



Perception of Sex Differences in Black-Capped Chickadee (*Poecile atricapillus*) Chick-A-Dee Calls

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Abstract – Black-capped chickadee (*Poecile atricapillus*) chick-a-dee calls differ acoustically depending on flock membership, individual identity, and species identity. Other chickadee vocalizations, including their *tseet* call and *fee-bee* song, differ depending on the sex of the signaler. In Experiment 1, we used an operant go/no-go discrimination task to investigate if black-capped chickadees perceive any acoustic differences between male- and female-produced chick-a-dee calls. Manufactured calls that included both male- and female-produced portions were also tested. We conducted a second experiment in which the terminal “-dee” portions of the same chick-a-dee stimuli as used in Experiment 1 were removed. In both experiments, there was no evidence for category learning. Birds did not transfer responding from learned contingencies to untrained stimuli. These results indicate that, while it may be biologically relevant to attend to sex of a signaler in reproductive-critical vocalizations such as the *fee-bee* song, there may be no benefit for this information to be transmitted in chick-a-dee calls, which are mainly used in situations unrelated to reproduction.

Keywords – Operant conditioning, Songbird, Acoustic perception, Sex differences, Categorization

As a species that typically inhabits sparse to dense forest across much of North America, black-capped chickadees (*Poecile atricapillus*) often rely on vocalizations to communicate between a signaller and a receiver (Smith, 1991). This is true of a variety of avian species that rely on acoustic, rather than visual, signals to discriminate between con- and heterospecifics as acoustic cues travel farther than visual cues, and vegetation, among other obstructions, can interfere with visual cues (Becker, 1982). In addition to containing species-specific cues, avian vocalizations also allow for individual recognition (Falls, 1982; Nelson & Poesel, 2007), identification of individual dominance rank (Hahn et al., 2017; Massen et al., 2014), and recognition of a signaller’s sex (Hoelzel, 1986; Pavlova et al., 2005).

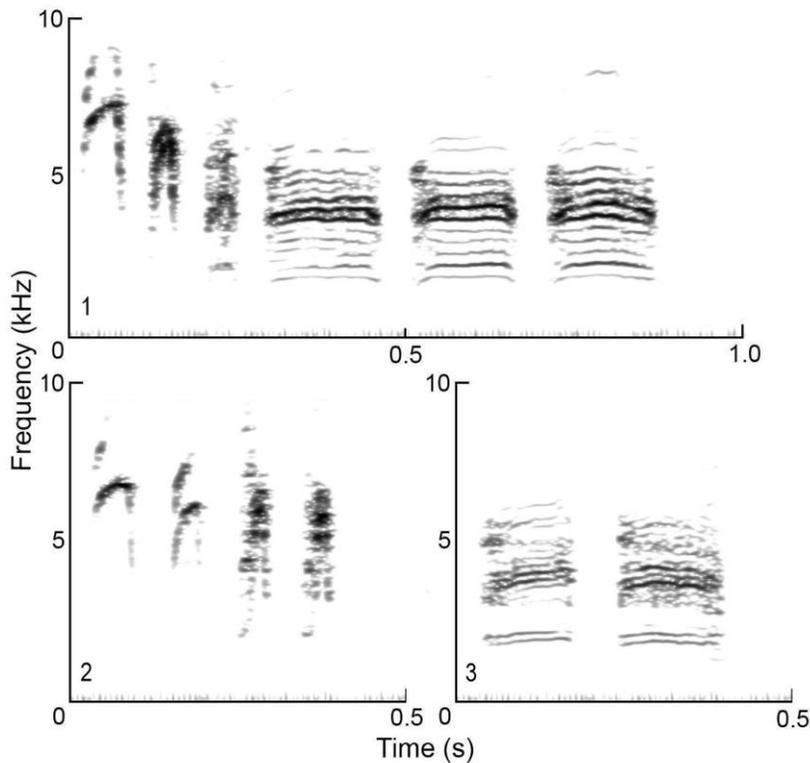
Most songbirds produce acoustically-complex learned vocalizations (i.e., songs) that function in territory defense and mate attraction, in addition to comparatively simple vocalizations (i.e., calls), which may or may not be learned and are produced in situations typically unrelated to mating behaviors (Catchpole & Slater, 2008). Unlike most songbirds, black-capped chickadees produce a single acoustically-simple song (i.e., *fee-bee* song), and numerous calls.

Here we focus on the chick-a-dee call, one of the most complex (in both acoustics and usage) and versatile vocalizations that black-capped chickadees produce. This call consists of four note-types that

occur in a relatively fixed order (A→B→C→D), though each note-type may be repeated or omitted, allowing for numerous and varied combinations (see Figure 1; Ficken et al., 1978). This variation makes it possible for the call to serve multiple functions, including informing conspecifics regarding the presence of food (Smith, 1991), the coordination of con- and heterospecifics to assist in mobbing behavior against predators (Hurd, 1996), and maintaining flock cohesion (Nowicki, 1983). Additionally, the *chick-a-dee* call has been found to differ acoustically based on a caller's individual identity (Charrier et al., 2004), flock membership (Mammen & Nowicki, 1981; Nowicki, 1989), and species (Bloomfield et al., 2003; Bloomfield & Sturdy, 2008).

Figure 1

Sound Spectrogram of Black-capped Chickadee Calls



Note. 1) a Black-capped Chickadee Chick-A-Dee Call with Composition A, B, C, D, D, D (Window Size = 256 Points, Frequency Precision = 43.1 Hz), 2) a Truncated Black-Capped Chickadee Chick-A Call with Composition A, B, C, C (Window Size = 256 Points, Frequency Precision = 43.1 Hz), and 3) a Truncated Black-Capped Chickadee -Dee Call with Composition D, D (Window Size = 256 Points, Frequency Precision = 43.1 Hz).

Sex differences have been documented in black-capped chickadee vocalizations, including their *fee-bee* songs (Hahn et al., 2013) and *tseet* calls (Guillette et al., 2010), as well as in the *chick-a-dee* calls of the closely-related Carolina chickadee (*P. carolinensis*; Freeberg et al., 2003). Conceptually, determining the sex of an unknown signaler may be beneficial in informing a receiver's actions. For example, if an individual male hears another male in his territory, the correct response would be to defend the territory aggressively; however, this response would not be appropriate if the intruder is a female as there may be an opportunity to mate. Bioacoustic analyses of black-capped chickadee *chick-a-dee* calls found evidence of some acoustic differences between A notes produced by males and females (Campbell et al., 2016). This featural analysis was conducted using a series of measurements related to call duration and frequency at various time points on a sound spectrogram. These features were selected by humans for

inclusion in the analysis and, as such, chickadees may or may not attend to these human-selected acoustic features, or they may attend to other components within the call not captured by the bioacoustic analysis.

