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Discrimination of male black-capped chickadee songs: Relationship between acoustic preference and performance accuracy

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Many species form social groups with dominance hierarchies. Often, individuals possess a status signal that indicates dominance rank. Songbirds produce songs that are used to attract mates or repel rivals and acoustic features within songs can also indicate an individual's quality, including dominance rank. Acoustic status signals have been reported in the songs of male black-capped chickadees (*Poecile atricapillus*), a non-migratory North American songbird. Here we used two operant conditioning tasks to examine acoustic preference for and discrimination of conspecific songs produced by males varying in dominance rank. We used a choice preference task to examine birds' preferences for listening to dominant or subordinate songs and conducted an instrumental learning task to determine if chickadees considered dominant and subordinate songs as belonging to separate signal categories based on acoustic features. Overall, our results provide little evidence that birds used open-ended categorization when discriminating, but there is evidence that songs from different geographic regions may contain acoustic similarity based on dominance rank. Consistent with previous song discrimination studies with black-capped chickadees, we found sex differences in discrimination abilities, with females learning the discrimination faster than males. We also found evidence that performance accuracy during the instrumental learning task correlates with acoustic song preference. Overall, these results suggest that when biologically relevant signals (e.g., male songs) are used as stimuli during a perceptual task, the birds' responses may be differentially affected based on individual differences among the subjects performing the task (including sex and underlying preference) and the salience associated with the stimuli (e.g., dominance rank of the singer).

Keywords: acoustic discrimination, black-capped chickadee, individual differences, operant conditioning, preference, song

Introduction

Dominance ranks were first described by Schjelderup-Ebbe (1922/1975) studying the hierarchical social structure of group-living domestic chickens (*Gallus gallus*). However, dominance ranks and social group interactions have been examined in numerous species (Allee, 1942/1975; Dewsbury, 1982). Dominance ranks are often established through quantifying behavioural dyadic interactions, with these interactions usually occurring during disputes focused around access to resources. Although dominance is a relative trait (i.e., an individual may be dominant over another individual, while also being subordinate to a third individual; Drews, 1993), within social groups with consistent membership over time, dominance hierarchies are usually stable (Wiley, Steadman, Chadwick, & Wollerman, 1999). When the social hierarchy is stable, individuals do not need to engage in constant confrontations to assert their dominance over other individuals. In the case of chickens, for example, the dominant individual does not need to continue to act aggressively toward lower-ranking individuals once the dominance hierarchy is established (Schjelderup-Ebbe, 1922/1975). Instead, once the dominance rank is established, few confrontations occur, and time and energy can be spent on other activities that are necessary for survival (e.g., foraging).

Although familiarity with opponents can facilitate rank stability (Archawaranon, Dove, & Wiley, 1991; Wiley et al., 1999), the formation and maintenance of dominance hierarchies does not imply individual recognition is necessary. Instead, individuals may possess a status signal that allows others to characterize that individual's dominance rank in the absence of individual recognition. If there is a status signal that varies with dominance rank, animals that live in large social groups could make rank discriminations without repeated confrontations with another individual (Cummins, 1996).

A status signal may be a visual trait that indicates dominance status (e.g., antler size in woodland caribou, *Rangifer tarandus caribou*, Barrette & Vandal, 1986; badge size in house sparrows, *Passer domesticus*, Møller, 1987; plumage coloration in black-capped chickadees, *Poecile atricapillus*, Mennill, Doucet, Montgomerie, & Ratcliffe, 2003), or an acoustic feature in an auditory signal (e.g., spotted hyena, *Crocuta crocuta*, Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010; rock hyrax, *Procavia capensis*, Koren & Geffen, 2009; fallow deer, *Dama dama*, Vannoni & McElligott, 2008). A behavioural trait can also indicate status, such as dominant individuals vocalizing more frequently compared to subordinates (domestic chicken, Leonard & Horn, 1995; black-capped chickadee, Otter, Chruszcz, & Ratcliffe, 1997).

If a signal indicates an individual's dominance status, how that signal is perceived will depend on who is receiving the signal. Traits that indicate an individual's fighting ability or quality, such as birdsong, can act as a signal of territoriality when directed at other males, or as a signal of mate quality when directed at females. Further, male birdsong often contains additional information regarding the individual that is signaling and, for species that live in social groups with dominance hierarchies, songs can contain information regarding a male's dominance status. In some species, such as brown-headed cowbirds (*Molothrus ater*), song is essential for the establishment of dominance relationships (Dufty, 1986); while subordinate brown-headed cowbird males are capable of singing the song preferred by females, only the dominant male sings these preferred songs (West, King, & Eastzer, 1981). If information regarding a male's dominance rank means something different for a listening female compared to a listening male, how the sexes respond to the signal should also vary. In addition, the type of signal produced by an individual may also vary depending on what audience is present (Dalziell & Cockburn, 2008).

Black-capped chickadees are common North American songbirds that live in winter flocks where social interactions are influenced by stable linear dominance hierarchies. Within a flock, males will usually dominate females, and once the winter flocks break up, birds mate assortatively - i.e. the highest-ranked male mates with the highest-ranked female, and vice versa for the lower-ranked pairs (Smith, 1991). The dominant male in the winter flock has preferential access to food resources (Smith, 1991). Once flock break-up occurs, dominant males more easily obtain a territory during the breeding season (Desrochers, Hannon, & Nordin, 1988) and obtain larger territories with more resources (Mennill, Ramsay, Boag, & Ratcliffe, 2004). Dominant males have higher lifetime reproductive success (Schubert et al., 2007) in part because they are preferred by females seeking extra-pair copulations (Mennill et al., 2004; Otter, Ratcliffe, Michaud, & Boag, 1998; Smith, 1988).

Black-capped chickadees produce two-note *fee-bee* songs. The song's first note (*fee* note) is produced at a higher frequency compared to the second note (*bee* note) and the frequency relationship between the two notes remains relatively consistent across song renditions (Horn, Leonard, Ratcliffe, Shackleton, & Weisman, 1992; Weisman, Ratcliffe, Johnsrude, & Hurly, 1990). Males (Mennill & Ratcliffe, 2004) and females (Mennill, Ratcliffe, & Boag, 2002) eavesdrop on male song contests and male dominance cues are contained within the songs (Christie, Mennill, & Ratcliffe, 2004; Hahn et al., 2013, Hoeschele et al., 2010). As males sing, they will shift the absolute frequency of their songs (Ratcliffe & Weisman, 1985; Hill & Lein, 1987); however, dominant males are more likely to maintain a consistent frequency relationship between the two notes compared to subordinate males (Christie et al., 2004). Dominant males also produce songs in which the relative amplitude between the two song notes is more consistent compared to the songs produced by subordinate males (Hoeschele et al., 2010).

Dominance-related acoustic cues in black-capped chickadee songs also vary between geographic regions. Specifically, the relative amplitude between the two song notes is a signal of dominance status in the songs produced by birds in northern British Columbia, but the relative amplitude between the two notes does not vary with dominance status for birds in eastern Ontario (Hahn et al., 2013). Since dominance-related cues in black-capped chickadee songs vary with geographic location, it allows us to test how birds from distant locations respond to songs produced by unfamiliar males from different geographic locations. For example, Hoeschele et al. (2010) found that females from one geographic location (i.e., central Alberta) responded differentially to dominance-related variation in songs produced by males that were the highest ranked within a flock compared to males that were the lowed rankest within a flock. In that study, the songs were produced by males from a distant geographic location (i.e., northern British Columbia), suggesting that females perceive acoustic variation relative to dominance in the songs, despite using stimuli not produced by males from the subject's own population.

Subsequent bioacoustic analyses and playback studies of songs produced by dominant and subordinate males have confirmed that male chickadee songs contain dominance cues (e.g., consistency of the relative amplitude between the two song notes, Hoeschele et al., 2010). This raises the possibility that receivers might use open-ended categorization to assess dominance rank without previous experience with the singing individual. With open-ended categorization individuals classify signals by means of perceptual similarity (Herrnstein, 1990). For example, if dominant individuals produce status signals with similar features, animals could identify a dominant individual by learning a general 'category' rule based on those similarities. If an individual's signal contains those features, the individual is considered to belong to that category (in this example the individual is classified as 'dominant'). If perceptual categories for a status

signal do not exist, open-ended categorization is not possible; however, animals could still discriminate using rote memorization. In contrast to open-ended categorization, rote memorization requires an individual to have prior experience with and memorize each signal (e.g., for an acoustic status signal, an individual would need to have prior experience with the vocalizing individual, evaluate the individual's dominance rank, and recognize the individual's vocalization). Open-ended categorization of dominance signals may be a more useful cognitive mechanism, and therefore selected for, compared to rote memorization, because open-ended categorization does not require an animal to recognize and remember each individual and their social status, which increases cognitive load as the number of individuals within the social group increases. Further, this could allow classifications of individuals from neighbouring social groups, with whom a receiver may have had more limited social interactions – a phenomenon common when chickadees interact with or settle near members of other wintering flocks.

In addition to the ability to categorize songs based on acoustic dominance cues, birds may also have a preference for listening to dominant or subordinate songs. Preference tests using conspecific song as the reinforcer have demonstrated in other songbird species that females prefer certain characteristics in male song (e.g., song complexity, chaffinch, *Fringilla coelebs*, Leitão, ten Cate, & Riebel, 2006; song bout length, European starling, *Sturnus vulgaris*, Gentner & Hulse, 2000).

