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'Chick-a-dee' calls of Carolina chickadees convey information about degree of threat posed by avian predators

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Individuals of many group-living species of birds respond to potential predators by giving alarm calls, and some species give different, spatially referential alarm calls in response to aerial predators (raptors in flight) and terrestrial predators (including perched raptors). In black-capped chickadees, *Poecile atricapillus*, characteristics of alarm calls also vary with predator size and level of perceived threat (Templeton et al. 2005, *Science*, **308**, 1934–1937). We examined whether the terrestrial alarm calls of Carolina chickadees, *P. carolinensis*, show similar variation. In 2007 and 2008, we monitored responses of eight flocks of Carolina chickadees in Madison County, Kentucky, U.S.A. to mounts of different species of raptors that varied in size. Chickadees responded to the raptors by uttering 'chick-a-dee' calls with different numbers and types of notes. Larger, lower-threat predators (e.g. red-tailed hawk, *Buteo jamaicensis*) elicited calls with significantly more introductory 'chick' notes and fewer 'dee' notes, whereas smaller, higher-threat predators (e.g. eastern screech-owl, *Megascops asio*) elicited calls with few or no 'chick' notes and significantly more 'dee' notes. In addition, playback experiments revealed that a greater percentage of Carolina chickadees responded to playback of 'chick-a-dee' calls previously given in response to a small predator than during playback of calls given in response to a large predator. These results suggest that the 'chick-a-dee' alarm call is a graded signal that informs conspecifics about the presence and behaviour (i.e. perched) of a predator and the degree of threat posed by that predator.

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Alarm calls often serve to alert members of a group to the potential threat of a predator, and several investigators have attempted to determine the type of information encoded in alarm calls (Seyfarth et al. 1980; Walters 1990; Stone & Trost 1991; Evans et al. 1993). Characteristics of the alarm calls of some species vary with the type of threat, and probably represent graded signals that inform conspecifics about the degree of perceived threat. For example, characteristics of the mobbing, or alarm, calls of black-capped chickadees, *Poecile atricapillus*, vary with predator size (Templeton et al. 2005). Specifically, Templeton et al. (2005) found a negative correlation between the number of 'dee' notes in 'chick-a-dee' calls and predator size (both wing span and body length) and suggested that the number of 'dee' notes conveyed information about the level of threat to conspecifics, with smaller, more manoeuvrable raptors eliciting more 'dee' notes because they posed a greater threat to chickadees.

Although black-capped and Carolina chickadees, *Poecile carolinensis*, give 'chick-a-dee' calls in similar contexts, the call of Carolina chickadees includes three B-note subtypes, whereas the A, C

and D notes remain similar (Fig. 1; Bloomfield et al. 2005). In both species of chickadees, the D note is the only one included in almost all 'chick-a-dee' calls (Charrier et al. 2004; Bloomfield et al. 2005) and, as just noted, variation in the number of D notes encodes information about predator size in black-capped chickadees (Templeton et al. 2005).

The vocal repertoire of Carolina chickadees has been described previously (Smith 1972; Freeberg & Lucas 2002; Freeberg et al. 2003; Clucas et al. 2004; Bloomfield et al. 2005). However, to date, no one has examined whether Carolina chickadees vary the characteristics of their 'chick-a-dee' call in response to different predators. We examined this possibility by exposing Carolina chickadees to various species of raptors and recording and analysing their 'chick-a-dee' calls. Following the protocol of Templeton et al. (2005), we also conducted experiments to determine whether the mobbing behaviour of Carolina chickadees varied when 'chick-a-dee' calls previously given in response to different predators were played back over speakers.

METHODS

We studied Carolina chickadees ($N = 8$ flocks, mean \pm SE flock size = 5.88 ± 0.55 birds, range 4–9 birds) during 15 January–8

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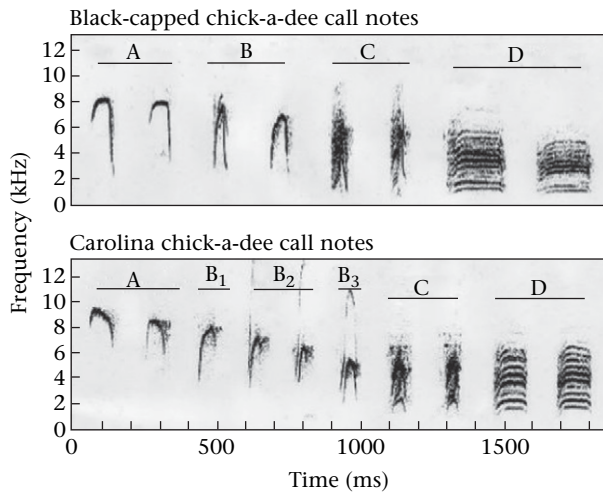