In the current study, we used an operant go/no-go discrimination task to evaluate if black-capped chickadees can discriminate between male- and female-produced *chick-a-dee* calls. We also manipulated calls to determine which portions of the call, if any, aid in this potential discrimination. Birds were, for example, trained to respond ('go') to male-produced *chick-a-dee* calls and withhold responding ('no-go') to female-produced calls; following training, birds were then tested with additional male- and female-produced calls, and manipulated calls. For the birds in the True groups, in which food-rewarded and unrewarded stimuli consisted of categories (i.e., male calls and female calls potentially forming perceptual categories), if the birds were using open-ended categorization to perform the discrimination, we would expect them to continue responding to these new calls in the Transfer stage using the same contingencies as they learned in Discrimination training (i.e., birds reinforced for responding to male calls would continue to respond to novel male calls). Conversely, if birds did not use categorization and instead relied on rote memorization to discriminate between rewarded and unrewarded stimuli in Discrimination training, we would expect to see non-differential responding to the novel calls presented in the Transfer stage as the learning would not transfer to new stimuli. Birds in the Pseudo groups, in which rewarded and unrewarded stimuli were randomly selected from between categories (i.e., random calls not forming perceptual categories based on sex of the caller), could rely only on rote memorization to discriminate between rewarded and unrewarded calls.

Experiment 1

Method

Subjects

Twenty-one (21) wild-caught black-capped chickadees (11 males, 10 females) captured between February 3, 2013 and January 20, 2015 participated in Experiment 1. Birds were captured in Edmonton (North Saskatchewan River Valley, 53.53°N, 113.53°W; Mill Creek Ravine, 53.52°N, 113.47°W) and Stony Plain (53.46°N, 114.01°W), Alberta, Canada and were aged as older than one year at time of capture using the shape and color of outer tail retrices (Pyle, 1997). Sex was determined using DNA analysis (Griffiths et al., 1998). All birds had previous experience with the operant discrimination paradigm, discriminating biological (owl calls, *fee-bee* songs; Congdon, et al., 2020; Hahn et al., 2015) and synthetic (tonal) stimuli (McMillan et al., 2017). Fourteen birds had experience discriminating between high- and low-arousal *chick-a-dee* calls (see Congdon et al., 2019), but none had experience with the calls used in the current experiment. Previous experience was balanced across groups.

Housing

Before and after the experiment, birds were housed in individual 30 × 40 × 40 cm cages (Rolf C. Hagen, Inc., Montreal, QC, Canada) in communal colony rooms, which allowed for visual and auditory, but not physical contact between conspecifics. Birds had *ad libitum* access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO, USA), water, grit, and cuttlebone. Water was supplemented with vitamins three days a week (Prime Vitamin Supplement; Hagen, Inc.). Food supplements included three to five sunflower seeds daily, one superworm (*Zophobas morio*) three times a week, and a mixture of egg and either parsley or spinach twice a week. The light:dark cycle was maintained to match the local day:night cycle for Edmonton, AB, Canada.

Apparatus

During the experiment, birds were housed individually in an experimental apparatus that consisted of a modified 30 × 40 × 40 cm home cage within a sound attenuating chamber. The chamber was supplied with a constant flow of air and lit by a 9W, full spectrum fluorescent bulb using an on-off schedule that matched the local day:night cycle for Edmonton, AB, Canada. An 11 × 16 cm opening on one side of the cage allowed the birds to access a motorized feeder. The cage contained three perches, a grit cup, a water bottle, and cuttlebone. Birds received one superworm, twice daily. Mazuri food was accessible only after a correct response as a reward. Infrared beams in the feeder and in the perch closest to the feeder tracked the position of the bird during testing. A single-board computer tracked responses and set up trials, sending and receiving data from a personal computer which also stored and played acoustic stimuli. Stimuli passed through an NAD310 Integrated Amplifier (NAD Electronics, London, UK) or a Cambridge A300 or 640A Integrated Amplifier (Cambridge Audio, London, UK) before coming through a Fostex FE108 Σ full range speaker beside the feeder (Fostex Corp., Tokyo, Japan; frequency response range: 80-18,000 Hz). See Sturdy and Weisman (2006) for a detailed description of the experimental setup.

Acoustic Stimuli

A total of 248 *chick-a-dee* calls were obtained from 44 black-capped chickadees (22 males, 22 females [sex determined using DNA analysis]) and used to create 268 acoustic stimuli (summarized in Table 1). Individuals that provided vocal stimuli were caught between December 30, 2008 and March 19, 2011 and, as such, are unfamiliar to those that served as subjects. High-quality vocalizations were recorded from individuals isolated in sound-attenuating chambers (1.7 m × 0.84 m × 0.58 m; Industrial Acoustics Company, Bronx, NY). Individual *chick-a-dee* calls were cut from recordings and bandpass filtered outside of frequency range of *chick-a-dee* calls (2000 - 5000 Hz) using GoldWave 6.19 (GoldWave, Inc., St John's, NL, Canada). These calls were prepared as outlined below and played at a volume of ~75 dB as measured at the request perch (Type 2239, Brüel & Kjær Sound & Vibration Measurement A/S, Nærum, Denmark; A-weighting, slow response) during the experiment.

Table 1

Summary of the 268 Acoustic Stimuli Presented in Experiment 1 and Modified for Experiment 2, Including Stimulus Type and Quantity

Introduction Stage	Natural Call Stimuli	Manipulated Call Stimuli						Total Call Stimuli
		Partial call		Spliced call	Single note-type spliced call			
		"chick-a"	"-dee"		A Note	B Note	C Note	
Discrimination training	120	-	-	-	-	-	-	120
Transfer testing	38	-	-	-	-	-	-	38
Test trials	-	20	20	40	12	12	6	110
Total	158	20	20	40	12	12	6	268

Note. Stimuli are listed under the experimental stage in which they were introduced, though stimuli introduced in Discrimination training were also presented during both Transfer training and Test trial stages.

Natural Call Stimuli. One hundred-and-twenty (120) unmanipulated calls from 24 individuals (12 males, 12 females) were used as stimuli for the Discrimination stage and 38 unmanipulated calls from 20 individuals (10 males, 10 females) were used as stimuli for the Transfer stage (see 'Procedure' below). Five milliseconds of silence was added to the beginning and end of each stimulus using SIGNAL 5.06.07

(Engineering Design, Berkeley, CA, USA), then each file was tapered to remove transients and amplitude was equalized. These unmanipulated stimuli were included to train subjects on the male-female discrimination and test for evidence of categorization or rote memorization as a mechanism for discrimination.

Manipulated Call Stimuli. Ninety additional calls from the same 20 individuals that provided stimuli for Transfer testing were modified as follows for Test trials.

Partial Call Stimuli. Ten male and 10 female calls (two calls each from 10 individuals) were cut into their initial “*chick-a*” portion (A, B, and/or C notes) and terminal “*-dee*” portion (D notes) such that each call yielded two stimuli (one “*chick-a*” and one “*-dee*” portion). These 40 portioned stimuli (10 male, 10 female “*chick-a*” stimuli; 10 male, 10 female “*-dee*” stimuli) were then prepared in the same manner as the natural call stimuli. These partial call stimuli were included to determine if subjects attended to acoustic features contained in the initial “*chick-a*” portion and/or the terminal “*-dee*” portion to perform the discrimination.

