

## Original Article

## Antipredator calls of tufted titmice and interspecific transfer of encoded threat information

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Birds in family Paridae (titmice and chickadees) produce complex and distinct alarm vocalizations in response to predator encounters. In 2 controlled aviary experiments, we tested for information transfer between 2 different species of parids. We first recorded the vocal and nonvocal alarm displays of captive tufted titmouse (*Baeolophus bicolor*) flocks responding to presentations of live predators and controls (no animal and quail). Second, we broadcast the recorded titmouse vocalizations to captive Carolina chickadees (*Poecile carolinensis*) and recorded their vocal and nonvocal responses. By evaluating the situational specificity of responses by, both, titmice (production specificity, H1) and chickadees (response specificity, H2) to their respective treatments, we could test for information transfer (H3) from titmice to chickadees. Analyses revealed that information content encoded in titmouse calls completely distinguished the different predation threats presented to them (confirming H1). Similarly, chickadee responses clearly distinguished the different predator threats encoded in titmouse calls they heard (confirming H2). Responses of the 2 species were, both, parallel and threat appropriate, confirming that heterospecific information transfer occurred (from titmice to chickadees; H3). Evidence abounds that parids convey important facilitative benefits to other species within Holarctic forest bird communities. We propose that information sharing about predation threats may underlie these benefits for species that participate in communication networks with parids and suggest titmice function as community informants. *Key words*: alarm calls, chickadee, heterospecific information transfer, mobbing, production and perception specificity, titmouse. [*Behav Ecol*]

## INTRODUCTION

Perhaps the most important of situations animals face is the risk of death or mortal injury during predator encounters (Lima 2009). Whereas direct attack obviously reduces individual fitness, nonlethal predation threats can reduce prey fitness in a variety of ways (Lima and Dill 1990; Lima 1998; Creel and Christianson 2008), including restriction of access to resources as a result of fear-based alteration of use of space (Dolby and Grubb 1998; Brown et al. 1999; Cresswell 2008). Accurate and precise information about predator quality, location, and activity can ease fear-based niche constriction by improving estimation of predation risk and effectiveness of predator avoidance (Griffin 2004; Fletcher and Sieving 2010). Socially derived information about predators is widely available in animal communities in the form of alarm calls and other vocalizations that encode prey species' perceptions of predation risk (Klump and Shalter 1984; Caro 2005; Sieving et al. 2010). Most alarm calls are considered to be overtly social and generally honest signals directed at kin (Maynard-Smith and Harper 2004; Otter 2007). It follows then that in diverse communities of animals, species

that share predators should be under strong selection pressure to accurately interpret each other's alarm calls.

The structures and social functions of alarm vocalizations are well-characterized in vertebrates, especially for certain birds (e.g., Hailman 1989; Otter 2007; Radford and Ridley 2007; Templeton and Greene 2007). Moreover, alarm calls are frequently used by heterospecifics through a process called interceptive eavesdropping (e.g., Dall et al. 2005; Peake et al. 2005; Koboroff and Kaplan 2006) or the use of alarm calls by nonkin. Through this process of eavesdropping, predator alarm signals likely represent the most frequent form of social communication across taxa (e.g., Nuechterlein 1981; Seyfarth and Cheney 1990; Blumstein 1995; Shriner 1998; Windfelder 2001; Bloomfield et al. 2005; Ellis 2008). The use of heterospecific alarm calls by animals occurs mostly among animal eavesdroppers of similar body size to signalers (see Templeton and Greene 2007) suggesting alarm communication networks are comprised of fellow prey species (Caro 2005). However, taxonomic similarity within alarm networks can vary from quite similar (within orders) to very different (between classes of vertebrates; Hoeksema and Schwartz 2001; Wong et al. 2005; Langham et al. 2006; Ratcliffe et al. 2007; Schmidt et al. 2008; Welbergen and Davies 2009). Our interest was in determining how accurately the information encoded in alarm calls can be transferred between different species.

We experimentally addressed the mechanics of information transfer between 2 species of birds in family Paridae. Parid species participate in a well-characterized alarm-calling communication network that is geographically widespread and

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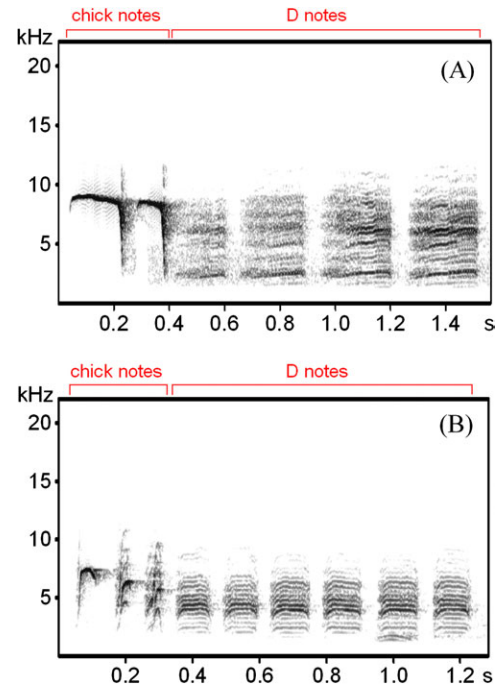
engages many nonparid species as participants (Hurd 1996; Sieving et al. 2004; Langham et al. 2006; Schmidt et al. 2008), thereby providing opportunity for field tests of how animals perceive, process, share, and respond to ecologically and socially important information (Schmidt et al. 2010; Sieving et al. 2010). Our design involved 2 linked aviary experiments. In the first (production) experiment, presentations of different live predators were made to one species, whose response behaviors were recorded. Then in a second (perception) experiment, the vocalizations produced in the first experiment were played to a second species whose responses reflected whether they perceived the same predation threats (types and intensities) as the respondents in the first experiment. If individuals in the first experiment (with live predators) produce unique responses to each stimulus, then this is termed ‘situational (production) specificity’ (H1). If in the second experiment respondents who only hear the calls given to predators also produce unique and distinctive responses, then this is termed “situational (perception) specificity” (H2; Evans et al. 1993; Macedonia and Evans 1993). Finally, confirmation that a transfer of predator-specific information from the first to the second species occurs lies in whether responses of both groups are appropriate antipredator behaviors for each predator species, whether directly observed or not (H3). This controlled experimental approach has previously been applied to intraspecific information transfer (Marler et al. 1986); here we apply this powerful experimental design to interspecific transfer of information.