Figure 1. Sonograms of the 'chick-a-dee' calls of a black-capped chickadee and a Carolina chickadee. A, B and C notes are the 'chick' or S1 syllables; D notes are the 'dee' or S2 syllables (Source: Bloomfield et al. 2003).

March 2007 and 15 October 2007–18 February 2008. Study sites were widely spaced (minimum distance apart = 1.53 km) to ensure that each flock consisted of different chickadees (locations ≥ 250 m apart ensures that flocks are independent; Freeberg & Lucas 2002). Eight sites in Madison County, Kentucky, U.S.A. were selected based on presence of apparently suitable habitat. Dominant tree species at these sites included oaks (*Quercus* sp.), hickories (*Carya* sp.), black walnut, *Juglans nigra*, white pine, *Pinus strobus*, eastern red cedar, *Juniperus virginiana*, and northern catalpa, *Catalpa speciosa*. Feeding stations (0.6 \times 0.6 m treated plywood platforms hung from a tree branch at a height of 1 m) were placed at study sites and were stocked with about 1 kg of black-oil sunflower seed once or twice per week to ensure the presence of chickadees.

Experimental protocols were similar to those of Templeton et al. (2005). However, because we studied free-living chickadees rather than captive chickadees (Templeton et al. 2005), some changes in protocol were necessary.

Predator Presentations

Specimens (study skins) representing six species of raptors were used in our experiments, including skins of an eastern screech-owl, *Megascops asio*, American kestrel, *Falco sparverius*, sharp-shinned hawk, *Accipiter striatus*, Cooper's hawk, *Accipiter cooperii*, great horned owl, *Bubo virginianus*, and red-tailed hawk, *Buteo jamaicensis* (Fig. 2). Great horned owls and red-tailed hawks were considered low-threat predators that rarely, if ever, prey on Carolina chickadees (Preston & Beane 1993; Houston et al. 1998), whereas the others were predators either known to prey on Carolina chickadees or assumed capable of doing so (Ritchison & Cavanagh 1992; Curtis et al. 2006). For controls, we used a platform with no raptor present (the same platform used in the experiments with raptors) and a study skin of a ruffed grouse, *Bonasa umbellus*.

Presentation trials were conducted during 8 February–8 March 2007 and 14 December 2007–18 January 2008. One trial was conducted per flock per day and all trials were conducted between 0900 and 1700 hours. Subsequent trials with a particular flock were at least 2 days apart, with order of presentation of different raptors and controls randomized. Each trial was 10 min in duration and consisted of pre-presentation and presentation periods. Prior to each trial, one of us (C.M.S.) placed a raptor study skin in a life-like position, covered by a sheet, on a 1 m high platform located about

1 m from the feeding station and allowed a 5 min acclimation period and then stood about 5 m away. After the acclimation period, the sheet was removed, and C.M.S. returned to the same position 5 m away. Trials began once chickadees were detected either visually or audibly, and chickadees were monitored for 5 min.

For each trial, we noted (1) the number of chickadees present, (2) the closest distance any chickadee approached the control or study skin of a raptor, (3) the percentage of birds in the flock that came within 1 m and within 3 m of the control or study skin, and (4) the number of 'chick-a-dee' calls given by flock members during the 5 min trial. During trials, calls were recorded with a cassette recorder (Sony TCM-400DV) and a directional microphone (Sennheiser MKH 60). We also noted the percentage of birds in the flock responding to account for differences in flock sizes. This was calculated by dividing the variable of interest by the number of chickadees detected responding during each trial, either visually or audibly.

To examine possible differences in responses by the chickadees among treatments, we used a Friedman's test (χ^2_r , $\alpha = 0.05$) and made pairwise comparisons using Nemenyi's post hoc test ($\alpha = 0.05$). These tests are nonparametric analogues to the repeated measures ANOVA with a Tukey's post hoc test.