Spliced Call Stimuli. These stimuli were created by randomly splicing together the “*chick-a*” and “*-dee*” portions created as partial call stimuli to form *chick-a-dee* calls made of notes from two different individuals. Ten stimuli were created from male “*chick-a*” and female “*-dee*” portions (M-F calls), ten were created from female “*chick-a*” and male “*-dee*” portions (F-M calls), ten were created with portions from two males (M-M calls), and ten were created with portions from two females (F-F calls), yielding a total of 40 spliced stimuli which were then prepared in the same manner as the natural call stimuli. The stimuli constructed from vocalizations produced by individuals of the same sex (e.g., M-M or F-F calls) were included to evaluate how subjects reacted to manipulated vocalizations (i.e., Do they treat a M-M spliced call similar to a natural male call?). The stimuli constructed from vocalizations produced by individuals of opposite sexes (e.g., M-F or F-M calls) were included to determine if subjects attended more to the initial “*chick-a*” portion and/or the terminal “*-dee*” portion to perform the discrimination (i.e., Do they treat a M-F spliced call more similar to a natural male call or a natural female call?).

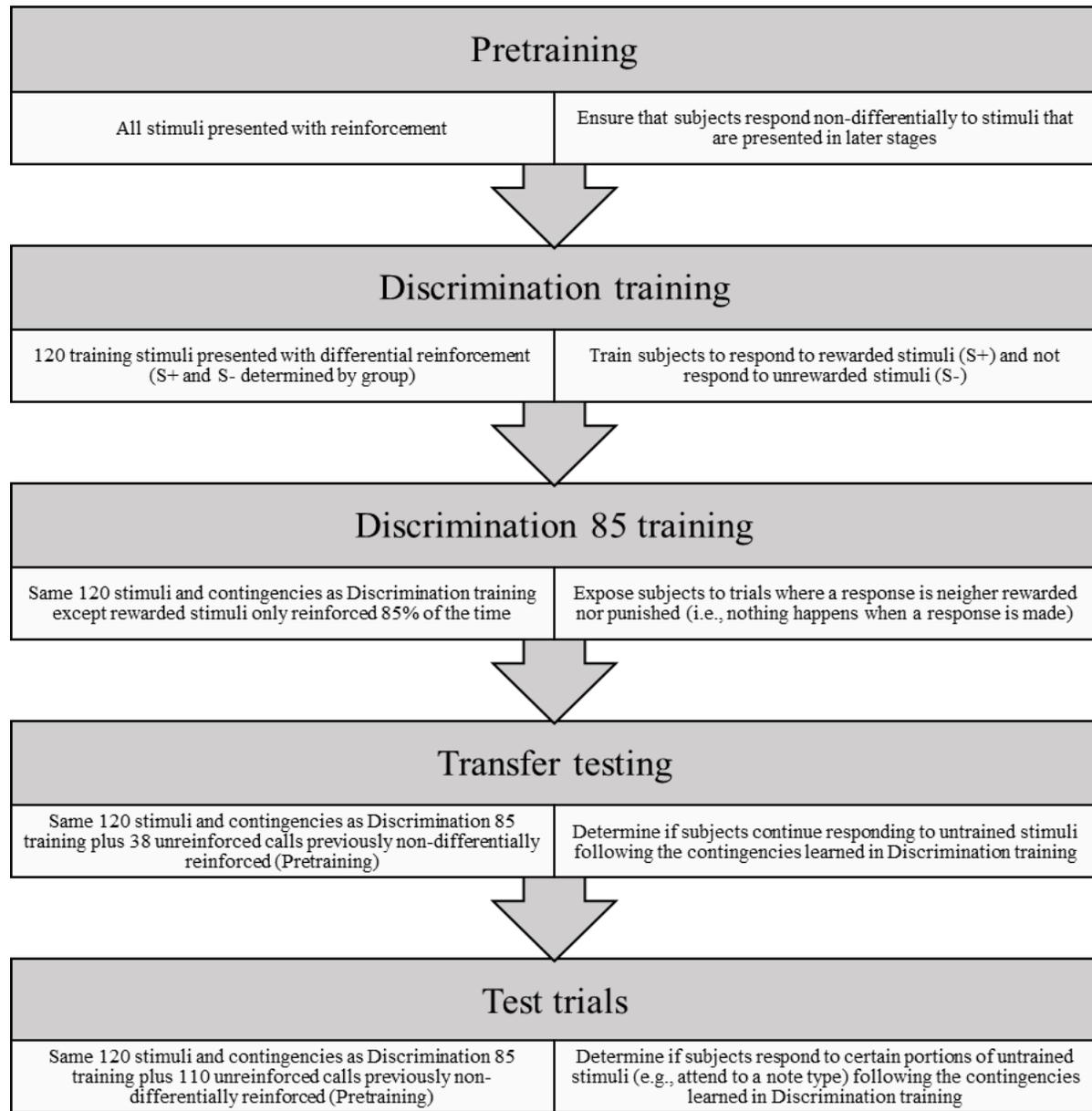
Single Note-Type Spliced Call Stimuli. To create these stimuli, a single note-type from one call was replaced with notes of the same type from another call. Care was taken to select calls that contained a similar number of the note-type that was exchanged in order to account for potential redundancy on call composition contained within call notes (see Freeburg et al., 2003). For example, replace the A notes from a call with five notes (e.g., AACDD) with A notes from a call with four to six notes of similar note structure (e.g., AADD). As with spliced call stimuli, single note-type spliced call stimuli were created from calls with all possible sex combinations (i.e., M-F, F-M, M-M, and F-F). These stimuli were created by splicing each of the three introductory note-types (A, B, and C notes) between calls from different individuals (the spliced call stimuli function as D-note splices). Due to limitations of call composition where certain note-types are produced less frequently than others (A notes are produced most often; C notes are produced least often; Campbell et al., 2016), fewer C-note splice stimuli were created than either A- or B-note splice stimuli. Overall, 12 A-note splice stimuli (5 M-F calls, 5 F-M calls, 1 M-M call, and 1 F-F call), 12 B-note splice stimuli (5 M-F calls, 5 F-M calls, 1 M-M call, and 1 F-F call), and six C-note splice stimuli were created (2 M-F calls, 2 F-M calls, 1 M-M call, and 1 F-F call). These 30 stimuli were then prepared in the same manner as the natural call stimuli. These manipulations were included for reasons similar to the spliced call stimuli, except these single note-type splices allow us to evaluate if subjects attend to any one note type (A, B, or C), rather than the initial “*chick-a*” portion and/or the terminal “*-dee*” portion, to perform the discrimination.

Procedure

The stages of the procedure are outlined in Figure 2.

Figure 2

Flowchart Outlining the Stages of the Experimental Procedure



Note. The name of each stage is provided in gray boxes. For each stage, a description of what is occurring in the stage is provided on the left and a description of the rationale for the stage is provided on the right.

