



ARTICLES

Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*

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The chick-a-dee call of the avian genus *Poecile* is a structurally complex vocal system because it possesses a set of simple rules that governs how the notes of the call are ordered, and variable numbers of each of the note types strung together can generate an extraordinary number of unique calls. Whereas it has been hypothesized that chick-a-dee calls with different notes may convey different information, no experimental evidence has been offered in support of the hypothesis. Previously published studies suggested that flock members use chick-a-dee calls in the context of moving to or from a feeding site. Here, we tested Carolina chickadees' responses to playbacks of chick-a-dee calls that differed in note composition. Playbacks were conducted in the field in the context of a novel food source. Our pilot data had indicated that chick-a-dee calls with relatively large numbers of 'C' notes were given by birds on their first contact with a novel seed stand. In the present study, we found that chickadees flew in close to the playback speaker and subsequently took seed from a seed stand more often during playbacks of chick-a-dee calls containing C notes than chick-a-dee calls not containing C notes or than control playbacks. Vocal responses of chickadees to the playbacks also differed in relation to the particular vocal signal being played back. These results indicate that receivers respond differently to chick-a-dee calls containing different compositions of note types and represent a first step to link variation in note composition and ordering in these calls to possible meanings.

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Vocal communication is important to maintaining social organization in many vertebrate species. Vocalizations that notify group members (i.e. receivers of the signal) of group movement, a located predator, or a found food source may be of adaptive value. This is particularly true for species in which a group's members are at times out of visual contact with one another while they move through the physical environment. Certain vocal signals in several avian and mammalian species have been shown to be associated with the presence and type of predator or food (Seyfarth et al. 1980; Dittus 1984; Gyger et al. 1987; Macedonia & Evans 1993; Evans & Marler 1994; Evans 1997; Evans & Evans 1999). In the majority of these cases, the animals possess distinct vocal signals within their repertoires that are context specific.

In many other species, individuals communicate with

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particular systems of calls that vary in the presence and/or number of note types that make up the calls. In some species in which a single call system shows a high degree of acoustic variability, there is an underlying structure, a simple syntax governing the order of the units, to that call system (Marler 1977). The most complex example of syntax governing a vocal system is, of course, human language. The rules that govern syntax in human languages result in a system that is functionally open-ended (it shows 'productivity', Hockett 1960). Vocal systems that are virtually open-ended due to simple ordering rules have been documented in a number of avian and nonhuman primate species and may provide clues to the evolution of systems of complex signals and perhaps human language (Snowdon 1990, 1993; Evans & Marler 1995; Ujhelyi 1996, 1998).

In avian species of the genus *Poecile*, a single call type, the chick-a-dee call, is highly variable but possesses ordering rules that govern the sequences of note types in the

call (Hailman 1989). The ordering rules are particularly well described in the black-capped chickadee, *Poecile atricapilla*, where there tend to be four major note types (A, B, C and D) that may or may not be present in a given chick-a-dee call and that, if present, can occur once or several times (Hailman & Ficken 1986). These four note types obey a general Markovian ordering rule, with high-frequency A notes virtually always coming first and lower-frequency D notes, if they occur, virtually always coming last in the call. B notes, if they occur, tend to follow A notes and to precede D notes, and C notes, if they occur, may occur alone or follow A notes or precede D notes. Because chick-a-dee calls are combinatorial, conforming to these basic ordering rules (while being highly variable), Hailman and colleagues have argued that the calls theoretically could convey a very large amount of information (Hailman et al. 1985, 1987).

Whereas chick-a-dee calls theoretically could convey a large amount of information, little experimental evidence to date has been offered to confirm or refute this (see also Snowdon 1993). Some observational data suggest possible variation in meanings, however. Hurd (1996) found that several other species (but not chickadees) responded differentially to playbacks of the 'mobbing' chick-a-dee call of black-capped chickadees relative to playbacks of a different chick-a-dee call. Ficken (1981), in a study of black-capped chickadees, showed that individuals frequently gave chick-a-dee calls upon finding food at feeders. Although Ficken (1981) did not report the note composition of the chick-a-dee calls she documented, the data suggested that the calls may have facilitated recruitment of flockmates to the feeder. Gaddis (1985), in a study of mountain chickadees, *P. gambeli*, found that the chick-a-dee calls given frequently when individuals arrived in a foraging patch were different in note composition from chick-a-dee calls given when individuals left a foraging patch or when individuals were startled. Smith (1972) found that different note types within the chick-a-dee call of Carolina chickadees were used in different contexts related to flock movement, often when feeding stations were nearby. In the present study, we used playbacks of Carolina chickadee chick-a-dee calls varying in note composition to test whether different variants of the calls resulted in different behavioural responses of receivers.

