in mobbing period; overall effect of chickadee rate:  $\beta = 0.14 \pm 0.06$ ).

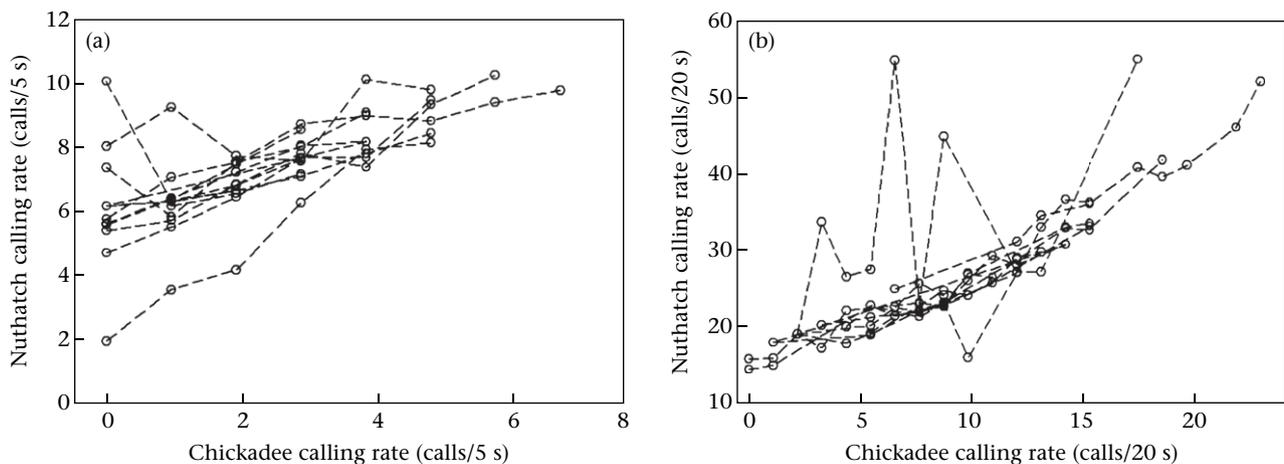
chickadees compared to the weak and variable mobbing by titmice suggests that the flow of vocal information during mobbing may often be from nuthatches or chickadees to titmice. Nuthatches may be important sources of local information about the presence of stationary predators because they have small territories relative to the home range size of flocks of chickadees and titmice (Offutt 1965; Grubb & Pravosudov 1993; Mostrom et al. 2002).

Differences in mobbing strategy between species are likely to be related to species-specific predation risk, physiological or structural constraints on vocal mobbing, and the constraints or benefits of conspecific sociality. Nuthatches' strong mobbing behaviour may be linked to the same factors that cause them to be satellite species in mixed-species foraging flocks (Dolby & Grubb 1998). The combination of a foraging position on a nonstandard substrate that obstructs vigilance (facing the tree trunk) (Lima 1992) and risk from an unknown owl in a small territory would make intense mobbing the best strategy when an owl gives away its location by calling. Because chickadees and titmice occur in conspecific social groups and use a foraging style that allows more vigilance relative to nuthatches (Grubb & Pravosudov 1994; Mostrom et al. 2002), the

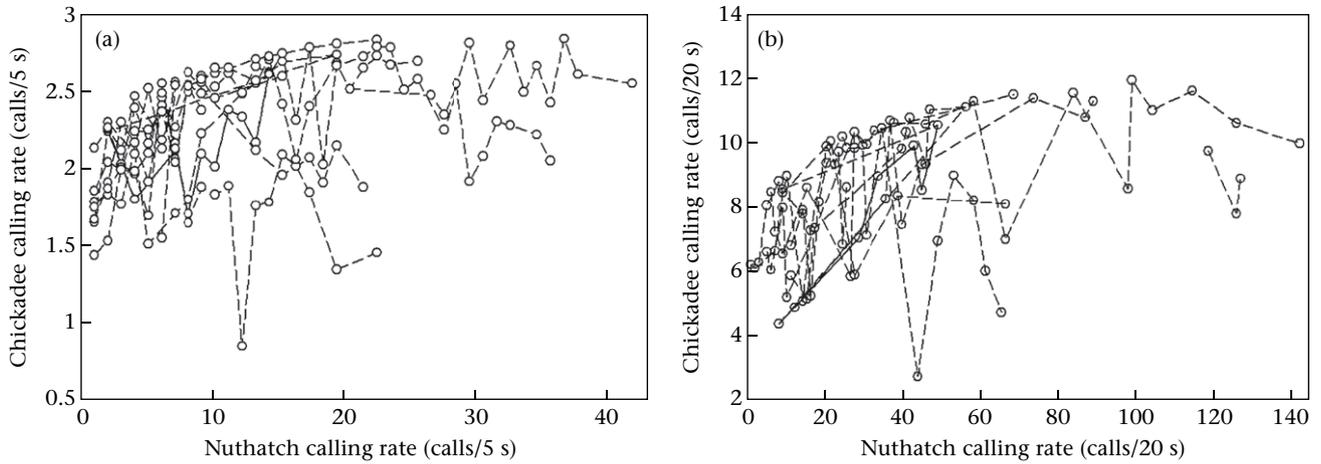
overall risk to these species from a distant owl may be lower. We did not attempt to separate the potential mechanisms underlying nuthatches' strong first response tendency; that is, their closer proximity to the owl at the start of the playback, their greater ability to detect the owl playback (Lucas et al. 2002, 2007), or their greater tendency to mob an owl (Pius & Leberg 1998). However, some of our observations did suggest that nuthatches may have had a greater tendency to mob before other species had approached the owl model. On three occasions when chickadees were present within 30 m but had not yet begun mobbing after the onset of playback, the chickadee(s) flew directly to within 5 m of the owl only seconds after a nuthatch began mobbing.