## MATERIALS AND METHODS

### Study species and their antipredator calls

We selected 2 parid species that inhabit woodlands in Florida. Tufted titmice (*Baeolophus bicolor*) and Carolina chickadees (*Poecile carolinensis*) are both in family Paridae, and though they are in different tribes, they share the same basic alarm communication system (Hailman 1989; Soard and Ritchison 2009; Courter and Ritchison 2010; Sieving et al. 2010; see below). The 2 species are sympatric; they occupy similar habitats and participate in winter foraging flocks (Brawn and Samson 1983; Farley et al. 2008) where titmice are socially dominant to chickadees (Waite and Grubb 1988; Cimprich and Grubb 1994). Titmice are “nuclear” species, around which mixed-species foraging flocks (6–15 satellite species) form during the winter months (Greenberg 2000; Fernandez-Juricic 2000; Farley et al. 2008; Contreras and Sieving 2011). Tufted titmice, like other nuclear species, manifest behavioral traits that support information transfer to con- and heterospecifics, including strong intraspecific sociality, high vocal complexity (variable predator alarm call structure, a variety of notes and call types, and variable production patterns of the latter; Freeberg 2008; Bartmess-LeVasseur et al. 2010), high vigilance, and overt aggression toward perched predators (e.g., Munn and Terborgh 1979; Gaddis 1983; Hutto 1994; Goodale et al. 2010). Tufted titmice (and other parid) antipredator calls stimulate vigorous mixed-species predator mobbing aggregations, which can attract more than 30 species of forest birds in Florida (Morse 1973; Sieving et al. 2004; Langham et al. 2006; Nocera et al. 2008). Thus, cross-species information exchange is likely to be common between the tufted titmouse and potentially many other species that associate with them across their range (Eastern United States).

The Paridae exhibit 2 main types of antipredator vocalizations: the seet alarm call also known as the high zee, high see, aerial predator, or attack call, and the mobbing or scold call (known variously as, churring, seejert, chick-a-dee; Smith 1972; Gaddis 1979; Alatalo and Helle 1990; Lucas and Freeberg



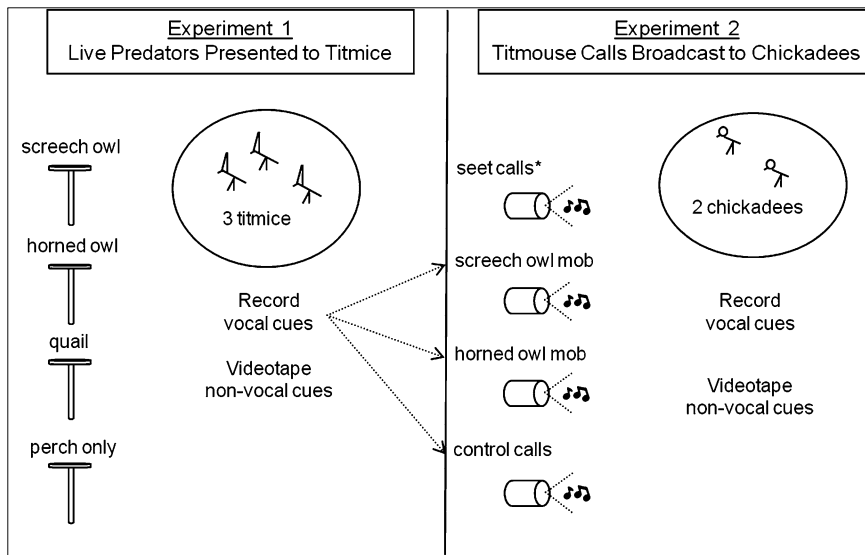
**Figure 1**

Sonograms of vocalizations analyzed in this study. The “chick-a-dee” mobbing calls of the tufted titmouse (A) and Carolina chickadee (B), each showing calls with fewer introductory chick notes (i.e., a shorter “chick sections”) than subsequent D notes (“D” sections). See Sieving et al. (2010) for sonogram of titmouse “seet” calls (like those used in experiment 2).

2007). Mobbing calls are variants of the “chick-a-dee” call, which is a complex call composed of combinations of introductory “chick” notes and subsequent “D” notes (dee notes, churr notes), with the number and presence of each note type being variable (Figure 1A,B; Latimer 1977; Hailman et al. 1985, 1987). The chick-a-dee call complex (or portions of it) is produced in many nonpredator situations in addition to being the dominant mobbing vocalization (Hailman 1989; Grubb and Pravosudov 1994; Freeberg et al. 2003; Freeberg 2008). Seet calls are frequently produced when a raptor flies close to parids, posing an immediate threat of aerial attack, whereas mobbing calls are typically given most vigorously to perched avian predators or snakes and mammals climbing or moving on the ground (Ficken 1989; Sieving et al. 2010). Mobbing calls are easily localizable and attract multiple prey species to harass (scold, approach, attack) perched or terrestrial predators (Hurd 1996; Langham et al. 2006). Whereas, seet calls are difficult to locate and their use results in either the complete, temporary cessation of all movements and vocalization (freezing) by nearby birds or in rapid escape to cover (Waite and Grubb 1988; Baker and Becker 2002; Templeton and Greene 2007; this study).