The chick-a-dee call in Carolina chickadees is similar to that described above for black-capped chickadees, and has been discussed by Smith (1972) as being produced in a variety of social contexts. The call is typically composed of relatively high-frequency A notes ('high-see', 'high-tee', and related notes in Smith 1972; see also Hailman 1989), occasionally followed by a single B note (variants of 'high-tee' note) or by one or more structurally complex C notes ('chick' notes), and concluded with lower-frequency D notes ('dee' notes). There is great variation in the number and even presence of each note type in the chick-a-dee calls of Carolina chickadees, although as is the case for black-capped chickadees (see Hailman et al. 1987), the ordering of note types in chick-a-dee calls virtually always follows an A-B-D or A-C-D pattern (Fig. 1).

In a pilot study, conducted in central Indiana, we analysed a small number of chick-a-dee calls recorded from Carolina chickadees as they initially arrived at feeding stations, and we found that a high proportion of these calls contained C notes (either with or without D notes following). Because C notes are less common than A and D notes in the chick-a-dee calls of this population (unpublished data), we hypothesized that these 'C-rich' chick-a-dee variants may: (1) signal increased arousal on the part of the producer in the context of a novel and nonthreatening environmental stimulus, or (2) be associated with the presence of food items in the environment. In either case, we predicted that in playback studies, Carolina chickadee receivers that heard any chick-a-dee call variant would respond by approaching and investigating the area of the playback speaker. However, we predicted that the receiver would take seed from a novel seed stand more often in response to 'C-rich' calls than would birds hearing alternative chick-a-dee calls or other vocalizations.

METHODS

Recordings

In the present study, we tested this hypothesis for C notes in chick-a-dee calls using playbacks at several sites containing a novel seed stand. The playbacks included variants of chick-a-dee calls with C notes ('C-rich' calls) and chick-a-dee calls without C notes ('long-D' calls). As a control for playbacks of chick-a-dee calls, we included in the playback design variants of the 'gargle' vocalization of Carolina chickadees. The gargle is distinct from the chick-a-dee call, but has a similar frequency range and pattern of high-frequency notes at the onset followed by notes generally decreasing in frequency over the course of the vocalization (Ficken et al. 1978; collectively also called 'T-slanks' and 'click-rasps' in Carolina chickadees, Smith 1972). As a control for playing back vocal signals of Carolina chickadees, we also played back a heterospecific vocalization, the 'quank' call of the white-breasted nuthatch, *Sitta carolinensis*, a species that commonly occurs with chickadees in multispecies flocks in central Indiana. As a control for playing back avian vocal signals in general, we also used a 'blank' playback, which was no playback whatsoever.

Carolina chickadee vocalizations used for playbacks included six chick-a-dee calls containing C notes (C-rich), six chick-a-dee calls without C notes but with several D notes (long-D) and six gargles, often used by this species in agonistic interactions (Smith 1972). We recorded each of these vocalizations in an indoor aviary to minimize noise and reverberation and to standardize recording conditions across calls. During recording, we housed chickadees individually in separate 1-m³ cages, but birds could hear other chickadees housed in the same room and in adjoining rooms. Each vocalization was recorded from a chickadee with a Saul Mineroff directional electret microphone, placed within 1 m of the bird, on Maxell XLII tape using a Marantz PMD 222 portable cassette recorder. We obtained the six C-rich and six long-D calls