In the current study, we used a series of operant conditioning tasks to examine (1) chickadees' preference for dominant or subordinate songs, (2) the abilities of chickadees to discriminate songs based on the singer's dominance rank in the absence of other dominance cues, and (3) how acoustic preference relates to discrimination performance. First, we used a choice preference task (similar to Gentner & Hulse, 2000) to examine chickadees' preference for

dominant or subordinate songs from two separate populations. Next, we used a go/no-go instrumental learning task (see Sturdy & Weisman, 2006) using a true category/pseudo category paradigm. The objective for the instrumental learning task was to examine if songs belong to acoustic categories that birds could discriminate based on the singer's dominance rank. Following the initial learning phase we presented birds with novel songs recorded in geographic regions that were different than the songs the birds were trained with, to examine how birds would categorize songs produced by dominant and subordinate males from other locations. Dominance cues in songs differ between populations (Hahn et al., 2013), so the rationale for presenting birds with songs from another geographic region was to test how animals would respond to completely unfamiliar songs from a different geographic region. Additionally we presented birds with songs in which we artificially manipulated an acoustic feature (i.e., relative amplitude of notes) that varies between dominant and subordinate songs (Hahn et al., 2013; Hoeschele et al., 2010). Last, we were interested in examining how a bird's underlying preference (as measured in the choice preference task) related to its performance in the instrumental learning task.

Methods

Subjects

Nineteen black-capped chickadees (ten males and nine females, sex determined by DNA analysis of blood samples; Griffiths, Double, Orr & Dawson, 1998) were tested between March and May 2012. Birds were captured in Edmonton (North Saskatchewan River Valley, 53.53˚N, 113.53˚W; Mill Creek Ravine, 53.52˚N, 113.47˚W), or Stony Plain (53.46˚N, 114.01˚W),

Alberta, Canada between January and March 2012 and were at least one year of age at capture (verified by examining color and shape of the outer tail retrices; Pyle, 1997).

When not in the experimental apparatus, birds were housed singly in cages (30 cm × 40 cm × 40 cm, Rolf C. Hagen, Inc., Montreal, QB) in colony rooms within the visual and auditory range of conspecifics. Birds had *ad libitum* access to food (Mazuri Small Bird Maintenance Diet; Mazuri, St Louis, MO), water (vitamin supplemented on alternating days; Prime vitamin supplement; Hagen, Inc.), grit, and cuttlebone. Birds received nutritional supplements, including: three to five sunflower seeds daily, one superworm (*Zophobas morio*) three times a week, and a mixture of eggs and greens (spinach or parsley) twice a week. The colony rooms were kept on a light:dark cycle that mimicked the natural light cycle for Edmonton, Alberta, Canada. Birds were naïve to all experimental procedures.

Apparatus

Choice preference task

During the choice preference task, birds were individually tested in a sound-attenuating chamber (117 cm × 120 cm × 200 cm; Industrial Acoustics Company, Bronx, NY). The testing space measured 67 cm × 116 cm × 116 cm. In the chamber, there were three perches (1.75 cm in diameter and 10 cm in length) each in front of a Fostex FE108E Σ full-range speaker (Fostex Corp., Japan; frequency response range 80-18,000 Hz). During testing, landing on two of the perches resulted in stimulus playback, while landing on the third perch resulted in no auditory playback (i.e., a neutral perch). The back wall and each side wall had one speaker mounted to it. Each perch was located 100 cm from the floor of the testing area. Each perch contained an

infrared beam used to monitor when a bird landed on the perch. A single-board computer (Palya & Walter, 2001) and personal computer controlled which stimuli played and recorded responses. Stimuli were played from a CD through a Cambridge Azur 640A Integrated Amplifier (Cambridge Audio, London, England) to the speakers within the chamber. During the testing session, birds had *ad libitum* access to Mazuri and water located on the floor of the testing space.

Instrumental learning task

During the instrumental learning task, birds were individually housed in modified home cages (30 cm × 40 cm × 40 cm) placed inside a ventilated, sound-attenuating chamber. Each chamber was illuminated by a 9 W, full spectrum fluorescent bulb following the natural light cycle for Edmonton, Alberta. The cage contained three perches, water (vitamin supplemented three times a week), grit, and cuttlebone. Birds were provided two superworms daily (one in the morning and one in the afternoon), other food (i.e., Mazuri; provided by a motor-driven feeder, Njegovan, Hilhorst, Ferguson, & Weisman, 1994) was only available following correct responding during the task. An opening (11 cm × 16 cm) on the side of the cage, gave the bird access to the feeder. The position of the bird was monitored by infrared cells in the feeder and request perch (perch closest to the feeder) and a personal computer connected to a single-board computer scheduled trials and recorded a bird's responses. Stimuli were played from a CD through an amplifier (Cambridge A300 or 640A Integrated Amplifier, Cambridge Audio, London, England; or NAD310 Integrated Amplifier, NAD Electronics, London, England) and a full-range speaker located in the sound-attenuating chamber (Fostex FE108 Σ or FE108E Σ, Fostex Corp., Japan; frequency response range 80-18,000 Hz). For a diagram and detailed description of the experimental apparatus see Sturdy and Weisman (2006).

Acoustic stimuli

A total of 160 (80 dominant; 80 subordinate) black-capped chickadee *fee-bee* songs were used as stimuli in the choice preference task (songs used as stimuli were produced by 20 dominant and 20 subordinate males). Seventy-four (38 dominant; 36 subordinate) *fee-bee* songs were used as stimuli in the instrumental learning task (songs used as stimuli were produced by 35 dominant and 33 subordinate males). Songs were recorded during the dawn chorus period in the spring (i.e. birds were no longer in winter flocks) from banded populations of black-capped chickadees. The dominance rank of male flockmates was assessed in the field (prior to audio recordings) by observing numerous interactions at winter feeding stations (see Mennill et al., 2004; Otter et al., 1998; van Oort, Otter, Fort, & Holschuh, 2006 for more information on dominance assessment). Within a flock, the highest-ranking male was considered a dominant male, and the lowest-ranking male was considered a subordinate male (i.e., middle ranking males in flocks with three or more males were not included). Songs were recorded between 27 April and 14 May 2000-2004 at the University of Northern British Columbia grounds (Prince George, British Columbia) with an Audio-Technica ATB815a (Audio-Technica U.S., Stow, OH), Sennheiser MKH70 or ME67 (Sennheiser Electronic, Old Lyme, CT) microphone and a Marantz PMD430 (Marantz America, Mahwah, NJ) tape recorder. Songs were also recorded between 25 April and 10 May 1999-2001 at the Queen's University Biological Station (near Kingston, Ontario) with an Audio-Technica AT815a or Sennheiser MKH70 microphone and a Sony Walkman Professional WM-D6C (Sony, Tokyo, Japan) or Marantz PMD222 tape recorder. Songs from these two locations (University of British Columbia and Queen's University Biological Station) were used as stimuli during both tasks; however, unique song exemplars were used in both tasks. During the instrumental conditioning task, we also

presented birds with songs recorded between 28 April and 16 May 2006, 2008 and 2009 during

the dawn chorus period at a field station in the John Prince Research Forest (Fort St. James,

British Columbia). Songs were recorded with an Audio-Technica ATB815a, Sennheiser MKH70

or ME67 microphone and a Marantz PMD430 tape recorder or Marantz PMD671 digital

recorder. The field recordings from the University of British Columbia and Queen's University

Biological Station were resampled from 22,050 Hz to 44,100 Hz (SIGNAL 5.10.29 software;

Engineering Design, Berkeley, CA).

Songs used during the choice preference task were bandpass filtered (2,000-6,000 Hz) to

remove background noise (GoldWave v5.58; GoldWave, Inc., St. John's, NL). Five ms before

and after the song were tapered and amplitude was normalized using SIGNAL. Songs were then

burned to a CD. Each stimulus track on the CD contained two songs produced by the same

individual and 1 s of silence separated the two songs. In total, there were 40 songs (20 stimulus

tracks) from each of the following groups: dominant songs from British Columbia, subordinate

songs from British Columbia, dominant songs from Ontario, and subordinate songs from

Ontario. Four songs produced by a given male were used (i.e., two stimulus tracks each

containing two songs each).

During the instrumental learning task, we presented birds with natural (i.e.,

unmanipulated) and manipulated song stimuli. All stimuli were presented at approximately 75

dB as measured by a Brüel & Kjær Type 2239 (Brüel & Kjær Sound & Vibration Measurement

A/S, Nærum, Denmark) decibel meter (A weighting, slow response) at the approximate position

of a bird's head when on the request perch. See below for specific details regarding further

stimulus preparation.

Natural Stimuli. Ten dominant and ten subordinate songs recorded at the University of

Northern British Columbia (Prince George, British Columbia) were used as stimuli during

discrimination training and an additional five dominant and three subordinate songs recorded

from this location were used as natural (unmanipulated) stimuli during testing (each song used as

a stimulus was produced by a different individual). There were two additional test sessions that

contained natural stimuli: one test session contained ten dominant and ten subordinate songs

recorded at the Queen's University Biological Station (near Kingston, Ontario; each song used a

as a stimulus was produced by a different individual) and one test session contained ten

dominant and ten subordinate songs recorded at the John Prince Research Forest (Fort St. James,

British Columbia; each song used as a stimulus was produced by a different individual).

Vocalizations were of high quality (i.e., no audible interference and low background noise when

viewed on a spectrogram with amplitude cutoffs of -35 to 0 dB relative to song peak amplitude).