Acoustic Analyses

Raven software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) was used to analyse all chickadee calls recorded during the presentation experiments. For each experiment, we determined the number of each type of note in each 'chick-a-dee' call (A, B, C and D) and the total number of syllables (pooled notes) in each section of the call ('chick' = S1 syllables: A, B and C notes; 'dee' = S2 syllables: D notes; Fig. 1). For each experiment, we then determined the mean number of syllables and notes per call for each flock.

We examined variability in the mean number of syllables and notes per call among treatments with a Friedman's test and made pairwise comparisons using Nemenyi's post hoc test. For each species of raptor (and grouse) used in our experiments, we determined their average size (body length and wing span) using information provided by Bump et al. (1947), Gehlbach (1995), Houston et al. (1998) and Clark & Wheeler (2001). Using linear regression, we examined the relationship between raptor size (body length and wing span) and the mean numbers of S1 and S2 syllables uttered per call. We used average body size rather than simply measuring the study skins because wing span was not measurable and because we assumed that chickadees base their responses both on predator species' identity and on relative size rather than on individual size alone (Kullberg & Lind 2002).

Two characteristics of the 'chick-a-dee' call, the interval between the 'chick' and 'dee' sections and the duration of the first D note were further analysed because calls uttered by black-capped chickadees in response to large versus small raptors differ in these characteristics (Templeton et al. 2005). We measured these durations for randomly selected, high-quality calls produced by Carolina chickadees in response to a red-tailed hawk, a large, low-threat predator, and an eastern screech-owl, a small, high-threat predator. For analysis, we determined the mean value for each call characteristic for each flock ($N = 4$ calls per flock), and we used a Wilcoxon signed-ranks test to compare characteristics of calls uttered in response to the two predators.

Playback Experiments

We conducted playback trials using chick-a-dee calls previously recorded from Carolina chickadees during the presentation trials

