Animal Behaviour 78 (2009) 1447–1453

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Chad M. Soard, Gary Ritchison*

Department of Biological Sciences, Eastern Kentucky University

ARTICLE INFO

Article history:
Received 28 October 2008
Initial acceptance 26 January 2009
Final acceptance 3 September 2009
Available online 24 October 2009
MS. number: A08-00703R

Keywords:
alarm call
Carolina chickadee
mobbing
Poecile carolinensis
predator
threat

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.

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 ± SE flock size = 5.88 ± 0.55 birds, range 4–9 birds) during 15 January–8

* Correspondence: G. Ritchison, Department of Biological Sciences, Eastern Kentucky University, Richmond, KY 40475, U.S.A.
E-mail address: gary.ritchison@eku.edu (G. Ritchison).

0003-3472/$38.00
doi:10.1016/j.anbehav.2009.09.026

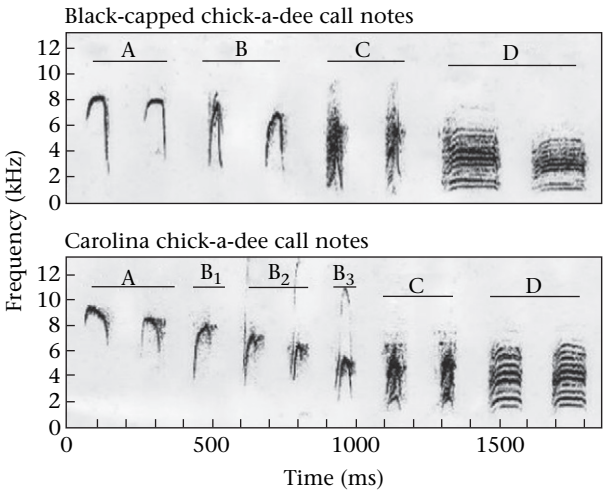

Figure 1. Sonagrams of the 'chick-a-dee' calls of a black-capped chickadee and a Carolina chickadee. A, B and C notes are the 'chick' or S1 syllables; D notes are the 'dee' or S2 syllables (Source: Bloomfield et al. 2003).

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 × 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