### Experimental design

We presented different live predators, representing known different predation threats, and controls to tufted titmice recorded their visual and vocal behaviors (experiment 1) and then played back titmouse vocalizations to a second species (Carolina chickadees) whose behaviors were also recorded (experiment 2; Figure 2). To fully characterize whether information encoded in the titmouse calls was transferred to chickadees, we tested 3 hypotheses. First,



**Figure 2**  
Diagrammatic representation of the experimental design (experiments 1 and 2). \*See text for sources of seet calls used in experiment 2.

vocalizations produced by tufted titmice to distinctly different perched live predators and controls would vary distinctly and predictably among treatments, demonstrating threat discrimination (H1, production specificity). Second, chickadee behavioral responses to playbacks of titmouse calls from the first experiment would vary distinctly and predictably among treatments (H2, response specificity). Finally, the third hypothesis is that information encoded in titmouse calls was reliably transferred to chickadees (H3, information transfer).

If H1 and H2 are valid, then the common prediction of both is that the responses in experiments 1 and 2 would uniquely identify each treatment (situational specificity; Macedonia 1990; Blumstein and Armitage 1997; Blumstein 1999; Griesser 2009). Alternatively, the null hypothesis for H1 and H2 is that vocal and visual responses of the titmice and chickadees would be indistinguishable among treatments. We could confirm that information transfer occurred or that chickadees understand the threats communicated by titmice in their calls (H3), if the responses of titmice and chickadees are parallel across treatments and if they reflect a risk-appropriate response to the treatment (predator type, level of danger). These predictions are reasonable because both species are known to encode predation threats in a similar way (Templeton et al. 2005; Soard and Ritchison 2009; Courter and Ritchison 2010). Alternative predictions for H3 include the following (suggesting no information transfer of predation threat occurred): chickadee responses would be inappropriate for the predator situation encoded in titmouse calls or chickadees could simply mimic the calls of titmice they heard. Both of these negative outcomes could be detected in analysis. Our judgment of predator threats and appropriate responses to the different treatments are based on Templeton et al. (2005), Templeton and Greene (2007), Sieving et al. (2010), and Soard and Ritchison (2009) who observed either perception and/or response specificity to similar predation threats for (collectively) 3 different parid species.

**Capture, handling, predator presentations, and playback trials**

Five groups of 3 titmice were captured in Gainesville, FL, between 13 October 2005 and 5 January 2006 at suburban seed feeders using mist nets and baited walk-in wire traps and were banded with uniquely colored leg bands. Only individuals that were captured together were subsequently

caged together to ensure familiarity and to minimize intra-group aggression. After capture, each group was released into a seminatural habitat within a 12 × 8 × 4 m outdoor aviary containing live potted trees and snags (USDA, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Gainesville, FL). After a 24-h habituation period, during which birds were monitored for normal feeding activity and general health, flocks were tested for each of 4 consecutive mornings. Ten pairs of Carolina chickadees were captured between 10 January 2006 and 5 March 2006 (all capture, housing, and handling as above; Hetrick 2006). In winter in Florida, we noted that titmice normally travel in groups of 3 or more and chickadees were nearly always in pairs. Thus, we adhered to this pattern in captivity to minimize social stress. Moreover, we elected to use social groups instead of lone individuals because alarm calls are social signals and might not be produced without social companions (Sieving et al. 2010). Sample sizes were estimated a priori using power analyses (for analysis of variance [ANOVA], global effects, 4 treatment groups, 4 response variables, error probability = 0.05; G\*Power, version 3.0.5), assuming a larger potential effect size for experiment 1 (0.40), where titmice faced live predators, than for experiment 2 (0.25), where chickadees only heard titmouse calls. Estimated necessary sample sizes were 5 titmouse groups and 9 chickadee pairs (exposed to 4 treatments each). We tested 5 titmouse groups and 10 chickadee pairs.

In experiment 1, we exposed titmice to 4 treatments representing 3 levels of predation threat (Figure 2): a live Eastern screech-owl (*Megascops asio*) representing a high-risk predator (one that preys often on small passerines), a live great horned owl (*Bubo virginianus*) representing a low-risk predator and 2 different controls, presentation of a live Northern bobwhite quail (*Colinus virginianus*, nonpredatory live animal), and an empty perch (no animal stimulus). The owls were nonreleasable, rehabilitated owls from Florida Wildlife Care, Inc. The 4 presentations were made in randomized order for each flock and spaced approximately 24 h apart. Diet studies indicate that both the Eastern screech owl (screech owl) and the Great horned owl (great horned) prey on birds, but small songbirds comprise a much greater proportion of the diet of the small, maneuverable screech owl than the larger, less maneuverable great horned, thus making the screech owl a higher risk predator for the titmice (reviewed in Templeton et al. 2005; Soard and Ritchison 2009).

Live birds presented to titmice in experiment 1 were settled on a 1.2-m high perch or small platform (for the quail) under a removable sheet approximately 10 min before each trial. Observers retreated to a camouflaged blind outside the aviary and removed the cover after 5 min using a pulley and string operated from the blind. Audio and video recordings were made for 5 min before uncovering the predator and for 7 min after that. Only the first 2 min after unveiling of the predator were included in analyses because most groups of titmice became habituated and stopped responding vigorously (calling, approaching) during the third minute after predators were unveiled. We used an omnidirectional microphone (Sennheiser ME 62) to record vocal responses directly onto a laptop using Raven Interactive Sound Analysis Software Version 1.1 with a sampling rate of 44 100 at 16-bit resolution. An observer (S.A.H.) was always present during trials and recorded the presence or absence of vocal responses that could not always be detected by the equipment (specifically, seet and chip notes).