Songs were bandpass filtered (2,500-4,800 Hz; outside the frequency range of songs) using

GoldWave version 5.58 (GoldWave, Inc). For each stimulus, 5 ms of silence was added at the

leading and trailing end of the song, which was then tapered to remove transients, and amplitude

was equalized using SIGNAL 5.10.29 software (Engineering Design).

Manipulated Songs. Three dominant and three subordinate songs recorded at the

University of Northern British Columbia were used during manipulated song tests. For these test

stimuli, we manipulated the relative amplitude between the first and second note of the songs,

because previous bioacoustic analyses have shown that the relative amplitude between the two

song notes varies with dominant status in birds from this population (Hahn et al. 2013;

Hoeschele et al. 2010). The relative amplitude is a measurement calculated by dividing the

maximum amplitude of the *bee* note by the maximum amplitude of the *fee* note. We selected a

random sample of songs (including some songs that were measured in Hahn et al. 2013) in order to have a subset of measurements from 90 songs produced by dominant males (nine songs produced by each of ten individuals) and 90 songs produced by subordinate males (nine songs produced by each of ten individuals). We used the standard deviations (SD) for the relative amplitude of the two notes within the song for the dominant and subordinate songs from the University of Northern British Columbia that were measured in the previous bioacoustic analysis to determine manipulations of the relative amplitude during the test session (the SD for dominant and subordinate songs was 0.083 and 0.123, respectively). To create the manipulated songs, we separated the two song notes and increased or decreased the amplitude of the *bee* note, so that the relative amplitude would decrease (i.e., become a smaller ratio) or increase (i.e., become a larger ratio), respectively. During the test session, each song was presented in five ways: (1) the relative amplitude was decreased by 1.5 SD, (2) the relative amplitude was increased by 1.5 SD, (3) the relative amplitude was manipulated to be equal, (4) the song was presented unmanipulated, and (5) sham manipulated: the two notes of the song were edited to separate the notes (similar to the manipulated songs), and then simply concatenated without altering the relative amplitude. Songs that were manipulated were not previously heard by the subjects, but the subjects were presented with other song exemplars produced by these same individuals during the natural test session.

Procedure

Choice preference task

The 160 stimulus songs were divided into two stimulus sets determined by the geographic origin of the songs (i.e., British Columbia or Ontario songs). Within a test session,

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birds heard songs from only one of the two sets (i.e., from one geographic location). The order that birds heard songs from each location was counterbalanced. Both stimulus sets contained songs produced by dominant and subordinate males. During the task, dominant songs were assigned to one perch, subordinate songs were assigned to a second perch, while the last perch had no acoustic stimuli associated with it. Birds were tested until they met criteria (see below) on one stimulus set (i.e., songs from one geographic location) before being tested with the other stimulus set (i.e., songs from the second geographic location). With three perches there were six possible configurations for stimuli (dominant, subordinate, or silent) to be associated with the perches. We randomly assigned the perch configuration for the first stimulus set presented. During the second test session (i.e., when a bird was tested with a new geographic location), we changed which perch was associated with dominant songs, subordinate songs and silence, so that no perch was associated with the same category of song for both geographic stimulus sets (i.e., the dominant, subordinate, and silent perches varied for the British Columbia and Ontario stimulus sets).

Each chickadee was tested in 2 h sessions between 0900 and 1600 hours (a bird never had more than one session per day). For testing, a bird was transported from the colony room to the testing room, removed from its home cage, and released into the testing chamber. After the 2 hr testing session ended, the bird was placed back in its home cage and returned to the colony room.

During the experimental session, when a bird landed on an acoustic (i.e., non-silent) perch, breaking the infrared beam, one stimulus track (i.e., two songs) played until completion. The stimulus track that played was sampled at random without replacement from the group of stimuli that were associated with that perch. If a bird remained on the perch after the songs had finished playing songs would not play continuously (a bird had to leave the perch and re-land on

it, breaking the infrared beam, before another stimulus would play). The number of times a bird landed on each of the three perches and the duration of time spent on each perch was recorded by the computer (while in the testing chamber, a bird could spend time in a location not associated with the perch, e.g., eating Mazuri on the floor of the testing space). A bird was tested in daily sessions until it had spent a total of at least 1 hr on the acoustic perches and heard all stimuli at least 5 times, or had completed a maximum of 5 experimental sessions. Once a bird had met these criteria with one stimulus set, it began sessions with the second stimulus set with a minimum of one day of rest in between testing (mean ± SD number of days between testing with two stimulus set = 3.4 ± 0.92). Following completion of the choice preference task, birds were tested on the instrumental learning task.

Instrumental learning task

During the instrumental learning task, chickadees were housed in the experimental apparatus (see Apparatus, above). Once birds met criterion on a given experimental stage, they moved onto the next stage. A summary of each experimental stage is provided in Figure 1 and below we provide the details about each stage.
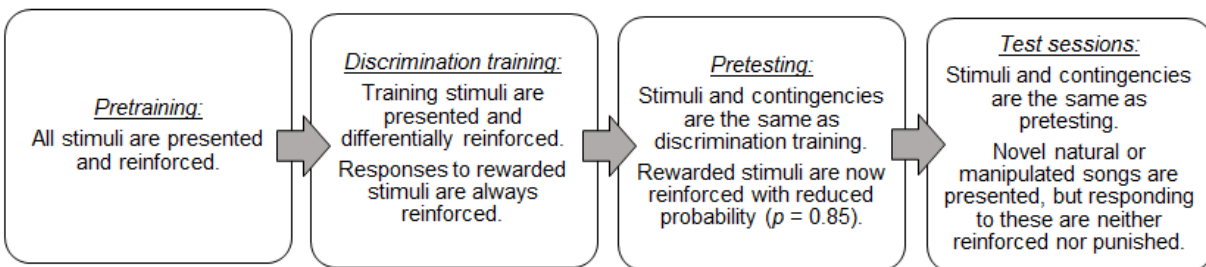
Figure 1. Flowchart showing the order and describing the experimental stages during the instrumental learning task.

Pretraining. Once the bird learned how to use the equipment to obtain food, pretraining began. The objective of pretraining was to ensure the bird stayed on the request perch for the duration of the song stimulus, had a high level of responding to all song stimuli, and responded non-differentially to songs that would be reinforced and non-reinforced during discrimination training. During pretraining, birds were presented with all songs that would be presented throughout the experiment and were reinforced for responding to all stimulus exemplars. In order for a trial to begin, the bird had to land and remain on the request perch for 900-1100 ms. Once the stimulus finished playing, if the bird entered the feeder within 1-s, it was given 1-s access to food and then a 30-s intertrial interval, during which the houselight remained on, but a new trial could not be initiated. An interrupted trial occurred if the bird left the request perch before the stimulus finished playing, which resulted in a 30-s timeout with the houselight turned off. If a bird stayed on the request perch during the song presentation and 1-s after the song finished, a 60-s intertrial interval occurred with the houselight on; however, this intertrial interval ended if the bird left the request perch. During pretraining, data were collected in blocks containing 294 trials (each stimulus played three times); the order that the stimuli played during each block was randomly-selected. Birds continued on pretraining until they completed six 294-trial blocks with ≥ 60% responding to all stimuli, at least four 294-trial blocks with ≤ 3% difference in responding to future rewarded and unrewarded stimuli and at least four 294-trial blocks with ≥ 60% feeding on future test stimuli.

Discrimination training. Following pretraining, each bird moved onto discrimination training. The procedure remained the same, but only 10 dominant and 10 subordinate songs were presented and responding to half of these songs (i.e., unrewarded songs) now resulted in a 30-s intertrial interval with the houselight off. Responding to the remaining 10 songs (i.e., rewarded

songs) resulted in 1-s access to food. Discrimination training continued until birds completed three 200-trial blocks with a discrimination ratio (DR) $\geq$ 0.75 with the last two blocks being consecutive. See response measures, below, for information regarding the DR calculations.

Black-capped chickadees were randomly assigned to either a true category ($n = 12$) or pseudo category discrimination group ($n = 5$). The true category discrimination group contained two subgroups: six birds discriminated rewarded dominant songs from unrewarded subordinate songs (dominant song group; three males and three females), and six birds discriminated rewarded subordinate songs from unrewarded dominant songs (subordinate song group; three males and three females). The pseudo category discrimination group was also separated into two subgroups. Each subgroup discriminated five rewarded dominant and five rewarded subordinate songs from five unrewarded dominant and five unrewarded subordinate songs. The rewarded songs for one subgroup were the unrewarded songs for the other subgroup, and vice versa. With this design, our intention was to combine the data from the two pseudo category subgroups in the data analyses comparing the true and pseudo category groups, as we had no reason to suspect that one pseudo category discrimination would be more difficult compared to the other. There were two males and one female in one subgroup and one male and one female in the other subgroup.

Pretesting. Pretesting was the same as discrimination training, with the exception that rewarded songs were reinforced with a reduced probability (i.e., $p = 0.85$). On trials in which a song in the rewarded category was not reinforced, a bird received no access to food and a 30-s intertrial interval with the houselight on. The purpose of pretesting was to introduce trials that were neither rewarded nor punished to prepare birds for test sessions (see below). Birds continued on pretesting until they completed two consecutive 200-trial blocks with a DR $\geq$ 0.75.

