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Chick-a-dee call syntax, social context, and season affect vocal responses of Carolina chickadees (*Poecile carolinensis*)

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Abstract Chick-a-dee calls in many chickadee (*Poecile*) species are common vocal signals used in a diversity of social contacts. The calls consist of four notes, A, B, C, and D, which follow simple rules of syntax (note ordering and composition) to generate many unique call types. We used field playbacks with Carolina chickadees, *P. carolinensis*, to ask whether violations of a syntactical rule affected their vocal responses. We show that chickadee responses to typical calls (e.g. AAAACCCC and CCC-CDDDD) differ from responses to atypical calls (e.g. CACACACA and DCDCDCDC) depending on playback note composition, season, and social context (presence of heterospecifics). In the fall/winter, playbacks of typical calls with A and C notes elicited the greatest number of A and B notes in chick-a-dee call responses and typical calls with D notes elicited the greatest number of C notes, when in the presence of heterospecifics. In contrast, the corresponding atypical calls did not elicit similar responses. This suggests communicative significance is lost in calls that violate a rule of syntax in the fall/winter. In the spring, neither chickadee feebeefebay song rate nor chick-a-dee calls responses differed by playback type. We suggest that call syntax is less salient for mated pairs in the spring than it is for fall/winter flocks that rely more on conspecific communication for foraging success and flock cohesion. This study represents the first experimental

evidence that chickadees attend to both note composition and ordering in chick-a-dee calls.

Keywords Carolina chickadee · Chick-a-dee call · *Poecile* · Syntax · Vocal communication

Introduction

Animals use vocal signals to accomplish a variety of social tasks and in some taxa selection may favor vocal repertoires of greater complexity (Kroodsma 1977; Blumstein and Armitage 1997; Bradbury and Vehrencamp 1998; Owings and Morton 1998; Ord et al. 2002). Certain species attain this complexity by varying the composition and possible order of different elements in structurally complex signals (Hailman and Ficken 1986). Additionally, the structure of the signals may follow simple rules of note composition and note ordering (e.g., Hailman et al. 1985, 1987) and it is suggested that this ‘syntax’ Note that throughout this paper, we are using ‘syntax’ to refer to note ordering and composition (Markovian syntax), and not in the language sense of different words being arranged in phrases or sentences such that changes in word ordering can alter phrase or sentence meaning might be important in communication (Robinson 1984; Hailman and Ficken 1986; Balaban 1988; Kanwal et al. 1994).

To demonstrate the importance of syntax in a vocal signaling system, it is not enough to show that signalers vary the syntax of their vocalizations; one must also show that receivers respond to variation in syntax. Many avian studies have shown that behavioral responses to local or typical birdsong syntax are different compared to foreign or atypical syntax (e.g., Baker et al. 1987; Okanoya et al. 2000; Holland et al. 2000). Similarly, several primate species that produce vocal signals governed by a rudimentary syntax give different behavioral responses to atypical compared to typical vocalizations (Mitani and Marler 1989; Ghazanfar et al. 2001; Zuberbuhler 2002). These studies suggest that animals attend to violations of

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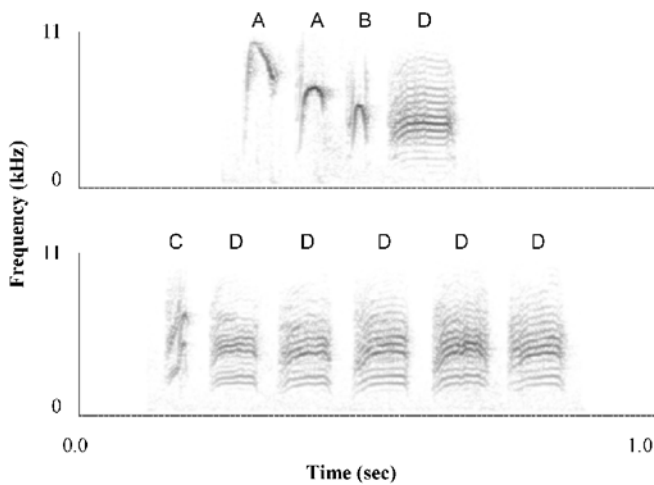


Fig. 1 Sonograms of two exemplars of chick-a-dee calls of Carolina chickadees (*Poecile carolinensis*). Sonograms were generated in Cool Edit Pro 2.0 on Windows XP platform, using the Blackmann-Harris windowing function at 256 band resolution. Note type classifications (based on note type designation from Hailman et al. 1985 and Freeberg and Lucas 2002) are indicated above each sonogram

syntactical rules, and provide further evidence that syntax potentially plays a functional role in communication for these species.

Here, we begin an investigation of the importance to conspecific receivers of call syntax in the chick-a-dee call of Carolina chickadees, *Poecile carolinensis*. The chick-a-dee call of *Poecile* species has been intensively analyzed in terms of the production rules governing the composition and ordering of its notes (Hailman et al. 1985, 1987; Hailman and Ficken 1986; Ficken et al. 1994). It is typically made up of four note types that are distinguished by unique acoustic properties, and traditionally designated as A, B, C, and D (Hailman and Ficken 1986; Ficken et al. 1994; Freeberg et al. 2003; Bloomfield et al. 2003). The notes follow a general A-B-C-D ordering (Hailman et al. 1985; see Fig. 1) and any note can be omitted or repeated up to 30 or more times in the call (Smith 1972). Therefore, the chick-a-dee call system has the potential to generate an enormous number of unique call types. The structural complexity of the chick-a-dee call is comparable to that of some birdsong. Yet unlike most song in songbird species, the chick-a-dee call is produced year round, during different social interactions and many environmental situations. Thus, in contrast to birdsong, chick-a-dee call syntax may accomplish more than communicating species identity or signaler status (e.g. mate choice and territorial functions). Several studies show that note composition (type and number of notes) in chick-a-dee calls correlates with the context of the vocalization (Gaddis 1985; Ficken et al. 1994) and can affect the behavior of signal recipients (Freeberg and Lucas 2002). However, no study has tested whether the order of the note types affect receiver perceptions and subsequent responses in a *Poecile* species.