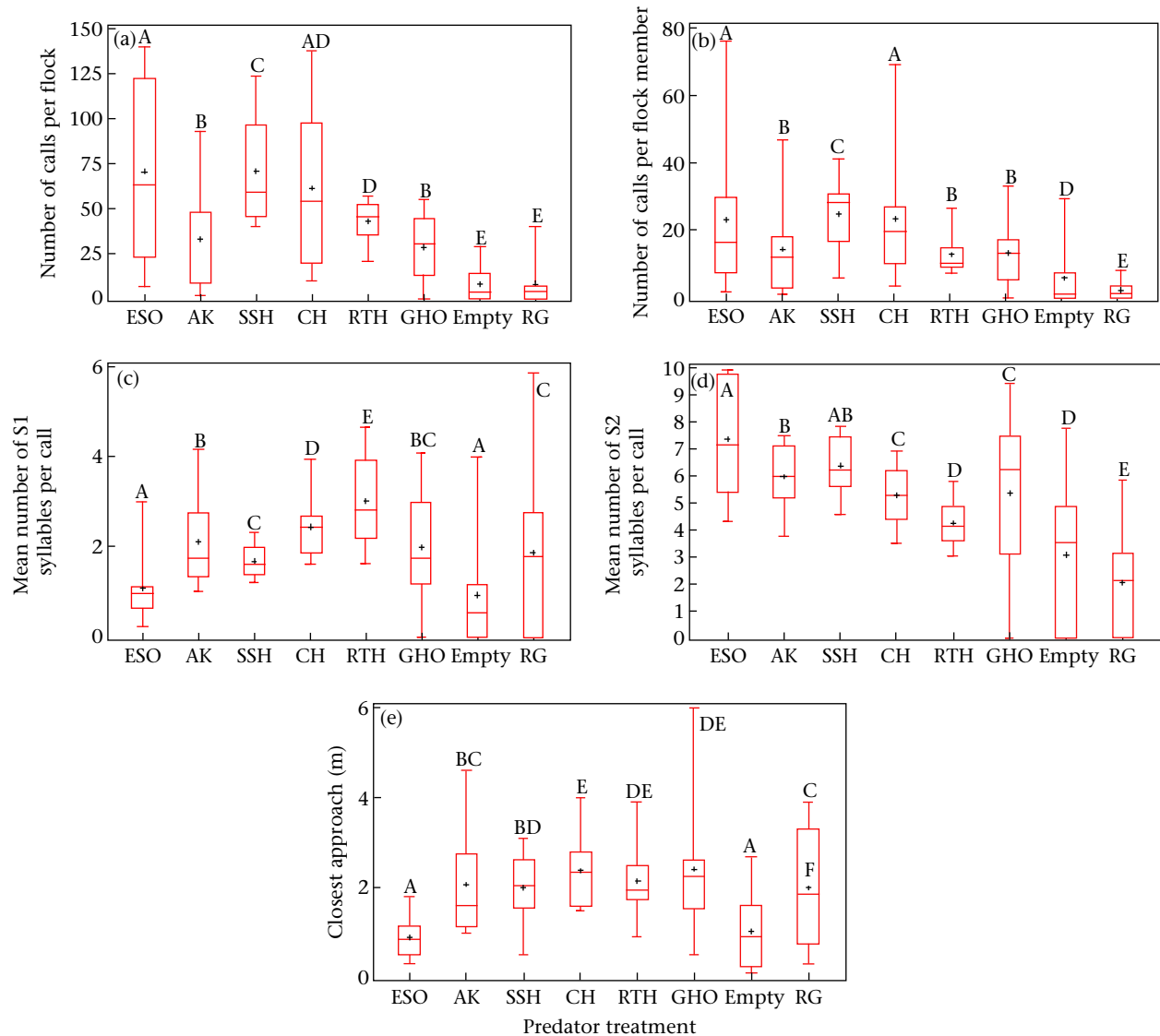


Figure 2. Behavioural responses of Carolina chickadees during 5 min predator presentation trials: (a, b) number of 'chick-a-dee' calls per flock, with data (a) uncorrected and (b) corrected for flock size; (c) number of S1 syllables (A, B and C notes) per 'chick-a-dee' call; (d) number of S2 syllables (A, B and C notes) per 'chick-a-dee' call; (e) closest approach to study skins and controls. Box plots show the mean (+), median, interquartile range, minimum and maximum values. Inset letters over box plots show pairwise comparisons from the Nemenyi post hoc test ($\alpha = 0.05$), with different letters indicating significant differences. Raptors are listed in order of increasing body length from left to right. ESO = eastern screech-owl; AK = American kestrel; SSH = sharp-shinned hawk; CH = Cooper's hawk; RTH = red-tailed hawk; GHO = great horned owl; Empty = empty platform; RG = ruffed grouse.

(14 February–18 February 2008). Specifically, we used calls given in response to a red-tailed hawk (large, low-threat predator) and an eastern screech-owl (small, high-threat predator). As a control, we played back the scolding calls of an American robin, *Turdus americanus*. Each playback trial included 15 s of 'chick-a-dee' calls (or control calls) at a volume of about 85 dB at 1 m, which was similar to the volume of calls uttered by chickadees during predator presentations. Each flock was tested using only high-quality calls recorded during predator presentations. Each 15 s tape ($N = 16$; two per flock) of 'chick-a-dee' calls included an average of 6.6 calls; the number of calls uttered in response to red-tailed hawks and in response to eastern screech-owls did not differ between tapes (dependent-sample t test: $t_{14} = 1.5$, $P = 0.16$). However, the number of D notes per 'chick-a-dee' call was significantly higher in response to eastern screech-owls (mean \pm SE = 9.1 ± 0.6) than in response to red-tailed hawks (4.2 ± 0.4) ($t_{14} = 7.2$, $P < 0.0001$). To prevent differences in response due to habituation, playback sessions were not conducted on consecutive days.

Each trial consisted of two periods, a 5 min pre-presentation (or acclimation) period and a 5 min presentation period. Prior to each trial, one of us (C.M.S.) approached the feeding station to disperse any chickadees from the immediate area. The speaker was placed in vegetation about 5 m from the feeding station and in a different location for each trial to reduce the likelihood of habituation. Once chickadees were detected, the 5 min pre-presentation period started and the playback trial began immediately thereafter. During playback trials, C.M.S. stood 5 m from the speaker and noted (1) the number of chickadees present, (2) the closest distance any bird approached the speaker, (3) the percentage of birds in the flock that came within 1 m and 3 m of the speaker, (5) the time until members of the flock stopped mobbing (cessation of alarm calling and approaches towards speaker) and (6) the number of 'chick-a-dee' calls produced by flock members for 90 s after playback ended. As with the predator presentations, we noted the percentage of birds in the flock responding to account for differences in flock sizes. This was calculated by dividing the variable of interest by the

number of chickadees that responded during each trial. A Friedman's test was used to examine differences in the response of Carolina chickadees to playback of different calls. Pairwise comparisons were conducted using a Nemenyi post hoc test. Values are presented as means \pm SE.

