



All “chick-a-dee” calls are not created equally Part II. Mechanisms for discrimination by sympatric and allopatric chickadees

L.L. Bloomfield, T.M. Farrell, C.B. Sturdy*

P-217 Biological Sciences Building, Department of Psychology, Canada

Received 6 February 2007; received in revised form 11 June 2007; accepted 18 June 2007

Abstract

The ‘chick-a-dee’ call, common to all members of the genus *Poecile*, is used by both sexes throughout the year to putatively co-ordinate flock movements and register alarm. In some regions, two or more chickadee species occupy overlapping territories, and therefore it is essential that these sympatric species learn to discriminate between the acoustically similar calls of the species. Previous work from our laboratory has shown that black-capped (*P. atricapillus*) and mountain chickadees (*P. gambeli*) discriminate between the species’ calls and treat each species’ calls as belonging to separate open-ended categories. In the current set of experiments we use an operant conditioning paradigm to gain an understanding of (1) how the birds perform this discrimination and (2) whether birds with different levels of experience with heterospecific calls perform this task differently. We use natural recordings of chick-a-dee calls and perform several manipulations to test the importance of the introductory ‘chick-a’ portion and the terminal ‘dee’ portion for discriminating among the calls of the two species. Evidence suggests that birds mainly use the terminal ‘dee’ portion, as all groups of birds responded similarly to these probe stimuli and control chick-a-dee calls. We propose that the terminal ‘dee’ portion, consisting of lower frequency notes, is more likely to be resistant to degradation, and therefore a more reliable species-specific marker.
© 2007 Elsevier B.V. All rights reserved.

Keywords: Allopatric; Chickadee; Operant discrimination; Mechanisms; Songbirds; Sympatric

1. Introduction

Acoustic communication is often the primary means by which many songbird species identify conspecifics and discriminate them from heterospecifics (see Becker, 1982), especially when natural obstructions such as vegetation can hinder visual communication. Songbirds spend a large proportion of their time defending territories, attracting mates, and foraging, and have evolved methods of recognizing species and individuals based on their auditory signals (Becker, 1982; Falls, 1982). Territory owners learn to recognize the acoustic signals of their neighbours to avoid unnecessary confrontations with familiar birds and mount strong aggressive responses towards invading strangers (see Stoddard, 1996), thereby increasing the fitness

of the individual and the species (McArthur, 1982). Furthermore, songbirds must be discriminating when selecting a mate, and avoid courting heterospecifics (Ratcliffe and Otter, 1996). Clearly, acoustic signals provide conspecifics, and perhaps heterospecifics, with cues critical to fitness and survival.

Chickadees (genus *Poecile*) provide an excellent model system for studying acoustic communication because both their song and some of their calls are learned (Shackleton and Ratcliffe, 1993; Hughes et al., 1998). Moreover, all members of the genus *Poecile* produce a species-typical variant of the chick-a-dee call (see Hailman and Ficken, 1996; Ficken et al., 1978, 1994, 1996; Smith, 1972; Gaddis, 1985). Finally, in some regions two or more species occupy the same areas, suggesting that both intra- and inter-specific vocal discriminations may occur.

The vocal repertoire of the black-capped chickadee is arguably the most well studied of all the chickadee species. Their chick-a-dee call, associated with mild alarm and flock communication and co-ordination (Smith, 1991; Ficken et al., 1978), consists of four note types; A, B, and C notes, which constitute

DOI of original article: [10.1016/j.beproc.2007.06.011](https://doi.org/10.1016/j.beproc.2007.06.011).

* Corresponding author at: Department of Psychology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. Tel.: +1 780 492 7843; fax: +1 780 492 1768.

E-mail address: csturdy@ualberta.ca (C.B. Sturdy).

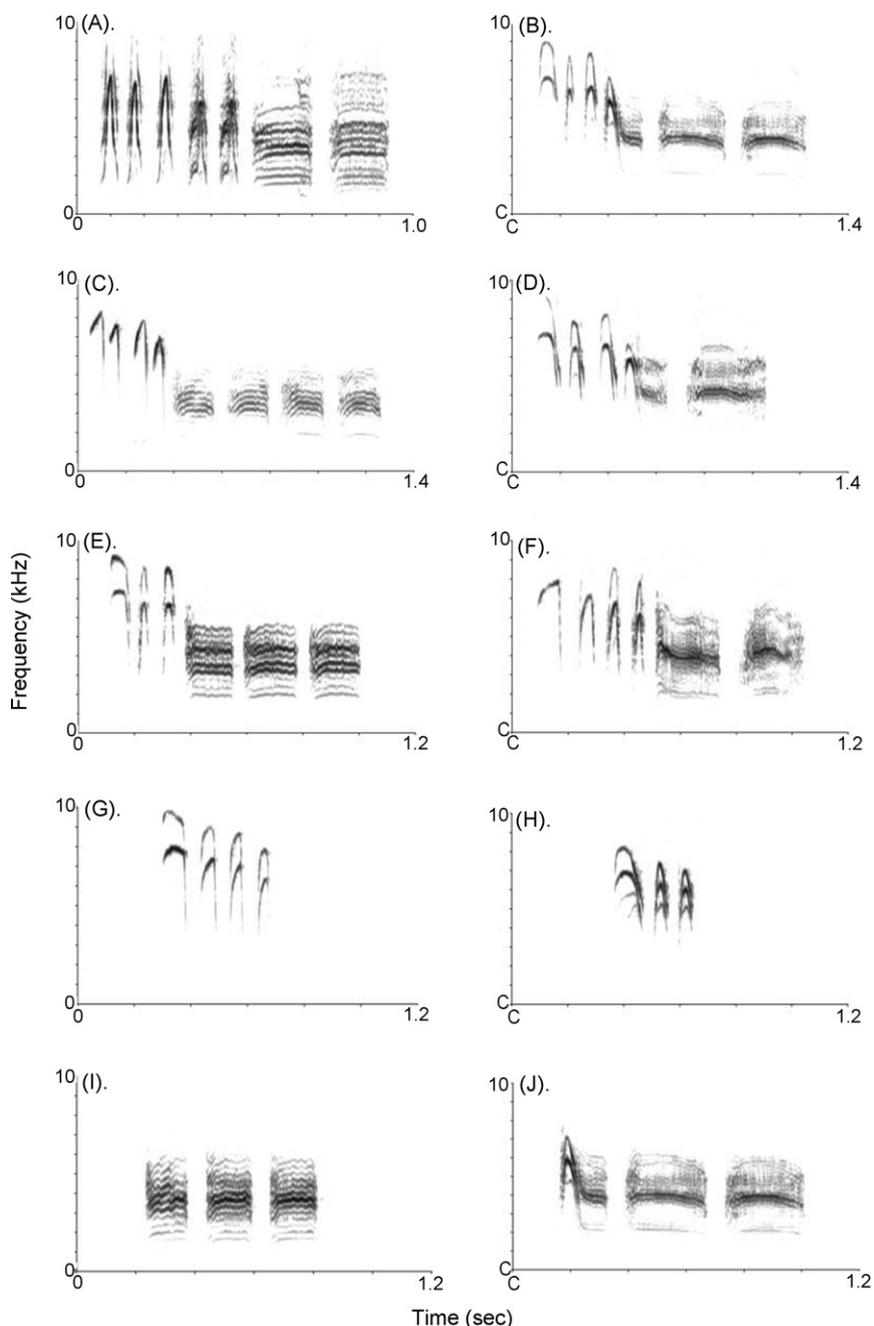


Fig. 1. Representative sound spectrogram of (A) a normal (i.e., unmanipulated) black-capped chick-a-dee call, (B) a normal mountain chick-a-dee call, (C) a Spliced Control black-capped chick-a-dee call, (D) a Spliced Control mountain chick-a-dee call, (E) a Multi-species Spliced chick-a-dee call consisting of mountain chickadee introductory portion and black-capped chickadee terminal portion, (F) a Multi-species Spliced chick-a-dee call consisting of black-capped chickadee introductory portion and mountain chickadee terminal portion, (G) a black-capped chickadee Introductory-only ‘chick-a’ portion (H) a mountain chickadee Introductory-only ‘chick-a’ portion, (I) a black-capped chickadee Terminal-only ‘dee’ portion, (J) a mountain chickadee Terminal-only ‘dee’ portion. Frequency (kHz) is on the y-axis and time (s) is on the x-axis in each spectrogram.

the introductory ‘chick-a’ portion, and D notes, which constitute the terminal ‘dee’ portion (see Fig. 1). While maintaining a fixed syntactical ordering of the notes within calls (A through D), any of the notes can be repeated or omitted to produce a seemingly infinite number of call types (Hailman et al., 1985). Black-capped chickadees perceive differences among chick-a-dee calls to discriminate flock mates from non-flock mates (Mammen and Nowicki, 1981), among different chickadee species (Bloomfield et al., 2003; Bloomfield and Sturdy, in press), and potentially

among individuals (Charrier et al., 2004). It therefore seems that chick-a-dee calls have the potential to convey a plethora of information to the conspecific listener.