We conducted field playbacks in the spring and fall/winter of chick-a-dee call variants containing notes in either typical (e.g. AAAACCCC and CCCCDDDD) or atypical (e.g. CACACACA and DCDCDCDC) order to test the possible effect of this syntax violation on the vocal responses by Carolina chickadees. The playback variants focused on C notes because previous work found that chickadees responded differently to the presence of a string of C notes in call playbacks compared to calls without these note types (Freeberg and Lucas 2002). We measured latency to arrive at playback site, vocalization rates, and note composition of chick-a-dee calls produced to test for differences in chickadees' responses to typical relative to atypical syntax call playbacks. Furthermore, we examined the effect of season because chickadees are in mated pairs in the spring and in small flocks (often heterospecific) in the fall/winter (Brewer 1961; Smith 1991) and these differences may influence vocal responses to playbacks. Differences in responses would suggest note order is important for communication.

Methods

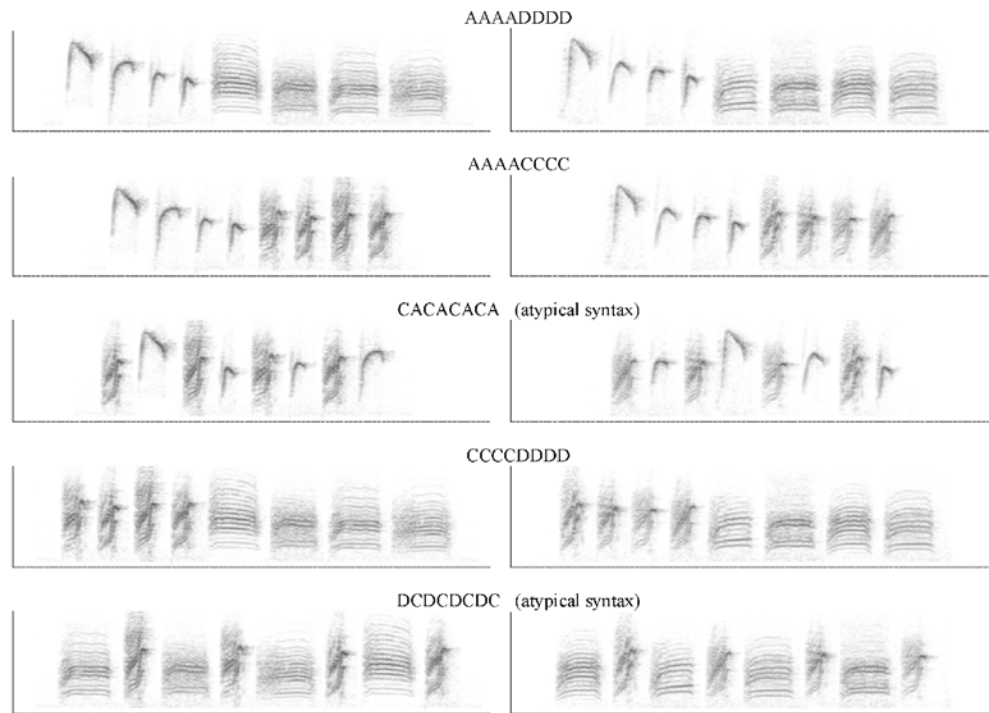
Generation of playback sets

We recorded individual Carolina chickadees in an anechoic room under identical conditions to generate a library of chick-a-dee calls. During recording, chickadees were housed individually in separate 1-m³ cages, where birds could hear and often see one another in adjoining cages or rooms. The chick-a-dee calls were recorded with Saul Mineroff directional electret microphones, placed within 1 m of an individual, on Maxell XLII cassette tape using Marantz PMD 222 portable cassette recorders. Calls were then digitized from cassette tape using Cool Edit Pro with 16-bit resolution and a 22 kHz sampling rate.

Carolina chickadees typically produce calls with the following note combinations: AC, AD, CD, ACD, or ABD using a range of note numbers (Smith 1972; Freeberg, unpublished data). Chick-a-dee calls in this Indiana population contain an average of 2.1 A notes (median 2, SD 1.9, range 0–18), 0.1 B notes (median 0, SD 0.4, range 0–5), 0.5 C notes (median 0, SD 1.1, range 0–9), and 3.4 D notes (median 3, SD 3.3, range 0–25), based on 1,653 calls recorded from birds at 13 independent field sites (Freeberg, unpublished data). We created eight-note calls that each had four notes of two types (A and C, C and D, or A and D), which controlled for note numbers across playback variants. For calls containing C notes, we made call types with typical note ordering (AAAACCCC and CCCCDDDD) and call types with atypical note ordering (CACACACA and DCDCDCDC). For calls not containing C notes, we made only typical note ordering (AAAADDDD). For each of the eight playback sites, a unique set of these five playback types was generated from previously recorded calls (sonograms of two of the eight sets are given in Fig. 2).

To demonstrate that the typical chick-a-dee calls we created do occur naturally, we analyzed the syntax of 1,653 field-recorded calls that were collected as part of a different study (Freeberg, unpublished data). Calls with the "AD" syntax that contained at least three A notes and at least three D notes occurred 149 times (calls from 12 of 13 sites). Calls with the "AC" syntax that contained at least three A notes and at least three C notes occurred 3 times (calls from 3 of 13 sites). Calls with the "CD" syntax that contained at least three C notes and at least three D notes occurred 22 times (calls from 11 of 13 sites). Calls containing an "ACA" or "CAC" note ordering (characteristic of the CACACACA note composition in our study), or containing an "CDC" or "DCD" note ordering (characteristic of the DCDCDCDC note composition in

Fig. 2 Sonograms of the five playback types from two of the eight playback sets. Scale of the axes and sonogram generation parameters are the same as in Fig. 1. The *left panel* of sonograms is the playback set for Playback Site 8, and the *right panel* of sonograms is the playback set for Playback Site 5. Note that within each playback set, individual A notes are identical (though ordering may differ) for the *top three rows*, individual C notes are identical (though ordering may differ) for the *bottom four rows*, and individual D notes are identical (though ordering may differ) for the *top row* and the *bottom two rows*



our study), at any point in the call's note composition, did not occur in that set of 1,653 calls. Thus, calls with the typical note ordering that we used in our playback study do occur in this population, and our field sampling to date has not obtained a call with the sort of atypical note ordering that we created.