In experiment 2, we played 4 acoustic treatments to chickadee pairs (Figure 2). The first 3 were recorded during experiment 1 in the presence of 1) high- (screech) and 2) low-risk (great horned owl) perched predators and 3) a procedural control (titmice vocalizations produced before live predators or controls were present). The fourth playback treatment consisted of recordings of titmouse seet calls. Five unique seet call recordings (2 min each, 123–217 seet calls per min) were obtained from another study with captive titmice responding to presentations of high threat predators in close proximity (accipiter, screech owl or cat;  $n = 4$  different titmice) and from one flock of free-living titmice responding to a predator (Sieving et al. 2010). For all playback treatments, there were 5 unique, independent exemplars (i.e., recordings from different individual titmice). Each of the 20 playback recordings (5 variants of each of 4 treatment types) was used twice for a total of 40 playbacks ( $n = 40$ ). Each of 10 chickadee pairs received one each of the 4 treatments presented in random order and spaced approximately 24 h apart. Audio stimuli were presented to chickadees using camouflaged speakers (RadioShack Model 40–1431) in the aviary on a 1.2-m platform. For each treatment, the speakers were randomly placed (at least 5 min prior to trial initiation) in 1 of 3 locations in the aviary in order to reduce directional habituation. Playback stimuli were broadcast for 2 min and then stopped. Recordings and behavioral observations (videotaping) began 5 min before playbacks were initiated, continued during the 2-min playback period, and for 5 min after the playback of titmouse calls ceased. Unlike titmice responding to the unveiling of live predators, chickadees did not always vocalize as soon as the playbacks began. Several flocks waited until after the playback stopped to vocalize most vigorously (i.e., during the third minute). Therefore, acoustic data used in statistical analyses of treatment differences for chickadees were extracted from the first 3 min after initiation of the playbacks. However, chickadee positional responses (approaches, freezing behavior) began immediately, and so we used the first 2 min after initiation of playback for those analyses. Other methods (videotaping, behavioral observations, and recording procedures) follow experiment 1.

Finally, we did not conduct any playbacks of titmice to other titmice or chickadees to other chickadees because in our experience, the broadcast of any conspecific calls generates aggressive–investigative behaviors in parids. Such responses should confound interpretation of antipredator behaviors with intraspecific aggression. Also, we assumed that signals produced by titmice and chickadees would reflect honest perceptions because deceit in alarm calling by social species is

thought to be rare due to kin selection or reciprocity (Maynard-Smith and Harper 2004). Because our study species occur in social/kin groups during the winter (Harrap and Quinn 1995; Hetrick 2006), we assumed that detectable responses to threats we presented reflected the birds' true perceptions (Blumstein and Daniel 2004; Kelley et al. 2008; Griesser 2009; Sieving et al. 2010).

### Response measures

Spectrographic analyses were performed on recordings using Avisoft SASLabPro 4.39. Sound files were finite impulse response low-pass filtered at 12 kHz and high-pass filtered at 1.8 kHz to edit out noise. The spectrogram parameters used were fast Fourier transformation = 512, frame size = 75%, window = hamming, and overlap = 87.5%. The notes in each call, or chick-a-dee call complex, were visually classified as introductory chick notes or subsequent D notes (Figure 1). Seet calls and chip notes were omitted from acoustic analysis because they were too soft to pick up across the large distances within the aviary and songs were omitted in order to focus on explicitly anti-predator calls (Latimer 1977; Gaddis 1979; Sieving et al. 2010). The observer in the blind could, however, detect the presence or absence of these calls during trials (Hetrick 2006).

Chick-a-dee calls were produced in 13 of the 20 presentations to titmice ( $n = 5/5$  screech,  $n = 4/5$  great horned, and  $n = 4/10$  controls), and in 21 of 40 chickadee trials (1/10 seet call trials, 7/10 screech, 8/10 great horned, and 5/10 controls). Because there were no differences between titmouse responses to procedural and experimental controls (empty perch and quail), those treatments were pooled (as controls) for some analyses. Only one titmouse contributed the majority of vocal responses in 4 out of the 5 flocks (probably the alpha male; Brawn and Samson 1983). If more than one titmouse responded, we isolated and measured the calls of the individual that called most frequently and clearly. We relied on other studies to select acoustic metrics to use (Baker and Becker 2002; Freeberg et al. 2003; Templeton et al. 2005; Table 1). Two kinds of acoustic data were summarized from recordings of both species' calls: 1) acoustic production patterns (numbers) of notes and calls (# chick, D notes, and chick-a-dee calls) and 2) acoustic structures of notes, calls, and sections of calls (e.g., duration, #, or proportion of note types or calls produced; Table 1). In analyses of acoustic production data, we used the total counts of each variable for the entire 2 min (titmice) or 3 min (chickadees) after initiation of stimuli (unveiling predators or starting playbacks of titmouse vocalizations). Because the taped calls of titmice being broadcast in experiment 2 trials sometimes overlapped with chickadee vocalizations, structural measures for some chickadee notes and calls produced could not be measured; but this did not restrict sampling because of the typically high numbers of notes and calls produced.

Nonvocal behaviors recorded during trials and analyzed statistically included: 1) the closest distance (m) any bird approached the stimulus and the proportion of birds that came 2) within 1 m and 3) within 3 m of the stimulus, respectively (Table 1; Templeton et al. 2005). Whether or not birds froze, becoming motionless was noted but not included in analyses.