Most closely related to the black-capped chickadee is the mountain chickadee (Gill et al., 1993). While the black-capped chickadee inhabits the northern United States and most of Canada, the mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (Smith, 1993; McCallum et al., 1999). In some regions the two species live

sympatrically and engage in interspecific activities such as foraging (pers. obs.), however in the sympatric regions of the western Rocky Mountains, birds do not appear to interbreed or exhibit interspecific competition (Hill and Lein, 1989). In common with the black-capped chick-a-dee call, the chick-a-dee call of the mountain chickadee is used in similar contexts (Gaddis, 1985) and consists of the ‘standard’ A, B, C and D notes, as well as two unique intermediary notes, A/B notes in the introductory ‘chick-a’ portion and D_{hybrid} notes in the terminal ‘dee’ portion (Bloomfield et al., 2004). Call notes are produced in a fixed syntactical order of $A \rightarrow D$, and note types may be omitted entirely or repeated. Also in common with black-capped chickadees, mountain chickadees perceive differences between their own chick-a-dee calls and the chick-a-dee calls of heterospecifics (black-capped chickadees, Bloomfield and Sturdy, in press), however the important or salient species-specific features used for these discriminations, and whether different strategies are used by the different species or those from differing geographic origins, are not known.

Here we employ a ‘go/nogo’ operant discrimination task to gain an understanding of (1) whether chickadees use the introductory ‘chick-a’ portion or the terminal ‘dee’ portion of chick-a-dee calls for discriminating conspecific chick-a-dee calls from heterospecific chick-a-dee calls, (2) whether there are differences between black-capped and mountain chickadees in the features used for these discriminations, and (3) whether black-capped chickadees with previous experience with mountain chickadees (i.e., sympatric chickadees) rely on different portions or features of chick-a-dee calls for species’ discriminations compared to inexperienced (i.e., allopatric) black-capped chickadees. Our logic here is that given their extensive experience with mountain chickadee’s calls, sympatric black-capped chickadees may be more adept at using *either* the introductory *or* terminal portions for discriminating between the calls of the two species. Alternatively, the allopatric chickadees, with no experience with the calls of mountain chickadees, may rely on only the terminal ‘dee’ portion, the portion that, at least to human ears, is easier to distinguish between the species.

2. General methods

2.1. Animals

A total of 31 birds (19 black-capped chickadees and 12 mountain chickadees) at least 1 year of age (determined by the shape and coloring of the outer tail retrices, Pyle, 1997) and naïve to the experimental procedures served in the current set of experiments. All birds were captured between December 2003 and February 2005. Eleven black-capped chickadees were caught in several regions of Edmonton Alberta (53°06’N, 113°04’W) and had no prior exposure to mountain chickadees (the *allopatric* group), as chickadees are non-migratory and mountain chickadees do not naturally occur in these areas. Eight black-capped chickadees and 12 mountain chickadees were caught in several regions in Kananaskis Country, Alberta, Canada (51°02’N, 115°03’W) and therefore these 8 black-capped chickadees had prior exposure to mountain chickadees (the *sympatric* group),

as both species are prolific to these areas (pers. obs.). Sex identification was conducted by DNA analysis (Griffiths, 2000).

Each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages (0.3 m wide \times 0.4 m high \times 0.4 m deep; Rolf C. Hagen, Inc., Montreal, Canada) for a minimum of 1 month prior to the commencement of the experiments. The housing conditions allowed for auditory and visual but not physical contact among birds of the same species. Birds were maintained on a day-light cycle consistent with the natural cycle for the time of year (January–August). Therefore, daylong sessions ranged from about 7.5 h (January) to 17 h (June).

Prior to experimentation birds were given *ad libitum* access to lab food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), cuttle bone, grit, and water (vitamin-supplemented on alternate days, Hagen, Rolf C. Hagen, Inc., Montreal, Canada). Birds were also given 1 meal worm three times per week and hard-boiled egg and spinach mixture twice a week.

During the experiment, standard rations were available only when an appropriate operant response was produced. Birds were given *ad libitum* access to cuttle bone, grit and water (vitamin-supplemented on alternate days). Two meal worms were provided daily to ensure good health throughout the duration of the experiments.

2.2. Apparatus

Modified budgerigar cages (0.3 m wide \times 0.4 m high \times 0.4 m deep) provided continuous housing for the birds during training and testing periods. To ensure the birds did not have access to spilled food, a mesh floor was attached near the bottom of the cage. Each cage was contained in a ventilated, sound-attenuated chamber illuminated by a 9-W twin-tube full-spectrum fluorescent bulb and had several perches and dispensers for water and grit. Infrared cells monitored a motor-driven feeder (Njegovan et al., 1994) mounted beside the cage, and a perch opposite the feeder entrance monitored the bird’s position. Access to the feeder was made possible by an opening (11 cm wide \times 16 cm high) in the cage. A single-board computer (Palya and Walter, 2001) interfaced to a personal computer controlled a standard CD-ROM, scheduled the experiment and recorded responses to stimuli. Stimuli were played at 75–85 dB (A weighting, slow response, measured using a Radio Shack Sound Level Meter) from a CD to either a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or a NAD 310 Integrated Amplifier (NAD Electronics, London, England) and then to a Fostex FE108 Σ full-range speaker (Fostex Corp., Japan) located beside the feeder (effective frequency response 200–16,000 Hz). The center of the speaker was at the height of the bird’s head when the bird stood on the perch.

2.3. Stimuli preparation

A total of 112 chick-a-dee calls (56 black-capped chick-a-dee calls and 56 mountain chick-a-dee calls, see Fig. 1A and B), recorded using a variety of microphones and recorder types, were randomly selected from several sources (our own database, recordings provided by other researchers, commercially avail-

able compact disks, bioacoustics libraries) for use in the current set of experiments. A small proportion of the recorded calls originated from birds that had been captured from the same location as the experimental birds on previous trapping years. That said, because there was at least 12 months between successive trapping events, it is unlikely that birds trapped on successive years would be familiar with previously trapped birds, and certainly not with their particular calls that were recorded in the laboratory and used as stimuli. Further, to reduce any possible influence of familiarity on discrimination, all call stimuli were randomly assigned to the training and testing stimulus sets (see below), and therefore overall performances by the birds in the current study were unlikely to be influenced by potential familiarity with a few of the recorded birds.

Calls were randomly assigned to either one of the two training sets or one of the four probe stimulus types. The first training set, used during the acquisition phase, consisted of 10 calls of each species (see Fig. 1A and B). The second training set, used during the Transfer 1 phase, consisted of 10 different calls of each species. The four probe stimulus types included—(1) Spliced Control calls: 6 calls of each species created using introductory and terminal portions from 12 calls of each species; (2) Multi-Species Spliced calls: 12 calls created using introductory portions of one species' calls and terminal portions of the other species' calls; (3) Introductory-only calls: 6 introductory 'chick-a' portions of each species calls (terminal portion removed); (4) Terminal-only calls: 6 terminal 'dee' portions of each species calls (introductory portion removed).

All calls were bandpass filtered (1000–10,000 Hz) using GoldWave Version 5.12 (GoldWave, Inc., St. John's, NF) to remove background noise, and using SIGNAL 4.0 sound analysis software (Engineering Design, CA) each call was viewed in a spectrogram (cutoff amplitude –35 dB relative to peak amplitude) to equalize call amplitude and taper the leading and trailing 5 ms of silence to remove transients, and was subsequently saved as an individual 2 s sound file by inserting silence after the end of the call. All calls to be used as probe stimuli ($n = 72$ calls) were further prepared according to the methods below. It is important to note that none of the recorded chick-a-dee calls was used more than once, either in whole or in part.

