

The effect of schedules of reinforcement on the composition of spontaneous and evoked black-capped chickadee calls

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SUMMARY

Songbirds often modify elements of their songs or calls in particular social situations (e.g. song matching, flock convergence, etc.) but whether adult individuals also make vocal modifications in response to abiotic environmental factors (e.g. food availability) is relatively unknown. In the present study we test whether two different schedules of food reinforcement, fixed ratio continuous reinforcement and variable ratio partial reinforcement, cause adult black-capped chickadees to change the structure of their chick-a-dee calls. We also examine how these calls differ in two contexts: being alone *versus* when experiencing an alarming event. Wild-caught black-capped chickadees were housed in isolation to prevent social interaction and recorded weekly for seven weeks. Baseline recordings on week one show that calls given alone differed from those given during an alarming event in both note type composition and frequency (i.e. pitch). Calls also changed over time between birds on the two different schedules of reinforcement. In addition, birds on different reinforcement schedules responded differently during the two recording conditions. Our results suggest that call characteristics can be modified rapidly and may reflect abiotic environmental conditions. If call structure varies consistently with particular abiotic environmental conditions, much can be gained from bioacoustic analyses of calls from wild birds. However, vocal patterns must be consistent across dialects, and we must disentangle vocal changes due to the abiotic environment from those due to social interaction. Further research is needed from natural populations and across multiple regions.

Key words: songbird, black-capped chickadee, communication, operant conditioning.

INTRODUCTION

Songbird vocalizations have the potential to tell us much about the individuals that produce them. In some species we can assess the structure of the habitat where a bird resides based on the pitch and duration of its vocal components (Morton, 1975; Hunter and Krebs, 1979; Boncoraglio and Saino, 2007). For others we can assess dominance status or likelihood of mating success based on song complexity or repertoire size (Ballentine et al., 2004; Mennill and Ratchliffe, 2004). In some species of songbirds, elevated anthropogenic noise can result in populations elevating the pitch of their songs (Slabbekoorn and Peet, 2003; Fernández-Juricic et al., 2005; Wood and Yezerinac, 2006). Additionally, nutritional stress during development is manifest in both neuroanatomical and vocal features observed in these birds as adults (Nowicki et al., 2002; Searcy et al., 2004). In a similar vein, Laiolo et al. (Laiolo et al., 2008) showed that healthy adult Dupont's larks (*Chersophilus dupontis*) had more complex songs, suggesting that health and vocal output are correlated. This is not surprising because song is used to announce identity, declare flock membership, attract mates and repel rivals, to name a few functions (Slater, 2003).

Despite this wealth of information, we have a limited knowledge of how birds modify the structure of their vocalizations in an ongoing manner in response to changes in their abiotic environment. This is not to imply that we poorly understand vocal learning in songbirds because this is clearly not the case (for reviews, see Marler, 1997; Beecher and Brenowitz, 2005). Rather, we suggest that our understanding of plasticity in vocal production after crystallization still needs further exploration. Much of the available literature

suggests that vocal characteristics are set during development or modified due to social interaction. Buchanan et al. found that nutritional stress during development affects the quality of adult songs, with individuals having better access to food singing longer songs and possessing larger repertoires (Buchanan et al., 2003). While the 'nutritional stress hypothesis' has gained further empirical support (e.g. Spencer et al., 2005; Macdonald et al., 2006), and may explain much of the vocal variation related to dominance and individual recognition, it does not suggest that the parameters of adult vocal production are closed entirely to modification. In fact, examination of seasonal changes in the avian brain (Brenowitz, 2004) and monitoring of variation in adult zebra finch songs (*Taeniopygia guttata*) (Tumer and Brainard, 2007) suggests that the adult brain is open to vocal adjustments, and that these adjustments are designed to convey or modify encoded messages (i.e. social facilitation). Further, zebra finches deafened as adults show degradation of their stereotyped songs over time (Nordeen and Nordeen, 1992), with deafening-induced degradation progressing more rapidly in younger adults (Lombardino and Nottebohm, 2000), demonstrating a reliance on auditory feedback for the maintenance of adult vocalizations.

Songbirds are also sensitive to external auditory stimulation and can rapidly adjust their ongoing pattern of vocal output as a result. Adult birds can quickly switch song types (e.g. Stoddard et al., 1992; Vehrencamp, 2001) or modify song characteristics [e.g. pitch (Fitzsimmons et al., 2008)] to match that of a counter-singing individual or novel playback (Franco and Slabbekoorn, 2009). Adult black-capped chickadees [*Poecile atricapillus* (Linnaeus 1766)] also

modify the structure of their chick-a-dee call when joining a new flock to converge on the flock's current call structure (Nowicki, 1989). A few studies have also demonstrated that individual birds can modify their vocalizations in the presence of predators (Bayly and Evans, 2003; Krama et al., 2008).

However, adult vocal modifications are probably not limited solely to situations dictated by social interaction. For example, changes to forest structure and ambient noise affect transmission properties (Morton, 1975; Slabbekoorn and Peet, 2003), and therefore may favor the ability of species to modify their vocal output as adults. Further, food availability may affect motivation to sing (Berg et al., 2005), behavioral state (Goldberg et al., 2001; Rafacz and Templeton, 2003; Lindqvist et al., 2009) or levels of stress (Pravosudov et al., 2001), again perpetuating modifications in the structure of vocalizations. Yet, to our knowledge, no study has evaluated, in a controlled setting, whether individual adult birds can modify the structure of their vocalizations in the presence of abiotic environmental changes such as food availability. To understand if avian vocalizations correlate with changes to the abiotic environment and whether these abiotic changes affect vocal response in two different calling contexts, we evaluated the vocal structure of spontaneous and evoked chick-a-dee calls from black-capped chickadees maintained on fixed ratio continuous food reinforcement or variable ratio partial food reinforcement [hereafter referred to as continuous and partial reinforcement; for extensive treatment of schedules of reinforcement see Ferster and Skinner (Ferster and Skinner, 1957)] under controlled laboratory conditions. We predict that chickadees will modify their calls (1) in response to intrusion of a human in the recording chamber, representing a context leading to alarm and evoking a vocal response; (2) in response to the introduction of a partially reinforced feeding schedule, representing an abiotic environmental change; and (3) that the modification of feeding schedules will differentially affect how black-capped chickadees call in the evoked and spontaneous recording conditions.