Within-region natural test session: University of Northern British Columbia. Following pretesting, all birds completed this test session to examine generalization before being tested with songs from other geographic regions or manipulated songs. The rationale for this test session was to examine if birds would continue to respond to new stimuli based on the contingencies from discrimination training (i.e., would birds in the true category group show generalization). The stimuli and reinforcement contingencies from pretesting were continued during test sessions; however, additional songs not heard during discrimination or pretesting were also presented. These new (i.e., test) stimuli included five dominant songs and three subordinate songs recorded at the same location as the songs used during discrimination (i.e., University of Northern British Columbia). The stimuli from pretesting were presented ten times each and each test stimulus was presented once during a 208-trial block. Responses to these test songs resulted in a 30-s intertrial interval with the houselight on, but no access to food. All birds completed at least three blocks of this test session, followed by one 200-trial block of pretesting with a DR ≥ 0.75 before moving onto the next test session.

Novel region natural test sessions: Queen's University Biological Station and John Prince Research Forest. We also had two test sessions with other natural (i.e., unmanipulated) song stimuli that were recorded at two different locations (i.e., Queen's University Biological Station and John Prince Research Forest). In one test session we presented ten dominant and ten subordinate songs recorded at Queen's University Biological Station, Ontario, and in the other test session we presented ten dominant and ten subordinate songs recorded at the John Prince Research Forest, British Columbia. The order that these two test sessions were presented was randomized between subjects. During these test sessions, the stimuli and contingencies from pretesting remained (each stimulus from pretesting was presented ten times) and each test

stimulus was presented once in a 220-trial block. Responses to these test songs resulted in a 30-s intertrial interval with the houselight on, but no access to food. Birds completed a minimum of three blocks, followed by one 200-trial block of pretesting with a DR ≥ 0.75 before moving onto the next test session.

Manipulated song test session. The remaining test stimuli ($n = 30$) were presented in the last test session. Similar to the other test sessions, each test stimulus was presented once and the stimuli from pretesting were presented ten times each. This resulted in a 230-trial block and birds completed a minimum of three blocks before completing the experiment. As in the previous test sessions, responses to the test songs resulted in a 30-s intertrial interval with the houselight on, but no access to food. One bird (a male in the subordinate song group) only completed two bins of the manipulated song test due to experimenter error (removed from the experiment too early) and these two bins were included in the analysis.

Response measures

During the choice preference task, we recorded the absolute amount of time spent perched and the absolute number of visits that each bird made to the three perches. Because the number of sessions required for a bird to reach criterion varied, we took the absolute amount of time that each bird spent on each of the three perches and divided it by the number of two-hour sessions that it completed in order to get a per session rate for each individual. We calculated a similar per-session rate for the number of visits made by each individual. We calculated these response measures separately for British Columbia songs and Ontario songs. One bird (a male) only completed the choice preference task with one set of songs (see Ethical note below), so we

only included data from the British Columbia song set for this bird. The silent perch was not

working during one of the sessions for two females on the British Columbia song sets, one

female on the Ontario song set, and one male on the Ontario song set, so these birds could not be

included in the analyses examining all three perches.

In order to quantify acoustic preference we used two dependent measures: (1) proportion

of time on the acoustic perches, and (2) proportion of visits to the acoustic perches. To determine

whether there was a preference for dominant over subordinate songs, we calculated a preference

score by taking the amount of time spent on the dominant song perch and dividing it by the

amount of time spent on the two acoustic perches. Specifically, we used the formula: preference

score = (time on dominant song perch)/[(time on dominant song perch) + (time on subordinate

song perch)]. We calculated a similar preference score by calculating the number of visits to the

dominant song perch and dividing it by the number of visits to both acoustic perches. A

preference score close to 1 indicates a preference for the dominant song perch, a score near 0.5

indicates no preference, and a score near 0 indicates a preference for the subordinate song perch.

We calculated each of these response measures separately for British Columbia songs and

Ontario songs.

During the instrumental learning task, we calculated the percent response for each

stimulus exemplar with the formula: $(R+/(N\text{-}I)) \times 100$, in which we divided the number of trials

where the bird went to the feeder (R+) by the total number of trials (N) not including trials in

which the bird left the perch before the entire stimulus played (I). In order to measure how well

birds discriminate rewarded songs from unrewarded songs, we calculated a discrimination ratio

(DR) for each 200-trial block during discrimination training and pretesting. A DR is calculated

by dividing the average percent response to the rewarded stimuli by the average percent response

to the rewarded stimuli plus the average percent response to the unrewarded stimuli during a given trial block. Perfect discrimination (i.e., responses only to rewarded songs) is represented by a DR of 1.0, while a DR of 0.50 represents equal responding to rewarded and unrewarded songs.

We calculated a modified two-tailed 95% confidence interval (CI) using the mean (M) and standard deviation (SD) of the percentage response to all unrewarded songs on the final day of discrimination training during the instrumental conditioning task with the formula: $CI = M \pm 1.96 \times SD$. Using this measure, we determined how many rewarded songs were well discriminated. If the percentage response to an individual rewarded song was $\geq$ 95% CI, it suggests that birds were significantly discriminating that rewarded stimulus from the unrewarded stimuli.

Individual subjects varied in their response levels to the test stimuli during the instrumental learning task, so we scaled the proportion of response for each subject. Each test stimulus was presented three times during the test session. For each test stimulus, we calculated the proportion of response using the individual's response to each of the three presentations. In order to scale the proportion of response across stimuli, we took the highest proportion of response to a test stimulus within a test session and rescaled it to 1. We then rescaled the proportion of response to the other stimuli by calculating a ratio between each stimulus and the stimulus with the highest proportion of responding. We rescaled each test session separately.

Statistical analyses

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For each stimulus set (i.e., British Columbia songs or Ontario songs) in the choice preference task, we conducted a repeated measures ANOVA to examine the amount of time spent on each of the three perches. We conducted a similar repeated measures ANOVA to examine the number of visits to each of the three perches.

To examine acoustic preference, we used a binomial test for dichotomous data to determine if the preference scores (see "response measures" above for preference score calculation) for each individual differed significantly from chance level (i.e., 0.5). We also conducted one-sample Wilcoxon signed-ranked tests using the preference scores to examine the preference of male and female subjects.

To examine the acoustic variation between the reward and unrewarded songs for the true category and pseudo category discrimination groups we conducted an acoustic analysis on the stimuli during discrimination training and discriminant function analyses to determine if songs could statistically be categorized into groups based on acoustic features. For this acoustic analysis, we measured six acoustic features that have been measured in previous bioacoustics analyses of *fee-bee* songs (Hahn et al., 2013; Hoeschele et al., 2010): total duration, *fee* proportional duration, *fee* glissando, interval ratio, relative amplitude and relative loudness of the *fee* note. We then conducted stepwise discrimination function analyses to classify the rewarded and unrewarded songs from discrimination training. For these analyses, we used the leave-one-out method of cross-validation, which withholds one song and derives a discriminant function from the remaining cases. Using this derived discriminant function the withheld case is classified and this process is repeated until all vocalizations are classified (Betz, 1987).

To examine responding during the instrumental learning task, we conducted an ANOVA on the number of trials to criterion and DRs for the true category and pseudo category groups during discrimination training. Birds required a varying number of trials to complete discrimination training. In order to compare learning acquisition among birds during discrimination, we Vincentized the acquisition curves to 14 blocks of data (the minimum number of blocks for a bird to reach criterion). To calculate the Vincentized blocks, we took the number of trial blocks it took an individual bird to reach criterion and divided it by 14. The actual number of blocks that the bird completed was then divided into the Vincentized blocks equal to the whole-number quotient, while any remaining blocks were placed into the middle two Vincentized blocks (i.e., the 7th and 8th Vincentized blocks). For example, if an individual bird took 32 blocks to reach criterion, each Vincentized block would consist of 2 actual blocks (i.e., 32/14 = 2 with a remainder of 4), and the remaining blocks (i.e., 4) would be divided between the 7th and 8th Vincentized blocks. The middle Vincentized blocks would each have 2 + 2 = 4 actual blocks grouped into it. The DRs for the trial blocks that were grouped into a Vincentized block were averaged (see Hahn et al., 2015; Hoeschele, Guillette, & Sturdy, 2012; Kling & Riggs, 1971).

In order to determine if the number of song exemplars that were responded to during discrimination training differed among groups, we examined the number of rewarded songs responded to ≥ 95% CI. We conducted additional ANOVA and Tukey's planned comparisons on the proportion of responding to the test stimuli using the arcsine square-root transformed proportions of responses (to correct for non-normality) using the following formula: arcsin(sqrt(x)), where x equals the untransformed preference score.

To determine if a bird's underlying preference for dominant or subordinate songs, as measured by the choice preference task, could be predicted by the bird's performance during the instrumental learning task, we conducted multiple regression analyses. We conducted two multiple regression analyses to predict our two measures of preference strength: (1) proportion of time on the acoustic perches, and (2) proportion of visits to the acoustic perches. For these analyses, we used the preference strength for the British Columbia stimulus set, because the songs used during discrimination training in the instrumental learning task were from this location. For the dependent variables, we used the proportion of time or the proportion of visits to the acoustic perch associated with the song category that was rewarded during the instrumental learning task; therefore, we only included birds in the true category groups in this analysis. By examining the data in this way, we could determine if the preference strength for a particular category of songs could be predicted by learning speed (defined as the number of 200-trial bins to complete discrimination training) or performance accuracy (defined as the DR during the final bin of discrimination training or the DR during the first bin during pretesting) when that category of songs was reinforced with food during the instrumental learning task. We included sex as an independent variable, along with the following learning scores from the instrumental learning task: one measure of learning speed (the number of 200-trial bins to complete discrimination training) and two measures of performance accuracy (the DR during the final bin of discrimination training and the DR during the first bin during pretesting). Previous studies have used the number of trials to criterion as a measure of learning speed and DRs as a measure of performance accuracy (e.g., Guillette et al. 2015). Statistics were conducted in Statistica v12 (StatSoft, Inc) or SPSS v23 (SPSS, Inc., Chicago, IL, USA). Figures depict the untransformed data.