2.4. Spliced Control calls

Calls ($n = 12$ of each species) were examined in sound spectrograms to ensure that both the introductory portion of each call (consisting of A-, B-, and C-type notes) and the terminal portion of each call (consisting of D-type notes) contained a minimum of two notes. Any call that did not meet this criterion was randomly exchanged with a call from one of the training sets, ensuring that no call, in whole or in part, was used more than once. Six of the 12 calls were randomly selected for their introductory portion and were randomly paired with the remaining six calls in which the terminal portions would be used. The sound spectrogram of each introductory-portion call was opened in SIGNAL 4.0 and the terminal portion of the call was removed at the point of the start of the first D-type note. The leading and trailing 5 ms of silence was tapered and each introductory-portion call

was saved as an individual file. Similarly, the sound spectrogram of each of the remaining six calls was opened in SIGNAL 4.0 and the introductory portion of the call was removed at the point of the end of the last introductory note (either A, B, or C note). The leading and trailing 5 ms of silence was tapered and each terminal-portion call was saved as an individual file. Subsequently, paired introductory and terminal portions were opened in Signal, spliced together, and each call was saved as an individual 2 s sound file by inserting silence after the end of the manufactured call (see Fig. 1C and D).

2.4.1. Multi-Species Spliced calls

Calls ($n = 12$ of each species) were examined in sound spectrograms to ensure that both the introductory portion of each call (consisting of A, B, and C note types) and the terminal portion of each call (consisting of D note types) contained a minimum of two notes. Any call that did not meet this criterion was randomly exchanged with a call from one of the training sets, ensuring that no call, in whole or in part, was used more than once. Methods for separating introductory portions and terminal portions were identical to methods used for creating Spliced Control calls (above). Six of the 12 black-capped chickadee calls were randomly selected for their introductory portion and the remaining 6 calls would be used for their terminal portions. The same random selection was conducted with the 12 mountain chickadee calls. Once separated, the leading and trailing 5 ms of silence was tapered and each introductory and terminal portion was saved as an individual file. Subsequently, introductory and terminal portions were spliced together in Signal 4.0, resulting in 12 unique calls; 6 calls consisting of black-capped chickadee introductory portions (and mountain chickadee terminal portions), and 6 calls consisting of mountain chickadee introductory portions (and black-capped chickadee terminal portions). Each call was saved as an individual 2 s sound file by inserting silence after the end of the call (see Fig. 1E and F).

2.4.2. Introductory- and terminal-only calls

Calls ($n = 6$ of each species) were separated into introductory and terminal portions using methods identical to those for creating Spliced Control and Multi-Species Spliced calls (above), however in this case introductory and terminal portions remained separated and only *either* the introductory portion or the terminal portion was retained for use. The leading and trailing 5 ms of silence was tapered and each portion was saved as an individual file. Calls were saved as a 2 s sound file by inserting silence after the end of the call (see Fig. 1G and H). The 40 training stimuli and the 48 probe stimuli were then transferred to compact disks, one call per track.

2.5. Procedure

2.5.1. Nondifferential training

Nondifferential training began after a bird had learned to use the perch and feeder. When a bird landed on the perch, breaking an infrared beam, the within-trial sequence began. Remaining on the perch for 1 s on average (range 900–1100 ms) resulted in a single call being randomly selected and played once (70–80 dB).

If the bird flew or hopped to the feeder after the stimulus was played, breaking another infrared beam, it was rewarded with 1 s access to food, followed by a 30-s inter-trial interval (ITI). If the bird left the perch without entering the feeder the trial ended after 1 s. If the bird failed to leave the perch the trial ended after 1 and a 60-s ITI followed. The 60-s ITI was used to increase the probability of the bird leaving the perch on all trials. Leaving the perch before the stimulus had finished playing resulted in the trial ending and the chamber lights turning off during a 30 s ITI. These procedures helped us to ensure that birds heard and attended to the calls and subsequently left the perch. During nondifferential training, we presented all the calls in the training sets but none of the calls created for the probe sets. The purpose of nondifferential training was to ensure that the birds heard and responded to all the calls and to gather similar percentages of responses to each call as a baseline for the evaluation of training during probe sessions.

2.5.2. Acquisition training

Acquisition training began after nondifferential training and continued throughout the experiment. During acquisition training, visits to the feeder after S+ (positive, or reinforced) calls were rewarded with access to food, but visits to the feeder after S– (negative, or nonreinforced) calls resulted in no reward and a 30-s ITI with the chamber lights off. Other procedures initiated during nondifferential training remained in effect during acquisition training. For example, as during nondifferential training, on each trial a single call was selected randomly and without replacement from the stimulus set. Further details about the stimulus calls used are presented in the methods sections for each experiment. Typically, each daylong session generated about 1000 trials.

2.5.3. Response measures and statistical analyses

We calculated a percentage of response measure for each stimulus (whether S+ or S–) using the following formula: $(R+ / (N \text{ trials} - N \text{ interrupted trials})) \times 100$, where $R+$ is the number of trials on which the bird flew or hopped to the feeder, N trials the total number of trial presentations for that stimulus, and N interrupted trials is the number of trials in which the lights were extinguished for the bird leaving the perch before the stimulus was played in its entirety. To facilitate comparisons among groups of birds, we scaled the percentages of responses to probe stimuli for each individual subject. Specifically, the highest percentage of response obtained for a probe stimulus was rescaled to 100%, and all other percentages of responses were represented as a ratio of the highest percentage of responding. This method was conducted on the average probe responses for each bird, and ultimately eliminated the problem of individual variation in the overall levels of responding, and allowed for a more critical analysis of the distribution of responses. We conducted analyses of variance (ANOVAs) and planned comparisons (Tukey's) on percentages of responses using STATISTICA, version 6, StatSoft, Inc. (2003). When percentages of responses are near 0% or 100%, sample values may not be normally distributed. We therefore conducted parallel ANOVAs using arcsine square-root transformations of the percentages of responses. Analysis of

transformed data virtually yielded the same pattern of results with virtually the same levels of significance as untransformed data, with two minor exceptions. Therefore, results for ANOVAs of the untransformed data are reported here, as well as the two differing results obtained with the transformed data in the probe analysis.

3. Training phase 1: acquisition

3.1. Methods

Prior to testing the putative mechanism(s) used by black-capped and mountain chickadees for discriminating each species' chick-a-dee calls, a baseline for discrimination was established during the initial phase of training (acquisition phase). Birds were presented with 10 black-capped chick-a-dee calls and 10 mountain chick-a-dee calls; calls of one species provided food reinforcement (S+) 100% of the time for flying to the feeder, and calls from the other species did not provide food reinforcement (S–). Birds were randomly assigned to either the black-capped chick-a-dee S+ call group (BCCH-S+ group, $N=15$, 3 male and 3 female mountain chickadees, 2 male and 2 female sympatric black-capped chickadees, and 3 male and 2 female allopatric black-capped chickadees) or the mountain chick-a-dee S+ call group (MOCH-S+ group, $N=16$, 3 male and 3 female mountain chickadees, 2 male and 2 female sympatric black-capped chickadees, and 3 male and 3 female allopatric black-capped chickadees). This phase of training continued until the birds completed a minimum of six 500-trial bins with a discrimination ratio (DR) ≥ 0.8 , with the last two bins occurring consecutively.

3.2. Results

3.2.1. Nondifferential training

During nondifferential training, birds were presented with all 40 chick-a-dee calls that would be used during training phases 1 and 2 (acquisition and Transfer 1), and were provided with 100% reinforcement for flying to the feeder following each call. This provided us with a consistent level of responding to all calls prior to acquisition/discrimination training. Once birds were responding at least 60% of the time to all calls and no statistical differences in responding occurred between each set of calls (i.e., between black-capped chick-a-dee calls and mountain chick-a-dee calls, examined daily using individual t -tests, $p < 0.05$, see Fig. 2), acquisition training began.