RESULTS

Predator Presentations

Because we studied free-ranging chickadees, flock composition varied among and within study sites. The mean number of chickadees present during presentation trials ($N = 64$) was 3.13 ± 0.20 birds (range 1–9) and flocks often included other species (tufted titmice, *Baeolophus bicolor*, white-breasted nuthatches, *Sitta carolinensis*, downy woodpeckers, *Picoides pubescens*). Although we corrected for chickadee flock size in our analyses, we did not attempt to quantify the possible effect of the presence of other species on chickadee behaviour.

We recorded 2584 'chick-a-dee' calls ($N = 8$ flocks) during the predator presentation trials. The number of calls per 5 min trial given in response to each treatment varied significantly for both uncorrected ($\chi^2 = 32.1$, $P < 0.0001$) and corrected (for flock size: $\chi^2 = 28.9$, $P = 0.0001$) data (Fig. 2a, b), with skins of an eastern screech-owl, sharp-shinned hawk and cooper's hawk eliciting more calls than those of the other raptors and controls.

The distance of closest approach by chickadees to the skins of different raptors and controls differed significantly ($\chi^2 = 20.2$, $P = 0.0052$), with chickadees coming closer to the eastern screech-owl and the empty platform than to the other raptors and the ruffed grouse (Fig. 2e). We found similar variability for the percentage of chickadees in flocks that approached to within 1 m ($\chi^2 = 16.0$, $P = 0.025$) and to within 3 m ($\chi^2 = 22.1$, $P = 0.0025$; Table 1). A significantly greater percentage of chickadees in flocks approached to within 1 m and 3 m during trials with the eastern screech-owl and an empty platform (Table 1) than during trials with the other raptors and the ruffed grouse.

Acoustic Analyses

The mean number of S1 syllables (A, B and C notes) per call varied between treatments ($\chi^2 = 17.3$, $P = 0.015$), as did the number of A ($\chi^2 = 14.9$, $P = 0.038$), B ($\chi^2 = 20.7$, $P = 0.0042$) and C ($\chi^2 = 16.9$, $P = 0.018$) notes. Calls uttered in response to the skins of the red-tailed hawk and the Cooper's hawk included significantly

Table 1

Mean \pm SE percentage of individuals in flocks of Carolina chickadees that approached to within 1 and 3 m of the study skins of different raptors and controls

	Approach to within 1 m		Approach to within 3 m	
	% Individuals	Pairwise comparison*	% Individuals	Pairwise comparison*
Eastern screech-owl	46.7 \pm 12.4	A	87.1 \pm 5.3	A
American kestrel	7.5 \pm 7.5	B	77.1 \pm 13.0	B
Sharp-shinned hawk	4.9 \pm 3.4	B	45.8 \pm 9.7	C
Cooper's hawk	0 \pm 0	C	43.8 \pm 7.0	C
Red-tailed hawk	6.3 \pm 6.3	B	56.7 \pm 9.8	D
Great horned owl	4.2 \pm 4.2	BC	75.6 \pm 14.2	B
Empty platform	40.0 \pm 17.7	D	92.5 \pm 7.5	A
Ruffed grouse	17.5 \pm 8.6	E	56.3 \pm 15.1	D

Raptors are listed from top to bottom in order of increasing size.

* Nemenyi post hoc test ($\alpha = 0.05$). Different letters indicate significant differences.

more S1 syllables than did calls given in response to the other raptors and controls (Fig. 2c). However, relationships between the mean number of S1 syllables per call and predator body length ($r^2 = 0.49$, $P = 0.12$) and wing span ($r^2 = 0.41$, $P = 0.17$) were not significant.

The mean number of S2 syllables (D notes) also varied between predator treatments ($\chi^2 = 25.0$, $P = 0.0008$), with smaller raptors eliciting calls with more S2 syllables (Fig. 2d). In contrast to the S1 syllables, the mean number of S2 syllables per call was inversely related to both predator body length (linear regression: $r^2 = -0.73$, $P = 0.03$; Fig. 3) and predator wing span ($r^2 = -0.64$, $P = 0.06$).