MATERIALS AND METHODS

Birds

Eleven male black-capped chickadees were captured in the Edmonton River Valley, Edmonton, Alberta, Canada, in winter 2006. Chickadees were sexed using genetic markers (see Griffiths et al., 1998). Only male chickadees were used to prevent sex-based differences and thus reduce the number of animals needed for the experiment. All individuals were identified as after second year males (ASY) by plumage (see Pyle, 1997). Prior to the experiment, birds resided in animal care facilities at the University of Alberta, Canada. In this facility they were housed in individual cages (30 cm wide×40 cm deep×40 cm high) but within auditory and visual range of conspecifics. Chickadees had *ad libitum* access to food, water, grit and a cuttlebone. To maintain a high standard of health, birds were supplemented with a mealworm three times per week, ground hardboiled egg and spinach twice a week and 3–5 whole sunflower seeds daily. Water had liquid vitamin (Hagen, Rolf C. Hagen, Inc., Montreal, PQ, Canada) added three times per week. Birds were kept under a natural light cycle throughout the experiment with rooms maintained at about 20°C.

Apparatus

In March of 2007 all birds were moved from animal care facilities into individual ventilated sound-attenuating chambers (see Bloomfield et al., 2008; Sturdy and Weisman, 2006). Thus, birds were visually and acoustically isolated from conspecifics. Sound-attenuating chambers were lit with a twin tube, 9 W full-spectrum

fluorescent bulb and were maintained on a natural light schedule. Each chamber contained a modified budgerigar cage similar to those in the animal care facility (30 cm wide×40 cm deep×40 cm high). Cages were equipped with several perches, a water bottle, grit cup and cuttlebone. An 11 cm wide×16 cm high opening provided access to an automated feeding apparatus (see Sturdy and Weisman, 2006). A 'request perch', placed opposite the feeder entrance, monitored the birds' use of the perch *via* an infrared (IR) beam. If the IR beam was interrupted by the bird landing on the perch it was recorded as a 'request' *via* a single experiment controller (EC) board computer (Payla and Walter, 2001). A red LED, positioned about 5 cm above the food cup, was then illuminated in the feeding chamber for 1 s to indicate the availability of food. If a bird entered the feeder when the red light was illuminated, its presence was detected by IR cells, and food became available for 1 s (Njegovan et al., 1994).

Procedure

For two weeks birds were gradually trained to request food by landing on the request perch and entering the feeding chamber once the red light was illuminated. Birds were considered to be trained on the task when food requests were followed by food visits more than 80% of the time, on two consecutive days. All individuals were maintained on a continuous reinforcement schedule for one week after task acquisition. Following this period, five individuals were placed on a variable ratio partial reinforcement feeding schedule, and six were maintained on the original schedule. The partial reinforcement feeding schedule was programmed so that food would become available in the chamber in response to 50 out of 100 food requests, in a randomized (i.e. variable) order. No upper limit was placed on the number of food requests an individual could make in either feeding schedule. Throughout the experiment the number of food requests and number of food rewards was logged for each individual. Birds were maintained on this schedule for seven weeks.

Recordings

A baseline recording session was conducted one week after birds were fully trained on a continuous reinforcement schedule but before any birds were moved to a partial reinforcement feeding schedule. Both spontaneous and evoked calls were recorded during baseline sessions. Once partial reinforcement feeding schedules were introduced for five individuals, all birds were recorded weekly at the same time of day and in the same order for six additional weeks. For each recording session, birds were moved from their ventilated sound-attenuating chamber into a walk-in sound-attenuating chamber (1.83 m×1.83 m×1.83 m; Industrial Acoustics Corporation, Bronx, NY, USA) but kept in the budgerigar cage used for operant conditioning. This provided easier access for audio equipment and human observation. The walk-in sound-attenuating chamber contained an AKG C 1000S microphone and a Marantz (PMD 670) solid-state recorder (Ciné Audio Visual, Edmonton, AB, Canada). Since birds remained in the same budgerigar cage and adjusted to their new environment quickly, recording began once the subject was inside the chamber and the equipment was ready for recording (~1 min). All calls were recorded from the individual for 12 minutes with no external stimulation. These calls were designated as 'spontaneous' calls. Immediately follow this 12 minute session, a second set of calls was collected during an addition six minute period. During this period one experimenter positioned himself briefly in front of a window in the sound-attenuating chamber (less than 1 m from the bird) and waved his hands. This was repeated several times within the six minute period to ensure agitation and prevent habituation. Calls collected during this period were

designated as ‘evoked’ calls. In total we obtained seven weekly recording sessions from each individual. Each session contained a spontaneous and evoked recording period.

Acoustic measures

The total call duration and the number of A, B, C, D and D hybrid (Dh: the case where the final A note is combined with the first D note to form one unique hybrid note) notes per call were calculated for all calls in all sessions [for description of note types see (Charrier et al., 2004; Ficken et al., 1978)]. Rate of calling (calls/min) was assessed for all spontaneous calling recording sessions. Rate was not calculated for evoked calls because human disturbance was designed to clearly agitate the subject and elicit calls but was not conducted using a strictly quantified protocol. Rate of note use (notes/call) was assessed for all spontaneous and evoked recording sessions. Six exemplars of each note type (except Dh) were randomly selected from each session for further bioacoustic analyses. In some cases, especially for C notes, less than six exemplars were available. In these cases all available exemplars were analyzed. Similar to Charrier et al. (Charrier et al., 2004) for A, B and C notes we took three measures of duration [total (TD), ascending (AD) and descending (DD)], and four measures of frequency (i.e. pitch) [start (SF), end (EF), highest (Fmax) and peak (PF; frequency at peak amplitude)] (Fig. 1). For D notes we measured TD, Fmax, lowest frequency (Fmin) and PF. Fmax and Fmin were calculated by measuring the frequency of the highest and lowest peak (frequency band) that fell within -35 dB of the maximum amplitude. All duration measures were taken on spectrograph images with a spectral cutoff of -35 dB relative to the maximum amplitude and a window size of 256 points. Frequency measures, with the exception of PF, Fmin and Fmax were also measured on spectrograph images with a spectral cutoff of -35 dB relative to the maximum amplitude and a window size of 1024 points. All frequency measures excluded above were taken using a power spectrum (i.e. an FFT) with a window size of 4096 points and 88.2 Hz smoothing width for a frequency resolution of 10.8 Hz. When multiple harmonics occurred on A, B or C notes, all measurements were taken from the most intense (darkest) band. Graphical measurements were conducted in

SIGNAL 4.0 sound analysis software (Engineering Design 2003, Berkeley, CA, USA).