3.2.2. Acquisition training

Chickadees in both S+ groups learned to fly to the feeder following S+ stimuli and learned to withhold flying to the feeder following S– stimuli in a minimum of 4000 trials (i.e., the fewest number of trials required by some subjects to reach criterion). We conducted a mixed model Birds (sympatric black-capped chickadee, allopatric black-capped chickadee, mountain chickadee) \times S+ Group (BCCH-S+, MOCH-S+) \times sex (male, female) \times exemplar set (black-capped chick-a-dee calls, mountain chick-a-dee calls) \times trial blocks (1–8) ANOVA on the

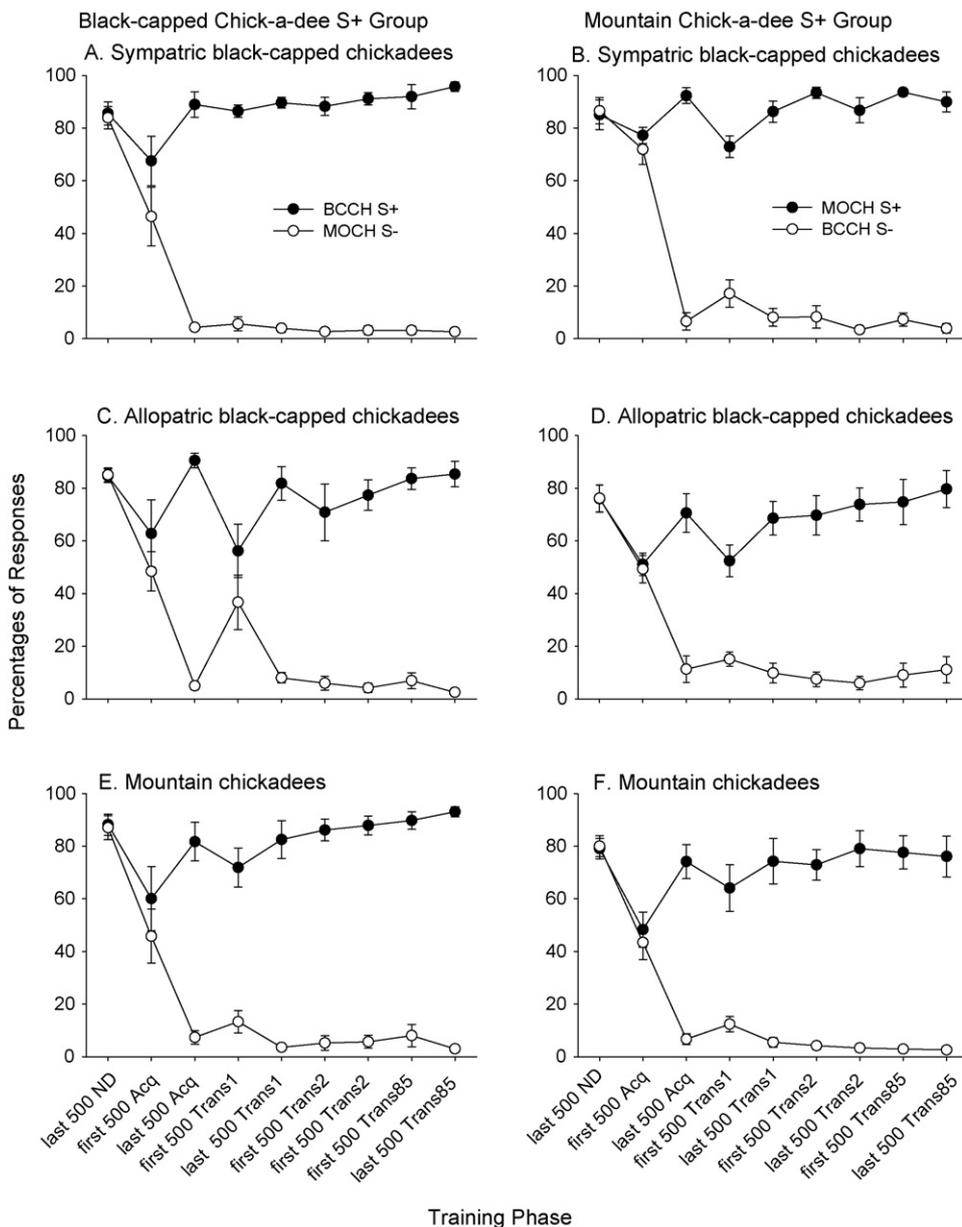


Fig. 2. Average percentages of responses (y-axis) to black-capped chick-a-dee calls (BCCH) and mountain chick-a-dee calls (MOCH) by (A and B) sympatric black-capped chickadees, (C and D) allopatric black-capped chickadees, and (E and F) mountain chickadees during the last 500 trials of nondifferential training (ND), and the first and last 500 trials of Acquisition (Acq), Transfer 1 (Trans1), Transfer 2 (Trans2), and Transfer 85 (Trans85) training phases (x-axis). Black-capped chick-a-dee S+ groups are in the left-hand side of the figure while mountain chick-a-dee S+ groups are in the right-hand side of the figure. Error bars represent average standard errors of the means.

percentages of responses obtained in each 500-trial block to examine whether there were any differences among black-capped and mountain chickadees in their discrimination abilities. There were no main effects of species, sex, or group, $p > 0.266$, however there was a main effect of exemplar set, $F(1, 19) = 4.93, p = 0.039$, of blocks, $F(7, 133) = 11.30, p < 0.001$, and several higher-order interactions, indicating that birds in each group learned over trials to respond to the S+ stimuli and to withhold responding to the S- stimuli.

We further investigated our *a priori* prediction that learning rates may differ between sympatric and allopatric black-capped

chickadees and mountain chickadees by conducting planned comparisons (Tukey's, $p < 0.05$). We chose to exclude the sex factor because (1) there was no main effect of sex in the omnibus ANOVA, (2) previous studies investigating chick-a-dee call perception in chickadees have yielded virtually no differences in discrimination abilities between males and females (e.g., Bloomfield et al., 2003; Bloomfield and Sturdy, in press), and (3) group sizes become increasingly smaller ($ns < 3$) when considering the remaining factors (species and group assignment). To further facilitate comparisons we present the results below based on group assignment.

3.3. BCCH-S+ group

After the first 500 trials, sympatric, allopatric, and mountain chickadees responded significantly less to the mountain chick-a-dee S– exemplars than to the black-capped chick-a-dee S+ exemplars. All birds continued to discriminate S+ from S– exemplars throughout the duration of training phase 1 (i.e., 4000 trials, see Fig. 2A, C and E).

3.4. MOCH-S+ group

After the first 1500 trials sympatric black-capped chickadees and mountain chickadees responded significantly less to the black-capped chick-a-dee S– exemplars than to the mountain chick-a-dee S+ exemplars. After 2500 trials all birds successfully discriminated S+ from S– exemplars, and maintained their discriminations throughout the duration of training phase 1 (i.e., 4000 trials, see Fig. 2B, D and F).

4. Training phase 2: Transfer 1

4.1. Methods

Once birds learned the contingencies associated with the two sets of chick-a-dee calls in the first phase of training, the calls were replaced with 10 novel calls of each species and the same category reinforcement rules established during acquisition were maintained during Transfer 1. The purpose of this phase of training was to ensure that birds understood the rule (i.e., contingency) associated with each stimulus set and were not simply responding based on rote memorization of each stimulus and its related contingency. This phase of training continued until the birds completed a minimum of six 500-trial bins (i.e., 3000 trials) with a discrimination ratio (DR) ≥ 0.8 , with the last two bins occurring consecutively.

4.2. Results

Birds in both groups continued to respond according to the category rules learned during acquisition training. To examine our *a priori* prediction that allopatric and sympatric chickadees may differ in their species' discriminations and generalizations, we conducted planned comparisons (Tukey's, $p < 0.05$) on the percentages of responses to S+ and S– exemplar sets during the last 500 trials of acquisition training and the percentages of responses to S+ and S– exemplar sets during the first 500 trials of training in Transfer 1. The logic here is that each stimulus is presented 25 times in a 500-trial bin and we were interested in determining whether all birds maintained their species' discriminations upon initial exposure to the novel stimuli and not following extensive training with these stimuli.

4.3. BCCH-S+ group

After the first 500 trials of Transfer 1, all birds continued to respond at high levels to S+ black-capped chick-a-dee

call exemplars and at significantly lower levels to S– mountain chick-a-dee call exemplars (see Fig. 2A, C and E). Allopatric black-capped chickadees responded significantly less to novel S+ calls and significantly more to novel S– calls compared to responding during the last 500 trials of acquisition, however responding to novel S+ and S– exemplars sets remained significantly different (56% and 37%, respectively, see Fig. 2C).

4.4. MOCH-S+ group

After the first 500 trials of Transfer 1, all birds continued to respond at high levels to S+ mountain chick-a-dee call exemplars and at significantly lower levels to S– black-capped chick-a-dee call exemplars (see Fig. 2B, D and F). Sympatric and allopatric black-capped chickadees responded slightly but significantly less to novel S+ mountain chick-a-dee calls compared to responding to S+ calls during the last 500 trials of acquisition, however responding to novel S+ and S– exemplars sets remained significantly different for sympatric chickadees (73% and 17%, respectively) and for allopatric chickadees (52% and 15%, respectively, see Fig. 2B and D).