For 'chick-a-dee' calls given in response to a red-tailed hawk (large, low-threat predator) versus an eastern screech-owl (small, high-threat predator), the interval between the 'chick' and 'dee' portions of the call did not differ (Wilcoxon signed-ranks test: $S = 10.5$, $P = 0.16$). However, the duration of the first 'dee' note was significantly shorter for calls given in response to an eastern screech-owl (mean = 77.9 ± 0.01 ms) than for calls given in response to a red-tailed hawk (mean = 100.4 ± 0.01 ms; $S = 15$, $P = 0.039$).

Playback Experiments

A greater percentage of individuals in flocks of Carolina chickadees approached within 3 m of the speaker during playback of 'chick-a-dee' calls previously uttered in response to an eastern screech-owl skin (EASO-elicited calls) than during playback of calls given in response to a red-tailed hawk skin (RTHA-elicited calls)

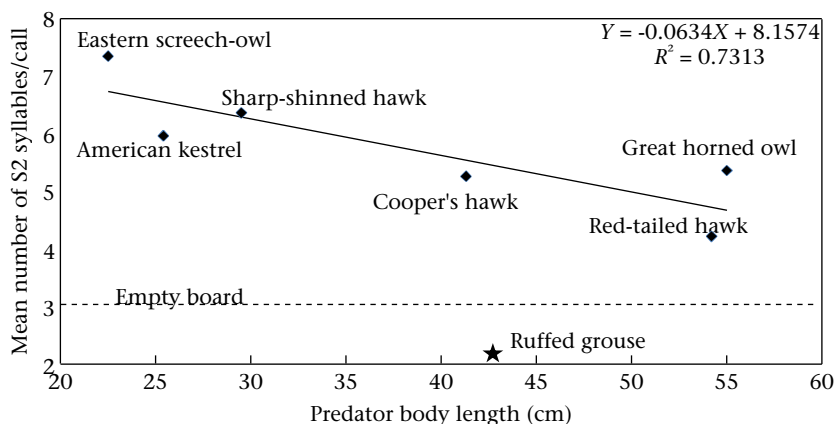


Figure 3. Mean number of S2 syllables (D notes) per 'chick-a-dee' call given by Carolina chickadees in relation to body length of raptors. Two control treatments, ruffed grouse (star) and empty platform (dashed line), are also included.

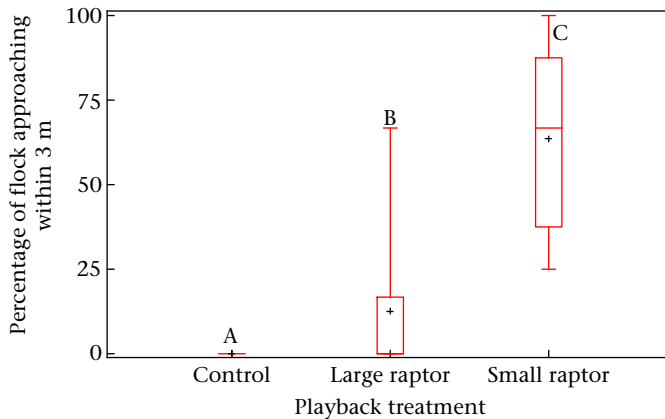


Figure 4. Percentage of individuals in Carolina chickadee flocks that approached to within 3 m of the speaker during playback of control calls (American robin scolding calls), 'chick-a-dee' calls previously given in response to a large raptor (red-tailed hawk) and 'chick-a-dee' calls previously given in response to a small raptor (eastern screech-owl). Box plots show the mean (+), median, interquartile range, minimum and maximum values. Inset letters over box plots show pairwise comparisons from the Nemenyi post hoc test ($\alpha = 0.05$), with different letters indicating significant differences.

or during playback of the scolding calls of an American robin ($\chi^2_r = 15.1, P = 0.0005$; Fig. 4). In addition, chickadees came closer to the speaker during playback of EASO-elicited calls than during playback of either RTHA-elicited calls or the scolding calls of a robin ($\chi^2_r = 13.0, P = 0.0015$; Fig. 5). Neither the percentage of chickadees in a flock approaching within 1 m of the speaker ($\chi^2_r = 4.0, P = 0.14$) nor the number of 'chick-a-dee' calls uttered by flock members during a 90 s period following playback ($\chi^2_r = 1.3, P = 0.51$) differed between treatments.