### Data analysis and assessment of predictions

To address predictions for H1 and H2, that responses to stimuli (live predators or alarm calls) would be specific and identifiably different, we submitted all continuous metrics extracted from recordings to univariate ANOVA with the least significant

**Table 1**  
**Behavioral measures recorded and compared among treatments for titmice and chickadees**

Response measures	Treatment rankings from post hoc tests	
Acoustic structure	Titmouse	Chickadee
Mean duration D notes	gh > (con = scr), <i>n</i> = 1492 <sup>a</sup>	scr > gh > con, <i>n</i> = 775
Mean duration chick notes	gh > scr > con, <i>n</i> = 131	scr > (gh = con), <i>n</i> = 723
Mean duration chick-a-dee call	scr > gh > con, <i>n</i> = 266	scr > gh > con, <i>n</i> = 335
Mean # chicks/chick-a-dee call	scr < gh < con, <i>n</i> = 266	scr < (gh = con), <i>n</i> = 338
Mean # Ds/chick-a-dee call	scr > gh > con, <i>n</i> = 266	scr > gh > con, <i>n</i> = 338
Prop chick notes per call	scr < gh < con, <i>n</i> = 14	scr = gh, scr < con, gh = con, <i>n</i> = 27
Mean # notes/chick-a-dee call	scr > gh > con, <i>n</i> = 266	scr > gh > con, <i>n</i> = 338
Acoustic production	Titmouse <i>N</i> = 20 <sup>b</sup>	Chickadee <i>N</i> = 30 <sup>b</sup>
Total # D notes	scr > gh > con	scr = gh, scr > con, gh = con
Total # chick notes	NS; scr = gh = con	scr = gh, scr = con, gh > con
Total # chick-a-dee calls	scr > (gh = con)	(scr = gh) > con
Visual behaviors	Titmouse <i>N</i> = 20 <sup>c</sup>	Chickadee <i>N</i> = 40 <sup>c</sup>
Closest approach (m)	scr < (gh = con)	scr < (gh = con) < seet
Prop w/in 1 m	scr > (gh = con)	scr > (gh = seet = con)
Prop w/in 3 m	scr > (gh = con)	scr > gh, scr = con, gh = con, scr > seet, gh = seet, con > seet

Results for acoustic structure and production measures were summarized over the first 2 min after presentation of predator stimuli in titmouse trials and for 3 min after initiation of titmouse playbacks in chickadee trials. Visual behaviors were summarized over the first 2 min after initiation of stimuli in both titmouse and chickadee trials (see text). Abbreviations of treatments: con, control; gh, great-horned owl; scr, screech owl; and seet, seet call treatment. Significance was set at alpha = 0.05.

<sup>a</sup> *N* values corresponding to the total number of notes or calls produced by all flocks during trials in which any vocalizations were produced (13 and 21, respectively, for titmice and chickadees).

<sup>b</sup> *N* values corresponding to the total number of trials with the exception of seet trials for chickadees that did not elicit any vocalizations.

<sup>c</sup> The *N* value for the visual behaviors corresponds to the total number of trials.

difference post hoc test to conduct pairwise comparisons among the treatments. For analysis of the acoustic production data, we submitted the total numbers of calls or notes produced during a trial as the sample unit. In analyses of the acoustic structure data, we used measures on all the useable notes and calls produced during trials for each treatment. Therefore, samples sizes for the acoustic production data were the same as the number of trials, and for acoustic structure data, sample sizes were equal to the total number of measurable calls or notes produced in the trials. We transformed the data when appropriate to meet the assumptions of the analysis using  $\sqrt{n}$ ,  $\arcsin(\sqrt{n})$ , and  $\log(n + 1)$  transformations (Sokal and Rohlf 1995). For the visual behaviors, Kruskal–Wallis nonparametric test with Mann–Whitney *U* post hoc tests were used to generate pairwise comparisons. All statistical analyses were conducted using SPSS 11.5 and significance in all statistical tests was set at alpha = 0.05.

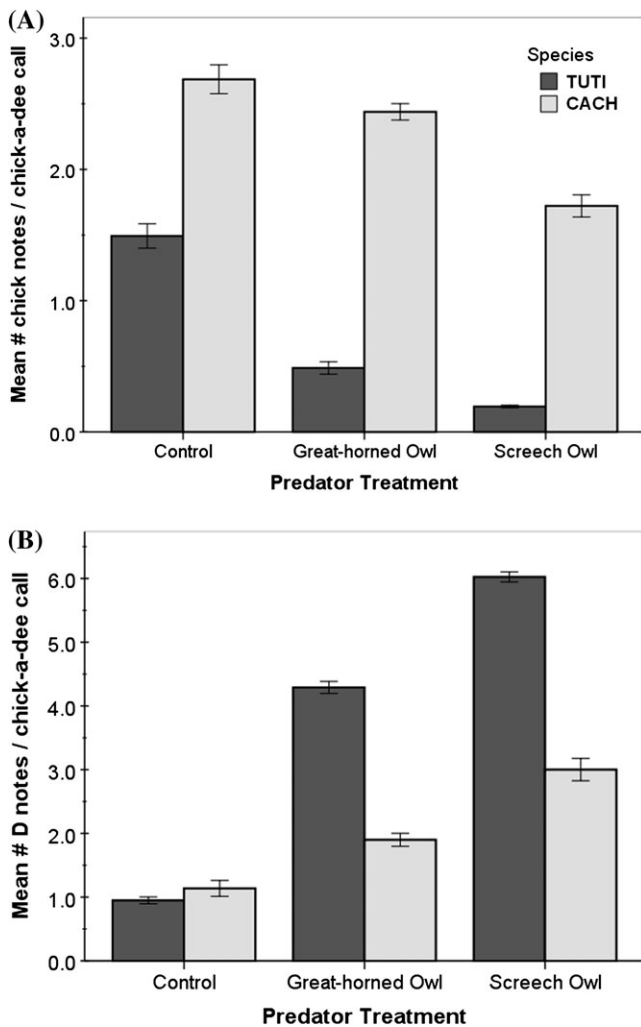
We used previous work on parid antipredator behavior to determine whether vocal and visual cues produced reflected appropriate responses to predation threat. Parids respond to higher threat levels by increasing their mobbing call rate and increasing the number of D notes per call (e.g., Apel 1985; Templeton et al. 2005; Courter and Ritchison 2010; Sieving et al. 2010). Some parids decrease or drop the introductory (chick) notes of the mobbing call while extending the D note section as the level of risk increases (Latimer 1977; Soard and Ritchison 2009). Parids also vary temporal measures and the acoustic structure of certain notes when presented with different predation threat levels (Templeton et al. 2005; Sieving et al. 2010). Regarding behavioral responses, the perched predator treatments should generate mobbing behaviors; more birds approaching more closely to more dangerous species is characteristic of appropriate predator mobbing behaviors (Caro 2005; Templeton et al. 2005; Langham et al. 2006; Soard and Ritchison 2009). In response to seet call playbacks, chickadees were expected to exhibit escape or highly vigilant behaviors include freezing, silence, fleeing, and/or alarm vocalizations (Haftorn 2000; Templeton and Greene 2007).