There is a fairly smooth transition in the spectral properties of notes given multiple times in a call (Freeberg et al. 2003). This transition is disrupted by definition when calls are made (artificially) with atypical syntax. To ensure that the effect of note order on chickadees' responses to our playbacks was not confounded by this, we constructed all calls (i.e., both typical and atypical calls) by combining a single note taken from eight different calls to make a single playback call consisting of eight notes. Thus, a complete set of playback calls for one playback site would be $A_1A_2A_3A_4C_5C_6C_7C_8$, $C_7A_4C_5A_1C_8A_2C_6A_3^*$, $A_1A_2A_3A_4D_9D_{10}D_{11}D_{12}$, $C_5C_6C_7C_8D_9D_{10}D_{11}D_{12}$, and $D_9C_6D_{11}C_5D_{12}C_8D_{10}C_7^*$ (notes derived from the same bird are indicated with the same subscript and an asterisk indicates that the call has atypical note ordering, with the note ordering for each of these playback types determined randomly).

Cool Edit Pro was used to construct each playback type for each playback set by cutting single notes from the recorded calls. Inter-note intervals were set at approximately 0.03 s for all notes, the mean inter-note intervals measured from chickadee calls in this population (Freeberg and Lucas, unpublished data). To control for geographic variation in note structure (Freeberg et al. 2003), all playback calls were constructed from notes recorded from birds captured from the same population as those given playbacks. Constructed playback types were then recorded onto Maxell UR cassette tapes with a Marantz PMD 222 portable cassette recorder. Each playback type was dubbed onto a different tape at roughly one vocalization every 10 s for 3 min (the duration of the playback period in each 10-min block of trials).

Playback presentations

Playbacks were conducted at the Ross Biological Reserve in West Lafayette, Indiana, during spring 2001 (March–May) and fall/winter 2001–2002 (September–January). There were eight playback sites, each at least 250 m apart to ensure independence of sites (see

Freeberg and Lucas 2002). Not all birds responding to the playbacks were banded; however in this study banded birds consistently responded at only one site, within a season. It is possible that an unbanded bird responded at more than one site; however, assuming flock and pair membership were stable (see Brewer 1961; Dixon 1963), this is unlikely.

At each of the eight sites, we conducted five different playback presentations, each on separate days with at least 7 days between consecutive playbacks. One playback type was broadcast during a presentation and the order of playback type was randomized across sites. Therefore, 40 playback presentations were completed in each season. Playbacks started between 0700 and 1030 hours EST with a 10-min 'pre-playback' observation period to obtain data on background call rate unaffected by playback calls. A novel seed stand (2 m high) was placed near a playback speaker (hung about 2 m high from a tree) on arrival to the site and was filled with sunflower seeds at the end of the 'pre-playback' period.

The experimental design was similar to that used by Freeberg and Lucas (2002). Briefly, we played back calls with a Marantz PMD 222 portable cassette recorder through a Saul Mineroff powered speaker. Trials lasted 60 min, which was divided into six 10-min sections. Each 10-min section began with a 3-min playback of a certain call type and ended with 7 min of silence. Trials (including the pre-playback period) were recorded with a second portable cassette recorder for subsequent analysis.

Data collection and analyses

We collected data on the following:

1. Number of chickadees vocalizing during the pre-playback period and number responding to each playback.
2. Rates of major vocalizations during the pre-playback period. These data would allow us to determine whether there were seasonal differences in production rates (number calls/h/bird) of chick-a-dee calls, gargle vocalizations (an agonistic vocal signal of *Poecile* species), and feebeefeebay songs (the territorial song of the species, given only by males).

3. Arrival time (min) for Carolina chickadee receivers to approach to within 20 m of the playback speaker and seed stand.
4. Rates of chick-a-dees, gargles, and feebeefebays during the playback trial.
5. Note composition of chick-a-dee call responses of Carolina chickadee receivers. Analysis of note composition was restricted to those calls given starting 10 min before the first bird broke the 20-m barrier around the feeder and ending 10 min after the bird(s) first broke the 20-m barrier. We used this 20-min subset of calls to ensure that our data reflect a response to the playback.

Recordings of each playback trial allowed us to analyze receivers' calls (Cool Edit Pro sound analysis program) to obtain the exact composition of all chick-a-dee call responses given within the 20-min criterion time. Identifying individual receivers was not possible from these recordings. However, limiting calls analyzed to a 20-min period (see previous paragraph) ensured calls analyzed were responses from birds that approached close to the playback speaker and were not multiple pairs/flocks approaching and departing from the playback site. We determined the average number of A, B, C, and D notes in calls produced by receivers at the playback sites. The introductory A and B notes were sometimes difficult to distinguish from each other, and inter-individual reliability for these notes was low (50%); therefore we combined these note types in our analysis. A total of 1,502 chick-a-dee calls constituted the complete data set for analysis of note composition in birds responding to our playbacks. B.A.C. scored the 1,502 calls that went into the statistical analyses and T.M.F. independently scored 490 calls for inter-observer agreement measures. Independent scoring was within ± 1 note agreement for 428 of those calls (87%).

We analyzed the data on arrival times, vocal rates, and numbers of A+B, C, and D notes in calls of receivers using repeated measures ANCOVAs with a first-order autoregressive covariance structure (Proc MIXED; SAS Institute 1994). The distributions of the data were highly skewed; therefore we log-transformed $[\ln(n+1)]$ the data for all of the data sets except the pre-playback vocal rates, where we log-log-transformed $\{\ln[\ln(n+1)+1]\}$ the data, to normalize residuals in the ANCOVA models. For the pre-playback data, we tested for effects of season (fall/winter vs spring) and playback type. For the playback trial data, we tested for main effects of season, playback type, and social context (presence or absence of tufted titmice, *Baeolophus bicolor*, or white-breasted nuthatches, *Sitta carolinensis*). We also tested for the effect of number of chickadees responding to our playbacks because vocalization rates will obviously vary with this number. Less obviously, the note composition of chick-a-dee calls given by responders might also vary if the syntax reflects, in part, communication between birds. To account for these effects, we included the number of chickadees we detected as covariates in the ANCOVA models. Playback site was used as the subject variable. All two-way interactions between the main effects and the three-way interaction were added to the models. Non-significant interaction terms were dropped from the model in order of decreasing P -value until all remaining interactions were significant ($P < 0.05$). Note that the degrees of freedom may vary depending on the interaction terms left in the model. Where significant effects were detected, we tested for significant differences between playback types, season, or social context using the DIFF option of the LSMEANS calculation in Proc MIXED. Below we only report differences that were significant at $\alpha = 0.05$.