Pretraining. Following basic training (i.e., shaping) to familiarize birds with the process of obtaining food from the experimental apparatus, Pretraining began. This stage ensured that birds responded in sufficient quantity and non-differentially to stimuli that would be rewarded and unrewarded during later stages. During Pretraining, birds were exposed to all stimuli that would be presented throughout the experiment and reinforced for responding to all stimuli. Each trial began with the bird landing on the request perch, breaking the perch's infrared beam and triggering a stimulus to play. Stimuli were grouped into 536-trial bins and were presented in a random order, without replacement, until all stimuli had been heard. The bird was required to remain on the request perch for 1084-2825 ms after

initiating a trial in order to ensure the whole stimulus was heard. If the bird left the perch before the stimulus finished playing, the trial was considered interrupted and the bird received a 30-s timeout in which the houselight was off and a new trial could not be initiated. If the bird flew to the feeder within 1 s of the completion of the stimulus, the bird was rewarded with 1 s access to food followed by a 30-s intertrial interval during which the houselight was on and a new trial could not be initiated. Remaining on the perch for 1 s longer than the stimulus triggered a 60-s intertrial interval during which the houselight was on and a new trial could not be initiated. However, this interval would end if the bird left the perch. Birds continued on Pretraining until they displayed at least 60% responding for six 536-trial blocks, a less than 3% difference in responding to rewarded and unrewarded stimuli for four blocks, and a less than 3% difference in responding to categories of future testing stimuli for four blocks. During this stage, one male was removed from the study after failing to feed at a sufficiently high rate and one female was removed from the study due to equipment failure. Both birds were returned to the colony room for use in later experiments.

Discrimination Training. Birds were randomly assigned to either a True category discrimination group or a Pseudo category discrimination group. The True category discrimination group consisted of two subgroups that were rewarded for either male calls ($n = 6$; 3 males, 3 females) or female calls ($n = 6$; 3 males, 3 females). The Pseudo category discrimination group consisted of two subgroups (Pseudo 1: $n = 3$; 2 males, 1 female; Pseudo 2: $n = 3$; 1 male, 2 females) that were rewarded for responding to 60 randomly-selected calls (30 male, 30 female) and unrewarded for responding to the remaining 60 calls (30 male, 30 female).

In this stage, the method of stimulus presentation remained the same as in Pretraining, however only 120 stimuli (unmanipulated natural call stimuli from 12 males, 12 females) were presented here. Additionally, these stimuli were differentially rewarded such that half remained rewarded (S+) and the other half were reassigned to be unrewarded (S-). Responding to these unrewarded stimuli now resulted in a 30-s intertrial interval in which the houselight was off and a new trial could not be initiated. Birds' experimental group determined which stimuli were rewarded and which were unrewarded.

Birds continued with Discrimination training until they completed six 120-trial blocks with a discrimination ratio (DR) of at least 80%. The last two of these blocks needed to be consecutive. DR was calculated by dividing the mean percentage of response to all rewarded stimuli by the mean percentage of response to rewarded stimuli plus the mean percentage of response to unrewarded stimuli, then multiplying by 100. With this calculation, a DR of 50% indicates equal responding to rewarded and unrewarded stimuli, while a DR of 100% indicates responding to only the rewarded stimuli (i.e., perfect discrimination). During this stage, two males, one in the Female S+ group and the other in the Pseudo 1 group, were removed from the experiment for failing to learn the discrimination in more than double the number of trials required for the other subjects to complete this stage (91 and 110 calculations, respectively).

Discrimination 85 Training. This training stage was identical to Discrimination training except that the rewarded stimuli were now reinforced only 85% of the time. This meant that on 15% of trials, when a stimulus from the rewarded category was played, entering the feeder resulted in a 30-s intertrial interval in which the houselight remained on without access to food. The purpose of this stage was to expose birds to trials in which responses to stimuli were neither rewarded nor punished, as would be encountered in both Transfer and Probe trials. As with the Discrimination stage, birds continued on Discrimination training until they completed six 120-trial blocks with a discrimination ratio (DR) of at least 80%, where the last two of these blocks needed to be consecutive.

Transfer Testing. The stimuli and associated reward-contingencies from Discrimination 85 training were maintained in Transfer testing. Additionally, birds were exposed to 38 calls (19 male, 19 female calls provided by different individuals than those that produced the calls used in Discrimination training) that had previously been non-differentially reinforced (i.e., had been played during Pretraining), but were not heard during Discrimination training. Responding to these novel Transfer stimuli resulted in a 30-s intertrial interval in which the houselight remained on without access to food being provided, meaning that the trials were neither rewarded nor punished. These stimuli were presented once during

278-trial blocks in which the stimuli presented during Discrimination training were presented twice each. Stimuli were randomly selected for playback from the total pool of available stimuli without replacement. Birds remained on Transfer until they completed three 278-trial blocks. Following this, they returned to Discrimination 85 training until they completed two 120-trial blocks with a discrimination ratio (DR) of at least 80%, where these blocks needed to be consecutive. Transfer calls were introduced to test for the method of learning that birds employed to discriminate between the rewarded- and unrewarded-contingencies presented in Discrimination training.

Test Trials. Similar to Transfer testing, the stimuli and associated reward-contingencies from Discrimination 85 training were maintained in Test trials. Additionally, birds were exposed to 110 manipulated calls (40 partial call stimuli, 40 spliced call stimuli, and 30 single note-type spliced call stimuli provided by different individuals than those that produced the calls used in either Discrimination training or Transfer testing) that had previously been non-differentially reinforced (i.e., had been played during Pretraining) but were not heard during other stages. Responding to these novel Test stimuli resulted in a 30-s intertrial interval in which the houselight remained on without access to food being provided; these trials were neither rewarded nor punished. These Test stimuli were randomly divided into four unique 267- or 268-trial blocks. Within each block, the 27-28 Test stimuli were presented once and the Discrimination training stimuli were presented twice each. Stimuli were randomly selected for playback from the total pool of available stimuli without replacement. Birds remained on Test trials until they completed three 267- or 268-trial blocks. Between each Test trial session, birds returned to Discrimination 85 training until they completed two 120-trial blocks with a discrimination ratio (DR) of at least 80%, where these blocks needed to be consecutive.

Response Measures

In order to analyze responding to each type of stimulus, we calculated the proportion of responding by dividing the number of trials where the bird went into the feeder by the total number of trials in which the bird either went into the feeder or left the request perch after hearing the full call stimulus (i.e., all non-interrupted trials). To account for individual differences in responding to non-trained stimuli, we scaled the proportion of responding to each type of Test trial stimuli separately for each bird. The highest proportion of responding for each individual was rescaled to equal 1 and all other proportions of responding were proportionally rescaled. For example, if the highest proportion of responding was 0.5 and all others were 0.25, the values would be scaled to 1 and 0.5, respectively.

Statistical Analyses

We first evaluated whether the two True groups differed from one another in speed of acquisition. We conducted an independent-samples *t*-test on the number of 120-trial blocks individuals took to reach criterion during Discrimination training. We also compared speed of acquisition between the two Pseudo groups. To compare rate of learning between True and Pseudo groups, we conducted an independent-samples *t*-test on the number of 120-trial blocks individuals took to reach criterion during Discrimination training.

All statistics were conducted in IBM SPSS Statistics v.22 (IBM Corp., Armonk, NY, USA).