Regarding H3, information transfer, we predicted the following responses would be observed. In control and both owl treatments, chickadee acoustic structure and production and visual behaviors should closely parallel those of titmice (Hailman 1989). We assessed this using the multiple comparisons tests—their rankings should be parallel for both experiments. In the case of the seet call trials, however, the appropriate response for chickadees hearing seet calls is not to produce these calls, but rather to be still, or escape, and not make any noise (Morse 1973; Gaddis 1979; authors’ personal observations of multiple hawk attacks on mixed flocks where titmice gave seet calls and all nearby species went silent, dived to cover, or froze in place).

**RESULTS**

**Situational specificity in perception and response**

Considering only the 3 treatment types common to both experiments, both titmice and chickadees fully distinguished controls from great horned from screech owl treatments, confirming H1 and H2. Titmice separated the 3 treatments completely (i.e., pairwise comparisons all significant) based on 7 of 13 response measures (Table 1) including 6 of 7 acoustic structural traits (all except mean duration of D notes) and total number of D notes produced within 2 min. Chickadees cleanly separated the 3 treatments (i.e., all 3 pairwise comparisons were significant) based on 4 of 13 response measures, all of which were acoustic structural traits and including mean duration of D notes (in contrast to titmice, this measure was similar for control and screech owl treatments). Key patterns observed included an increase in the numbers and duration of chick-a-dee calls (Table 1) and number of D notes per call with increasing threat level of the predator (screech > great horned > control) for both species. As the number of D notes/chick-a-dee call increased, the number of chick notes/chick-a-dee call decreased, although this was more pronounced for titmice than chickadees (Figure 3A,B). Titmice



**Figure 3** Representative acoustic responses of titmice to predators and chickadees to playbacks of titmouse calls. (A) The mean number of chick notes per chick-a-dee call and (B) the mean number of D notes per chick-a-dee call, for each species given to the control, great horned, and screech owl treatments. TUTI, tufted titmouse and CACH, Carolina chickadee. Error bars = 1 standard error.

largely dropped chick notes from the chick-a-dee calls during screech owl treatments. Therefore, although both species produced the longest chick-a-dee calls and the most notes per call to the worst predator (screech owl), the 2 species varied their chick-a-dee call structure in subtly different ways. The screech owl treatment generated significantly different responses from the other 2 treatments for 11 of 13 measures for titmice and 8 of 13 for chickadees (Table 1), whereas the great-horned owl and controls were not distinguishable by as many measures. Rankings of treatments based on the 13 measures were largely parallel in both species except the duration of individual D and chick notes varied among treatments but not in the same pattern as the production of those notes. Titmice produced the longest D and chick notes in response to the great-horned owl but chickadees did the same to the screech owl (Table 1, Figure 4A,B).

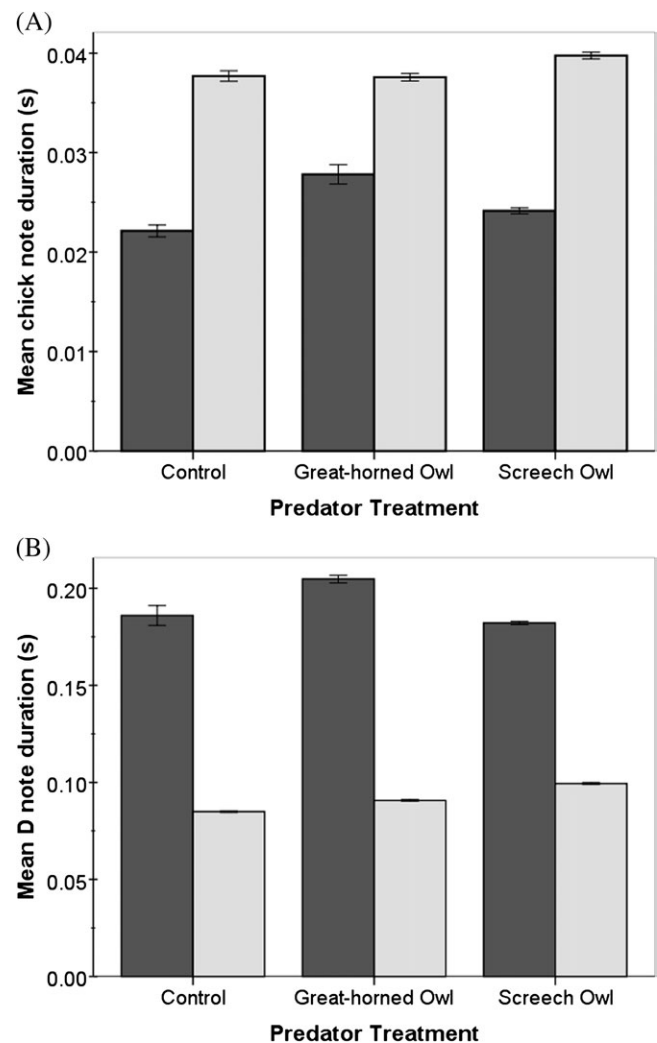
Finally, considering the seet call treatments experienced by chickadees, we observed responses not observed during other trials. Chickadee pairs did not stop being active in any of the playback trials except the seet playbacks in which they froze

(completely unmoving) for 100% of the 3 min experimental periods (often for many minutes after the playback stopped). The latter behaviors are reflected in the large approach distances (Table 1). Moreover, chickadees were completely silent in 9 of the 10 seet call trials, uttering no vocalizations.