We divided the calls into their component parts (A+B, C and D notes) to evaluate the effect of season, playback type and social context on call syntax. Doing so may inflate the probability of a type I error by underestimating the true P -value (since each call is analyzed three times). Therefore, we use a Bonferroni correction of the α level to account for these multiple tests ($\alpha = 0.05/3$).

Finally, we used repeated measures Poisson regression (GLIMMIX SAS macro in Littell et al. 1996) to evaluate whether the number of responding birds changed between seasons, or changed as a function of playback type.

Results

Number of chickadees vocalizing/number responding to playbacks

The number of chickadees responding to our playbacks ranged from 1–4 birds and did not vary with playback type ($F = 0.90_{4,41}$, $P = 0.4735$) season ($F = 0.18_{1,41}$, $P = 0.6710$), and social context ($F = 0.16_{1,41}$, $P = 0.6914$).

Rates of chick-a-dees, gargles, and feebeefebays during the pre-playback period

Combining pre-playback intervals across all sites, there was a significant effect of season on rates of chick-a-dee call production ($F_{1,14} = 5.1$, $P = 0.041$). More chick-a-dee calls were produced in the fall/winter than in the spring (Fig. 3), and chick-a-dee rate increased with the number of chickadees observed ($F_{1,15} = 6.31$, $P = 0.0001$). We did not detect an effect of season on rates of gargle production ($F_{1,14} = 0.00$, $P = 0.96$; see Fig. 4). Gargle rates did increase significantly with an increase in the number of chickadees ($F_{1,15} = 10.3$, $P = 0.006$). Finally, for feebeefebay rates there was a significant interaction between the number of chickadees and season ($F_{1,14} = 11.3$, $P = 0.005$), with a stronger effect of number of birds on song rate in spring than in fall/winter.

Arrival time to approach within 20 m

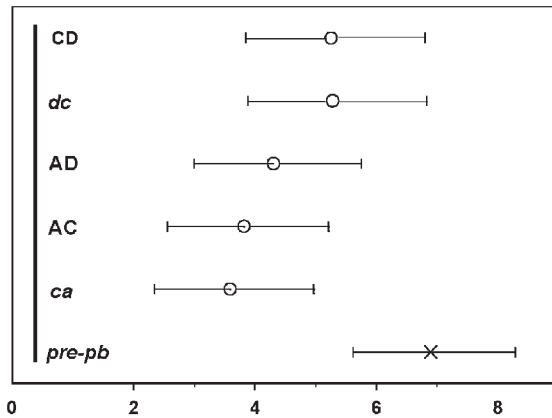
Carolina chickadee receivers generally approached the speaker and seed stand within about 20 min of the start of the playback (spring: 18.3 ± 2.8 SE min; fall/winter: 17.7 ± 3.1 SE min). We did not detect an effect of playback type ($F_{4,31} = 0.65$, $P = 0.63$) or season ($F_{1,8} = 0.52$, $P = 0.49$) on arrival times of chickadees. However, arrival time was shorter with an increase in the number of responding birds ($F_{1,9} = 12.6$, $P = 0.0062$; $\beta = -1.20 \pm 0.34$, with log $(n+1)$ transform of arrival time).

Rates of chick-a-dees, gargles, and feebeefebays during the playback trial

Chick-a-dee rates

The main effect of playback type on chick-a-dee rates was not significant ($F_{4,73} = 1.1$, $P = 0.35$). We did not detect an effect of season ($F_{1,73} = 0.00$, $P = 0.99$; Fig. 3) or social context ($F_{1,73} = 0.12$, $P = 0.73$) on rates of chick-a-dee calls produced by receivers. However, when we analyze patterns in chick-a-dee rates separately for each season, the number of chickadees responding contributes to variance in chick-a-dee rates (Table 1).

A) Fall



B) Spring

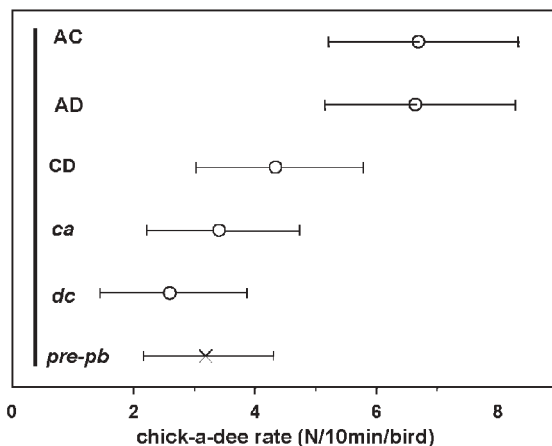


Fig. 3 Chick-a-dee rates (least squares means \pm SE) elicited by each playback type in the fall (A) and spring (B). Playback types: “AD”=AAAADDDD; “AC”=AAAACCCC; “CD”=CCCCDDDD; “ca”=CACACACA; “dc”=DCDCDCDC. SE were back calculated from the $\log(n+1)$ transformation. Multiple comparisons suggest that none of the means within each season are significantly different from one another ($\alpha=0.05$)