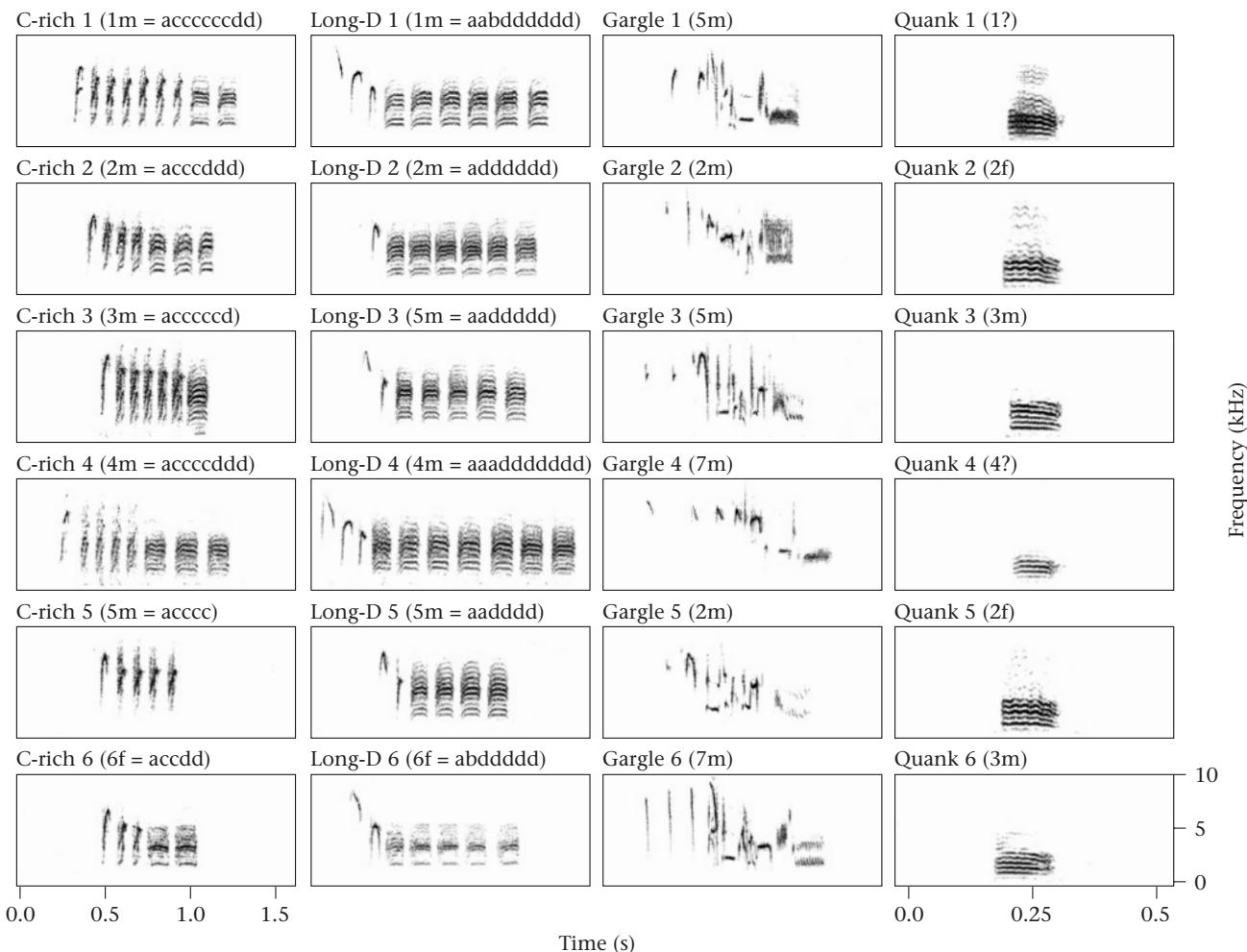


Figure 1. Sonograms of the Carolina chickadee C-rich chick-a-dee calls, long-D chick-a-dee calls and gargles, and white-breasted nuthatch 'quank' calls used as playbacks. The Y axis represents the same frequency range (0–10 000 Hz) in each figure. The X axis for each figure indicates time: C-rich, long-D and garge sonograms are all represented on a 1.5-s scale; nuthatch quank vocalizations are represented on a 0.5-s scale. In parentheses above each call are the birds' sex (m=male, f=female, ?=unknown) and ID numbers, and for the C-rich and long-D calls, the note compositions of the calls. Sonograms were generated with Cool Edit using the Blackman–Harris windowing function with a resolution of 128 bands.

from five adult male and one adult female Carolina chickadee (we determined sex by wing chord according to known distributions from the population; [Thirakupt 1985](#)). We obtained the six gargles from three adult male chickadees; and the six heterospecific quank calls from four nuthatches (one male and one female accounted for four of the quanks; the other two were recorded from the field within 1 m and with the same recording equipment, and the sex of the caller was not documented at the time of the recording). Sonograms of the vocalizations used in the playbacks are displayed in [Fig. 1](#).

All of the vocalizations were obtained from birds from the Ross Biological Reserve, or, in the case of two of the nuthatches, the Martell Forest Reserve, two forest tracks located approximately 20 km west of Purdue University's campus. This area is near the northern edge of the Carolina chickadee's range and the southern edge of the black-capped chickadee's, with whom it shares some similarities in plumage, morphology and behaviour. We

confirmed species identity using differences in size (see [Merritt 1981](#); [Thirakupt 1985](#)) and characteristics of territorial songs and chick-a-dee calls ([Ficken et al. 1978](#)); the birds of the present study produced songs and chick-a-dee calls characteristic of Carolina chickadees.

Playbacks

As a first attempt to test for differences in behavioural responses of receivers hearing chick-a-dee calls of different note compositions, we chose to use unmanipulated calls. The recorded calls used as playbacks were digitized using the Cool Edit sound analysis program (version 96, using a sampling rate of 22 050 at 16-bit resolution). We then recorded the vocalizations onto endless loop tapes (TDK EC-3M) or onto nonloop tapes (Maxell UR60) with a Marantz PMD 222 portable cassette recorder. The vocalizations were recorded onto the tapes at a rate of six vocalizations/min, at roughly one vocalization every 10 s.

We attempted to sample the variation in C-rich and long-D chick-a-dee calls in choosing our playback sample, while balancing recording quality of the calls. We generated six sets of playback calls, with each set played back at two different sites (see below). In each set, we paired the C-rich and long-D calls by overall number of notes: in each pair, calls had to possess the same overall number of notes to within a two-note difference. It should be noted, however, that controlling for number of notes in the calls resulted in the long-D calls being longer in duration than the C-rich calls, as D notes are longer in duration than C notes (Fig. 1). We tried to control for the possibility of differential dominance status of the birds from which we obtained the recordings by pairing C-rich and long-D calls from the same bird within each playback set. Five of the six playback sets contained C-rich and long-D calls recorded from the same individual (Fig. 1).