Frequency and duration measures within each note type are likely to be correlated and were, therefore, analyzed in separate univariate statistical models. As we were interested in which of these elements are open to change, we chose to retain all measures in the analysis. However, when differences are found in several measures within a particular note type, they are potentially correlated and do not necessarily represent stronger evidence of an effect.

Statistical analyses

A univariate analysis of variance (ANOVA) was computed to assess the effect of the two feeding schedules on request rate and number of times food was accessed in the chamber. General linear mixed models (GLMMs) were conducted on baseline data to detect differences in evoked and spontaneous calls prior to the introduction of the partial reinforcement feeding schedule. Additionally, this model was used to detect baseline difference between the individuals assigned to the continuous reinforcement and partial reinforcement feeding schedules. A second set of GLMMs included acoustic measures from all seven recording sessions. Fixed factors included in the models were week, food treatment group (termed ‘group’), recording condition (termed ‘type’) and the interactions between group and the other main effects (Systat V12, Systat Software Inc., 2008, Chicago, IL, USA). Subject ID was entered as a random factor to account for correlations of repeated measures within each subject (Cnaan et al., 1997).

This second set of models was designed to detect changes from baseline in calls between birds on the two feeding schedules. To present our data in an easily interpretable manner, however, we retained absolute measures, rather than correcting measures relative to baseline. Therefore, difference in the main effect of group may be attributed to intrinsic differences between individuals, rather than a result of our treatment. Thus, to avoid incorrectly interpreting the effects of feeding schedules we evaluated only whether groups diverge or converge in vocal measures over time by examining the interaction terms, including group \times week and group \times type \times week. Further, we address only those interactions that were significant and

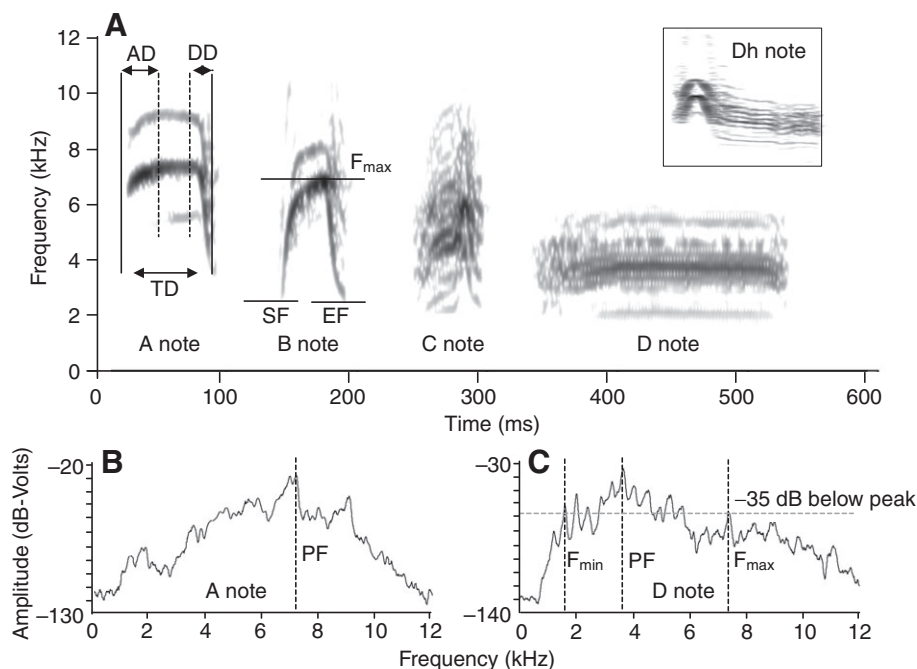


Fig. 1. Representative chick-a-dee call notes and measurements taken on each note. (A) Spectral measures for call notes. Duration measures for A, B and C notes include total duration (TD), ascending duration (AD) and descending duration (DD). TD was also measured on D notes. Frequency measures for A, B and C notes included start frequency (SF), end frequency (EF) and highest frequency (Fmax). A Dh note is a case where the final A and initial D note in a chick-a-dee call are merged, leaving no gap between the two notes. (B) Peak frequency (PF) was taken from the power spectra of A, B and C notes. (C) Frequency measures for D notes. PF, Fmax and lowest frequency (Fmin). Fmax and Fmin represent the lowest and highest harmonic at -35 dB relative to the loudest frequency.

also demonstrated clear patterns of change over time. Finally, although isolation alone may affect how birds call, our baseline recording occurred three weeks after birds were isolated. In addition, we are primarily interested in differences between group responses and therefore do not address the main affects of isolation in this paper.

Any P value ≤ 0.05 is considered to be significant. Results are reported as means \pm standard error of the mean (\pm s.e.m.).

RESULTS

Effect of feeding schedules on food received

Birds in both groups increased the number of food requests made after feeding schedules were introduced ($F_{1,521}=113.31$, $P<0.001$) but partially reinforced birds increased significantly more than continuously reinforced birds ($F_{1,521}=17.49$, $P<0.001$) (Fig. 2). A group \times feeding condition interaction showed that by making more requests, continuously reinforced birds increased their food rewards as the experiment progressed but in comparison with baseline, partially reinforced birds had less overall food rewards after the introduction of a reduced feeding schedule despite their increase in requests ($F_{1,521}=18.50$, $P<0.001$) (Fig. 2).

Acoustic differences between spontaneous and evoked calls

A comparison between calls in the two recording conditions prior to the introduction of feeding schedules reveals that evoked calls contained significantly more B notes ($F_{1,506}=118.73$, $P<0.001$) and fewer A, D and Dh notes ($F_{1,504}=6.14$, $P<0.014$; $F_{1,506}=37.31$, $P<0.001$; $F_{1,505}=28.19$, $P<0.001$, respectively). Evoked calls were also significantly shorter in duration ($F_{1,504}=36.16$, $P<0.001$). Overall evoked calls were composed of more high frequency notes than those given spontaneously (Fig. 3). This pattern of note use in the evoked condition remained stable throughout the experiment, except for the use of A notes, which became non-significant between the two recording conditions in the full analysis ($F_{1,2702}=0.58$, $P<0.449$).