To ensure that birds continued to respond appropriately to S+ and S– exemplar sets throughout the duration of Transfer 1, we conducted planned comparisons (Tukey's, $p < 0.05$) on each 500-trial block of Transfer 1. All birds in both S+ groups continued to respond at high levels to S+ exemplars and at significantly lower levels to S– exemplars (see Fig. 2).

5. Training phase 3: Transfer 2

Following their training with the novel calls in Transfer 1, birds were required to maintain their levels of responding when presented with all 20 black-capped chick-a-dee calls and all 20 mountain chick-a-dee calls used during acquisition and Transfer 1. Transfer 2 training continued until birds had completed six bins of 500 trials with DRs ≥ 0.8 .

5.1. Results

We compared the percentages of responses to S+ and S– exemplar sets during the last 500 trials of Transfer 1 training with the percentages of responses to S+ and S– exemplar sets during the first 500 trials of Transfer 2 training (Tukey's, $p < 0.05$). All birds, regardless of group assignment, continued to respond at high levels to S+ exemplars and respond at low levels to S– exemplars, as there were no significant differences in responding to the S+ and S– exemplar sets at the end of Transfer 1 and the start of Transfer 2 (see Fig. 2).

To ensure that birds maintained their species' discriminations throughout the duration of Transfer 2, we conducted planned comparisons (Tukey's, $p < 0.05$) on each 500-trial block. Indeed all birds continued to respond at high levels to S+ exemplars and at significantly lower levels to S– exemplars (see Fig. 2).

6. Probe tests

6.1. Methods

Once evidence of category-associated responding to all 20 calls of each species was observed during Transfer 2, all 20 calls of each species were presented for a minimum of 1000 trials (2 training blocks) with the percentage of reinforcement for S+ stimuli lowered to 85% (Transfer 85). This was done to decrease the notice-ability of differential reinforcement between training and test (probe) stimuli. During the testing phase, birds were required to maintain their species' discriminations of the two sets of 20 chick-a-dee training calls while probe stimuli were intermittently presented. Each probe session ($n = 3$) consisted of four stimuli (two black-capped chickadee stimuli types and two mountain chickadee stimuli types) from each of the four probe sets (Spliced Control, Multi-Species Spliced, Introductory-only, and Terminal-only). Each of the 16 probe stimuli in each session was randomly selected without replacement and presented only once in a 416-trial block (10 presentations each of the 40 training stimuli and 1 presentation each of the 16 probe stimuli) with a percentage of reinforcement set at 15%. This low rate of reinforcement was chosen in an effort to maintain responding by birds, but also to avoid the possibility that birds treat probe stimuli as nonrewarded and subsequently withhold responding to them. Once 3 blocks of 416 trials were collected, 1 block of 500 trials of Transfer 85 stimuli (i.e., training stimuli) was interspersed prior to commencing the next probe session. Once all three probe sessions had been presented, the sequence began again, ultimately resulting in each probe session being presented twice, resulting in each of the 48 probe stimuli being presented a total of 6 times. Birds completed, on average, 1–3 blocks of trials per day, and therefore probe sessions were conducted on different days.

6.2. Results

To ensure that birds continued to discriminate among the S+ and S– training calls despite the change in reinforcement value from 100% to 85%, we conducted a mixed model birds \times group \times exemplar set \times training phase ANOVA on the percentages of responses during the last 500 trials of Transfer 2 and the first 500 trials of Transfer 85 training phases. There were no significant differences in the responding by birds to the S+ and S– exemplars at the end of Transfer 2 and the start of Transfer 85, $F(1, 25) = 0.125$, $p = 0.726$ (see Fig. 2). Therefore birds continued to discriminate among black-capped and mountain chick-a-dee calls despite a reduction in the percentage of reinforcement value.

In the following analyses we conducted planned comparisons (Tukey's, $p < 0.05$) on the percentages of responses by chickadees to training calls presented during the last 500 trials of Transfer 85 and the average percentages of responses to the 6 presentations of each of the 8 probe types (4 black-capped chickadee types and 4 mountain chickadee types). One female sympatric black-capped chickadee in the mountain chickadee S+ group was omitted from the following analyses due to an equip-

ment failure that occurred during one of the six probe-session presentations.

In general, all three groups of birds in both S+ discrimination groups responded significantly less to the probe stimuli compared to responding to the S+ training stimuli, suggesting that birds could indeed discriminate between the training and testing exemplars. To examine the distribution of responses to the eight probe types (four S+ associated and four S– associated stimulus types) we compared the scaled percentages of responses (see Section 2.5.3) to each probe type by birds in both S+ discrimination groups. To facilitate comparisons we present the results below based on group assignment.

6.3. BCCH-S+ group

Sympatric birds responded most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and both Multi-species Spliced stimuli, with no significant differences among them in levels of responding (see Fig. 3A). Birds responded significantly less to the black-capped chick-a-dee Introductory-only stimuli and mountain chick-a-dee Spliced Control, Introductory-only, and Terminal-only probe stimuli, (see Fig. 3A).

Allopatric birds responded in a similar manner to the sympatric black-capped chickadees by responding most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and Multi-species (black-capped terminal) Spliced probe stimuli. However, when the data were transformed, a significant difference in responding to Spliced Control calls and Terminal-only stimuli was observed. Allopatric birds responded significantly less to black-capped chick-a-dee Introductory-only stimuli and all mountain chick-a-dee probe stimuli (see Fig. 3C).

Mountain chickadees responded most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and Multi-species (black-capped terminal) Spliced probe stimuli. However, when the data were transformed, a significant difference in responding to Spliced Control calls and Terminal-only stimuli was observed. Mountain chickadees responded significantly less to black-capped chick-a-dee Introductory-only stimuli and all mountain chick-a-dee probe stimuli (see Fig. 3E).

6.4. MOCH-S+ group

Sympatric birds responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli. Compared to these probe types, sympatric chickadees responded significantly less to mountain chick-a-dee Introductory-only stimuli, Multi-species (mountain terminal) Spliced stimuli, and all black-capped chick-a-dee probe stimulus types.

Allopatric birds responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli, but responded significantly less to the mountain chick-a-dee Introductory-only and Multi-species (mountain terminal) Spliced probe stimuli (see Fig. 3D). Allopatric birds also responded significantly less to all black-capped chick-a-dee probe types.