Ethical note

Studies were conducted with approval from the Animal Care and Use Committee for Biosciences for the University of Alberta (AUP 108) and all procedures were in accordance with the Canadian Council on Animal Care (CCAC) Guidelines and Policies and the ABS Guidelines for the Use of Animals in Research. During the choice preference task, birds were in the testing apparatus for two hours a day, during which they had free access to food and water. Birds were then returned to their home cage and the colony room. During instrumental learning task, birds were provided with free access to water, grit and cuttlebone and given two superworms daily. Birds were monitored at least two times a day. One bird (a male) was found dead in its home cage in the colony room as the choice preference task testing procedures were being conducted; a post-mortem conducted by the University of Alberta veterinarian determined that the bird had a tumor on its lung. One bird (a female) was found dead during pretesting on the instrumental learning task; a post-mortem conducted by the veterinarian suggested that the bird died from a heart defect. In both cases, these deaths were unrelated to the experimental procedures. All other birds remained healthy during the experimental procedures. Following the experiment, birds were returned to the colony room to be used in future studies. Chickadees were captured under an Environment Canada Canadian Wildlife Service Scientific permit, Alberta Fish and Wildlife Capture and Research permits, and City of Edmonton Parks Permit.

Results

Responses to all three perches

We conducted a repeated measures ANOVA with the amount of time on each perch (dominant, subordinate, silent) as the dependent variable and sex and presentation order (British Columbia songs heard first or Ontario songs heard first) as between subject factors separately for British Columbia and Ontario songs. For songs from both populations, there was a significant main effect of perch (British Columbia songs: $F_{2,26} = 4.84$, $p = 0.016$; Ontario songs: $F_{2,24} = 4.29$, $p = 0.026$). A Tukey's post-hoc test on the British Columbia songs revealed that birds spent significantly more time on the silent perch compared to the dominant perch ($p = 0.013$) and subordinate perch ($p = 0.049$). A Tukey's post-hoc test on the Ontario songs revealed that birds spent significantly more time on the silent perch compared to the dominant perch ($p = 0.011$). See Figure 2.

We conducted a repeated measures ANOVA with number of visits to each perch (dominant, subordinate, silent) as the dependent variable and sex and presentation order (British Columbia songs heard first or Ontario songs heard first) as between subject factors separately for British Columbia and Ontario songs. For British Columbia songs, there was no significant difference in the number of visits to the three perches or any interactions (Fs $_{2,26} \leq 1.41$, ps ≥ 0.26; Fs $_{1,13} \leq 0.35$, ps ≥ 0.56). For Ontario songs, there was no significant difference in the number of visits to the three perches or any interactions (Fs$_{2,24} \leq 1.03$, ps ≥ 0.37; Fs$_{1,12} \leq 0.80$, ps ≥ 0.39).
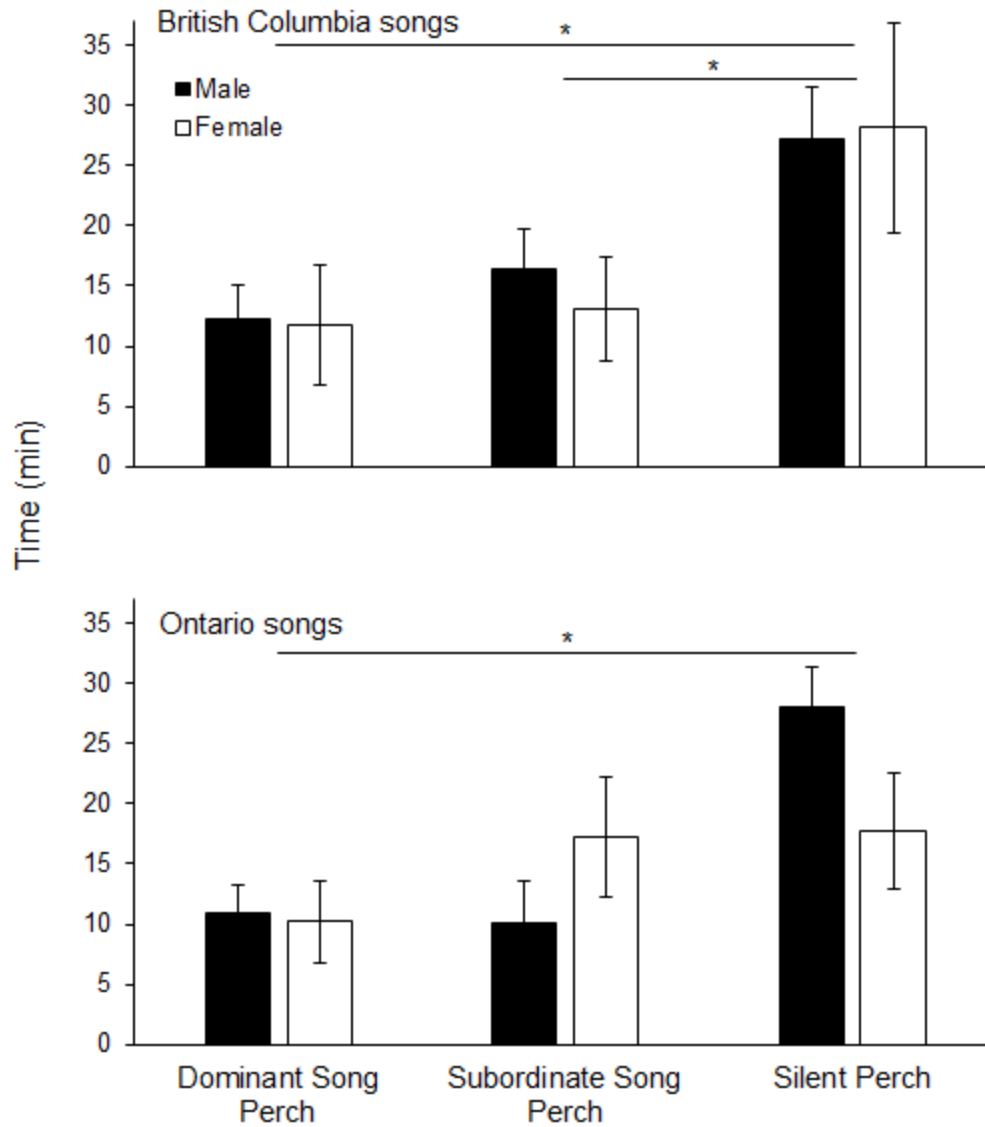
**Figure 2.** The average ± SE amount of time spent on each perch by male (black bars) and female (white bars) black-capped chickadees for British Columbia songs (top graph) and Ontario songs (bottom graph) during the choice preference task. *Indicates a significant difference ($p \leq 0.05$).

Acoustic preference

Time on acoustic perches. Using the proportion of time on the acoustic perches as the behavioral measure for British Columbia songs, two males and three females significantly preferred dominant songs and four males and three females significantly preferred subordinate songs. As a group, neither males (Wilcoxon signed-rank test, $W = 19.0$, $p = 0.39$) nor females (Wilcoxon signed-rank test, $W = 17.0$, $p = 0.52$) demonstrated a significant preference (Figure 3). For Ontario songs, four males and two females significantly preferred dominant songs and two males and four females significantly preferred subordinate songs. As a group, neither males (Wilcoxon signed-rank test, $W = 30.0$, $p = 0.37$) nor females (Wilcoxon signed-rank test, $W = 18.0$, $p = 0.59$) demonstrated a significant preference (Figure 3).