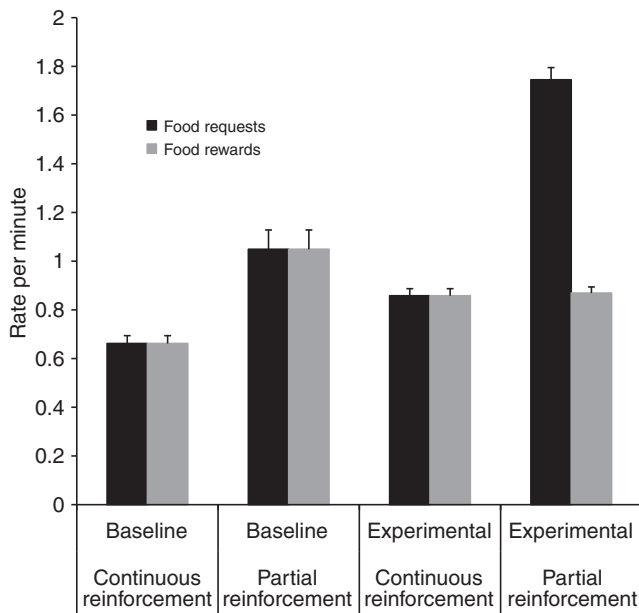


Fig. 2. Food requests and food rewards received in response to food requests made at baseline and after the introduction of a 50% feeding schedule for partially reinforced birds. Continuously reinforced birds remained at 100%. Means are plotted with error bars representing \pm s.e.m.

In comparison with the spontaneous (sp) condition, evoked (ev) A notes were produced at higher frequencies (SF: ev=6034.56 \pm 161.91 Hz, sp=5342.98 \pm 192.52 Hz, $F_{1,50}=4.11$, $P<0.048$; EF: ev=4029.55 \pm 132.38 Hz, sp=3331.75 \pm 156.26 Hz, $F_{1,50}=6.23$, $P<0.016$; Fmax: ev=7485.30 \pm 53.26 Hz, sp=7141.69 \pm 83.81 Hz, $F_{1,50}=6.50$, $P<0.014$), evoked B notes descended faster (DD: ev=22.40 \pm 0.84 ms, sp=26.24 \pm 1.44 ms, $F_{1,52}=4.12$, $P<0.047$) and evoked C notes ended at higher frequencies (EF: ev=2660.09 \pm 85.25 Hz, sp=2162.51 \pm 176.36 Hz, $F_{1,13}=5.41$, $P<0.037$). Only D notes remained unchanged in frequency and duration between the two conditions.

Acoustic differences between continuous reinforcement and partial reinforcement schedules

Baseline

During the baseline recording session all birds were maintained on a continuous reinforcement feeding schedule. However, birds were categorized according to their assigned feeding treatment and evaluated for vocal differences prior to treatment. Although not reported here, rate of note use, frequency and duration differed in several cases, justifying our use of interaction terms rather than the main effect of group in subsequent analysis.

Whole call measures

Calling rate did not vary by food treatment group ($F_{1,54}=1.20$, $P<0.278$). Total call duration decreased significantly by week for both groups in the spontaneous condition but only for birds on partial reinforcement in the evoked condition ($F_{6,2702}=3.06$, $P<0.005$) (Fig. 4A).

Rate of note use

A group \times type \times week interaction ($F_{7,2702}=4.22$, $P<0.001$) revealed that A note use dropped off quickly in partially reinforced birds in the spontaneous condition while A note use in all other treatments increased over time (Fig. 4B). No interactions were significant for B notes (Fig. 4C). C note use differed for the group \times type \times week interaction ($F_{1,2702}=3.31$, $P<0.003$) (Fig. 4D), revealing that C note use increased over time in spontaneous calls from continuously reinforced birds while they decreased in all other conditions. A group \times type \times week interaction also revealed that D notes use decreased significantly by week ($F_{1,2702}=4.35$, $P<0.001$) but less so in evoked calls from continuously reinforced birds and spontaneous

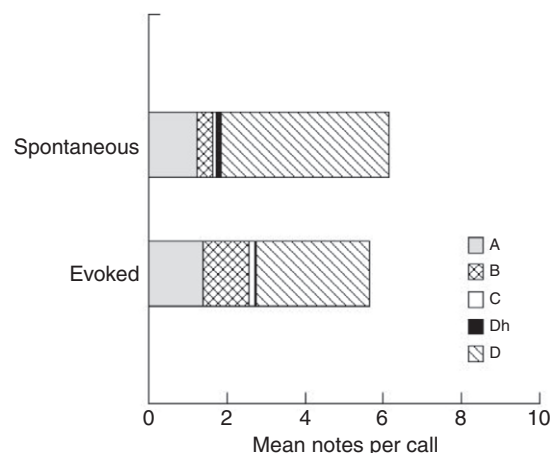


Fig. 3. Mean number of A, B, C, D and Dh notes used per call during baseline recording. Calls are categorized as spontaneous or evoked.