Ethical Note

Throughout the experiments, birds remained in the testing apparatus to minimize stress and discomfort caused by transport and handling. Following the experiments, birds were returned to the colony room for use in future experiments. Birds were closely monitored and remained healthy during the experiment. All procedures were conducted in accordance with the Canadian Council on Animal Care (CCAC) Guidelines and Policies with approval from the Animal Care and Use Committee for Biosciences for the University of Alberta (AUP 107 and 108), which is consistent with the Animal Care

Committee Guidelines for the Use of Animals in Research. Birds were captured and research was conducted under an Environment Canada Canadian Wildlife Service Scientific permit (#13-AB-SC004), Alberta Fish and Wildlife Capture and Research permits (#56076 and #56077), and City of Edmonton Parks Permit.

Results

Trials to Criterion

The average \pm SD number of trial blocks required for each group to complete Discrimination training are as follows: Male S+ group = 29.17 ± 8.98 ; Female S+ group = 24.50 ± 5.68 ; Pseudo group 1 = 22.00 ± 7.07 ; and Pseudo group 2 = 39.00 ± 23.90 . Independent-samples *t*-tests on the number of 120-trial blocks individuals took to reach criterion during Discrimination training revealed no significant difference between either the two True category groups (i.e., Male S+ and Female S+ groups; $t(10) = 1.076$, $p = .307$, 95% CI [-5.00, 14.33]) or the two Pseudo category groups ($t(3) = -0.934$, $p = .419$, 95% CI [-74.90, 40.91]). There was also no difference between the True and Pseudo category groups ($t(15) = -0.839$, $p = .415$, 95% CI [-19.01, 8.28]).

Transfer Testing

To determine if individuals in the true category groups continued to respond to the reward-contingencies learned in Discrimination training when presented with novel stimuli in Transfer testing, we conducted a Subject Sex \times Group \times Stimulus Type mixed model ANOVA on the scaled proportion of responding during the first three 278-trial blocks of Transfer testing with Stimulus Type (e.g., Discrimination male calls, Discrimination female calls, Transfer male calls, Transfer female calls) as a within-subjects factor, category group (e.g., Male S+ group, Female S+ group) and subject sex as between-subjects factors. There was a significant main effect of Stimulus Type ($F(3, 24) = 4.330$, $p = .014$, $\pi^2 = 0.117$) and a significant Stimulus Type \times Group interaction ($F(3, 24) = 32.070$, $p < .001$, $\pi^2 = 0.495$). All other main effects and interactions were not significant (all $ps > .296$).

We conducted post hoc comparisons using Bonferroni corrections to determine the nature of the significant interactions. For the main effect of Stimulus Type, there was no significant pairwise comparison (all p values $> .189$). We conducted pairwise comparisons on the proportion of responding to each stimulus type for each True group separately. For the Male S+ group, birds responded significantly more to rewarded male-produced calls than to unrewarded female-produced calls (adjusted $p < .001$, 95% CI [-0.785, -0.470]). Birds in the Female S+ group also responded more to rewarded calls than unrewarded calls (adjusted $p = .004$, 95% CI [0.237, 0.868]), and also responded significantly more to Transfer female calls than to unrewarded Discrimination male calls (adjusted $p = .023$, 95% CI [-0.909, -0.086]). All other pairwise comparisons were not significant (adjusted $ps > .051$). Four independent-samples *t*-tests were conducted to compare the proportion of responding to each Stimulus Type (e.g., Discrimination male calls, Discrimination female calls, Transfer male calls, Transfer female calls) between the two True groups (e.g., Male S+ group, Female S+ group). The adjusted p -value for significance here and all subsequent four *t*-test comparisons became $p = .05/4 = .013$ with Bonferroni corrections for four comparisons. There was a significant difference in responding between groups such that birds rewarded for responding to male stimuli (e.g., Male S+ group) responded more to male stimuli than did birds that were rewarded for responding to female stimuli ($t(10) = -4.984$, $p = .001$, 95% CI [-0.795, -0.304]) and birds rewarded for responding to female stimuli (e.g., Female S+ group) responded more to female stimuli than did birds that were rewarded for responding to male stimuli ($t(10) = 10.071$, $p < .001$, 95% CI [0.491, 0.770]). All other between-group comparisons were not significant (all $ps > .690$).

Test Trials

To determine if individuals in the true category groups responded to the novel stimuli presented in Test trials, we conducted six Subject Sex \times Group \times Stimulus Type mixed model ANOVAs; one for each type of Test stimulus, on scaled proportion of responding during the first three 267-trial or 268-trial blocks of Transfer testing with Stimulus Type (e.g., Discrimination male calls, Discrimination female calls, Probe M-M calls, F-F calls, M-F calls, and F-M calls) as a within-subjects factor, category group (e.g., Male S+ group, Female S+ group) and subject sex as between-subjects factors.

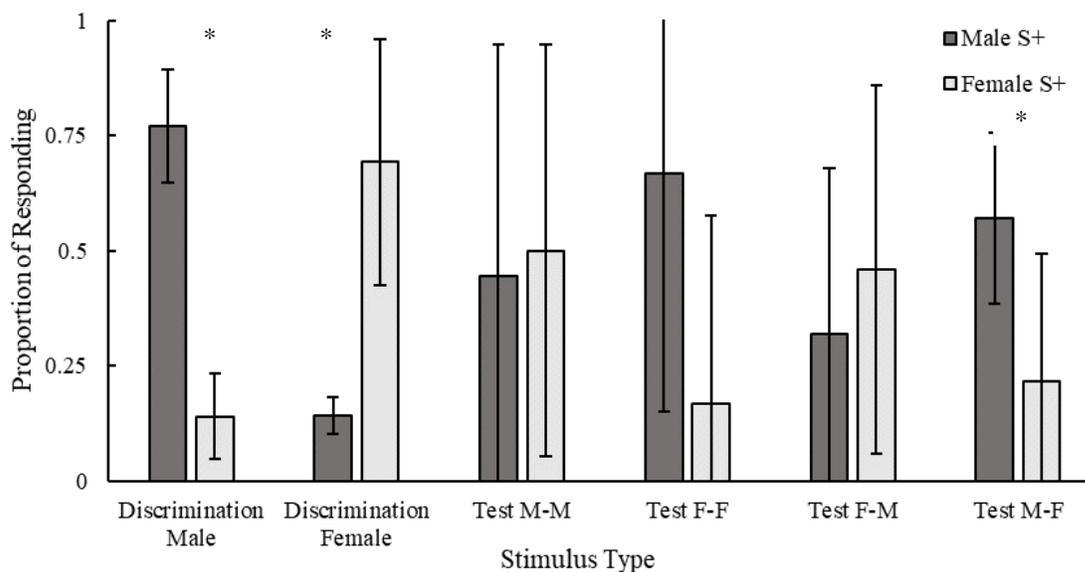
Partial Call Stimuli. Two Subject Sex \times Group \times Stimulus Type mixed model ANOVAs were conducted, one on scaled proportion of responding to *chick-a* stimuli and one on scaled proportion of responding to *-dee* stimuli. In both cases, there was a significant Stimulus Type \times Group interaction (*chick-a*: $F(3, 24) = 27.519$, $p < .001$, $\pi^2 = 0.526$; *-dee*: $F(1.42, 11.35) = 20.998$, $p < .001$, $\pi^2 = 0.447$). Greenhouse–Geisser correction was used whenever assumptions of sphericity were violated. In addition to the same difference between rewarded and unrewarded Discrimination stimuli reported for the Transfer testing results (as the same proportion of responding to Discrimination stimuli is compared to all Transfer and Test trial responses), there was a significant difference in responding such that birds in the Female S+ group responded more to Discrimination female stimuli than to Partial call male “*chick-a*” stimuli (adjusted $p = .028$, 95% CI [0.060, 0.878]). All other pairwise comparisons were not significant (adjusted $ps > .057$). Two independent-samples t -tests were conducted for each type of Partial call stimulus to compare the proportion of responding to male- and female-produced stimuli (e.g., “*chick-a*” male stimuli, “*chick-a*” female stimuli, “*-dee*” male stimuli, “*-dee*” female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). The adjusted p -value for significance here and all subsequent two t -test comparisons became $p = .05/2 = .026$ with Bonferroni corrections. None of these tests were significant ($ps > .131$).