Visits to acoustic perches. Using the proportion of visits to the acoustic perches as the behavioral measure for British Columbia songs, two males and three females significantly preferred dominant songs and five males and three females significantly preferred subordinate songs. As a group, neither males (Wilcoxon signed-rank test, $W = 15.0$, $p = 0.20$) nor females (Wilcoxon signed-rank test, $W = 21.0$, $p = 0.86$) demonstrated a significant preference (Figure 3). For Ontario songs, four males and two females significantly preferred dominant songs and two males and three females significantly preferred subordinate songs.. As a group, neither males (Wilcoxon signed-rank test, $W = 29.0$, $p = 0.44$) nor females (Wilcoxon signed-rank test, $W = 15.0$, $p = 0.37$) demonstrated a significant preference (Figure 3).
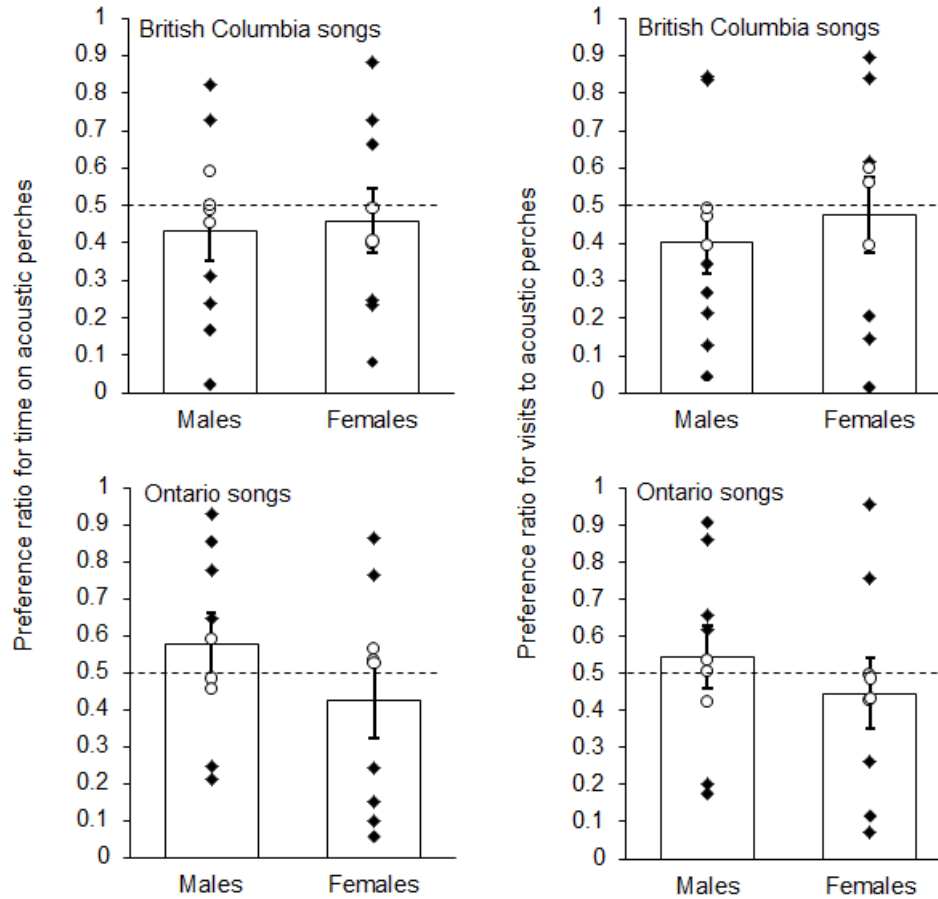
Figure 3. Preference ratios for British Columbia songs (top graphs) and Ontario songs (bottom graphs). Preference ratios were calculated by taking the time (left panel) or visits (right panel) spent on the dominant song perch divided by the total amount of time or visits on both acoustic perches. Filled shapes represent individuals with preference ratios significantly different from chance and open circles represent individuals without a significant preference ($p \leq 0.05$). A preference ratio above 0.50 indicates a preference for dominant songs and a preference ratio below 0.50 indicates a preference for subordinate songs. Bars represent the mean preference ratio for each sex and error bars represent standard error of the mean.

Comparison of true and pseudo category discriminations during instrumental learning task

Acoustic analysis. The purpose of the acoustic analyses were to determine if there is an acoustic feature or features in the songs used as discrimination stimuli that are statistically different between the rewarded and unrewarded songs. We conducted a discriminant function analysis to classify the rewarded and unrewarded songs for the true category group. The overall Wilks' λ was significant (Wilks' $\lambda = 0.79$; $\chi^2 = 4.16$; $p = 0.041$), which indicates that overall the discriminant function used the predictor variables to discriminate between dominant and subordinate songs. The squared canonical correlation coefficient (R_c^2) denotes how much of the variation is explained by the predictor variables used in the discriminant function. The discriminant function (eigenvalue = 0.269; $R_c^2 = 0.21$) assigned 75.0% of the cross-validated cases to the correct category (i.e., rewarded or unrewarded stimuli; which in this case, were also the categories of dominant or subordinate songs). Of the six acoustic features that we measured, the only feature used by the discriminant function was the relative amplitude. This result is consistent with previous bioacoustics and statistical analyses (including a previous discriminant function analysis) on dominant and subordinate *fee-bee* songs (Hahn et al., 2013; Hoeschele et al., 2010). We also conducted a discriminant function analysis to classify the rewarded and unrewarded songs for the pseudo category group; however, using the stepwise method none of our predictor variables were entered into the model and no discriminant function was created. This indicates that the acoustic features in the rewarded and unrewarded songs for the pseudo category group did not contain significant acoustic differences for statistical classification.

Trials to criterion. The average ± SD number of 200-trial blocks required for birds in each discrimination group to complete discrimination training was: 42 ± 16.37 (range: 28-60) and 25.67 ± 10.21 (range: 14-33) for males and females (respectively) in the dominant song

group, 25.67 ± 11.59 (range: 15-38) and 31 ± 9.54 (range: 20-37) for males and females (respectively) in the subordinate song group, and 46 ± 1.73 (range: 44-47) and 22.5 ± 3.54 (range: 20-25) for males and females (respectively) in the pseudo category group. To determine whether males and females in the two true category discrimination groups (dominant song group and subordinate song group) differed in their speed of acquisition, we conducted a sex × group (dominant song, subordinate song) ANOVA on the number of 200-trial blocks required to complete discrimination training. There were no significant main effects or interactions ($Fs_{1,8} \leq 2.36$, $ps \geq 0.16$), revealing that birds rewarded for responding to dominant songs learned the discrimination as quickly as birds rewarded for responding to subordinate songs.

To determine whether males and females in the two pseudo category groups differed in their speed of acquisition, we conducted a main effects ANOVA with sex and group (pseudo group 1, pseudo group 2) as categorical predictors and the number of 200-trial blocks to complete discrimination training as the dependent variable. There was a significant main effect of sex ($F_{1,2} = 70.90$, $p = 0.014$) with females requiring fewer trials to complete discrimination training. There was no main effect of group ($F_{1,2} = 0.02$, $p = 0.89$), so we combined the two pseudo groups in the remaining analyses.

In order to compare the speed of acquisition of birds in the true and pseudo category groups, we conducted a sex × group (dominant song, subordinate song, pseudo) ANOVA on the number of 200-trial blocks to complete discrimination training. There was a main effect of sex ($F_{2,11} = 4.98$, $p = 0.0474$), but no other main effects or interactions. Overall, females learned the discrimination in fewer trials compared to males (average ± SE for males = 37.89 ± 4.57; females = 26.88 ± 2.98). See Figure 4.
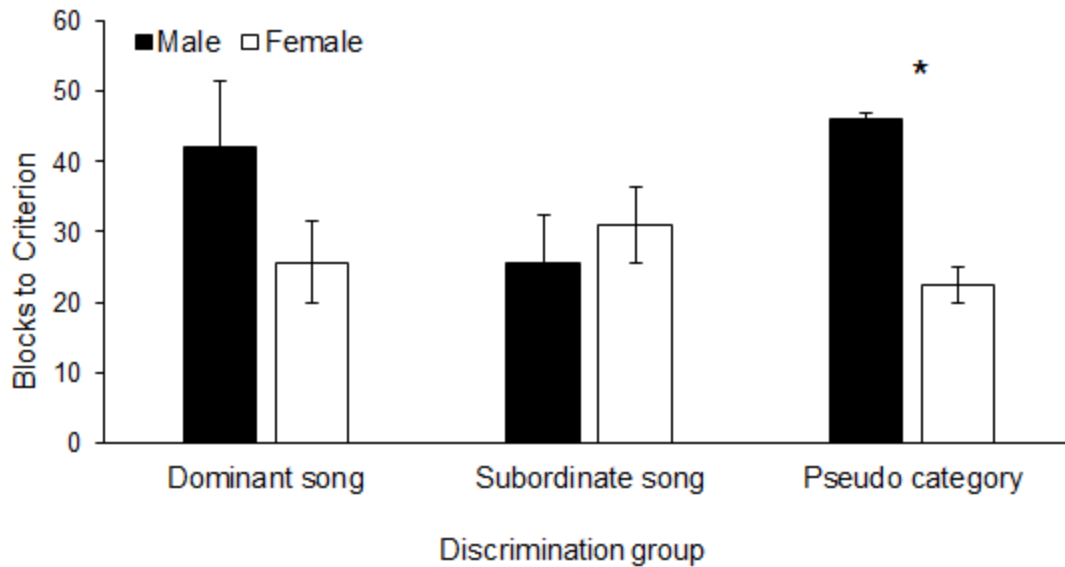
Figure 4. The average ± SE number of 200-trial blocks to complete discrimination training for male (black bars) and female (white bars) subjects in each discrimination group. *Indicates a significant difference in the number of trial blocks to reach criterion between male and female subjects ($p \leq 0.05$) for that discrimination group.

Acquisition performance. We compared task acquisition across Vincentized blocks using a repeated measures ANOVA with sex and group (dominant song, subordinate song, pseudo) as categorical predictors and the DR calculated for each Vincentized block (1-14) as dependent variables. There was a significant main effect for Vincentized block $F_{13, 143} = 73.52$, $p < 0.001$. The DRs increased across Vincentized blocks. There was also a significant main effect of group $F_{2, 11} = 4.41$, $p = 0.039$. A Tukey's post hoc test for the group main effect revealed that the DRs were significantly different between the dominant song group and the subordinate song group ($p = 0.034$), with the subordinate song group having overall higher DRs.

Final day performance. We conducted a sex × group (dominant song, subordinate song, pseudo) ANOVA on the DR on the final day of discrimination training. There were no significant differences (Fs ≤ 1.11, all ps ≥ 0.37) suggesting that by the final day of discrimination training all birds had reached a similar level of performance.