DISCUSSION

Carolina chickadees in our study varied their mobbing (alarm) behaviour and the characteristics of their 'chick-a-dee' calls when responding to different raptors. Mobbing chickadees uttered significantly more 'chick-a-dee' calls in response to smaller raptors than in response to larger raptors or controls, and chickadees approached an eastern screech-owl skin more closely than they did

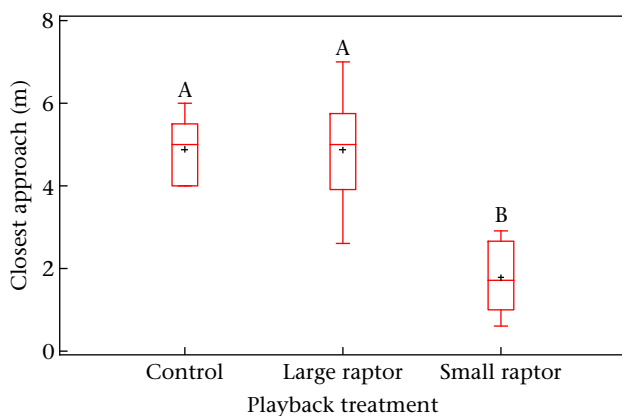


Figure 5. Closest approach (m) by Carolina chickadees to the speaker during playback of control calls (American robin scolding calls), 'chick-a-dee' calls previously given in response to a large raptor (red-tailed hawk) and 'chick-a-dee' calls previously given in response to a small raptor (eastern screech-owl). Box plots show the mean (+), median, interquartile range, minimum and maximum values. Inset letters over box-plots show pairwise comparisons from the Nemenyi post hoc test ($\alpha = 0.05$), with different letters indicating significant differences.

skins of other raptors. Similarly, Templeton et al. (2005) noted that black-capped chickadees uttered more 'chick-a-dee' calls when responding to smaller raptors, and Apel (1985) found that presentation of a mount of a sharp-shinned hawk elicited a higher rate of calling by black-capped chickadees than did mounts of larger predators. Thus, chickadee calling rates appear to inform conspecifics about the degree of threat, with smaller, more agile raptors eliciting more calls than larger, less agile raptors.

Smaller raptors probably represent a greater threat to chickadees because, as stated by Templeton et al. (2005, page 1937), 'maneuverability is extremely important in determining the outcome of predator-prey interactions and is inversely related to wing-span and body size in birds (Howland 1974; Dial 2003)'. Other investigators have also noted that smaller birds should be most vulnerable to smaller raptors because flight performance (ability to accelerate faster and show a wider range of speeds) improves as body size decreases (Tobalske & Dial 2000; Adams et al. 2006; Dial et al. 2008).

Increased calling rates and closer approaches are also perceived by predators, and various hypotheses have been proposed to explain the function of such mobbing behaviour. The move-on hypothesis proposes that a predator should leave an area sooner in response to more intense mobbing (Curio 1978). In support of this hypothesis, evidence suggests that mobbing calls may agitate and stress predatory raptors (Shalter 1978; Flasskamp 1994). In addition, Pettifor (1990) found that European kestrels, *F. tinnunculus*, move greater distances to new perches or wind-hovering sites after being mobbed than when they are not mobbed. Although additional study is needed to clarify the function(s) of mobbing by chickadees and other species, the increased intensity of mobbing in response to smaller, more agile predators suggests an attempt to agitate and, perhaps, cause the potential predator to move a greater distance where they would represent less of a threat.

During trials, Carolina chickadees in our study approached an eastern screech-owl study skin (and an empty platform) more closely than they did skins of other raptors. Reasons for the close approach of the empty platform are unclear, but chickadees may have considered the platform (because of its resemblance to the feeding stations) a potential source of food. The closer approaches to the eastern screech-owl may indicate that these owls represent a greater threat to chickadees than the other raptors, perhaps because, as nocturnal predators, screech-owls can prey on chickadees when they are roosting (sleeping or, if awake, with limited vision due to low-light conditions) and, therefore, more vulnerable. Eastern screech-owls prey on wide variety of invertebrates and vertebrates (Allen 1924; Gehlbach 1995), including chickadees (Allen 1924).