Spliced Call Stimuli. A Subject Sex \times Group \times Stimulus Type mixed model ANOVA was conducted on scaled proportion of responding to spliced call stimuli. There was a significant Stimulus Type \times Group interaction ($F(1.87, 14.94) = 20.550$, $p < .001$, $\pi^2 = 0.384$). For the Stimulus Type \times Group interaction, there was a significant difference in responding such that birds in the Male S+ group responded more to Discrimination male stimuli than to Spliced call M-M stimuli (adjusted $p = .044$, CI [0.010, 0.681]) and birds in the Female S+ group responded more to Discrimination female stimuli than to Call splice F-M stimuli (adjusted $p = .010$, 95% CI [0.138, 0.786]). All other pairwise comparisons were not significant (adjusted $ps > .060$). Four independent-samples t -tests were conducted for each type of Spliced call stimulus to compare the proportion of responding to male- and female-produced stimuli (e.g., M-M stimuli, F-F stimuli, F-M male stimuli, M-F female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). None of these tests were significant (all $ps > .188$).

Single Note-type Spliced Call Stimuli. Three Subject Sex \times Group \times Stimulus Type mixed model ANOVAs were conducted, one on scaled proportion of responding to each type of single note-type spliced call stimuli (e.g., A note spliced calls, B note spliced calls, and C note spliced calls). There was a significant Stimulus Type \times Group interaction (A note: $F(2.35, 18.83) = 8.280$, $p = .002$, $\pi^2 = 0.278$; B note: $F(2.33, 18.62) = 8.642$, $p = .002$, $\pi^2 = 0.313$; C note: $F(2.07, 16.55) = 6.764$, $p = .007$, $\pi^2 = 0.321$). For the pairwise comparisons for both A note and B note spliced call stimuli, there was a significant difference in responding where birds in the Female S+ group responded more to Discrimination female stimuli than to the single note-type call splice F-M stimuli (A note: adjusted $p = .013$, 95% CI [0.132, 0.909]; B note: adjusted $p = .020$, 95% CI [0.089, 0.885]). For the pairwise comparisons for C note spliced call stimuli, birds in the Male S+ group responded significantly more to single note-type call splice M-F stimuli than to the Discrimination female stimuli (adjusted $p = .017$, 95% CI [-0.762, -0.090]; see Figure 3). All other pairwise comparisons were not significant (adjusted $ps > .060$). Four independent-samples t -tests were conducted for each type of Single note-type spliced call stimulus (e.g., A note, B note, and C note spliced) to compare the proportion of responding to male- and female-produced stimuli (e.g., M-M stimuli, F-F stimuli, F-M male stimuli, M-F female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). None of these tests were significant ($ps > .027$).

Figure 3

Mean \pm SE Scaled Proportion of Responding to C Note Splice Call Stimuli for True Groups (e.g., Male S+ and Female S+) in Experiment 1



*Indicates a significant difference in responding between the two groups ($p < .05$)

Rationale for Experiment 2

From the results of Experiment 1, we found that birds can discriminate between male- and female-produced *chick-a-dee* calls. However, they did not respond to new calls in the Transfer stage using the same contingencies as they learned in Discrimination training, suggesting that they simply memorized individual stimuli during training. Previous research on sex differences in *chick-a-dee* calls of black-capped chickadees (Campbell et al., 2016) and Carolina chickadees (Freeberg et al., 2003) found differences in the preliminary, “*chick-a*” portion of the call (e.g., the portion made of A, B, and C notes). The terminal “*-dee*” portion of the call (e.g., the D notes) is known to change based on individual flock identity (Mammen & Nowicki, 1981; Nowicki, 1989) and the presence of predators (Hurd, 1996). With this flexibility, it could be argued that the “*-dee*” portion of *chick-a-dee* calls may be unreliable for identifying a stable trait like individual sex, and this portion may serve as a distractor from any potential information contained within the “*chick-a*” portion. With this in mind, and knowing that “*chick-a*” only calls are commonly produced in nature (Smith, 1991), we designed Experiment 2 to investigate how removing the “*-dee*” portion of *chick-a-dee* calls affects the perception of sex differences by black-capped chickadees.

Experiment 2

Method

The methods for Experiment 2 were identical to those of Experiment 1 except for the modifications noted below.

Subjects

Eighteen wild-caught black-capped chickadees (9 males, 9 females) captured between January 14, 2014 and January 30, 2016 participated in Experiment 2. Birds were captured in Edmonton (North Saskatchewan River Valley, 53.53°N, 113.53°W; Mill Creek Ravine, 53.52°N, 113.47°W), Alberta, Canada and were aged as older than one year at time of capture using the shape and color of outer tail retrices (Pyle, 1997). Sex was determined using DNA analysis (Griffiths et al., 1998). Eight birds had previous experience with the operant discrimination paradigm, discriminating biological stimuli (*chick-a-dee* calls: Scully et al., 2020; *chick-a-dee* and owl calls: Congdon, et al., 2020), but none had experience with the calls used in the current experiment. Previous experience was balanced across groups.

Acoustic Stimuli

Experiment 2 used the same acoustic stimuli as Experiment 1; however, the vocalizations were modified as follows: Natural call stimuli were truncated, removing the *-dee* portion of all calls. For the manipulated call stimuli, partial call stimuli were not modified; however, both spliced call and single note spliced call stimuli were also shortened to remove the *-dee* portion of the calls using SIGNAL 5.06.07 (Engineering Design, Berkeley, CA, U.S.A.) before being tapered and equalized as for Experiment 1.

Results

Trials to Criterion

The average \pm SD number of trial blocks required for each group to complete Discrimination training are as follows: Male S+ group = 65.67 ± 26.99 ; Female S+ group = 62.00 ± 22.36 ; Pseudo group 1 = 75.00 ± 33.15 ; and Pseudo group 2 = 60.00 ± 26.51 . Independent-samples *t*-tests on the number of 120-trial blocks individuals took to reach criterion during Discrimination training revealed no significant difference between either the two true category groups (i.e., Male S+ and Female S+ groups; $t_{10} = 0.256$, $p = .803$, 95% CI = -28.21, 35.55) or the two Pseudo category groups ($t_4 = 0.612$, $p = .574$, 95% CI = -53.05, 83.05). There was also no difference between the True and Pseudo category groups ($t_{16} = -0.292$, $p = .774$, 95% CI = -30.33, 22.99).