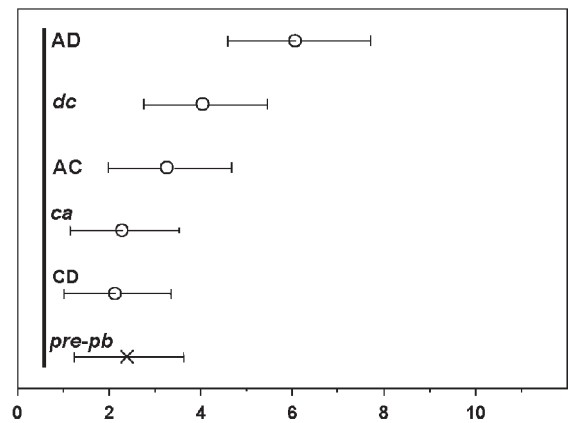
Gargle rates

Chickadee receivers produced no more gargle vocalizations to playbacks in the spring than they did in the fall/winter (Fig. 4; $F_{1,73}=2.67$, $P=0.11$). We also did not detect an effect of playback type or social context on gargle rates (Table 1). In both seasons, gargle rates increased significantly from pre-playback to playback intervals (Fig. 4; fall/winter: $F_{1,60}=32.3$, $P<0.0001$; spring: $F_{1,60}=26.1$, $P<0.0001$), indicating that birds were responding to our playbacks.

Feebeefebay rates

The interaction of season, number of responding birds and playback type had an effect on rates of feebeefebay production ($F_{1,61}=3.0$, $P=0.005$). Therefore, analysis of

A) Fall



B) Spring

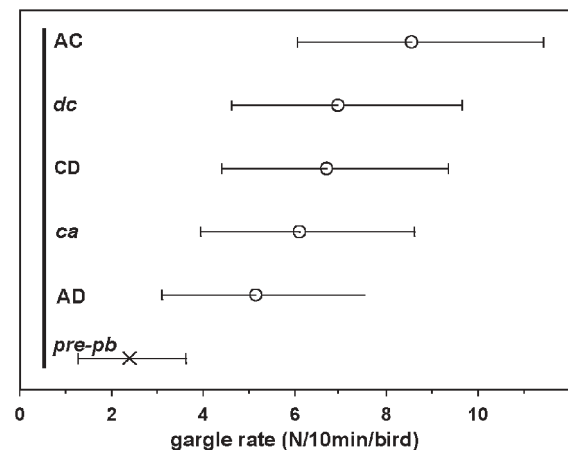
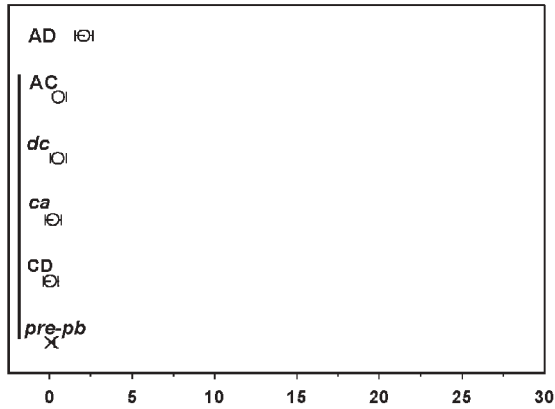


Fig. 4 Gargle rates (least squares means \pm SE) elicited by each playback type in the fall (A) and spring (B). SE were back calculated from the $\log(n+1)$ transformation. Multiple comparisons suggest that none of the means within each season are significantly different ($\alpha=0.05$). Playback type and social context designations are the same as in Fig. 3

feebeefebay rates is clearer when the data for the two seasons are evaluated separately. In the fall/winter, the chickadees rarely responded with feebeefebay song but the few songs given were to AAAADDDD playbacks (Fig. 5a; Table 1). Not surprisingly, male chickadees sang more in the spring and the only factor that correlated (positively) with song rates was the number of responding birds (Fig. 5b; Table 1). We added pre-playback feebeefebay rates to the model to test whether our playbacks elicited a change in song rates. The pre- versus during-playback main effect was significant for both seasons (Fig. 5; fall/winter: $F_{1,60}=9.52$, $P=0.003$; spring: $F_{1,60}=9.41$, $P=0.003$), with the average pre-playback rate significantly lower than the during-playback rate. This demonstrates that feebeefebay rates of receivers were strongly influenced by our playbacks, especially in the spring when singing is most prevalent.

A) Fall



B) Spring

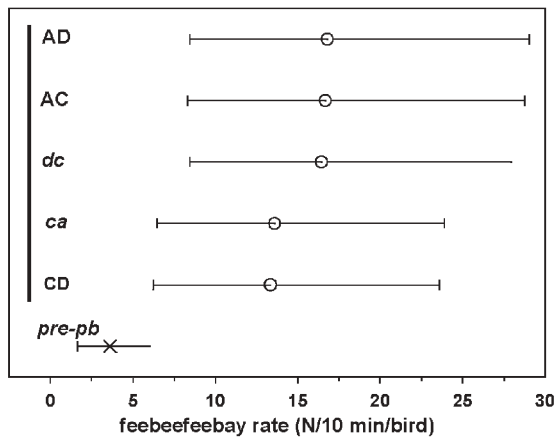


Fig. 5 Feebeefebay rates (least squares means±SE) elicited by each playback type in the fall (A) and spring (B). SE were back calculated from the log(*n*+1) transformation. Multiple comparisons are indicated with lines to the left of the playback designations; those connected by a line are not significantly different at $\alpha=0.05$. Playback type designations are the same as in Fig. 3

Note composition of chick-a-dee calls of Carolina chickadee receivers

We analyzed the effect of playback type and social context (presence or absence of titmice or nuthatches) for

each note type in the chickadee call separately. In addition, we focus on trends within seasons following the rationale that playback type and social context are the most critical effects that we are evaluating with respect to the note composition of chick-a-dees given by responding birds (noting that these relationships can nonetheless vary across seasons).

A+B notes

There were on average 1.85 A+B notes per call across all calls we analyzed for this study (median=1, lower quartile=1, upper quartile=3, range=0 to 17 A+B notes per call). In the fall/winter, the number of introductory notes given by the responding birds was affected by each of the independent variables through a significant 3-way interaction (Table 2). Interestingly, holding number of birds responding and social context constant, the number of introductory notes was highest in response to the playbacks with typical syntax (especially AC playback), compared to calls with atypical syntax (Fig. 6a). In the spring, there were no significant trends (Fig. 6b).