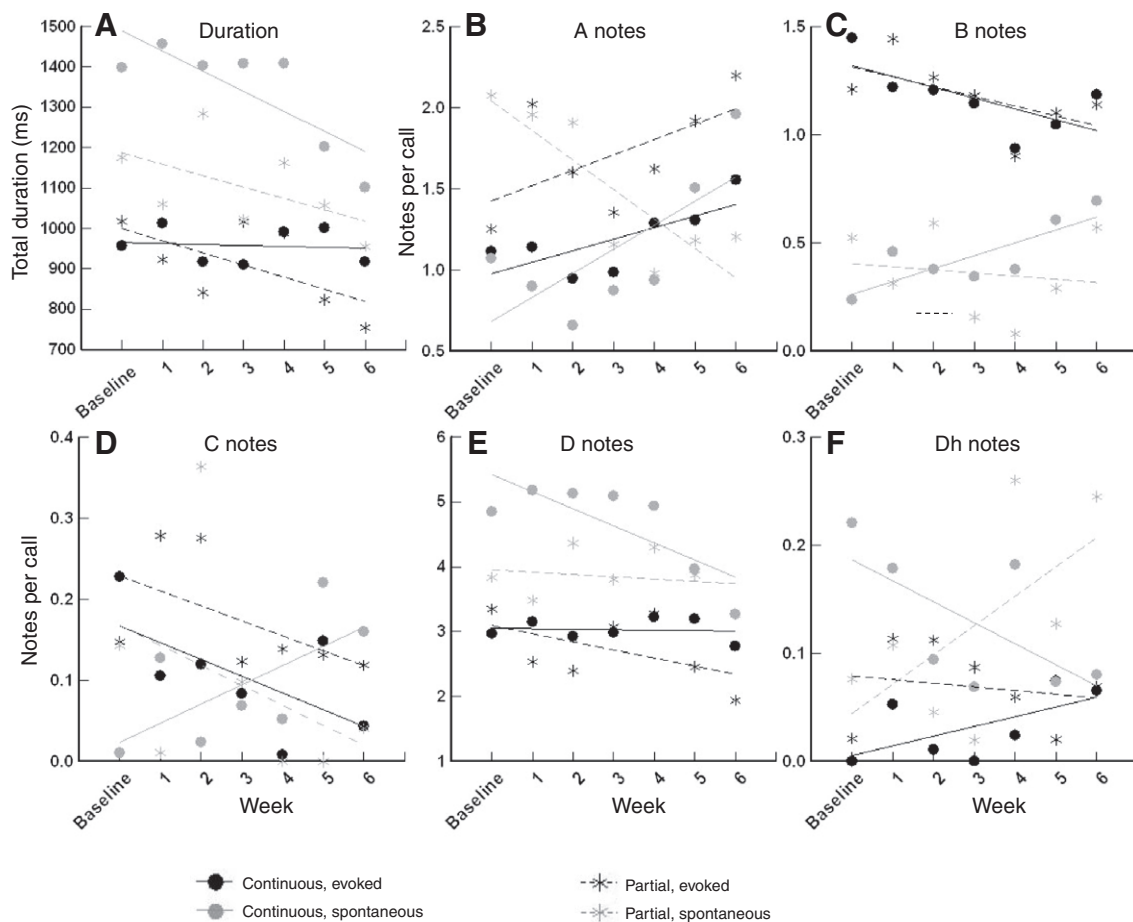


Fig. 4. Scatter plot of mean number of notes used per call (for A, B, C, D and Dh) in chickadee calls by week. Four treatment conditions are represented to show how feeding schedules and human intrusion affect note use. Best fit linear line added to show trends over time.

calls from partially reinforced birds (Fig. 4E). Rate of Dh note use increased significantly by week in the partially reinforced group in the spontaneous condition ($F_{7,2706}=4.57$, $P<0.001$) (Fig. 4F) while remaining somewhat stable in other conditions.

Frequency and duration of note types

Three A note frequency measures (SF, Fmax and PF) increased over time in continuously reinforced birds but remained stable in partially reinforced birds (Table 1; Fig. 5). In B notes two frequency measures (SF and PF) become lower over time in only partially reinforced birds (Table 1; Fig. 6). SF increased over time in spontaneous C notes from partially reinforced birds while remaining stable in all other conditions (Table 1; Fig. 7). Partially reinforced birds reduced Fmin of their D notes over time, and raised Fmax of the same notes when calls were given in the spontaneous condition (Table 1; Fig. 8).

DISCUSSION

In the present study we show that adult, male, black-capped chickadees recorded in two different conditions (evoked and spontaneous) and maintained using two different feeding protocols (fixed ratio continuous reinforcement and variable ratio partial reinforcement) display markedly different patterns of vocal output. In general, birds recorded under evoked conditions produced higher pitched calls that contained more B notes and fewer A, D and Dh notes than the same birds when recorded in spontaneous conditions. Moreover, this pattern of vocal output was observed immediately

(i.e. at baseline) and was maintained (with the exception of A notes) throughout the experiment, indicating that vocal output is plastic on very short timescales and that some note types are more strongly associated with particular behavioral situations. However, longer term vocal flexibility was exhibited between birds on different feeding schedules as partially reinforced birds decreased their use of A notes, increased their use of Dh notes and lowered the pitches of their B and D notes over the course of the experiment. By contrast, continuously reinforced birds increased their use of C notes in spontaneous calls and maintained stable overall call durations in the evoked condition. Our results suggest that elements of the chickadee call can be modified in response to changes in the abiotic environment beyond the stage of song crystallization and external to social interaction. To our knowledge, this study represents one of the first documenting vocal modification in individual adult songbirds due to changes in feeding schedules and lays the baseline for further studies on call modification in response to abiotic environmental changes. While our original hypothesis posits only that calls will be modified under our treatments, we suggest a few potential mechanisms underlying these changes below. Additional research will reveal the plausibility of these explanations.

Our results reveal that in response to human disturbance chickadees produce calls with more B notes and fewer D and Dh notes. The increase in the use of B notes in association with imminent threat was noted by Baker and Becker (Baker and Becker, 2002), who found that black-capped chickadees increased B note production

Table 1. Results of univariate general linear mixed models for all frequency and duration measures of A, B, C and D note types