Despite investigations into mobbing function (Frankenberg 1981; Flasskamp 1994), the social transmission of predator identity (Curio et al. 1978; Vieth et al. 1980), and the potentially cooperative nature of nest defence mobs (Krams & Krama 2002; Olendorf et al. 2004; Krams et al. 2008), interspecific asymmetries in mob participation and their consequences remain largely unexplored. In contrast, behavioural asymmetries among species in mixed-species foraging flocks have received substantial attention (Bell 1980; Diamond 1987; Jullien & Thiollay 1998; Greenberg 2000; Goodale & Kotagama 2005b). Additionally, in many mixed-species nesting associations, individuals of smaller and more defenceless species place their nests close to those of aggressive protector species (reviewed in Caro 2005). It seems likely that particular species may also play central roles in multispecies mobbing behaviour if they use loud and harsh mobbing calls, have high rates of calling, or make close physical approaches towards the predator. If these asymmetries are consistent, they will set the stage for a consistent directionality of interspecific vocal information flow in multispecies mobbing as often occurs in mixed-species flocking behaviour.

Goodale & Kotagama (2006a) examined mobbing call mimicry by the greater racket-tailed drongo, *Dicrurus paradiseus*, a nuclear species in mixed-species foraging flocks of Sri Lanka, but did not report observations on the relative frequency of mobbing behaviour by different species in the flocks as they did for alarm calls (Goodale & Kotagama 2005a). The presence of particular prey species with particular mobbing tendencies and the presence of particular predators may change the species dynamics of a mob assemblage. For example, in contrast to our findings of variable and weak mobbing behaviour in tufted titmice, bridled titmice, *Baeolophus wollweberi*, are usually the first to locate and mob northern pygmy-owls in the mixed-species foraging flocks of southwestern North America (Nocedal & Ficken 1998). Northern pygmy-owls are



**Figure 4.** Effect of chickadee calling rate on nuthatch calling rate (a) per 5 s interval and (b) per 20 s interval. Each dashed line represents the least-squares mean values for a single playback ( $N = 11$  playbacks) from a repeated measures mixed model (model:  $\ln(\text{nuthatch rate}) = \text{chickadee rate} + \text{time}$ ; overall effect of chickadee rate: 5 s:  $\beta = 0.075 \pm 0.027$ ; 20 s:  $\beta = 0.059 \pm 0.019$ ).