C notes

The calls we analyzed had an average of 0.97 C notes in them (median=0, lower quartile=0, upper quartile=1, range=0 to 12 C notes per call). In the fall/winter, the number of C notes in chick-a-dee calls elicited from our playbacks was highest for playbacks with typical syntax, and this effect varied with playback note composition and was also affected by the presence of titmice and nuthatches. The two main effects, playback type and social context, and their interaction were significantly correlated with the number of C notes in the calls (Fig. 7a; Table 2). A multiple comparisons test indicates that the AAAADDDD and CCCDDDD playbacks in the presence of titmice and nuthatches elicit chick-a-dee calls rich in C notes. All other typical combinations of note composition and social context in the fall/winter elicited calls with fewer C notes, as did all of the atypical syntax playbacks (Fig. 7a; Table 2). The number of birds responding did not affect the number of C notes in the calls

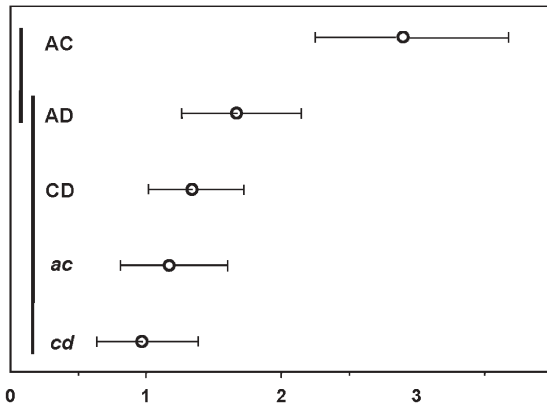
Table 1 Repeated measures analysis of the effect of playback type, social context (presence of titmice or nuthatches), and number of Carolina chickadees (*Poecile carolinensis*) responding on chick-a-dee, gargle, and feebeefebay call rates of responding Carolina chickadees. Call rates were number of calls/10 min of playback; this value was log(*n*+1) transformed to normalize the residuals. Only significant interaction terms were retained in each model

Call type	Independent variable	Spring	Fall
Chick-a-dee	Playback type	$F_{4,34}=0.54, P=0.71$	$F_{4,34}=0.18, P=0.95$
	Social context	$F_{1,34}=0.03, P=0.87$	$F_{1,34}=1.53, P=0.23$
	No. birds responding	$F_{1,35}=13.3, P=0.0009$	$F_{1,34}=73.6, P=0.0008$
Gargle	Playback type	$F_{4,34}=0.51, P=0.73$	$F_{4,34}=0.19, P=0.94$
	Social context	$F_{1,34}=0.02, P=0.89$	$F_{4,34}=0.00, P=0.98$
	No. birds responding	$F_{1,35}=34.0, P=0.0001$	$F_{1,34}=37.0, P=0.0001$
Feebeefebay	Playback type	$F_{4,34}=0.04, P=0.99$	$F_{4,34}=2.66, P=0.049$
	Social context	$F_{1,34}=0.46, P=0.50$	$F_{1,30}=2.59, P=0.12$
	No. birds responding	$F_{1,7}=23.3, P=0.002$	$F_{1,7}=4.01, P=0.09$

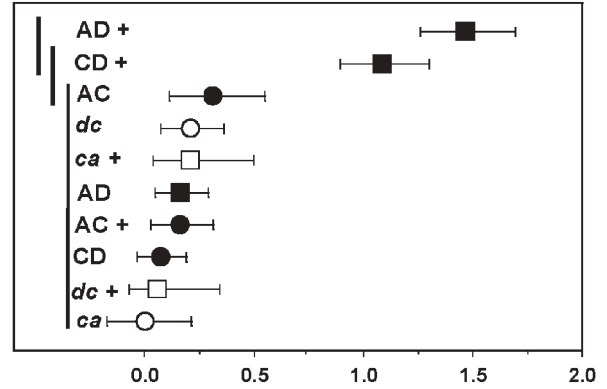
Table 2 Repeated measures analysis of the effect of playback type, social context (presence of titmice or nuthatches), and number of Carolina chickadees responding on note composition of chick-a-dee calls. The number of notes in a call was $\log(n+1)$ transformed. Only significant interaction terms were retained in each model

Note type	Independent variable	Spring	Fall
D	Playback type	$F_{4,19}=1.62, P=0.211$	$F_{4,17}=1.96, P=0.15$
	Social context	$F_{1,19}=1.55, P=0.228$	$F_{1,17}=2.41, P=0.139$
	No. birds responding	$F_{1,11}=19.21, P=0.001$	$F_{1,9}=1.96, P=0.195$
	No. birds \times social context	NS	$F_{1,9}=8.73, P=0.016$
C	Playback type	$F_{4,19}=0.03, P=0.99$	$F_{4,13}=5.39, P=0.009$
	Social context	$F_{1,19}=0.26, P=0.61$	$F_{1,13}=10.81, P=0.006$
	No. birds responding	$F_{1,11}=8.93, P=0.012$	$F_{1,16}=1.32, P=0.27$
	Playback \times social context	NS	$F_{4,13}=7.69, P=0.002$
A+B	Playback type	$F_{4,19}=2.68, P=0.063$	$F_{4,17}=5.06, P=0.007$
	Social context	$F_{1,19}=3.26, P=0.087$	$F_{1,17}=1.44, P=0.25$
	No. birds responding	$F_{1,11}=19.42, P=0.001$	$F_{1,12}=0.01, P=0.91$
	No. birds responding \times playback	NS	$F_{4,12}=3.92, P=0.029$