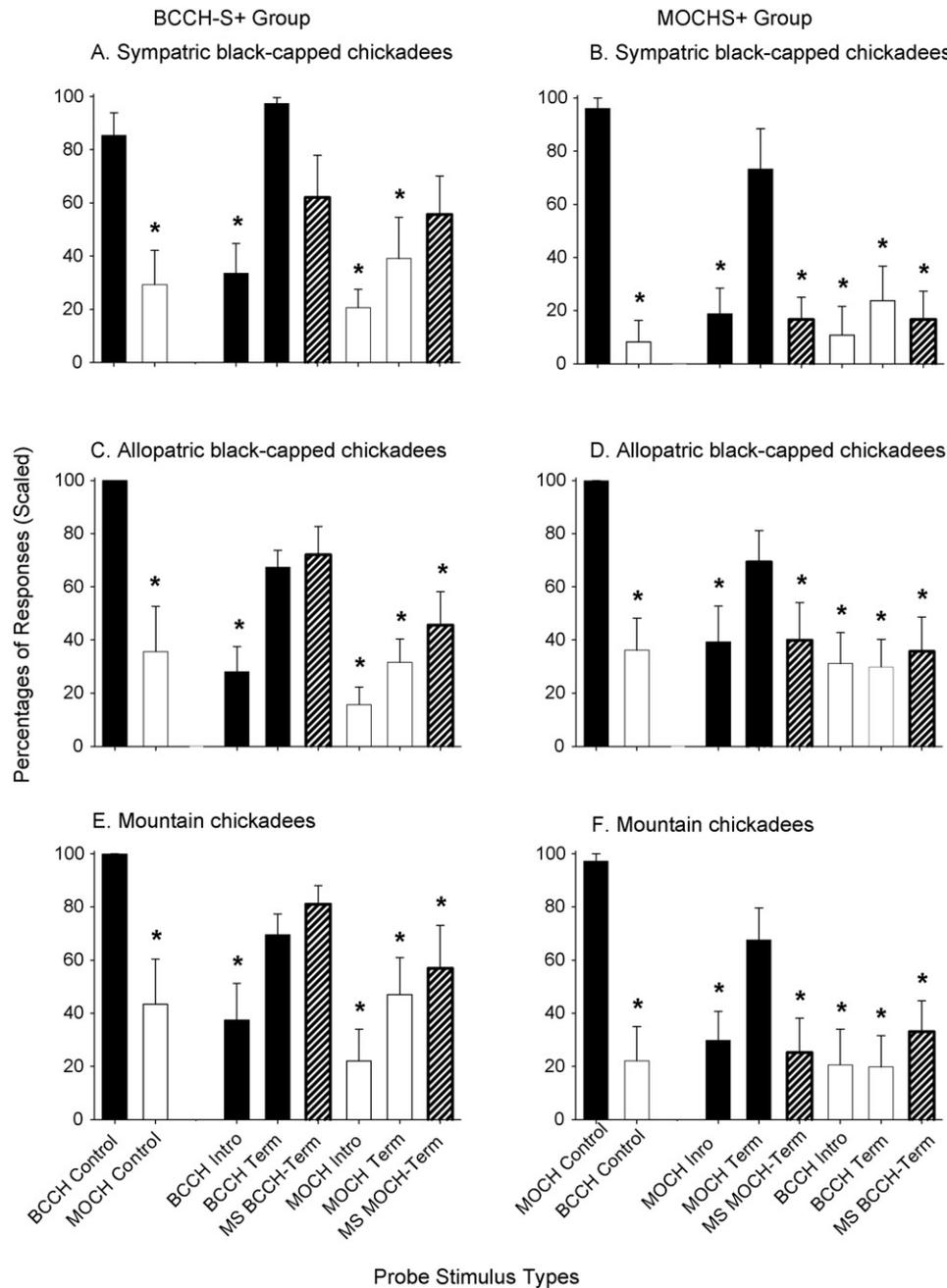


Fig. 3. Average percentages of responses (scaled to maximum responding, y-axis) by (A and B) sympatric black-capped chickadees, (C and D) allopatric black-capped chickadees, and (E and F) mountain chickadees to each of the eight probe stimulus types. Black-capped chick-a-dee (BCCH) S+ groups are in the left-hand side of the figure while mountain chick-a-dee (MOCH) S+ groups are in the right-hand side of the figure. Filled bars represent S+ associated probe stimuli, open bars represent S- associated probe stimuli, hatched bars represent probe stimuli consisting of both S+ and S- associated stimuli. Probe stimuli include: Spliced Control calls (BCCH Control and MOCH Control), Introductory-only stimuli (BCCH Intro and MOCH Intro), Terminal-only stimuli (BCCH Term and MOCH Term), and Multi-species Spliced calls with either a black-capped chickadee terminal portion (MS BCCH-Term) or a mountain chickadee terminal portion (MS MOCH-Term). Error bars represent average standard errors of the means. * Significant difference in responding ($p < 0.05$) compared to S+ associated Spliced Control probe stimuli.

Mountain chickadees responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli (see Fig. 3F), but responded significantly less to the mountain chick-a-dee Introductory-only and Multi-species (mountain terminal) Spliced probe stimuli. Mountain chickadees also responded significantly less to all black-capped chick-a-dee probe types.

We subsequently conducted planned comparisons (Tukey's, $p < 0.05$) to determine whether birds responded differently to each of the probe types. Sympatric black-capped chickadees, allopatric black-capped chickadees, and mountain chickadees responded about equally to each probe type (see Fig. 4), as there were no significant differences between groups of birds.

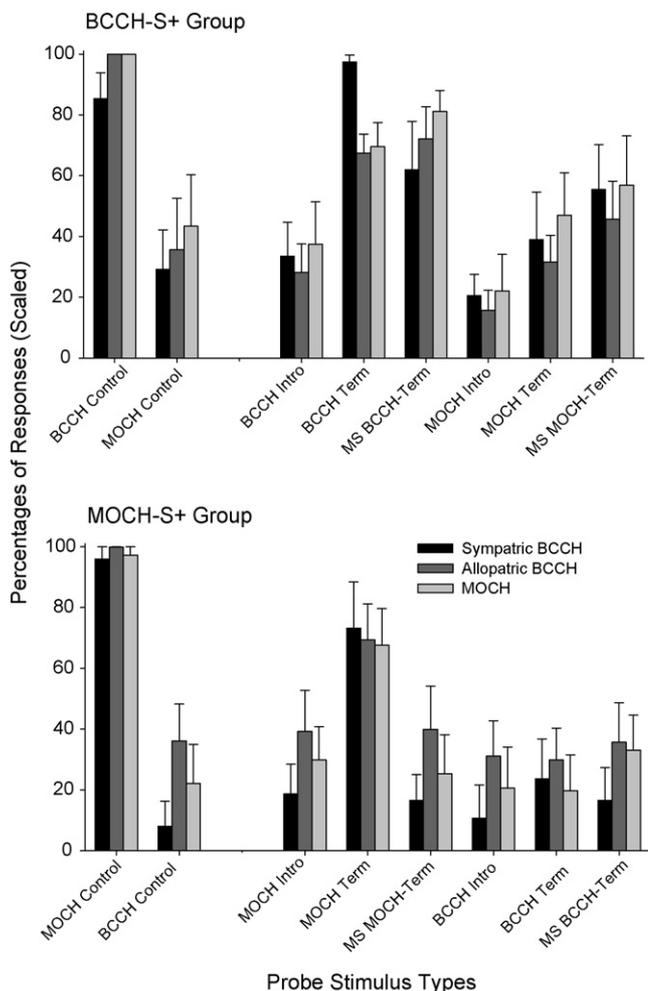


Fig. 4. Average percentages of responses (scaled to maximum responding, y-axis) by black-capped chickadees (BCCH, sympatric = black bars, allopatric = dark gray bars) and mountain chickadees (MOCH = light gray bars) in the black-capped chick-a-dee (BCCH) S+ group (top) and the mountain chick-a-dee (MOCH) S+ group (bottom), to each of the probe stimuli (x-axis). Error bars represent average standard errors of the means.

7. Discussion

Here we present the results of an operant discrimination performed by black-capped and mountain chickadees to determine the mechanisms for discriminating black-capped from mountain chick-a-dee calls. In addition, we examine whether experience affects the discriminations of black-capped chickadees and whether the two species of chickadees utilize different portions of the calls for discriminating. By establishing a baseline level of responding to each species' calls we were able to intermittently present experimenter-manipulated chick-a-dee calls and examine the responses by birds.

In a previous set of experiments (Bloomfield and Sturdy, in press) we provided evidence that black-capped and mountain chickadees discriminate their own from the other species' chick-a-dee calls, and perceive each species' calls as belonging to two separate, open-ended, perceptual categories. Further, there appeared to be several differences between sympatric and allopatric black-capped chickadees in their discrimination

speed and accuracy. At the outset of the current experiment we hypothesized that black-capped chickadees may discriminate black-capped and mountain chick-a-dee calls differently, depending on their previous histories with mountain chickadees. Given the extensive experience of the sympatric black-capped chickadees with mountain chick-a-dee calls, we predicted that these birds would be better able to discriminate between the species' calls using either the introductory 'chick-a' portion or the terminal 'dee' portion compared to allopatric chickadees.

Sympatric and allopatric black-capped chickadees performed relatively similarly in the current set of experiments. Birds learned to discriminate black-capped from mountain chick-a-dee calls over a minimum of 4000 trials, taking approximately 200 presentations of each stimulus to master the initial task. Birds in the black-capped chick-a-dee S+ group were the first to acquire the discrimination by responding significantly more to black-capped chick-a-dee calls than to mountain chick-a-dee calls after the first 500 trials whereas sympatric black-capped and mountain chickadees in the mountain chick-a-dee S+ group required 1500 trials. Allopatric birds in the mountain chick-a-dee S+ group required 2500 trials to learn to respond to mountain chick-a-dee calls and withhold responding to black-capped chick-a-dee calls. Although the methods were slightly different between the current study and the previous study examining open-ended categorization in chickadees (Bloomfield and Sturdy, in press), similar discrimination results appeared in each study. Specifically, in the previous study sympatric black-capped chickadees and mountain chickadees assigned to the mountain chick-a-dee S+ group required more trials to discriminate S+ mountain chick-a-dee calls from S- black-capped chickadee calls compared to birds in the black-capped chick-a-dee S+ group. While the cause(s) for the differences in speed of acquisition between the two groups is (are) unclear, all birds nonetheless learned the discrimination by 4000 trials.