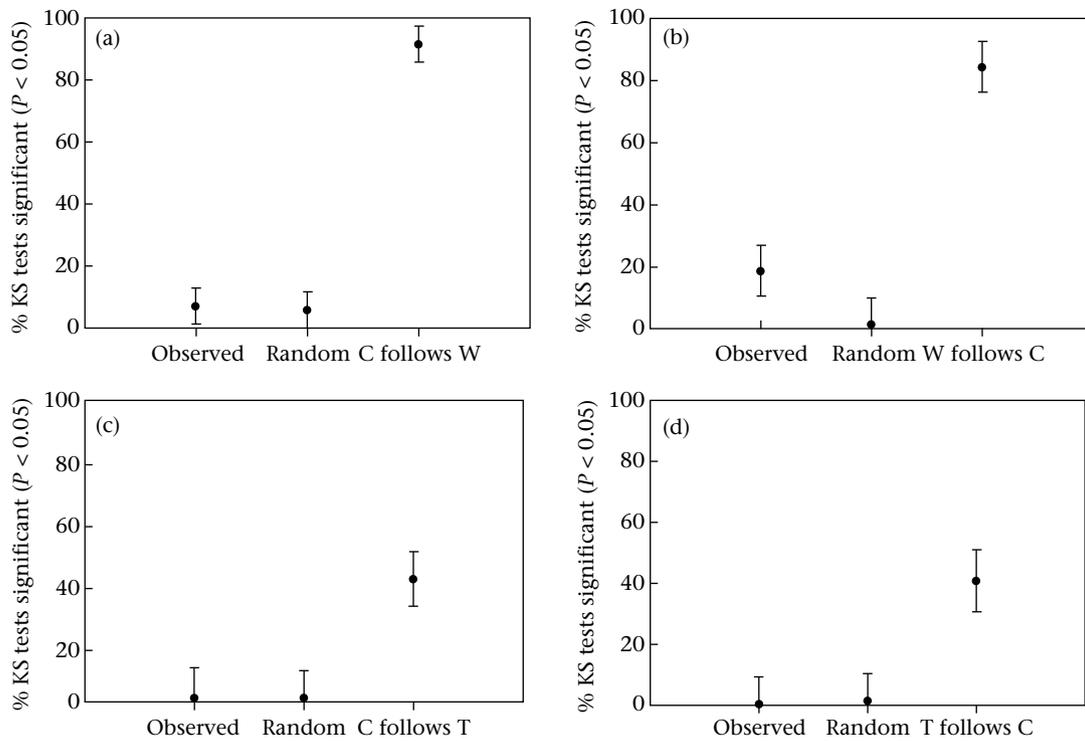


**Figure 5.** Effect of nuthatch calling rate on chickadee calling rate (a) per 5 s interval and (b) per 20 s interval. Each dashed line represents the least-squares mean values for a single playback ( $N = 11$  playbacks) from a repeated measures mixed model (model: chickadee-rate =  $\ln(\text{nuthatch rate}) + \text{time} + \ln(\text{nuthatch rate}) \times \text{time}$ ; overall effect of nuthatch rate: 5 s:  $\beta = 0.21 \pm 0.09$ ; 20 s:  $\beta = 1.23 \pm 0.47$ ).

common diurnal predators of small birds and may thus be more threatening than screech-owls (Holt & Petersen 2000). It is also possible that the behaviour of the predator may influence mob assemblage and species' roles in a mobbing association through changes to the relative risk faced by each species. While nuthatches show strong mobbing behaviour in response to a stationary and vocalizing eastern screech-owl, it is possible that nuthatches would show reduced mobbing in response to a more dangerous active or silent owl. We observed one instance of birds mobbing a live calling owl in the field. Both nuthatches and titmice approached to within 10 cm of this owl.

*Interspecific Interactions during Mobbing Behaviour*

Although our results suggest that nuthatches may play a key role in the initiation of mobbing behaviour, both chickadees and nuthatches appear to contribute to the overall mobbing intensity after the onset of mobbing behaviours. Regardless of which species tend to initiation mobbing, the general phenomenon of interspecific interactions during mobbing may be common. Although multispecies mobbing choruses have been previously reported, the behavioural dynamics of these choruses have not been examined. Hypotheses explaining the apparent clumping of mobbing calls



**Figure 6.** Percentage of significant Kolmogorov-Smirnov tests ( $N = 1000$ ) from randomization simulations comparing simulations conducted using the observed temporal calling patterns and simulations conducted using two known patterns (random versus following, a pattern where the following species calls on average 0.5 s after the leading species). The patterns tested were as follows: (a) chickadee calls follow nuthatch calls, (b) nuthatch calls follow chickadee calls, (c) chickadee calls follow titmouse calls and (d) titmouse calls follow chickadee calls. C: chickadee; W: white-breasted nuthatch; T: titmouse.

during single-species mobbing (Ficken 1989) have been rarely discussed and are untested. We hypothesized that if mobbing intensity is correlated across species, this may be apparent in positive feedback among species' calling rates. Alternatively, heterospecific behaviour may simply represent simultaneous but uncorrelated responses to the same predator stimulus, or heterospecific calls may actually interfere with communication among conspecifics.