Transfer Testing

We conducted a Subject Sex \times Group \times Stimulus Type mixed model ANOVA in the same manner as in Experiment 1. There was a significant Stimulus Type \times Group interaction ($F_{3,24} = 23.362$, $p < .001$, $\pi^2 = 0.581$). All other main effects and interactions were not significant ($ps > .103$).

As in Experiment 1, we conducted pairwise comparisons on the proportion of responding to each stimulus type for each True group separately. For the Male S+ group, birds responded significantly more to rewarded male-produced calls than to unrewarded female-produced calls (adjusted $p = .004$, 95% CI = -0.744, -0.210). Birds in the Female S+ group also responded more to rewarded calls than unrewarded calls (adjusted $p = .008$, 95% CI = 0.164, 0.761), and also responded significantly more to both Transfer male calls and Transfer female calls than to unrewarded Discrimination male calls (male: adjusted $p = .012$, 95% CI = -0.626, -0.106; female: adjusted $p = .011$, 95% CI = -0.987, -0.171). All other pairwise comparisons were not significant (adjusted $ps > .059$). Four independent-samples *t*-tests were conducted to compare the proportion of responding to each Stimulus Type (e.g., Discrimination male calls, Discrimination female calls, Transfer male calls, Transfer female calls) between the two True groups (e.g., Male S+ group, Female S+ group). There was a significant difference in responding between groups such that birds in the Male S+ group responded more to Discrimination male stimuli than did birds in the Female S+ group ($t_{10} = -5.087$, $p < 0.001$, 95% CI = 0.283, 0.725), birds in the Female S+ group responded more to Discrimination female stimuli than did birds in the Male S+ group ($t_{10} = -4.438$, $p =$

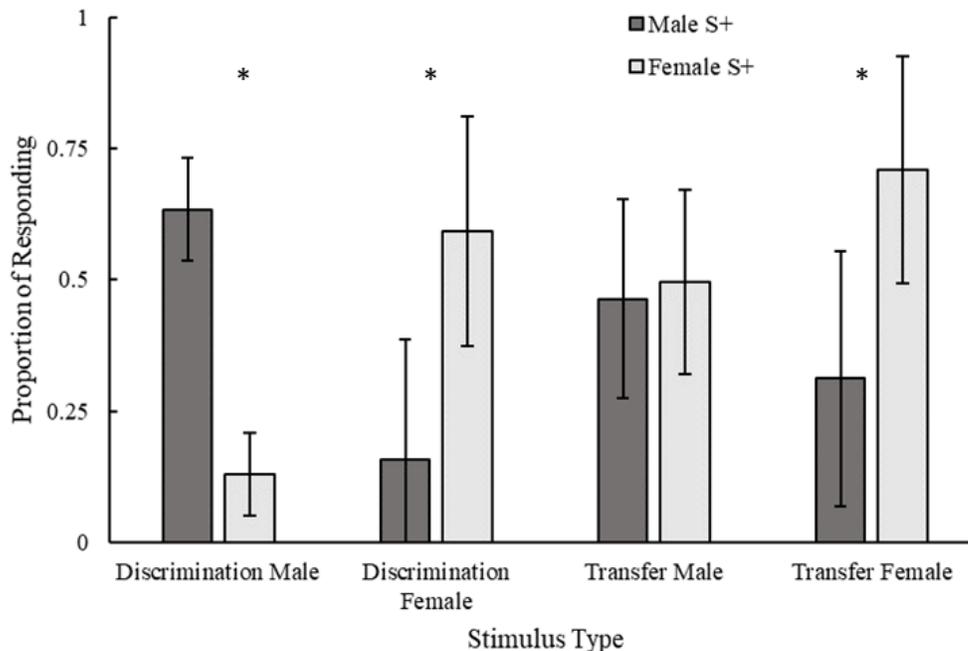
.001, 95% CI = -0.653, -0.217), and birds in the Female S+ group responded more to Transfer female stimuli than birds in the Male S+ group did ($t_{10} = -3.388$, $p = .007$, 95% CI = -0.659, -0.136). All other between-group comparisons were not significant ($ps > .793$; see Figure 4).

Test trials

Partial Call Stimuli. Two Subject Sex \times Group \times Stimulus Type mixed model ANOVAs were conducted, one on scaled proportion of responding to *chick-a* stimuli and one on scaled proportion of responding to *-dee* stimuli. In both cases, there was a significant main effect of Stimulus type (*chick-a*: $F_{3,24} = 5.723$, $p = .004$, $\pi^2 = 0.247$; *-dee*: $F_{1,52,12.19} = 5.167$, $p = 0.030$, $\pi^2 = 0.267$); however, there was no significant pairwise comparison (*chick-a*: $p > 0.056$; *-dee*: $p > 0.146$). There was also a significant Stimulus Type \times Group interaction for both “*chick-a*” and “*-dee*” Partial call stimuli (*chick-a*: $F_{3,24} = 26.250$, $p < .001$, $\pi^2 = 0.602$; *-dee*: $F_{1,42,11.35} = 20.998$, $p < .001$, $\pi^2 = 0.580$). There was a significant difference in responding such that birds in the Male S+ group responded more to Discrimination male stimuli than to either Partial call male or Partial call female “*chick-a*” stimuli (male: adjusted $p = .034$, 95% CI = 0.042, 0.865; female: adjusted $p = .032$, 95% CI = 0.043, 0.803). Birds in the Male S+ group also responded more to Discrimination male stimuli than to either Partial call male or Partial call female “*-dee*” stimuli (male: adjusted $p = .013$, 95% CI = 0.166, 1.035; female: adjusted $p = .030$, 95% CI = 0.064, 1.076). All other pairwise comparisons were not significant (adjusted $ps > .066$). Two independent-samples t -tests were conducted for each type of Partial call stimulus to compare the proportion of responding to male- and female-produced stimuli (e.g., “*chick-a*” male stimuli, “*chick-a*” female stimuli, “*-dee*” male stimuli, “*-dee*” female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). None of these tests were significant ($ps > .037$).

Figure 4

Mean \pm SE Proportion of Responding to Stimuli During the Transfer Testing Stage for True Groups (e.g., Male S+ and Female S+) in Experiment 2



* Indicates a significant difference in responding between the two groups ($p < .05$)

Spliced Call Stimuli. A Subject Sex \times Group \times Stimulus Type mixed model ANOVA was conducted on scaled proportion of responding to spliced call stimuli. There was a significant Stimulus Type \times Group interaction ($F_{1,87,14.94} = 20.550$, $p < .001$, $\pi^2 = 0.526$). For the Stimulus Type \times Group interaction, there was a significant difference in responding such that birds in the Male S+ group responded more to Discrimination male stimuli than to Spliced call M-M stimuli (adjusted $p = .044$, CI = 0.012, 0.856), Spliced call F-F stimuli (adjusted $p = .044$, CI = -0.966, -0.013), and Spliced call M-F stimuli (adjusted $p = .039$, 95% CI = 0.026, 0.893). All other pairwise comparisons were not significant (adjusted $ps > .184$). Four independent-samples t -tests were conducted for each type of Spliced call stimulus to compare the proportion of responding to male- and female-produced stimuli (e.g., M-M stimuli, F-F stimuli, F-M male stimuli, M-F female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). None of these tests were significant ($ps > .191$).