		Frequency and duration measures by note type													
		TD		AD		DD		SF		EF		Fmax		PF	
A note	d.f.	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<
Group	1, 395	1.344	0.247	0.698	0.404	0.369	0.544	0.081	0.776	1.869	0.172	3.295	0.070	4.786	0.029
Type	1, 395	0.267	0.606	18.414	0.001	0.365	0.546	13.469	0.001	2.960	0.086	30.826	0.001	28.672	0.001
Week	6, 395	0.885	0.506	2.314	0.033	1.387	0.219	2.459	0.024	2.079	0.055	3.839	0.001	2.744	0.013
Group × week	6, 395	0.680	0.666	2.353	0.030	0.818	0.556	4.196	0.001	1.430	0.202	3.637	0.002	3.729	0.001
Group × type × week	7, 395	1.064	0.384	2.033	0.060	1.745	0.109	1.224	0.293	2.777	0.012	1.157	0.329	1.793	0.099
		TD		AD		DD		SF		EF		Fmax		PF	
B note	d.f.	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<
Group	1, 406	4.276	0.039	2.183	0.140	0.828	0.363	0.566	0.452	0.628	0.429	0.223	0.637	7.583	0.006
Type	1, 406	4.009	0.046	1.334	0.249	0.265	0.607	0.075	0.784	0.117	0.733	0.259	0.611	0.001	0.982
Week	6, 406	2.949	0.008	0.649	0.691	2.524	0.021	1.985	0.067	1.258	0.276	2.775	0.012	2.110	0.051
Group × week	6, 406	1.264	0.273	1.600	0.146	1.195	0.308	2.150	0.047	1.410	0.209	2.088	0.054	2.146	0.047
Group × type × Week	7, 406	1.380	0.221	0.520	0.793	1.576	0.153	1.827	0.092	0.989	0.432	1.028	0.406	1.302	0.255
		TD		AD		DD		SF		EF		Fmax		PF	
C note	d.f.	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<	F	P<
Group	1, 90	3.376	0.069	3.107	0.081	0.407	0.525	3.186	0.078	1.055	0.307	0.779	0.410	0.615	0.435
Type	1, 90	0.838	0.362	3.028	0.085	1.993	0.162	0.416	0.521	0.725	0.397	0.686	0.410	1.151	0.286
Week	6, 90	2.028	0.070	1.862	0.096	0.767	0.598	1.974	0.078	0.744	0.615	2.622	0.022	1.737	0.121
Group × week	6, 90	0.626	0.709	1.544	0.173	0.363	0.901	1.452	0.204	0.648	0.691	1.464	0.200	1.138	0.347
Group × type × week	7, 90	1.168	0.330	0.790	0.588	0.393	0.813	2.736	0.034	0.542	0.705	1.422	0.233	0.609	0.658
		TD		Fmax		Fmin		PF							
D note	d.f.	F	P<	F	P<	F	P<	F	P<						
Group	1, 411	5.769	0.017	5.589	0.019	6.303	0.012	0.798	0.372						
Type	1, 411	4.938	0.027	7.719	0.006	0.125	0.724	0.936	0.334						
Week	6, 411	4.083	0.001	0.659	0.683	4.403	0.001	3.144	0.005						
Group × week	6, 411	1.467	0.188	1.670	0.127	2.591	0.018	3.196	0.004						
Group × type × week	7, 411	2.251	0.038	2.400	0.027	1.909	0.078	1.679	0.125						

Feeding schedule is represented by 'group' and recording condition by 'type'. TD=total duration, AD=ascending duration, DD=descending duration, SF=start frequency, EF=end frequency, Fmax=highest frequency, Fmin=lowest frequency, PF=peak frequency.

in response to predator mounts at one meter when compared with the same mounts at six meters. Our results strengthen their suggestion that B notes function in situations of surprise or imminent threat. The reduction of D notes is in line with research by Templeton et al. (Templeton et al., 2005), suggesting that threat level can be encoded in the number of D notes produced. As such, humans are probably a lower level threat to an aerial species like the black-capped chickadee. Additionally, reducing D and Dh notes is in line with an overall shift in production to higher pitch note types and calls of shorter duration in situations of surprise or imminent threat. This is further supported by our finding that A notes are produced at higher frequencies in the evoked condition.

The function of this overall shift in vocal production to higher frequencies in situations of surprise or immediate threat may serve to reduce the ability of a predator to localize the vocalizing individual. A closely related species, the Carolina chickadee (*Poecile carolinensis*) also increases the use of higher pitch note types and decreases the use of lower pitch note types in the presence of predators (Freeberg, 2008). Another chickadee species, the Mexican chickadee (*Poecile sclateri*), elevates the frequency of their 'high zee' call when predators are in the vicinity (Ficken, 1990). In a non-chickadee species, the white-browed scrubwren (*Sericornis frontalis*) increases the pitch of their aerial trill alarm call as predators become more proximal (Leavesley and Magrath, 2005). In our case, it is also possible that the increased use of high pitch notes (i.e. B

notes) may function to alert nearby conspecifics of imminent danger. However, the repeated observation that songbirds shift vocalizations to higher frequencies in close proximity to predators merits further investigation. Behavioral field studies that examine the response of predators and conspecifics to these pitch-shifted vocalizations are needed to establish their function.

Partially reinforced birds reduced their production of A notes after week three, primarily in the spontaneous recording condition. This suggests that A note production is sensitive to environmental changes. Moreover, pitch characteristics of B and D notes in experimental birds changed (i.e. became lower and broader spectrum) over the course of the experiment in spite of the fact that their rate of occurrence (i.e. usage) was not reduced. Taken as a whole, the decrease in A note production and the use of lower pitches in B and D notes in partially reinforced birds, resulted in chick-a-dee calls being produced at overall lower pitches over time.

In the wild, birds in areas with lower resources often establish larger territories (Marshall and Cooper, 2004) and are more likely to forage beyond their established territory (Fort and Otter, 2004). The food-value theory predicts that territory size is inversely related to food availability (Stenger, 1958). This is predicted because animals must forage at increasing distances when food is scarce. The chick-a-dee call is used to communicate, at the very least, within a flock, and chickadee flocks maintain a winter territory (Odum, 1942). Flocks theoretically should become more highly dispersed

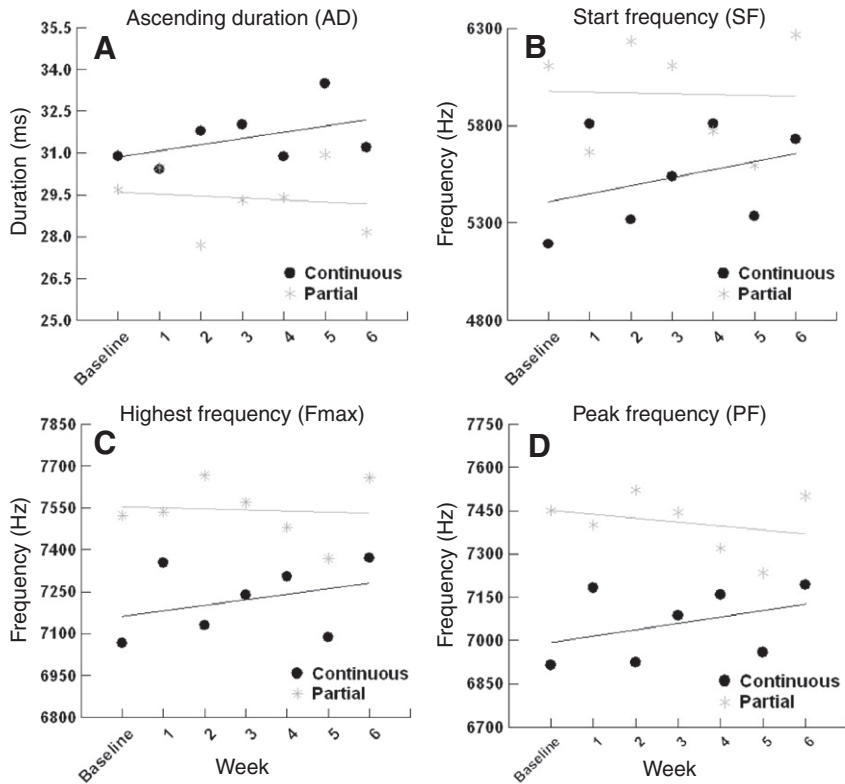


Fig. 5. Scatter plot of mean (A) duration and (B–D) frequencies of A notes in chickadee calls by week, broken into continuous reinforcement and partial reinforcement feeding schedules. Best fit linear line added to show trends over time.