We tested the playback types at 12 sites in the Ross Biological Reserve and Ross Hills County Park, West Lafayette, Indiana (which is adjacent to the Ross Biological Reserve) from 18 March to 6 May 2000. These two forest tracts combined comprise approximately 90 ha of largely mature *Quercus*–*Carya* forest (Von Culin & Lindsey 1973) surrounded by farms, disturbed forests and the Wabash River. To increase our chances of playing back calls to different flocks and to ensure that each site was largely independent, we established the 12 playback sites so that each site was separated from the next closest site by at least 250 m. In support of our contention that these distances between playback sites resulted in reasonable independence between sites, of 11 banded Carolina chickadees observed during the playbacks at six different sites, we observed 10 only at one site and the 11th at two different sites (we observed only unbanded chickadees at the other six sites).

We tested each playback type (C-rich, long-D, garge, nuthatch and blank) once at each playback site, with at least 4 days separating consecutive playbacks at the same site. The total study was comprised of five rounds: one playback at each site per round. We randomized presentation of playback types except for the fact that we balanced the five playback types across rounds, such that only two or three of each type occurred within a round. For example, the first round contained two C-rich, three long-D, two garge, three nuthatch and two blank playbacks. Over the course of the study across the 12 sites, each individual playback variant was used at two different sites.

We conducted the playback trials between 0830 and 1330 hours Eastern Standard Time. Before each playback, we gathered 10 min of preplayback data on vocalizations heard at the playback site. We played back each call type with a Marantz PMD 222 portable cassette recorder through a Saul Mineroff Electronics powered speaker. Playback trials lasted 60 min and were broken into six 10-min blocks. Each of these 10-min blocks was made up of 3 min of playback of the vocalization (or blank) being tested that morning, followed by 7 min of silence. Approximately 5 min before collecting preplayback data, we placed a seed stand (post=2 m high, seed tray=10 cm diameter) into the ground and placed a playback speaker

within 1 m of the seed stand (we either hung the speaker from a tree or placed it on a 1.5-m-high stand). After the 10-min preplayback observation period, we filled the seed tray with sunflower seeds, and began the 60-min playback period. The observers conducted the playbacks while seated and motionless from behind a tree or vegetation, 10–12 m from the playback speaker. We collected the seed and removed the seed stand from the site after each playback was finished.

Data Collection and Analyses

We collected data on the following:

(1) Number of sites at which at least one Carolina chickadee approached to within 20 m of playback speaker and the number of different Carolina chickadees to arrive within 20 m of the playback speaker. We were able to determine the number of chickadees to approach unambiguously for some of the sites where most of the birds to approach the speaker were banded. At the sites where the birds were unbanded, given that birds would sometimes approach the speaker and then leave for several minutes before again approaching the speaker, we chose to be conservative and only counted more than one chickadee when we saw two or more birds in the area simultaneously.

(2) Taking seed from the seed stand: a Carolina chickadee landed on the seed stand, took a seed, and ate it there or flew off with it to eat or cache it elsewhere.

(3) First-approach vocal response: the first time a Carolina chickadee approached to within 10 m of the playback speaker during a playback, we documented the vocal behaviour of that bird in the next 1-min period.

(4) Total vocal production: during the entire 60-min playback period (60 1-min bins of data), we documented every chick-a-dee, garge and fee-bee-fee-bay (the territorial song of the species, Smith 1972) we were able to hear, regardless of the distance from the playback site.

In our analyses of receivers approaching to within 20 m of the playback speaker and taking seed from the seed stand, our dependent variable was dichotomous (yes versus no; take versus no-take). To test whether birds responded differently by playback type for these variables, we used the Cochran Q test, a nonparametric test for categorical data for more than two related samples (see Siegel & Castellan 1988). When we detected a significant effect of playback type on chickadees' responses, we used the McNemar change test to determine whether there were differences between the C-rich playbacks and the other playbacks (Siegel & Castellan 1988). To test whether the number of birds to approach within 20 m was affected by playback type, we used the Friedman two-way analysis of variance (ANOVA) by ranks. We used site as the repeated measure for these tests, as well as for the vocal response tests described below, under the assumption that the response to repeated playbacks at each site should be more strongly correlated than playbacks at different sites. Note, however, that there is some pseudoreplication in this analysis, because we used each of the six unique sets of playbacks at two different sites.

To normalize residuals from the data for the first-approach vocal responses in the ANCOVA models, we log-transformed ($\log(n+1)$) the number of chick-a-dees and fee-bee-fee-bays and double-log-transformed ($\log(\log(n+1))$) the number of gargles given in response to the playback types. For the total vocal production data (all vocalizations recorded during the 60-min of playback observation), we double-log-transformed the data to obtain normal distributions of residuals. These transformations were needed because the distribution of number of calls was highly skewed. We used repeated measures analysis of covariance (ANCOVA) with first-order autoregressive covariance structure (Proc Mixed; **SAS Institute 1994**) to test for differences in vocalization rates between sites. Finally, when significant results were detected for fixed effects of playback type with ANCOVAs using the mixed procedure in SAS, we performed multiple contrasts comparing the C-rich playbacks to the other four playback types. In the Results section, we report only significant contrasts (at $P \leq 0.05$).