Single Note-type Spliced Call Stimuli. Three Subject Sex \times Group \times Stimulus Type mixed model ANOVAs were conducted, one on scaled proportion of responding to each type of single note-type spliced call stimuli (e.g., A note spliced calls, B note spliced calls, and C note spliced calls). There was a significant Stimulus Type \times Group interaction (A note: $F_{5,40} = 5.474$, $p = .001$, $\pi^2 = 0.261$; B note: $F_{1,49,11.93} = 8.642$, $p = .046$, effect size = 0.311; C note: $F_{5,40} = 8.250$, $p < .001$, $\pi^2 = 0.444$). For the pairwise comparisons for B note spliced call stimuli, there was a significant difference in responding where birds in the Male S+ group responded more to Discrimination male stimuli than to the single note-type call splice M-F stimuli (adjusted $p = .003$, CI = 0.218, 0.705). For the pairwise comparisons for C note spliced call stimuli, birds in the Male S+ group responded significantly more to Discrimination male stimuli than to single note-type call splice M-M stimuli (adjusted $p = .016$, CI = 0.142, 1.126) and birds in the Female S+ group responded significantly more to Discrimination female stimuli than to single note-type call splice F-F stimuli (adjusted $p = .033$, CI = 0.050, 1.023). All other pairwise comparisons were not significant (adjusted $ps > .132$). Four independent-samples t -tests were conducted for each type of Single note-type spliced call stimulus (e.g., A note, B note, and C note spliced) to compare the proportion of responding to male- and female-produced stimuli (e.g., M-M stimuli, F-F stimuli, F-M male stimuli, M-F female stimuli) between the two True groups (e.g., Male S+ group, Female S+ group). None of these tests were significant ($ps > .019$).

General Discussion

Natural Call Stimuli

We evaluated the ability of black-capped chickadees to perceive sex differences in their *chick-a-dee* calls. We also compared responding to full *chick-a-dee* calls to truncated *chick-a* calls in order to determine if the *-dee* portion of the calls influences how birds perceive the sex of a caller. We found that, for birds hearing either full calls or shortened calls, training with stimuli forming a True category (based on sex of the caller) provided no benefit in speed of acquisition over training using a Pseudo category. This suggests that there may not be an advantage in using categorization by sex (i.e., True category group) instead of rote memorization (i.e., pseudo category group) in this particular task.

We tested responding to novel male- and female-produced *chick-a-dee* and *chick-a* calls to determine if birds had in fact learned a category, rather than simply memorizing the trained vocalizations. In Experiment 1, birds did not respond to new *chick-a-dee* calls following the reward contingencies introduced in Discrimination training. This suggests that birds did not learn to categorize calls based on the sex of the caller. Even though the birds in Experiment 2 that were rewarded for responding to female-produced *chick-a* calls in Discrimination training (e.g., female S+ group) responded significantly more to novel female-produced *chick-a* calls (e.g., Transfer stimuli) than birds rewarded for responding to male stimuli (e.g., male S+ group), they also responded more to all Transfer stimuli than they did to unrewarded male Discrimination *chick-a* calls, suggesting that birds may simply have been responding to Transfer stimuli nondifferentially (i.e., at chance levels).

Manipulated Call Stimuli

Test trial stimuli were presented to evaluate whether exchanging certain portions of the *chick-a-dee* call would influence how birds perceived that call. We asked, for example whether birds in the female S+ group could be made to respond to a male-produced call by exchanging the male-produced A notes with female-produced A notes. In Experiment 1, we found that birds in the male S+ group responded significantly more to M-F C note spliced stimuli than to unrewarded female-produced Discrimination stimuli. However, since there was no evidence of category learning in this group, this result may simply be due to birds responding non-differentially to this type of test stimulus. Supporting this idea, the remainder of significant differences observed for Test trials in both experiments revealed that birds responded more to their rewarded Discrimination stimuli than to Test stimuli. This difference in responding indicated that they perceive the Test stimuli as different from the trained Discrimination stimuli.

We conducted Experiment 2 after seeing no evidence of category learning with full *chick-a-dee* calls in Experiment 1. Previous bioacoustic analyses of sex differences in both black-capped chickadees and Carolina chickadees identified sex differences in acoustic features of A notes, which occur in the “*chick-a*” portion of calls (Campbell et al., 2016; Freeberg et al., 2003). Additionally, the terminal “-*dee*” portion of the call changes with individual flock identity (Mammen & Nowicki, 1981; Nowicki, 1989) and the presence of predators (Hurd, 1996), which could indicate that the “-*dee*” portion of *chick-a-dee* calls would be unreliable for identifying an invariable quality, such as individual sex. As such, we expected the removal of the “-*dee*” portion of the call to facilitate category learning as the D notes might not contain information related to sex. The difference in Transfer testing results between Experiment 1 where there were no significant interactions involving Transfer stimuli and Experiment 2 where birds in the True groups responded differently to Transfer female calls support this prediction. However, given that the birds in the female S+ group responded more to both types of Transfer stimuli than to unrewarded stimuli, this evidence is not strong. When investigating perception of sex differences in the black-capped chickadee *fee-bee* song, solid evidence of category learning was observed when employing a much smaller training stimulus set (30 male, 30 female song stimuli used by Hahn et al., 2015, versus 60 male, 60 female call stimuli employed here). As such, we suggest that knowing sex of a signaler may be more biologically relevant for reproductive-critical vocalizations like *fee-bee* song, but it may be less critical for *chick-a-dee* calls, which are used for situations outside of reproduction (Smith, 1991). If this is the case, birds would be unlikely to learn “male-produced” or “female-produced” as perceptual categories in this operant discrimination paradigm.

Conclusions

Overall, our results provide evidence that black-capped chickadees can learn to discriminate between male- and female-produced full *chick-a-dee* calls as well as shortened *chick-a* calls, but are unlikely to rely on category learning to do so. Considering that chickadees attend to sex differences in their *fee-bee* song but do not appear to do the same with their *chick-a-dee* calls, the biological relevance of the vocalization and the conditions within which it is employed may play a role in whether or not a vocalization differs between the sexes. *Chick-a-dee* calls differ acoustically between individuals, which would allow for a receiver to identify familiar signalers (Charrier et al., 2004). Since *chick-a-dee* calls function to indicate the presence of food (Smith, 1991), to coordinate mobbing behavior against predators (Hurd, 1996), and to maintain flock cohesion (Nowicki, 1983), it is possible that knowing the identity of an individual is sufficient and knowing the sex of the signaler independently provides no benefit. Future studies should be conducted to investigate black-capped chickadees' perception of sex differences in other chickadee vocalizations such as *tseet* or *gargle* calls, which serve different biological functions (Smith, 1991) to determine if function may be related to the presence or absence of sex differences in the vocalizations.

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