## DISCUSSION

### Information transfer from titmice to chickadees

Titmouse acoustic responses were clear and concise in distinguishing among the threats they faced and chickadees clearly “got the message” from titmice. Titmouse calls we recorded in experiment 1 reflected their perceptions of 3 distinct situations: nothing or little to worry about (control, large owl) and detection of a perched predator worthy of vigorous mobbing behavior (small owl). Titmouse and chickadee responses to the large and small owl were similar to those of free-living conspecifics faced with similar situations (e.g., chickadees,



**Figure 4** Representative acoustic responses of titmice to predators and chickadees to playbacks of titmouse calls. See Figure 3A for relevant figure legend. (A) The mean duration of chick notes per chickadee call produced by titmice and chickadees in response to 3 treatments. (B) The mean duration of D notes per chickadee call produced by titmice and chickadees in response to 3 treatments. Error bars = 1 standard error.

Soard and Ritchison 2009; titmice, Courter and Ritchison 2010) signifying that we elicited typical and appropriate vocal signals from both species. With respect to situational specificity, our findings are consistent with similar analyses of parid acoustic structure variation in response to perched predators representing different kinds or degrees of predation threat (Baker and Becker 2002; Templeton et al. 2005; Sieving et al. 2010). Moreover, we observed consistently appropriate responses in all treatments for both species: mobbing behaviors in the owl treatments and extreme attack–escape reactions in the chickadee seet call treatments (freezing, silence, and retreat to edges of aviary, indicated by the largest approach distances; Table 1; Lima 1993). Taken altogether, results provide overwhelming confirmation of parallel situational specificity in both experiments (H1, H2), and that both species' behavioral responses in each treatment were highly appropriate for the stimuli received (e.g., Sieving et al. 2004; Langham et al. 2006; Templeton and Greene 2007; Courter and Ritchison 2010; Sieving et al. 2010). Therefore, our findings support the conclusion that accurate and precise information transfer occurred from titmice to chickadees (H3).

An alternative explanation for observed patterns in chickadee responses, other than the correct perception of threats encoded in titmouse calls, is that they simply copied or mimicked what they heard titmice doing. However, 3 lines of evidence contradict this alternative. First, chickadees in experiment 2 produced mobbing calls to the 2 predator species that were more similar to the calls of chickadees in Soard and Ritchison (2009; ratio of D to chick notes per chick-a-dee call produced) than to the titmice in our experiment 1. Second, chickadees in experiment 2 could not see titmice whose calls they heard, thus they could not copy their visual behaviors. Yet, chickadees had positional behaviors similar to those of titmice in our treatments (Table 1) and to those of free-living Carolina chickadees and other parids presented with similar treatments (Templeton and Greene 2007; Soard and Ritchison 2009). Finally, if chickadees were just copying what they heard then they should have produced their own version of seet calls when exposed to titmouse seet calls; but they produced no vocalizations whatsoever and exhibited freezing/escape behaviors not observed in any other treatment that were highly appropriate if we assume that chickadees perceived imminent attack (Marler 1955; Waite and Grubb 1988; Lima 1993; Templeton and Greene 2007). Avian alarm calls across taxa vary in acoustically similar ways with perceived predation risk (Klump and Shalter 1984) yet there is no general or specific evidence that this is ever a result of mimicry (Kelley et al. 2008). Therefore, given the parallel nature of both production and perception specificity across both experiments, and because chickadees are unlikely to have simply copied titmouse responses, we conclude that interspecific transfer of information encoded in titmouse calls occurred.

Despite the striking similarities in acoustic parameters of the 2 parids, we noted some subtle differences that could be important for characterizing antipredator communication within family Paridae. Both species relied heavily on varying the number of D notes per mobbing call with threat level but titmice appear to have a greater range of D note production (up to twice as many as chickadees; Figure 3B) whereas chickadees produced up to twice as many chick notes per mobbing call (Figure 3A). In this regard (high upper range of D note number per call), tufted titmice and black-capped chickadees may be more similar to each other than to Carolina chickadees (Freeberg et al. 2003; Templeton et al. 2005; Lucas and Freeberg 2007; Soard and Ritchison 2009; Sieving et al. 2010). Furthermore, the 2 species in our study altered the duration of their chick and D notes in different ways. Despite having parallel patterns of chick and D note numbers per call, chick-

adees identified the most dangerous owl with the longest notes, and titmice lengthened their notes for the less dangerous owl. The latter was unexpected for 2 reasons. First, titmice produced significantly longer seet notes in response to more dangerous predator threats in a companion study (Sieving et al. 2010) and, second, in general, longer alarm call notes in response to greater threats is the norm (e.g., Yorzinski and Vehrencamp 2009). Perhaps, titmice face a unique signaling constraint in mobbing call production in that their propensity to produce so many D notes per call prevents simultaneous lengthening of the same notes. Given the high degree of conservation of alarm call signals across the Paridae (Hailman 1989), both the similarities and differences in their production may be of significance in studies of information use within their communication networks (Schmidt et al. 2010; Sieving et al. 2010).