RESULTS

Birds Approaching the Playback Speaker

The probability that at least one Carolina chickadee receiver approached within 20 m of the playback speaker varied significantly with playback type (Fig. 2a; Cochran Q test: $\chi^2_4=12.97$, two-tailed $P < 0.05$). Contrasts of the responses to C-rich playbacks compared with the other playbacks indicated that birds approached to within 20 m at more sites to playbacks of C-rich calls than to playbacks of nuthatch quank calls (McNemar change test: $\chi^2_1=6.13$, two-tailed $P < 0.05$). None of the other contrasts was significantly different. The number of different individuals to approach within 20 m of the playback speaker was marginally dependent upon the playback type, but was not statistically significant (Fig. 2b; Friedman repeated measures ANOVA on ranks: $\chi^2_4=8.38$, NS).

We detected no effect of playback type on the latency with which Carolina chickadees approached to within 20 m of the playback speaker ($F_{4,13}=0.52$, $P=0.72$), or to within 10 m of the playback speaker ($F_{4,9}=0.40$, $P=0.80$). We also detected no effect of playback type on the preplayback rates of vocalizing. For rates of vocalizing over the 10-min interval before each playback, we could not detect any effect of playback site on the total vocal production data ($F_{4,44}=0.78$, $P=0.54$). Thus, even though Carolina chickadees tended to be more active in general at some sites relative to others (see Discussion), any possible site differences did not appear to affect our playback results.

Taking Seed from the Seed Stand

The probability that chickadees took seed from the novel seed stands varied with playback type (Fig. 2c; Cochran Q test: $\chi^2_4=18.53$, two-tailed $P < 0.01$). Chickadees took seed from the seed stand more often at sites during playbacks of C-rich calls (7 of the 12 sites)

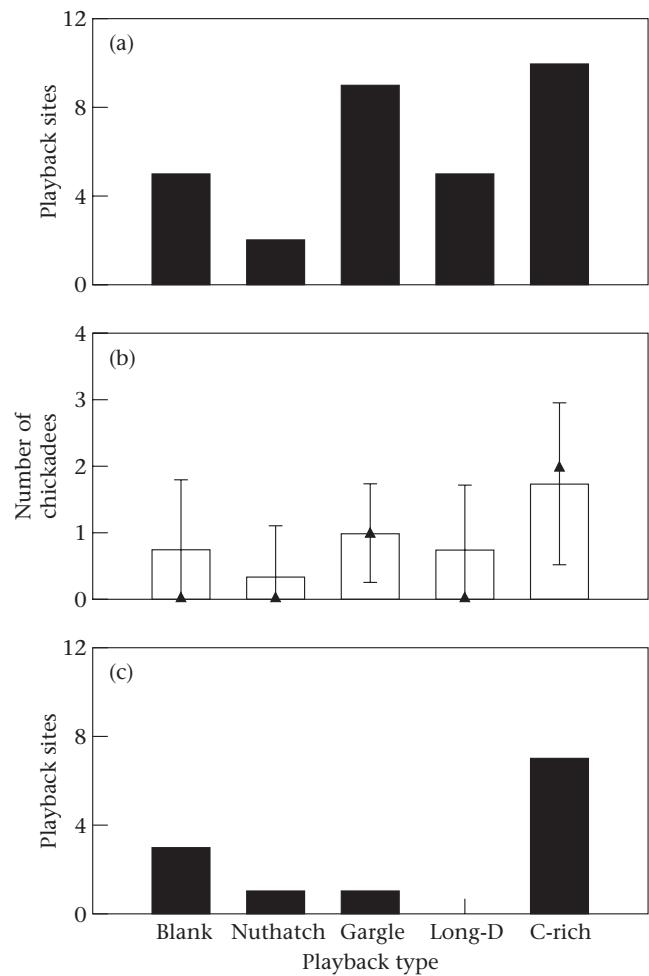


Figure 2. Behavioural responses of chickadee receivers approaching the playback speaker and taking seed from seed stand, as a function of playback type. (a) Number of playback sites at which at least one chickadee approached within 20 m of the playback speaker. (b) Average (\pm SD) number of chickadee receivers to approach within 20 m of the playback speaker across the 12 playback sites (\blacktriangle =median number). (c) Number of playback sites at which at least one chickadee took seed from the seed stand.

than during playbacks of long-D calls (0 of the 12 sites; McNemar change test, $\chi^2_1=5.14$, two-tailed $P < 0.05$). None of the other contrasts differed significantly. Carolina chickadees took no seed during any playback at five of the playback sites. However, birds approached to within 10 m of the playback speaker during at least one of the playbacks at every site.