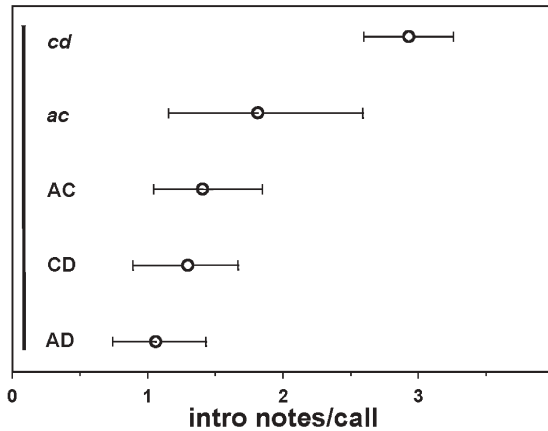
A) Fall



A) Fall



B) Spring



B) Spring

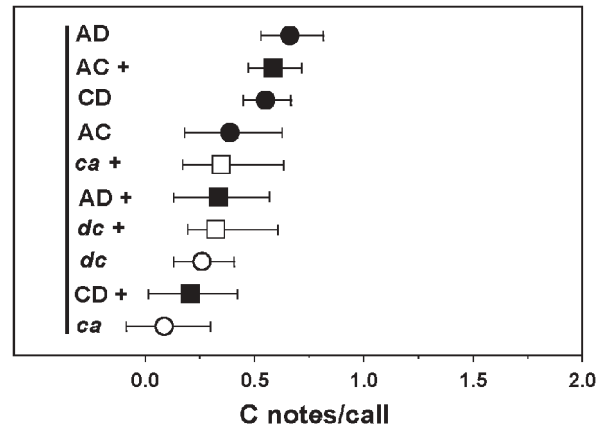
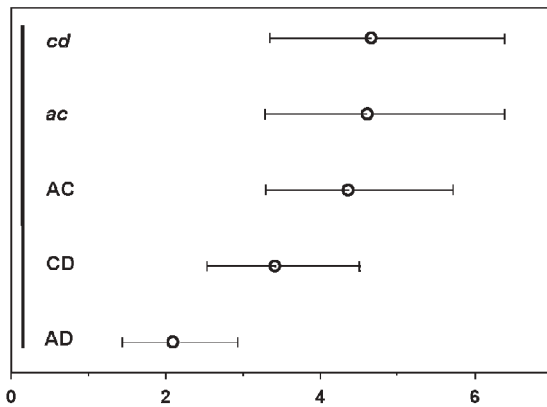


Fig. 6 Number of A+B notes (least squares means \pm SE) in chick-a-dee calls as a function of playback type in the fall (A) and spring (B). Playback type designations are the same as in Figure 3

Fig. 7 Number of C notes (least squares means \pm SE) in chick-a-dee calls as a function of playback type and social context in the fall (A) and spring (B). Playback types: “AD”=AAAADDDD; “AC”= AAAACCCC; “CD”=CCCCDDDD; “ca”=CACACACA; “dc”=DCDCDCDC. Social context: + modifier to call playback = presence of titmice and/or nuthatches; no modifier to call playback = absence of titmice and/or nuthatches. SE were back calculated from the $\log(n+1)$ transformation. Multiple comparisons are indicated with lines to the left of the playback designations; those connected by a line are not significantly different at $\alpha=0.05$

(Table 2). In contrast to these fall/winter results, we did not detect an effect of playback type or social context on C notes in the spring (Fig. 6b; Table 2), although the number of C notes in the calls did increase with the number of birds responding ($\beta=0.20\pm 0.07$).

A) Fall



B) Spring

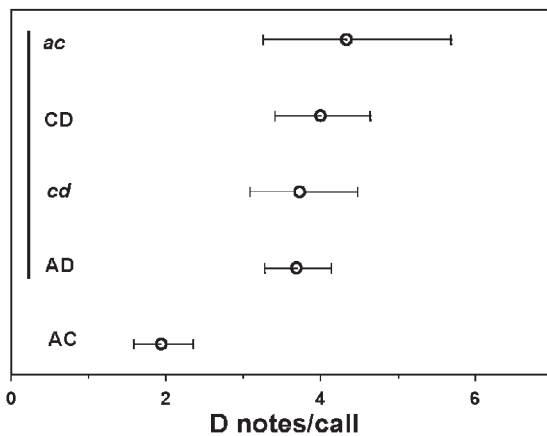


Fig. 8 Number of D notes (LSM \pm SE) in chick-a-dee calls as a function of playback in the fall (A) and spring (B). Playback type designations are the same as in Figure 3

D notes

The calls we analyzed had an average of 4.56 D notes (median=4, lower quartile=2, upper quartile=6, range=0 to 25 D notes per call). In the fall/winter, we did not detect an effect of playback type on the number of D notes in a call (Fig. 8a), but there was a significant effect of social context, through an interaction with the number of responding conspecifics. Chickadees increased the number of D notes with increasing number of conspecifics responding in the absence of titmice or nuthatches ($\beta=0.43\pm0.14$) but decreased the number of D notes with an increase in conspecifics responding in the presence of titmice or nuthatches ($\beta=-0.11\pm0.10$) (Table 2). Note that the reduction in number of D notes in the presence of heterospecifics is caused by a change in note composition compared to chick-a-dee calls given when no heterospecifics were present. This response is not a simple reduction in chick-a-dee rates.

In the spring, there was a statistically not significant effect of playback type on the number of D notes in the call and a significant interaction between playback type

and number of responding birds (Table 2). As the number of birds responding increased in the spring, the number of D notes decreased, but the strongest decrease was for typical AC calls ($\beta=-0.50\pm0.23$). In contrast, there was no effect of number of birds responding on the number of D notes given in response to typical CD calls ($\beta=0.01\pm0.20$). The other three calls had intermediate effects (CD atypical: 0.008 ± 0.22 ; AC atypical: -0.0026 ± 0.31 ; AD typical: -0.251 ± 0.21). Holding number of birds responding constant, the number of D notes per call given in response to normal AC calls was significantly less than the number of D notes given in response to any other call. All other comparisons were not significant.

Discussion

This study tested whether Carolina chickadees would attend to violations of a syntactical rule in their chick-a-dee call by responding differently to call playbacks of typical note order versus atypical note order. The results show that although vocalization rates did not vary with playback type, there were subtle differences in the note composition of chick-a-dee call responses to typically ordered calls compared to atypically ordered calls. Season (spring or fall/winter) and social context (presence or absence of heterospecifics) also contributed to these response differences and may reflect the effect of seasonal changes in chickadee social structure and heterospecific interactions on intraspecific communication. Thus, note order affects response behavior and the presence of this note order effect suggests that calls with atypical syntax can lose communicative significance.