Carolina chickadees varied the note composition and duration of 'chick-a-dee' alarm calls when responding to raptors of different sizes (and degrees of threat). As previously reported for black-capped chickadees (Templeton et al. 2005), we found that the number of S2 syllables (D notes) in the calls of Carolina chickadees was inversely related to raptor body length and wing span. Similarly, Ficken et al. (1994) found that Mexican chickadees, *P. sclateri*, uttered calls with more 'C' notes in response to playback of the calls of northern pygmy owls, *Glaucidium californicum*, than they did in response to a model great horned owl. In addition, we found that the duration of the first D note was shorter in calls given in response to a small raptor (eastern screech-owl), which probably represents a greater threat to chickadees, than it was in calls given in response to a large raptor (red-tailed hawk). Mostrom et al. (2002) noted that Carolina chickadees often give a rapid series of 'chick-a-dee' calls with especially short D notes when mobbing predators, but the authors did not indicate whether the duration of those notes differed for chickadees responding to different

predators. These results suggest that the 'chick-a-dee' alarm call is a graded signal that can inform conspecifics about the presence and behaviour (i.e. perched) of a predator and the degree of threat posed by that predator. In support of that hypothesis, we found, as did Templeton et al. (2005), that a greater percentage of chickadees responded and approached the speaker more closely during playback of 'chick-a-dee' calls previously given in response to a small predator than they did during playback of calls given in response to a large predator.

Thus, the 'chick-a-dee' call of Carolina chickadees appears to communicate threat along a graded continuum in a manner similar to, but slightly different from, the 'chick-a-dee' call of black-capped chickadees. In response to different-sized predators, both species of chickadees vary the number and duration of S2 syllables (D notes) at the end of each call. However, we found that Carolina chickadees may also vary the number of introductory S1 syllables (A, B and C notes). Thus, Carolina chickadees, like black-capped chickadees, and perhaps, Mexican chickadees, encode their calls with information about predators at two levels (i.e. a coarse and fine level; Templeton et al. 2005). At the coarse level, the alarm call provides a spatial reference, with 'chick-a-dee' calls indicating the presence of a terrestrial (perched) predator, and another call ('high see' call) indicating the presence of an aerial predator (Mostrom et al. 2002). The fine level involves variation in the 'chick-a-dee' call that communicates the level of threat.

Other species of birds also have calls that provide information about predators. For example, many species have different alarm calls for terrestrial and aerial predators, including domestic chickens, *Gallus gallus* (Evans et al. 1993), superb starlings, *Spreo superbus* (Seyfarth & Cheney 1990), and several other bird species (Marler 1955; Magrath et al. 2007). In addition, Siberian jays, *Perisoreus infaustus*, use different antipredator calls to provide conspecifics with information about a hawk's behaviour (perched, prey searching or attacking; Griesser 2008). 'Fine-level' communication has also been reported in species of birds other than chickadees. For example, Leavesley & Magrath (2005) found that white-browed scrub-wrens, *Sericornis frontalis*, give alarm calls with more elements when a predator appears closer to them, and the authors concluded that an alarm-calling system where fewer elements encoded greater urgency would be evolutionarily unstable because such calls would increase the risk of receivers not hearing the alarm and, thus, increase the chance for false alarms.

In addition to the direct threat of predation, detection of a predator causes birds to stop engaging in other activities (e.g. foraging). An alarm call like the 'chick-a-dee' call of Carolina chickadees that provides conspecifics with information about the behaviour (perched) and degree of threat posed by a predator allows members in a flock to both reduce the risk of predation and maximize their time and energy allocation relative to that threat. Lind et al. (2005) reported a similar finding for mobbing calls of great tits, *Parus major*: birds that were exposed to the alarm calls of conspecifics resumed foraging at the same time as those that could see the predator, indicating that the mobbing calls of great tits act as honest signals of predation risk.

In conclusion, we found that the 'chick-a-dee' calls of Carolina chickadees simultaneously convey information about both the type of predator (aerial versus terrestrial) and the degree of threat posed. The 'chick-a-dee' call of chickadees also serves other functions, including coordination of flock activities (Ficken et al. 1978; Hailman et al. 1985). The combinatorial nature of 'chick-a-dee' calls, with note types repeated or omitted to produce calls with a large number of combinations, shares many features with human speech (Hailman et al. 1985), with the number of notes and note-type occurrence changing with context (Ficken et al. 1978; Gaddis 1985; Freeberg & Lucas 2002). Additional study of this call and the

contexts in which it is used by Carolina, black-capped, Mexican, and other species of chickadees will probably provide further examples of how chickadees communicate in complex ways with conspecifics.

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