First-approach Vocal Responses

The first time an individual Carolina chickadee approached to within 10 m of the playback speaker, the vocal behaviour it gave in the next 1-min time period depended upon the playback type ($F_{4,7}=7.13$, $P=0.013$). However, the response to C-rich calls was not statistically different from the response to long-D calls for this response variable. Contrast analyses indicated that receivers produced significantly more chick-a-dees during

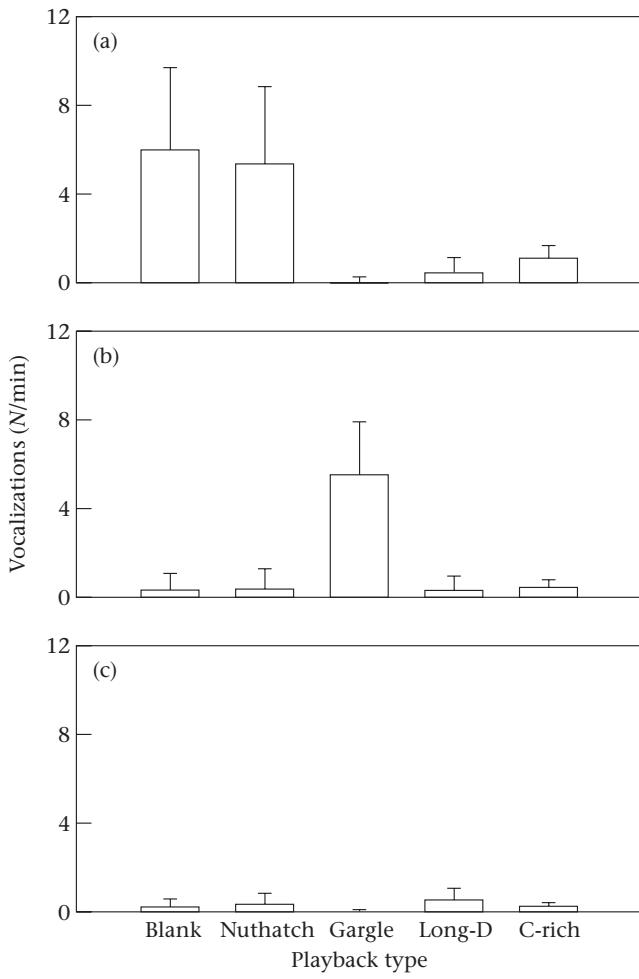


Figure 3. First-approach vocal responses: the vocal rates of Carolina chickadees in the 1-min period following the first time a bird approached within 10 m of the playback speaker during a playback trial. Least squares means (+SD) for (a) chick-a-dee, (b) fee-bee-fee-bay and (c) garge calls. To generate the figures, data were backtransformed from the repeated measures ANCOVA models (see text).

blank and nuthatch playbacks than during C-rich playbacks (Fig. 3a; blank: $F_{1,7}=8.67$, $P=0.022$; nuthatch: $F_{1,7}=6.94$, $P=0.034$). Furthermore, receivers produced significantly more chick-a-dees during C-rich playbacks than during garge playbacks (Fig. 3a; $F_{1,7}=6.61$, $P=0.037$). There was a significant effect of playback type on fee-bee-fee-bay rates in the first-approach vocal response data ($F_{4,7}=4.63$, $P=0.038$). Contrast analyses indicated that playbacks of garges evoked significantly more fee-bee-fee-bays than did playbacks of C-rich calls (Fig. 3b; $F_{1,7}=14.94$, $P=0.006$). The rate at which approaching chickadees produced garges was unaffected by playback type (Fig. 3c; $F_{4,7}=0.75$, $P=0.590$).

The time of day at which each playback was started was found to have a significant effect on the chick-a-dee rates of receivers ($F_{1,11}=5.35$, $P=0.04$). Carolina chickadees gave fewer chick-a-dees in their first-approach vocal responses the later in the morning the playback test began, across all playback types.