We conducted playbacks across two seasons, spring and fall/winter, because seasonal variation in social systems can affect the use of components of a vocal repertoire. An obvious example is the seasonal use of song in a wide variety of songbirds (see Kroodsma and Miller 1996). Male song provides a mechanism for territory defense and advertisement of its borders, and is often dropped entirely from male repertoires outside of the breeding season. Thus it was not surprising that male chickadees sang almost exclusively in the spring when they defend a territory with their mate, and very little the fall/winter when chickadees form small flocks (Smith 1972; Smith 1991). In the spring, male chickadees increased song rates during all of our playbacks suggesting territorial males investigate and aggressively respond to conspecific calls regardless of note order.

Chick-a-dee call responses were given at similar rates between season and rates did not differ between playback types within season. However, in the fall/winter the note composition of chick-a-dee call responses differed depending on the playback type. Specifically, chickadees produced chick-a-dee calls with the most introductory (A and B) notes in response to typical AC playbacks (regardless of the presence of heterospecifics) and calls with the most C notes in response to the other typical playbacks (AD and CD) when in the presence of het-

erospecifics. Atypically ordered playbacks with the same number and composition of notes did not elicit similar responses, suggesting that the chickadees do not perceive them as the same call as the typically ordered playbacks. In contrast to these fall/winter patterns, there was no difference in the note composition of chick-a-dee calls elicited by different playbacks broadcast in the spring. We suggest that this seasonal variation in vocal communication reflects seasonal changes in social structure. Unlike mated pairs in the spring, Carolina chickadees form small flocks of unrelated individuals during the fall that remain together throughout the winter (Brewer 1961; Dixon 1963). The chick-a-dee call is thought to play an important communicative role in maintaining flock cohesion and facilitating foraging (Smith 1991). Thus, we might expect chickadees to be more sensitive to differences in chick-a-dee call syntax from unknown birds (our playbacks) in the fall/winter compared to in the spring. However, what could explain the fact that different notes were produced dependent on playback type and social context in the fall/winter? More fundamentally, why might selection favor a call system that can generate many unique call types using rules for note ordering and composition?

Obviously, the benefit of communicating among conspecifics is not the only factor that may affect the production and perception of vocal signals. The production of signals is risky. By attracting the attention of unintended receivers, animals can expose themselves to social and predation costs. For example, subordinates that vocalize in the presence of a rich food source may elicit aggression from more dominant animals nearby (Wrangham 1977) and advertisement signals used during mating can be exploited by predators to localize and prey on signalers (Endler 1991; Ryan et al. 1982). One solution for minimizing the risks associated with communication would be a flexible repertoire where different signals can be given depending on circumstance. Thus, signalers might have the option of using a subset of calls that are 'cautious' in the sense that they are not easily heard or localized, and another, more conspicuous, subset for use under less risky conditions to produce a richer set of information. A classic example is the Túngara frog (*Physalaemus pustulosus*) whine-chuck call system where males omit the conspicuous "chuck" element when predation risk is increased (Ryan 1985).

During the fall/winter, chickadees often form mixed species flocks with other bird species, in particular with white-breasted nuthatches and tufted titmice (Brewer 1961). Although chickadees are known as a 'nuclear species' in the mixed species flocks, they are the subordinate members (Morse 1970; Cimprich and Grubb 1994). It is suggested that heterospecifics may exploit communication between chickadees to find food and this could incur competition costs for chickadees (Sullivan 1984). Indeed, Cimprich and Grubb (1994) showed that when tufted titmice were experimentally removed, chickadees experienced increased nutritional condition. Thus, in the context of titmice or nuthatches in close proximity, the

increased numbers of C notes in chick-a-dee calls in response to our typical call playbacks by chickadees may be related to competition with those more dominant species.

Alternatively, chickadees may only respond with more C notes when in the presence of heterospecifics because predation risk is decreased in larger mixed species flocks (Gaddis 1980; Pravosudov and Grubb 1999; Dolby and Grubb 2000). Krams (2001) found that sparrowhawks (*Accipiter nisus*) attacked models of great tits (*Parus major*) more during playbacks of long-range, trilled calls than during short-range, high-pitched calls. Similar to trilled notes, C notes are harsh 'chick' like notes that have a large bandwidth and are thus likely to be relatively easy to localize, by predators and heterospecifics alike (Marten and Marler 1977; Wiley 1991; Krams 2001). Therefore, chick-a-dee calls containing C notes may be riskier than calls with other note compositions. For example, introductory notes (A and B) are high frequency whistles and might be harder to locate. This might explain why chickadees increased the number of introductory notes in response to a typical call playbacks compared to their response to the atypical call playbacks. Nonetheless, studies of predator responses to chick-a-dee calls varying in note composition are needed (Lima 2002), as well as experiments that examine chickadee vocalizations given in varying degrees of predation risk.

Other playback studies have tested for the significance of note ordering in vocalizations by measuring differences in responses to typical versus atypical note ordering (Mitani and Marler 1989; Esser et al. 1997, Okanoya et al. 2000; Holland et al. 2000; Ghazanfar et al. 2001; Zuberbuhler 2002). However, it can be argued that demonstrating these different response behaviors to signals with atypical syntax that do not occur naturally is trivial (e.g., Evans and Marler 1995). Therefore, we are hesitant to make broad generalizations about the role of note ordering in the chick-a-dee call system at this point. Still, we do believe that simply demonstrating an effect of note ordering on receiver responses is an important initial step to take in understanding the perceptual, affective, and possibly referential aspects of the chick-a-dee call. We are also aware that the resolution of our results could improve by not only accounting for the number of birds responding to our playbacks, but by analyzing note composition of chick-a-dee responses by individual.

The importance of note order in the chick-a-dee calls of signalers has been suggested in several previous studies (Smith 1972, Hailman et al. 1985, Hailman and Ficken 1986). However, it was also important to demonstrate that behavioral responses varied dependent on syntactical properties. Additionally, the importance of the context in which signals are produced and received was demonstrated by the differences in vocal responses seen between seasons and by the differences due to social context. This study provides a preliminary examination of the importance of syntax and further experimental playbacks with Carolina chickadees and other *Poecile* species are needed to examine the functional role of syntax in this complex communication system.

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