Our results suggest that positive feedback does occur between the mobbing intensity of heterospecifics, as indicated by calling rate. However, randomization simulations showed that the correlation of calling rates was not driven by the tendency of individuals to call when a particular 'nuclear' species calls. The resultant pattern was a period during which many individuals of all species call frequently with calls often overlapping, creating a random chorus of noise. Such a pattern contrasts with the hypothesis that heterospecific calls may interfere with conspecific communication when conspecific communication is important, which would result in antiphonal patterns of calling between species (Brumm 2006). The interspecific correlation of calling rates can be generally explained under the hypothesis that mobbing serves to reduce the likelihood of predator attack through physical and vocal harassment (Curio 1978) and that this behaviour is costly (Curio & Regelmann 1986; Poiani & Yorke 1989; Sordahl 1990). However, the correlation of calling rates during mobbing supports two non-exclusive possibilities regarding the costs and benefits of mobbing for small birds.

First, coordination of vocal mobbing intensity with other species may dilute the risk of predation from the owl itself or from dangerous aerial predators (Ficken 1989), particularly if the species already mobbing is calling at a very high rate. The cost of high rates of calling could be substantial (Krams 2001; Krama & Krams 2005; Krams et al. 2007); *Accipiter* hawks interrupted several of our mobbing playbacks. If correlated fluctuations in vocal rate across species are linked to individual movements during mobbing, acoustic cues of heterospecific mobbing intensity could be used to coordinate movements towards the owl. Acoustic coordination of mobbing intensity would allow greater allocation of visual attention towards the owl and towards potential predators attracted by the noise and commotion of mobbing (Smith 1969). Although it is unclear whether the correlations of calling rate that we found were linked to correlated movements by both species towards and away from the owl model, previous work suggests this possibility. Curio & Regelmann (1985) found that mobbing great tits increased their calling rate during each approach towards a predator, but not during retreats, and they engaged in frequent approaches and retreats. Curio & Regelmann (1985) suggested that vocal behaviour during mobbing is linked to physical proximity to the predator. The threat from the predator may increase with proximity and so calling may be used to mitigate this risk by interfering with the predator's attention.

Second, if a coordinated group response is necessary for production of sufficient noise to harass the predator successfully or to attract larger mobbing partners (Curio 1978; Caro 2005), intense bouts of calling may occur irrespective of the calling individuals' momentary positions. Studies of owls' response to mobbing have found that owls increase movements while being mobbed, change or leave their roosts during or after mobbing events, and may have evolved cryptic roosting behaviours and plumage characteristics to avoid and confuse mobbing birds (Flasskamp 1994; Pavey & Smyth 1998; Deppe et al. 2003; Sunde et al. 2003; Hendrichsen et al. 2006). However, vocal constraints on calling rates and the small physical size of these birds may make sustained calling unprofitable without a large mobbing group or the attraction of larger, more powerful species. In strong support of this idea, Gehlbach (1994)

reported that eastern screech-owls were never flushed by multi-species mobs without the presence of a blue jay, *Cyanocitta cristata*, in observations of over 100 actual mobbing events. Similarly, during an observation of an actual mobbing event, we also observed a screech-owl immediately retreat into its cavity upon the arrival of blue jays, while it had been unresponsive to prior harassment by titmice and nuthatches.

There have been several investigations into the role of vocal information flow in the formation of heterospecific social groups (Goodale & Kotagama 2005b; Goodale & Kotagama 2006b) and many into the interspecific relevance of antipredator behaviours (Fitzgibbon 1990; Oda & Masataka 1996; Bshary & Noe 1997; Ramakrishnan & Coss 2000; Magrath et al. 2007; Lea et al. 2008). Recent work has also suggested that some mobbing behaviour among conspecifics may be more complex than previously thought. Pied flycatchers, *Ficedula hypoleuca*, apparently use a tit-for-tat-like strategy when making the decision to aid a neighbouring conspecific in mobbing a nest predator (Krams et al. 2008). However, the general importance of heterospecific mobbing behaviour and heterospecific mobbing calls to multispecies mobbing remains unknown (Ficken 2000). We have shown that vocal interaction among a set of species that show heterospecific sociality extends to the multispecies mobbing association. In complex multispecies mobs, species' vocal contributions should not only result in a diverse chorus of information about predation risk (Goodale & Kotagama 2005a), but also facilitate positive feedback among species' mobbing intensity. This complexity suggests that interspecific mobbing associations could lead to the potential for interspecific vocal communication (Kostan 2002) and interspecific manipulation (Munn 1986; Ridley et al. 2007), in addition to interspecific eavesdropping on conspecific-directed or predator-directed signals (Sullivan 1984; Phelps et al. 2007). Both experimental and careful observational studies are needed to distinguish among alternative hypotheses for the role of heterospecifics and heterospecific vocalizations in multispecies mobbing.

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## Supplementary Material

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