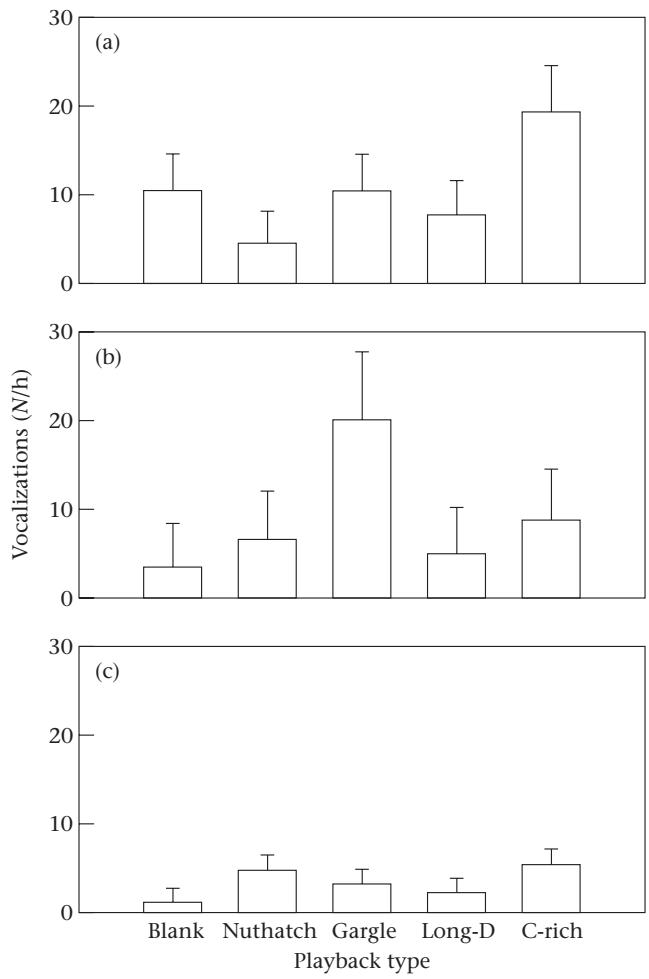


Figure 4. Total vocal production: the vocal rates of Carolina chickadees across each entire 60-min playback trial. Least squares means (+SD) for (a) chick-a-dee, (b) fee-bee-fee-bay and (c) garge calls. To generate the figures, data were backtransformed from the repeated measures ANCOVA models (see text).

Total Vocal Production

As was the case with first-approach vocal responses, the playback type affected total vocal production during the entire 60-min playback interval. We found significant effects of playback type on chick-a-dee rates ($F_{4,43}=4.72$, $P=0.003$) and on fee-bee-fee-bay rates ($F_{4,43}=6.42$, $P=0.001$). However, unlike the first-approach vocal responses, the chickadees' vocal response to C-rich calls differed significantly from their response to long-D calls. Contrast analyses for chick-a-dee responses in the total vocal production data indicated that chickadees produced more chick-a-dees during playbacks of C-rich calls than during the four other playback types (Fig. 4a; blank: $F_{1,43}=6.29$, $P=0.016$; nuthatch: $F_{1,43}=17.74$, $P=0.0001$; garge: $F_{1,43}=5.82$, $P=0.020$; long-D: $F_{1,43}=9.29$, $P=0.004$). Contrast analyses for fee-bee-fee-bay responses indicated that fee-bee-fee-bays were given to playbacks of garges more often than to C-rich playbacks (Fig. 4b; $F_{1,43}=11.12$, $P=0.002$). We found no effect of playback type on garge rates, as was the case for the first-approach vocal responses (Fig. 4c; $F_{4,43}=1.44$, $P=0.236$).

DISCUSSION

The social organization of Carolina chickadees changes from a male and female pair defending a territory during the breeding season to typically two or more pairs of unrelated males and females forming a flock and defending a joint territory during the autumn and winter months (Brewer 1961; Ekman 1989; Hogstad 1989; Matthysen 1990). Among several potentially adaptive reasons for forming flocks, the greater numbers of individuals may increase the possibility of detecting food resources on the flock's territory (Lucas et al. 1999). For this to be true, an individual locating a novel food source would need to be able to communicate some information to flockmates. One of the most efficient means of communicating over potentially large distances and out of visual contact is through acoustic signalling (Bradbury & Vehrencamp 1998). Previous work with different species of chickadees suggested the possibility that different variants of the chick-a-dee vocal system might be associated with the presence of different environmental stimuli or motivational states of the signaller (Smith 1972; Gaddis 1985; Ficken et al. 1994). In the present study, the number of sites at which Carolina chickadees approached within 20 m of the playback speaker was dependent upon the type of call being broadcast, with calls containing C notes (C-rich calls) eliciting approach more often than any other call type. Birds subsequently took seed from seed stands during playbacks of C-rich calls more often than they did during playbacks of chick-a-dee calls that did not contain C notes (long-D calls). Indeed, across the 12 playback sites, Carolina chickadees never took a seed from the seed stand during a playback of a long-D call.

In addition to the data on taking seeds, we found response differences between C-rich and long-D chick-a-dee playbacks in the total vocal production data. We observed more chick-a-dee calls during the 60-min playback trial when the playback was a C-rich call than when it was any other playback type. A possible explanation for this is that birds approaching the playback speaker closely in response to C-rich playbacks, and subsequently taking seed, tended to return again and again to the stand. Thus, the observed increased chick-a-dee rates to C-rich call playbacks may have been a consequence of slightly more chickadees in the area (although we did not detect significant differences among playback types for the number of birds approaching the playback speaker). Taken together, the data on taking seed and total vocal production indicate that C-rich and long-D calls produce different vocal and approach responses in receivers.

One interpretation of our results is that calls containing C notes convey some information about the presence of food and that the location of the signaller would provide information about the location of the food. Thus, the context in which the signal is given likely is important to receivers as well as the signal itself (Smith 1968; Leger 1993). The C-rich calls cannot be considered truly referential signals (see Evans 1997), referring exclusively to food, because they are used in nonfood contexts, as are other variants of chick-a-dee calls (Smith 1972; Ficken et al. 1978; Gaddis 1985). A relatively high number of C

notes in a chick-a-dee call may, however, be probabilistically associated with the presence of a rich food resource in the environment. Another interpretation of these results is that chick-a-dee calls with a relatively high number of C notes may signal novelty or a high motivation level on the part of the producer in the context of a novel but nonthreatening environmental stimulus (a large amount of seed on the seed stand). In this sense, the C-rich calls in the present study would conform to ideas about note composition, motivation and flock member movement conveyed by earlier work with chick-a-dee calls (Smith 1972; Hailman et al. 1985). Indeed, we might expect a call system that exhibits nondiscrete variation (such as the chick-a-dee call system, where C-rich calls could contain, for example, 3, 6, or even 10 C notes) to convey information about graded changes in the motivation of the producer (Owings & Morton 1998).