in conditions when food is less available. In this case it would be advantageous to use vocal frequencies that transmit over farther distances. Lower frequencies of sound are less subject to degradation and attenuation than higher frequencies (Wiley and Richards, 1982) and therefore present a communication advantage when signaling must occur over longer distances. If this is the case, it would provide one explanation for the observed shift to lower pitch calls when our birds were maintained, and recorded, under partial reinforcement schedules. However, this is applied to our results in a theoretical framework and needs to be explicitly examined in the field, under natural conditions.

Alternatively, these vocal changes could be due to differences in energy available to birds on the two schedules of reinforcement. Larger, older birds, presumably having good access to food, can vocalize closer to the species limits and produce longer and more complex vocalizations (Ballentine et al., 2004; Ballentine, 2009; Genevois and Bretagnolle, 1994; Martin-Vivaldi et al., 1998). It is

possible that by moving to lower frequencies, partially reinforced individuals are reducing their energetic allotment for vocal production. Although their small size, and thus short vocal tract, suggest that it should require more energy to vocalize at lower frequencies, body size does not appear to regulate frequency production in all species (see ten Cate et al., 2002).

Limited energy, however, is a likely explanation for the increase in Dh note production in the partially reinforced group. This differential production of Dh notes may potentially be associated with a higher energetic cost associated with maintaining a clean break between high pitch A, B and C notes and lower pitch, broadband D notes [see cost of birdsong production (Oberweger and Goller, 2001; Hasselquist and Bensch, 2008)]. In a similar vein, Barnett and Briskie found that wild male silvereyes (*Zosterops lateralis*) given supplemental food produced more complex songs than they had prior to supplementation (Barnett and Briskie, 2007). We suggest that the increased use of Dh notes in spontaneous calls

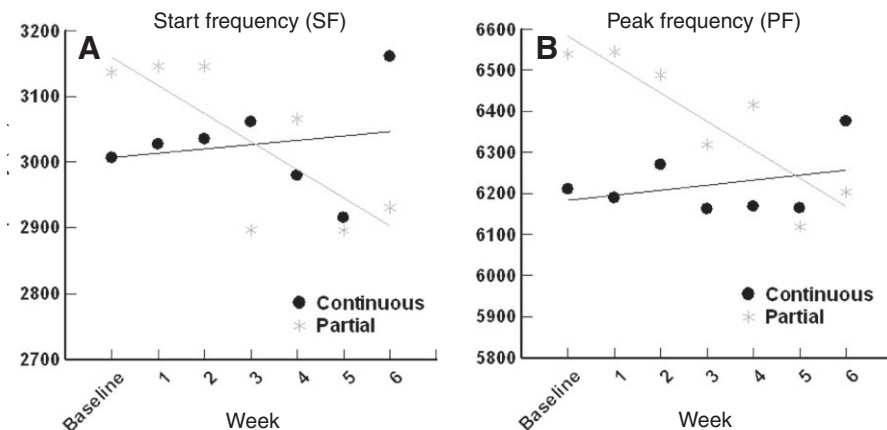


Fig. 6. Scatter plot of mean frequencies of B notes in chickadee calls by week, broken into continuous reinforcement and partial reinforcement feeding schedules. Best fit linear line added to show trends over time.

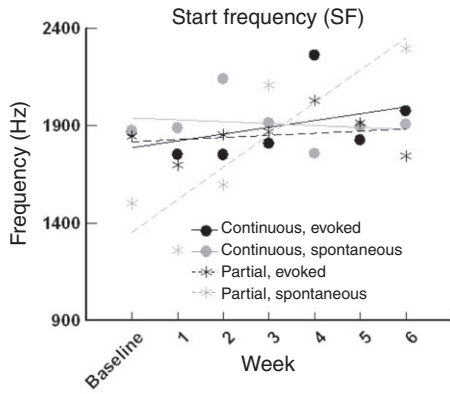


Fig. 7. Scatter plot of mean start frequency of C notes in chickadee calls by week. Four treatment conditions are represented to show how feeding schedules and human intrusion affect note use. Best fit linear line added to show trends over time.

from partially reinforced birds may be the result of a reduced ability or willingness to invest energy into vocal production, because more energy was required to access food. However, investing less energy into these calls may also result in a reduced ability to propagate high quality, unambiguous signals.

In the presence of a threat, failure to produce high quality, unambiguous calls has potential fitness costs. For example, in the presence of a threat, lesser short-toed larks (*Calandrella rufescens*) in better nutritional condition produced broader frequency calls than birds in poorer condition (Laiolo et al., 2004). By announcing their condition through their calls, these birds may inform a potential predator of their ability to escape predation. In turn, this may affect whether the predator continues its pursuit or searches for easier prey. The sudden appearance and movement of a human intruder used in this experiment to evoke calls produced alarm in the subjects, a case where the subject could reduce its perceived predation risk by producing higher quality calls. In addition, because black-capped chickadees are known to mob potential threats, and the chickadee call is used to alert nearby conspecifics (Smith, 1991; Baker and Becker, 2002; Ficken and Witkin, 1977), a clear, well-composed call increases the probability of drawing a quick response from conspecific individuals. In our simulated, threatening scenario several differences that had been observed between the two feeding groups in spontaneous calls are reduced. For example, A and Dh note production becomes similar between birds on the two feeding

schedules. This suggests that while energetic differences do produce vocal differences between individuals, many of these differences disappear when external motivation favors high quality calls. Further studies should evaluate how long partially reinforced birds can sustain high quality vocalizations in the presence of predators or potential mates.

One final observation is that in spontaneous calls C notes become more common in continuously reinforced birds and are produced at higher pitch in partially reinforced birds. This may represent a change in energy allocated to this note based on the quality of the food source the bird is experiencing. As noted by Freeberg and Lucas, C notes may be associated with a food source (Freeberg and Lucas, 2002). Thus, the higher quality food source experienced by the continuously reinforced birds may motivate them to produce more C notes, while partially reinforced birds maintain a stable production but increase the start frequency of their C notes; thus, potentially reducing the distance they will transmit. Interestingly, neither of these differences remains in the evoked calls, a case where food advertisement is a low priority.