Finally, we could interpret the greater number of significant distinctions (multiple comparisons at  $P < 0.05$ ) among treatments encoded in titmice acoustic responses to reflect a greater degree of vocal complexity than that exhibited by chickadees (Table 1). Vocal complexity is commonly listed among the traits associated with nuclear species in mixed flocks of birds that forage together (Spencer et al. 2004; Gros-Louis et al. 2008). Tufted titmice are socially dominant to chickadees in foraging flocks in continental North America (e.g., Morse 1973; Gaddis 1983; Greenberg 2000; Farley et al. 2008). Moreover, mobbing aggregations form more readily around titmice (and their alarm calls) than around chickadee species (Sieving et al. 2004; Langham et al. 2006). We suggest that the sharing of high-quality (i.e., accurate, precise) information about predation threats that titmice perceive could help explain the strong attraction of diverse species to be around them (in winter foraging and mobbing flocks; Greenberg 2000; Langham et al. 2006; Sieving et al. 2010).

### Broader implications: parids as community informants and facilitators

We carefully documented efficient and accurate information transfer between 2 species of family Paridae. Six distinct experiments with 4 parid species now provide strong evidence that within the Paridae, significant variation in chick-a-dee mobbing call structure clearly conveys perceived threat levels (Templeton et al. 2005; Soard and Ritchison 2009; Sieving et al. 2010; Courter and Ritchison 2010) and, in turn, these perceptions can be accurately transmitted to other species that are competent listeners (Templeton and Greene 2007; this study). Situational specificity in parid mobbing calls was high across all 6 experiments, suggesting that parids can carefully assess and accurately communicate abundant, reliable, and redundant social information about threats. Moreover, tufted titmouse contact calls encode precise variations in perceptions of threat in a similar manner as the chick-a-dee mobbing call (Sieving et al. 2010). Therefore, even when titmice are not producing overt alarm calls, they are using abundant contact calls throughout the day, creating a near-constant flow of threat-relevant information. Because they are widespread (Holarctic), have broad habitat use patterns (forest, woodland, and shrubland) and are highly social with other species in foraging and mobbing aggregations (Harrap and Quinn 1995), parids may represent an unparalleled information source for a high number of forest bird species.

We suggest that members of family Paridae should be viewed as “community informants”, whose copious production and dissemination of antipredator information may significantly influence forest bird community dynamics. Both mobbing and seet calls of parids are overtly social signals (Haftorn 2000; Lucas and Freeberg 2007) that are highly conserved in their basic structure

across the family (in genera *Parus*, *Baeolophus*, *Poecile*). Therefore, these 2 types of calls are common in the environments of a great number of forest animals across the Holarctic. The variety and specificity of information that can be encoded in parid alarm calls is tremendous (Hailman 1989; Freeberg 2008; Sieving et al. 2010; this study), and it is clear that a large number of forest songbirds, and other prey species sympatric with parids, comprehend and utilize these calls (Hurd 1996; Sieving et al. 2004; Langham et al. 2006; Schmidt et al. 2008, 2010).

Further support for their roles as community informants comes from literature that implicates parids in a broad array of positive, facilitative interactions that support survival and reproduction of species that associate with them. The presence of tufted titmice expands foraging niche breadth for heterospecific flock mates (Dolby and Grubb 1998), increases time spent foraging (Sullivan 1984; Hogstad 1990), and increases over-winter body weight and survival (Dolby and Grubb 1998). The presence of tufted titmice also increases access to more open habitats for forest birds (Dolby and Grubb 2000; Rodriguez et al. 2001; Sieving et al. 2004), expanding the diversity of available resources and, potentially, home range size. In Scandinavia and North America, plots with enhanced densities of parids attract higher settling densities of migrant breeding birds (Thomson et al. 2003; Forsman et al. 2009). Such “heterospecific attraction” likely increases settlement efficiency in climates with contracted breeding seasons (Mönkkönen and Forsman 2002). Moreover, enhanced reproductive success may accrue to heterospecifics that nest in close proximity to parid nests (Forsman et al. 2002, 2007). Collectively, these works demonstrate that the “presence” of parids has positive fitness consequences. Given the attentive perception and use of titmouse (and other parid) calls by diverse heterospecifics (this study; Langham et al. 2006; Schmidt et al. 2008; Huang 2010), we propose that information sharing and facilitation can be linked.

The provision and use of constantly updated, high-quality information about predation threats could underlie all observed fitness benefits of parids to fellow prey species. Information can be a commodity for exchange in biological markets, or simply a by-product benefit to eavesdroppers that, in turn, can support decision-making enabling facilitation and mutualism within animal communities (Bradbury and Vehrencamp 2000; Hoeksma and Schwartz 2001; Chapuis and Bshary 2010; Leimar and Hammerstein 2010). Parids could also be communicating other kinds of information sought by heterospecifics, for example, about food resources (Marler et al. 1986; Mahurin and Freeberg 2009) or competitors (Betts et al. 2010). Thus, eavesdropping heterospecifics could be using parid cues to adjust time budgets and use of space to reduce stress and energetic costs of gathering food and information and avoiding predators (Digweed et al. 2005; Vitousek et al. 2007; Danchin et al. 2008; Schmidt et al. 2008). We have demonstrated (with experimental precision) that information encoded in titmouse calls influenced decision making in chickadees; both their use of space and choice of behaviors varied appropriately given the information we knew was encoded in titmouse calls. Our studies expand a growing body of work documenting diverse interspecific exchanges of information in animal communities and that parids, in particular, may provide information with important consequences for other species' behavior, distribution, and community structure (Seppänen et al. 2007; Goodale et al. 2010; Schmidt et al. 2010). Many woodland species throughout the Holarctic participate in social groups and information networks with parids (e.g., Hurd 1996; Sieving et al. 2004; Langham et al. 2006; Schmidt et al. 2008, 2010). If parids, as Holarctic community informants, enhance fitness for a fraction of the species that participate in antipredator communication networks with them, then we suggest that the role of parids may be far-reaching in avian community organization.

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