Five of our playback sites occurred within an area of the Ross Biological Reserve that has had permanent seed stands in place for over a decade, although the specific sites we used for our seed stands never had permanent seed stands. Carolina chickadees approached and subsequently took seeds during playbacks of C-rich calls at all five of these playback sites, but did so only at two of the seven sites not near permanent seed stands. Chickadees never took seed during playbacks of long-D calls, regardless of playback site (note that we played back all five playback types at each of the 12 playback sites). While this is a small sample, the results suggest that C-rich chick-a-dee calls may be most effective at producing seed-taking behaviour on the part of receivers in contexts in which the birds are already used to obtaining seed on stands, whereas long-D calls are ineffective at producing seed-taking behaviour irrespective of the feeding history of the birds in the population.

It has been suggested that the ratio of D notes to other note types may convey information in chick-a-dee calls (Hailman et al. 1987). In other words, few or no D notes may convey a different meaning to a receiver than would many D notes, regardless of the presence of C notes in the calls. Under this interpretation, playbacks of the C-rich calls at the seed stands, because they had relatively few D notes, may have been acted on by responding individuals as a signal indicating a novel but not agonistic context. Each of the C-rich and long-D calls (and gurgles) were probably perceived by responding individuals as coming from nonflock members, as all of the playback calls were recorded from individuals that differed from those to which the calls were played back. Long-D calls may have been perceived as being aggressive or antagonistic, while C-rich calls with few or no D notes may not have been perceived as such, and the increased propensity to approach the speaker and seed stand may have simply been an incidental by-product of this. Further work is needed to clarify this issue.

This study represents a first step to determine whether chick-a-dee calls that vary in note composition have different meanings. We have focused on certain chick-a-dee call variants and possible differences in meaning from the standpoint of the signal receiver, the assessment side of the communication system (Owings & Morton 1998).

Future work will need to address more closely the management side of the communication system, focusing on the specific contexts in which calls varying in note composition (such as C-rich or long-D variants) are produced. Furthermore, future work will need to look more closely at how combinations of signals that vary in note composition are used by chickadees in different contexts (see [Smith 1991](#); [Leger 1993](#)). It seems possible that both note composition of individual calls and the ordering of chick-a-dee calls in a calling sequence of a bird might depend upon the relationships between the signaller and receivers, as well as upon whether the contexts of the vocalizations were food, a predator, an aggressive interaction, or the movement of the signaller. For example, in flycatchers in the genus *Sayornis*, different vocal types are used in different social contexts, and the 'string lengths' of vocal types (number of repetitions of a particular vocal type before the bird switches to another vocal type) predict a bird's subsequent behaviour ([Smith 1969, 1970](#)). Shifts between different vocal types are also predictive of behaviour in great crested flycatchers, *Myiarchus crinitus* ([Smith & Smith 1996a, b](#)).

The results of the present study support the suggestion of [Ficken et al. \(1994\)](#) that contextual differences in chick-a-dee call use vary considerably among chickadee species. In the Mexican chickadee, *P. sclateri*, birds produce calls with a relatively high number of C notes when near a playback speaker broadcasting predator calls ([Ficken et al. 1994](#)). Thus, in the Mexican chickadee, C notes appear to be used more in a predator mobbing context or when the birds are in a disturbed situation. However, strings of D notes appear to take on those functions in black-capped chickadees ([Apel 1985](#), cited in [Ficken et al. 1994](#)), and possibly Carolina chickadees (J. R. Lucas & M. Lorenz, unpublished data). The C note has been suggested to function in flock movement in black-capped chickadees ([Hailman et al. 1985](#)) and when birds leave a foraging patch in mountain chickadees (classified as Category II calls containing B elements in [Gaddis 1985](#)). Phylogenies based on mitochondrial DNA comparisons place Carolina chickadees close to the black-capped chickadee and mountain chickadee clade, and more distantly to Mexican chickadees ([Gill et al. 1993](#)). The admittedly small amount of empirical data thus far suggests that note type and context relationships of the chick-a-dee call in these four species correlate with these phylogenetic differences; more comparative research on this call system in these and other *Poecile* species is needed to understand these relationships better.

The hypothetical amount of information that could be conveyed in the chick-a-dee call system is immense ([Hailman et al. 1985](#)). This study provides the first experimental data in chickadee species to indicate that chick-a-dee calls differing in terms of their note composition can also differ in terms of their meaning to receivers. Together with the question of note composition relationships to possible meanings in chick-a-dee calls, the fact that characteristics of this call system, like human language, are learned ([Nowicki 1989](#); [Hughes et al. 1998](#)) suggests that this system may represent an informative analogue to human language.

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