Following the acquisition phase, birds were presented with 10 novel calls of each species and were required to maintain their species' discrimination. Allopatric birds in the black-capped chick-a-dee S+ group responded slightly less to novel black-capped chick-a-dee S+ calls and responded slightly more to novel mountain chick-a-dee S- calls. As well, sympatric and allopatric birds in the mountain chick-a-dee S+ group responded slightly less to novel mountain chick-a-dee S+ calls, however all birds continued to respond significantly more to the S+ stimuli compared to the S- stimuli, indicating that they understood the rules of contingency associated with each stimulus set (i.e., each species' category of calls).

Following training we intermittently presented experimenter-manipulated chick-a-dee calls to determine the mechanisms underlying species' discrimination by sympatric and allopatric black-capped chickadees and mountain chickadees. All chickadees performed about equally in the current study. Birds responded most to the S+ Spliced Control calls, created using the 'voice' of one individual for the 'chick-a' portion and the 'voice' of another individual of the same species for the 'dee' portion. However, responding to the Spliced Control calls rarely equaled the level of responding observed for the normal training calls.

Similar to the results seen at the beginning of Transfer 1 in the current study, and in other studies with chickadees (Bloomfield et al., 2003; Bloomfield and Sturdy, in press), this could be due to the fact that birds received extensive training with the normal calls and thus were able to detect the difference between the normal and the probe calls. Alternatively, the use of two voices to produce one call may have in fact been perceived by the birds as abnormal, resulting in lower responding.

Sympatric and allopatric black-capped chickadees and mountain chickadees all responded about equally to the S+ associated Spliced Control calls, Terminal-only calls, and the Multi-species calls consisting of the S+ associated terminal portion. Despite the difference in responding by allopatric and mountain chickadees in the BCCH-S+ group to Spliced Control and Terminal-only calls observed when the data were transformed, responding to the Multi-species calls with BCCH-term portion remained high, suggesting that the terminal ‘dee’ portion of the call is sufficient for inducing species-specific responses despite the mismatched introductory portion. By comparison, responding to the Introductory-only probe stimuli remained low, indicating that the ‘chick-a’ portion of the chick-a-dee call may not be a reliable species-indicator. In addition, chickadees responded to the Multi-species (black-capped terminal) Spliced probe stimuli. There are two possible explanations for these levels of responding. First, birds may not attend to the introductory portion of chick-a-dee calls for species discriminations when the terminal portion is present. Second, birds may not be able to discriminate between species using only the introductory portion. This second alternative remains a possibility, as all birds responded at low levels to both S+ and S– associated Introductory-only probe stimuli. Experiments currently underway will ultimately determine whether chickadees are capable of discriminating species on the basis of individual introductory and terminal notes of conspecific and heterospecific chick-a-dee calls, as would be suggested by a linear discriminant analysis conducted by Dawson et al. (2006).

In summary, it appears that the Terminal-only portion of the chick-a-dee call conveys more species-specific information compared to the Introductory-only portion, as birds responded significantly more to the Terminal-only probe type. However, if the birds only used the terminal “dee” portion of the calls for discriminating the calls of black-capped and mountain chickadees, then we might have expected to see higher levels of responding to the Multi-species calls with appropriate S+ terminal ‘dee’ portions. When the Terminal portion was combined with an Introductory portion of the other species, some differences in responding occurred. In particular, not only did sympatric black-capped chickadees in the BCCH-S+ group respond to the Multi-species Spliced stimuli consisting of the S+ associated Terminal portion, but these birds also responded to the Multi-species Spliced stimuli consisting of the S– associated Terminal portion. Thus perhaps birds were able to detect the S+ associated Introductory portion and responded accordingly. Therefore it remains possible that although birds appeared to mainly rely on the terminal portions of the calls for discriminating, the introductory portions provided some type of species information.

The terminal portions of the calls of black-capped and mountain chickadees are similar in at least one respect: mountain chick-a-dee calls and black-capped chick-a-dee calls almost always contain one or more D notes, and the D notes are similar in structure between the two species (Charrier et al., 2004; Bloomfield et al., 2004). However, the terminal portions of the calls of the two species also differ in at least one respect: mountain chickadees produce an additional note type, the D_{hybrid} note, present in a majority of their calls (Bloomfield et al., 2004). This note type is more tonal in nature at the outset of the note, appearing more like an introductory A- or B-type note, and quickly transitions to a note that appears more like a typical D note (see Fig. 1). It remains possible that this is the one main difference that the birds were attending to when discriminating black-capped from mountain chick-a-dee calls. The D-type notes may in fact prove to be reliable species markers, given that they are (1) present in nearly every chick-a-dee call, (2) longer in duration, and therefore may provide the birds with greater opportunity to attend to them and perceive the salient, species-specific information, and (3) lower in frequency compared to all other chick-a-dee call notes, and therefore would be more resistant to degradation in the birds’ natural habitats. However further evidence beyond the scope of the current study would be required to determine whether this is in fact the only feature used by the birds for discriminating. It remains possible that micro-acoustic features, such as spectral and temporal differences in these note types, provide birds with species-specific information.

Chickadees are not the only avian species to produce and perceive species-specific markers in their vocalizations. For example, Brenowitz (1982) found that Red-winged Blackbirds (*Agelaius phoeniceus*) can transmit the terminal ‘trill’ note of their song over 100 m, whereas the introductory and higher frequency components of the song were severely attenuated. Further, this portion of the song, in the absence of the introductory components, was both necessary and sufficient for inducing species-specific responses from flock and non-flock members. This trill note is similar in structure to the D notes of black-capped and mountain chickadees, with most of the energy occurring in the 2–4 kHz range, suggesting that perhaps the D notes of chickadees can also be transmitted over long distances without the loss of species-specific information. Brenowitz and others (e.g., Richards, 1981a,b) suggest that the high-frequency introductory notes may act as ‘alerting notes’, or alternatively function to convey individual identity or information about the distance of the singer. Because the chickadees in the current study did not appear to rely on the introductory notes in the chick-a-dee calls for species’ discriminations, it remains possible that these high-frequency notes also function in a manner not related to species-identity.

In American redstarts (*Setophaga ruticilla*) the initial trill of the male song, which is a brief repeated frequency-modulated note, would by itself invoke a species-typical response, however synthetic repetition of the terminal syllable would invoke a similar response, a response not seen when presented only once in the song (Date et al., 1991). This suggests that although a feature may convey less species-specific information than other features, redundancy, for example in the form of repetition,

may in turn provide more reliable information than singly presented features. In chickadees, the D notes are often repeated within a call (average 3.4 notes/call in black-capped chickadees, Charrier et al., 2004; average 1.6 notes/call in mountain chickadees, Bloomfield et al., 2004), possibly providing listening birds with redundant, and therefore more reliable, species information. With this in mind, further experimentation is currently underway to determine whether the repetition of any one chick-a-dee call-note type would facilitate species' discrimination by black-capped and mountain chickadees.

Nelson furthered our understanding of species-specific information in the features of songs with the discovery that the relatively invariant feature 'maximum note frequency' was most useful for multivariate discriminations of the songs of the field sparrow (*Spizella pusilla*) and the chipping sparrow (*S. passerine*), and that the frequency of field sparrow song needed to be presented within a species-typical range in order for birds to respond maximally (Nelson, 1988, 1989). Using four features measured in the D notes of black-capped and mountain chickadees, a discriminant analysis clearly indicated that these notes were sufficient for species identification, as the notes were classified according to species with an average accuracy of 94% (Dawson et al., 2006). Apparent differences in the average loudest frequencies (F_{\max}) of the two species' D notes may have been a significant contributor to this discrimination (see Table 4 in Charrier et al., 2004; Table 5 in Bloomfield et al., 2004).

Taken together, it appears that the D notes in the chick-a-dee calls of (at least) black-capped and mountain chickadees may be suitable for conveying species-specific information. First, they are lower in frequency and longer in duration than all other note types in the chick-a-dee calls of these two species, and are therefore more likely to be resistant to degradation and able to be heard at greater distances. Second, they are present in nearly every single chick-a-dee call produced and are typically repeated within a call, providing greater opportunity for listeners to perceive the pertinent information. Finally, based on only four acoustic measurements (one temporal and three spectral) a linear discriminant analysis was able to accurately classify these note types by species. However we are only beginning to understand the perceptual abilities and limits of songbirds, and therefore it remains possible that human-conducted acoustic measurements do not fully envelope all the possible features that birds may perceive. Therefore birds may in fact acquire more information from these notes than we are able to measure, thereby increasing the number of possible species-specific features in these notes.