We recognize two broader potential implications of our findings. First, determining whether vocalizations correlate consistently with abiotic environmental changes may have management applications. If abiotic environmental variables produce predictable changes in vocal structure (i.e. through reduced energy or motivation), and most individuals in an area display similar changes in their vocalizations, this could serve as an early warning for ecosystem disturbance. Furthermore, if the abiotic environmental variable related to these ‘altered’ vocalizations can be pinpointed, active management may reduce the likelihood of a population decline in that area. Such a system is currently being developed for the management of captive animals, including domestic pigs [*Sus scrofa*] (Duepjan et al., 2008), cattle [*Bos taurus*] (Grandin, 1998) and laboratory rats [*Rattus norvegicus*] (Burman et al., 2007)]. Songbirds in a natural ecosystem are subject to more interacting factors but vocal analysis of a few keystone species could still provide valuable information (see Laiolo et al., 2008). For example, if Dh notes are associated with lower food availability, an assessment of the regularity of which Dh notes occur in a black-capped chickadee population could provide information on the levels of food available to that population.

Second, we must also understand the particular timescales under which birds modify their vocal structure to reflect external conditions. For instance, does vocal output in adulthood accurately represent only conditions from development or do they also reflect conditions from the previous year, season, weeks or days? Changes are occurring in climate (Van Buskirk et al., 2009; Archaux, 2003),

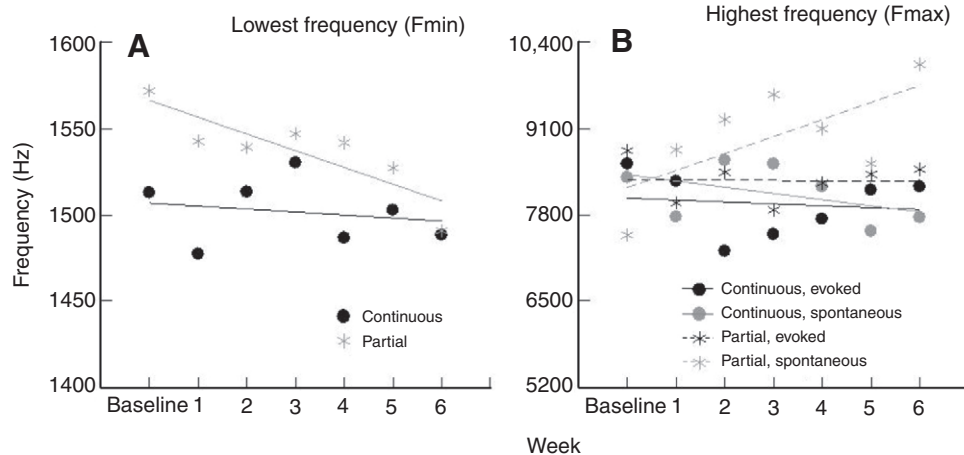


Fig. 8. Scatter plot of mean frequencies of D notes in chickadee calls by week, broken into (A) fixed ratio continuous reinforcement and partial reinforcement feeding schedules, and (B) four treatment conditions to show how feeding schedules and human intrusion affect note use. Best fit linear line added to show trends over time.

ambient noise levels (Bayne et al., 2008; Patricelli and Blickley, 2006), forest structure (Leonard et al., 2008; Betts et al., 2006) and plant communities (Ortega et al., 2006; Grant et al., 2004) throughout the ranges of many songbird species. Each of these changes may favor the transmission of vocalizations with different pitch, duration and note structure (Wiley and Richards, 1982). While some population differences have been observed in response to external changes [i.e. pitch shifting in urban noise (Slabbekoorn and Peet, 2003); higher pitch in open forest habitat (Hunter and Krebs, 1979)], little is known about the ability of an individual to modify vocal structure in these conditions. We show for the first time that individual black-capped chickadees can, in fact, modify the structure of their vocalizations in response to changes in their abiotic environment. Whether this ability is used to overcome changes in their natural habitat is yet to be seen and requires further research. Additionally, we must disentangle vocal modification that is in response to changes in the abiotic environment from modification due to due social interaction and local dialects.

We recognize two limitations of this study, both which should be addressed through further field and laboratory studies. First, although there are several diverging patterns in the call structure of black-capped chickadees on the two feeding schedules, much variability is also evident in the data. This variability may make it difficult to discern the abiotic conditions a bird is subject to based on absolute call measures procured in the field. Thus, studies are needed to establish a range of 'normal' call characteristics. When calls diverge from this norm they may then be attributed to changes in the abiotic environment. A second limitation is that our birds were kept in isolation from conspecifics throughout the experiment. Although this allowed us to control and standardize the birds' external environment, isolation alone may also contribute to the modification of vocal structure. This concern may be addressed through similar experiments where birds are able to interact with conspecifics, yet are limited to particular food sources.

In summary, we show that black-capped chickadees modify their chick-a-dee calls in response to changes to the abiotic environment. Our data supports the increased use of B notes and a shift to high pitch calls in situations of surprise and imminent threat. Birds maintained under a partially reinforced feeding schedule use lower pitch note types and lower the pitch of these notes. We suggest that the overall move to lower frequencies may represent an attempt to communicate over larger spatial scale. Alternatively this may represent an attempt to reduce the energetic costs of vocal production, especially in the case of Dh note production. Energetic costs as a mechanism underlying these vocal differences is further supported by our finding that observed differences are reduced in calls produced under a threatening scenario, a case when failing to produce high quality calls may have fitness consequences. Further studies should investigate chick-a-dee call modifications in natural environments differing in food availability and other relevant abiotic variables. If call modification in these natural environments parallels those found in our laboratory study, we may begin to be able to predict characteristics of the black-capped chickadee's external abiotic environment through vocal analysis of its calls.

LIST OF ABBREVIATIONS

ANOVA	analysis of variance
AD	ascending duration
ASY	after second year
DD	descending duration
EC	experiment controller
ev	evoked calls
EF	end frequency

Fmax	highest frequency
Fmin	lowest frequency
GLMM	general linear mixed model
IR	infrared
PF	peak frequency
sp	spontaneous calls
SF	start frequency
TD	total duration

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