Number of rewarded songs responded to ≥ 95% confidence interval (CI). Birds can achieve a high DR by only responding to a few rewarded stimuli, while responding less to the remaining rewarded stimuli and all unrewarded stimuli. To determine how many of the rewarded stimuli were well-discriminated, we examined how many rewarded songs were responded to ≥ 95% CI during the final block of discrimination training. We conducted a sex × group (dominant song, subordinate song, pseudo) ANOVA to determine if the true category and pseudo category groups differed in the number of exemplars responded to ≥ 95% CI. There was no significant main effect of sex ($F_{1,11} = 0.06$; $p = 0.81$), group ($F_{2,11} = 0.53$; $p = 0.60$) or significant interaction ($F_{2,11} = 0.57$, $p = 0.58$). Out of 10 rewarded stimuli, the mean ± SE for the number of stimuli responded to ≥ 95% CI were: dominant song group, 7.67 ± 2.33and 10 ± 0, for male and female subjects, respectively; subordinate song group, 8 ± 1.0 and 7.33± 2.67, for male and female subjects respectively; and pseudo category group, 9.67 ± 0.33and 9 ± 1.0, for male and female subjects, respectively.

Test sessions

Natural songs: University of Northern British Columbia, British Columbia. Following pretesting, birds in the true category and pseudo category discrimination conditions were presented with dominant and subordinate songs not heard during acquisition (but songs from the
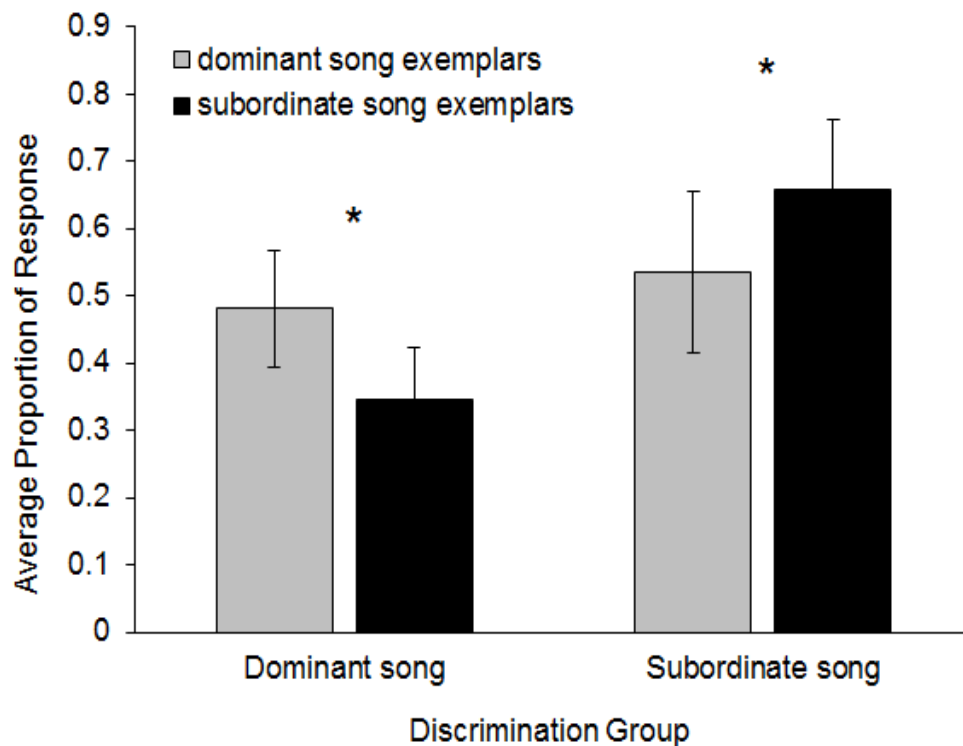
same region as the songs presented during acquisition). We conducted a sex × group (dominant

song, subordinate song, pseudo) × stimulus type (dominant song, subordinate song) ANOVA on

the scaled proportion of response. There were no significant main effects or interactions ($Fs_{2,11} \leq$

2.95, $ps \geq 0.09$; $Fs_{1,11} \leq 2.00$, $ps \geq 0.18$;). See Figure 5.
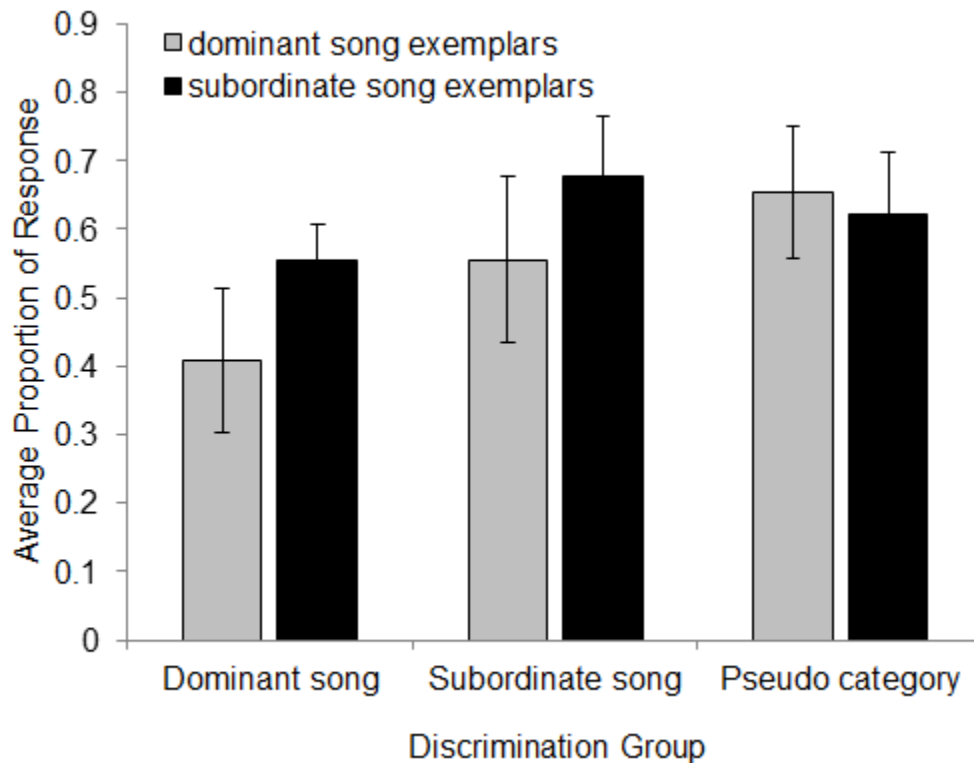
Figure 5. Average ± SE proportion of response by birds in each discrimination group to

untrained test songs produced by dominant (gray bars) and subordinate (black bars) males from

the University of Northern British Columbia.

Natural songs: Queen's University Biological Station, Ontario. We conducted a sex ×

group (dominant song, subordinate song) × stimulus type (dominant song, subordinate song) on

the scaled proportion of response to the songs recorded in Ontario. There was a significant stimulus type × group interaction $F_{1,8} = 104.31$, $p < 0.001$. To examine the interaction, we conducted a Tukey's post hoc analysis. Birds in the dominant song group responded significantly more to dominant songs ($X = 0.48$) compared to subordinate songs ($X = 0.34$), $p = 0.0005$. Birds in the subordinate song group responded significantly more to subordinate songs ($X = 0.66$) compared to dominant songs ($X = 0.53$), $p = 0.0006$. See Figure 6.

Figure 6. Average ± SE proportion of response by birds in each discrimination group to untrained test songs produced by dominant (gray bars) and subordinate (black bars) males from Ontario. *Indicates a significant difference ($p \leq 0.05$) in response to dominant and subordinate song exemplars by that discrimination group.

Natural songs: John Prince Research Forest, British Columbia. We conducted a sex ×
group (dominant song, subordinate song) × stimulus type (dominant song, subordinate song) on
the scaled proportion of response to the songs recorded at John Prince Research Forest, British
Columbia. There were no significant main effects or interactions ($Fs_{1,8} \leq 4.87$, $ps \geq 0.067$).

Manipulated songs. We conducted planned comparisons (Tukey's, $p \leq 0.05$) on the
average scaled proportion of response to the rewarded discrimination songs presented during the
manipulated song tests (reinforced 85% of the time) compared to average proportion of response
to each of the ten manipulated song types (i.e., dominant songs and subordinate songs with:
relative amplitude increased, relative amplitude decreased, equal relative amplitude, sham
manipulated songs, natural (i.e., unmanipulated) songs). We also conducted planned
comparisons (Tukey's, $p \leq 0.05$) on the average proportion of response to the unrewarded
discrimination songs presented during the manipulated song tests compared to average
proportion to each of the ten manipulated song types. In order to measure effect size for the
pairwise comparisons, we calculated Hedges' g using the unbiased correction for small sample
sizes: $((M_1 - M_2) / S_p)*(1 - (3 / (4*(n_1 + n_2 - 2) - 1)))$, where M = sample mean and S_p = square
root of the pooled variance estimate (Cohen, 2008). Because the training and the test songs were
presented a different number of times during each bin (i.e., test songs are each presented once
during a bin, while training songs were each presented ten times), we scaled the training songs
separately from the test stimuli. We compared the manipulated songs to the discrimination songs
because the results from the test session with songs from the University of Northern British
Columbia suggest that the discrimination may not generalize to novel songs, and comparing both
manipulated and unmanipulated songs to the songs from training allowed us to see whether there
was a difference in responding as the songs were manipulated.