It is perhaps important to clarify that the terminal notes in the chick-a-dee calls may not be the only features that can be used by the birds for discriminating. In the current study we provided the birds with one of two options: use the introductory 'chick-a' portion or use the terminal 'dee' portion. This design did not allow us to gain a greater understanding of the potential for each individual note type to convey species information. As a follow-up to the current study we are investigating this possibility by providing the birds with individually or repeatedly presented notes of each type and examining their responses. Further, other features, such as absolute and relative pitch (frequency) of the notes and of the whole call, as well as temporal characteristics (such

as note duration and call rate) can be manipulated and tested for their potential for species-identifying information. These proposed designs will ultimately answer the question whether birds rely on the terminal 'dee' portion of the calls or depend on the terminal 'dee' portion of the calls for discriminating black-capped from mountain chick-a-dee calls.

Acknowledgements

This research was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant (NSERC), Alberta Ingenuity Fund (AIF) New Faculty Grant, Canada Foundation for Innovation (CFI) New Opportunities Grant along with start-up funding and CFI partner funding from the University of Alberta, Edmonton, Alberta, Canada to CBS, an Alberta Ingenuity Studentship to LLB, and an NSERC USRA to TMF. This research was approved by the University of Alberta Biological Sciences Animal Care Committee and the University of Calgary Life and Environmental Sciences Animal Care Committee. Chickadees were captured under an Environment Canada Canadian Wildlife Service Scientific permit, and Alberta Fish and Wildlife Capture and Research permits.

The authors thank I. Lank, L. Omerzu, and H. Tischer for technical assistance, M. Avey, R. Smith, and C. Nickerson for their contributions, and two anonymous reviewers for their helpful suggestions.

References

- Becker, P.H., 1982. The coding of species-specific characteristics in bird sounds. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Acoustic Communication in Birds*. Cornell University Press, New York, pp. 213–252.
- Bloomfield, L.L., Charrier, I., Sturdy, C.B., 2004. Note types and coding in Parid vocalizations II: The chick-a-dee call of the mountain chickadee (*Poecile gambeli*). *Can. J. Zool.* 82, 780–793.
- Bloomfield, L.L., Sturdy, C.B., Phillmore, L.S., Weisman, R.G., 2003. Open-ended categorization of chick-a-dee calls by black-capped chickadees (*Poecile atricapilla*). *J. Comp. Psychol.* 117, 290–301.
- Bloomfield, L.L., Sturdy, C.B., in press. All "chick-a-dee" calls are not created equally. Part I. Open-ended categorization of chick-a-dee calls by sympatric and allopatric chickadees, *Behav. Process.*, doi:10.1016/j.beproc.2007.06.011.
- Brenowitz, E.A., 1982. Long-range communication of species identity by song in the Red-winged Blackbird. *Behav. Ecol. Sociobiol.* 10, 2–38.
- Charrier, I., Bloomfield, L.L., Sturdy, C.B., 2004. Note types and coding in Parid vocalizations I: the chick-a-dee call of the black-capped chickadee (*Poecile atricapilla*). *Can. J. Zool.* 82, 769–779.
- Date, E.M., Lemon, R.E., Weary, D.M., Richter, A.K., 1991. Species identity by birdsong: discrete or additive information? *Anim. Behav.* 41, 111–120.
- Dawson, M.R.W., Bloomfield, L.L., Charrier, I., Sturdy, C.B., 2006. Statistical classification of black-capped (*Poecile atricapillus*) and mountain chickadee (*Poecile gambeli*) call notes. *J. Comp. Psychol.* 120, 147–153.
- Falls, J.B., 1982. Individual recognition by sound in birds. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Acoustic Communication in Birds*. Cornell University Press, New York, pp. 237–278.
- Ficken, M.S., Ficken, R.W., Witkin, S.R., 1978. Vocal repertoire of the black-capped chickadee. *Auk* 95, 34–48.
- Ficken, M.S., Hailman, E.D., Hailman, J.P., 1994. The chick-a-dee call system of the Mexican chickadee. *Condor* 96, 70–82.
- Ficken, M.S., McLaren, M.J., Hailman, J.P., 1996. Boreal chickadee (*Parus hudsonicus*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, no. 254. The Birds of North America Inc., Philadelphia, Pennsylvania, pp. 1–23.

- Gaddis, P.K., 1985. Structure and variability in the vocal repertoire of the mountain chickadee. *Wilson Bull.* No. 97, pp. 30–45.
- Gill, F.B., Mostrom, A., Mack, A.L., 1993. Speciation in North American chickadees: Patterns of mtDNA genetic divergence. *Evolution* 47, 195–212.
- Griffiths, R., 2000. Sex identification using DNA markers. In: Baker, A.J. (Ed.), *Molecular Methods in Ecology*. Blackwell Science, Malden, MA, pp. 295–321.
- Hailman, J.P., Ficken, M.S., 1996. Comparative analysis of vocal repertoires, with reference to chickadees. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, New York, pp. 136–159.
- Hailman, J.P., Ficken, M.S., Ficken, R.W., 1985. The “chick-a-dee” calls of *Parus atricapillus*: a recombinant system of animal communication compared with written English. *Semiotica* 56, 191–224.
- Hill, B.G., Lein, M.R., 1989. Natural and simulated encounters between sympatric black-capped chickadees and mountain chickadees. *Auk* 106, 645–652.
- Hughes, M., Nowicki, S., Lohr, B., 1998. Call learning in Black-capped chickadees (*Parus atricapillus*): the role of experience in the development of “chick-a-dee” calls. *Ethology* 104, 232–249.
- Mammen, D.L., Nowicki, S., 1981. Individual differences and within-flock convergence in chickadee calls. *Behav. Ecol. Sociobiol.* 9, 179–186.
- McArthur, P., 1982. Mechanisms and development of parent-young vocal recognition in the pinyon jay. *Anim. Behav.* 30, 62–74.
- McCallum, D.A., Grundel, R., Dahlsten, D.L., 1999. Mountain chickadee (*Poecile gambeli*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, no. 559. The Birds of North America Inc., Philadelphia, Pennsylvania, pp. 1–27.
- Nelson, D.A., 1988. Feature weighing in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* 106, 159–182.
- Nelson, D.A., 1989. Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). *J. Comp. Psychol.* 103, 171–176.
- Njegovan, M., Hilhorst, B., Ferguson, S., Weisman, R., 1994. A motor driven feeder for operant training in song birds. *Behav. Res. Methods Instrum. Comput.* 26, 26–27.
- Palya, W.L., Walter, D.E., 2001. Document Set for the High-Performance Experiment Controller. Retrieved May 2, 2000 from <http://www.jsu.edu/depart/psychology/sebac/Exp-Ctl.html>.
- Pyle, P., 1997. *Identification Guide to North American Birds*. Slate Creek Press, Bolinas, CA.
- Ratcliffe, L., Otter, K., 1996. Sex differences in song recognition. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, New York, pp. 339–355.
- Richards, D.G., 1981a. Estimation of distance of singing conspecifics by the Carolina Wren. *Auk* 98, 127–133.
- Richards, D.G., 1981b. Alerting and message components in songs of Rufous-sided Towhees. *Behaviour* 76, 223–249.
- Shackleton, S.A., Ratcliffe, L.M., 1993. Development of song in hand-reared black-capped chickadees. *Wilson Bull.* No. 105, pp. 637–644.
- Smith, S.M., 1991. *The Black-Capped Chickadee: Behavioral Ecology and Natural History*. Cornell University Press, New York.
- Smith, S.M., 1993. Black-capped chickadee (*Poecile atricapilla*). In: Poole, A., Stettenheim, P., Gill, F. (Eds.), *Birds of North America* [No. 39]. Academy of Natural Sciences, Philadelphia, pp. 1–19.
- Smith, S.T., 1972. *Communication and other social behavior in Parus carolinensis*. Nuttall Ornithological Club, Massachusetts.
- Stoddard, P.K., 1996. Vocal recognition of neighbors by territorial Passerines. In: Kroodsma, D.E., Miller, E.H. (Eds.), *Ecology and Evolution of Acoustic Communication in Birds*. Cornell University Press, New York, pp. 356–374.