For birds in the dominant song group, birds responded significantly more to the rewarded discrimination songs compared to all manipulated song types (all $ts \geq 3.97$; all $ps \leq 0.003$, all gs between 1.76–3.77). Birds in the dominant song group responded significantly less to unrewarded discrimination songs compared to dominant songs sham manipulated ($t = 2.77, p = 0.022, g = 1.52$), subordinate songs sham manipulated ($t = 2.85, p = 0.019, g = 1.50$), natural subordinate songs ($t = 2.90, p = 0.017, g = 2.04$), and subordinate songs with equal relative amplitude ($t = 2.58, p = 0.030, g = 1.44$).

For birds in the subordinate song group, birds responded significantly more to the rewarded discrimination songs compared to all manipulated song types (all $ts \geq 2.59$; all $ps \leq 0.027$, all gs between 1.05-2.0) with the exception that birds did not respond significantly differently between subordinate songs with the relative amplitude increased and the rewarded discrimination songs ($t = 2.22, p = 0.051, g = 1.06$). Birds in the subordinate song group responded significantly less to unrewarded discrimination songs compared to subordinate songs with relative amplitude increased ($t = 2.29, p = 0.045, g = 0.57$), subordinate songs sham manipulated ($t = 3.34, p = 0.007, g = 1.13$), and subordinate songs with equal relative amplitude ($t = 3.39, p = 0.007, g = 0.95$). See Figure 7.
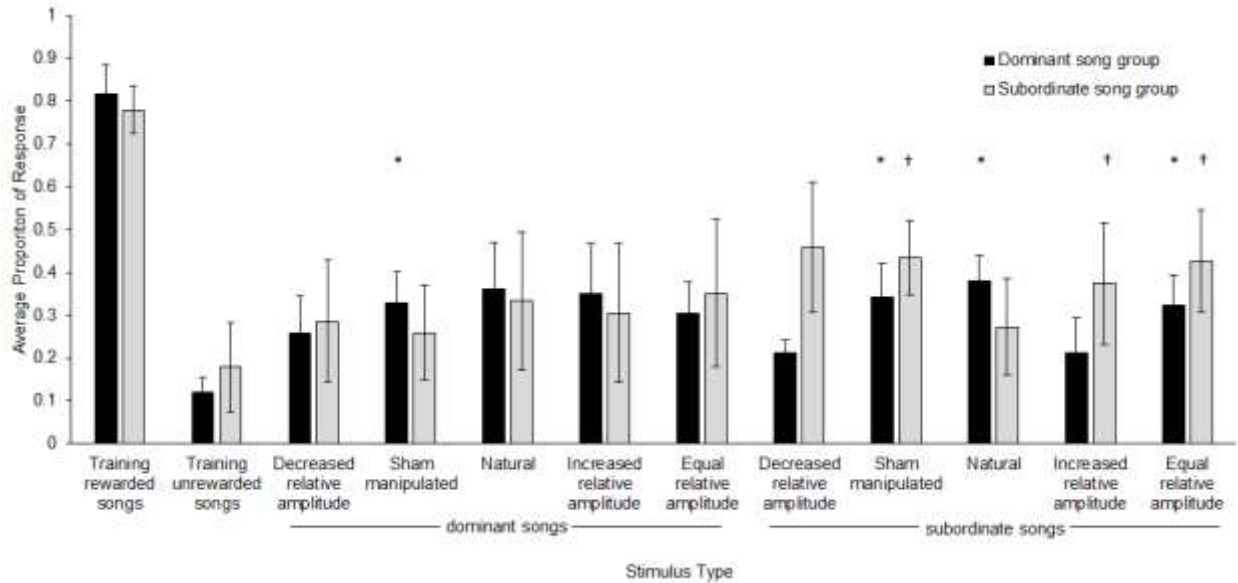
Figure 7. Mean ± SE proportion of response to manipulated test stimuli. Black bars represent the responding by birds in the dominant song discrimination group and gray bars represent the responding by birds in the subordinate songs group. Test stimuli were presented in five ways (relative amplitude of the two song notes decreased, song notes cut apart and put back together with no manipulation (sham manipulated), natural (unmanipulated) songs, relative amplitude increased, and relative amplitude made equal). *Indicates a significant difference ($p \leq 0.05$) compared to the training unrewarded songs for birds in the dominant song discrimination group. †Indicates a significant difference ($p \leq 0.05$) compared to the training unrewarded songs for birds in the subordinate song discrimination group (see text for details).
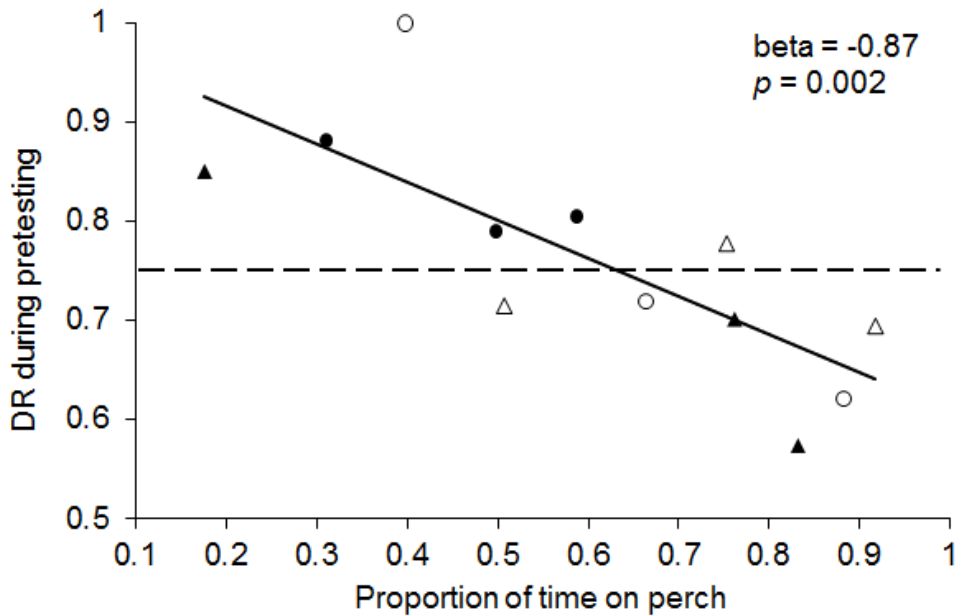
Relationship between acoustic preference and performance on the instrumental learning task

A multiple regression analysis was conducted to predict preference strength as measured by the proportion of time spent on each acoustic perch, using the measures of learning speed and performance accuracy as independent variables. The regression equation was significant, $R^2 =$

0.80, adjusted $R^2 = 0.69$, $F_{4,7} = 7.20$, $p = 0.013$. The DR during the first bin of pretesting was the only variable that significantly predicted the time on perch (beta = -0.87, $p = 0.002$). Birds that had lower DRs during the first bin of pretesting demonstrated a stronger preference towards future rewarded songs (i.e., the song category that was rewarded during acquisition). See Figure 8.

We also conducted a multiple regression analysis to predict preference strength as measured by the proportion of visits to each acoustic perch. We used the same measures of learning speed and performance accuracy as our independent variables as the analyses described above. The overall regression equation was not significant, $R^2 = 0.54$, adjusted $R^2 = 0.27$, $F_{4,7} = 2.04$, $p = 0.19$.

Figure 8. Relationship between the proportion of time during the choice preference task spent on the perch associated with the category songs rewarded during the instrumental learning task (*x*-axis) and the discrimination ratio (DR) during the first 200-trial bin of pretesting during the

instrumental learning task (y-axis). Beta and p values were determined with a multiple regression model ($n = 12$). Filled shapes represent male subjects and open shapes represent female subjects. Circles represent subjects in the dominant song group and triangles represent individuals in the subordinate song group. The dashed line represents the DR (i.e., 0.75) that birds were required to reach during pretesting.

Discussion

In the current study, we report the results from two operant conditioning tasks examining chickadees' responses to conspecific songs that vary with singer dominance rank. The first task was a choice preference task that allowed us to examine active responses by birds (i.e., selection of songs) in the absence of food reinforcement. The second task was an instrumental learning task, during which birds were differentially reinforced with food for responding to certain songs. We also examined the relationship between individual variation in performance during the instrumental learning task and individual variation in acoustic preference. Overall, our results suggest sex differences in learning speed, with females learning to discriminate among songs faster than males. We also found that performance accuracy varied depending on which category of songs was rewarded (i.e., when subordinate songs were rewarded birds achieved higher performance accuracy) and we found evidence that a bird's performance accuracy during the instrumental learning task correlates with its acoustic preference.

Perceptual categorization

One indication that animals are using open-ended categorization is to compare the number of trials required to complete discrimination training for birds in a true category group compared to birds in a pseudo category group, with birds in the former group completing the discrimination faster if in fact they are perceiving stimuli as open-ended categories. However, this predicted difference in learning speed assumes that there is a benefit (in terms of how long it takes to learn the task) for a bird to use open-ended categorization. In the current study, we found no difference in the number of trials to complete discrimination training for birds in the true category group compared to birds in a pseudo category group. It is possible that the acoustically simple structure of *fee-bee* songs (i.e., two-note tonal structure) result in all birds (regardless of group assignment) performing similarly. In other words, regardless of whether birds are using categorization or rote memorization, both mechanisms are equally efficient in terms of how long it takes to learn the task (e.g., Hahn et al., 2015). It is also possible that all birds were using rote memorization resulting in no difference in how many trials to reach criterion between the two groups.

While previous studies have found evidence that chickadees use open-ended categorization when discriminating among conspecific vocalizations (e.g., species-based cues in calls, Bloomfield et al., 2003; 2008; sex-based cues in songs, Hahn et al., 2015), it is possible that open-ended categorization is a less useful strategy when discriminating based on dominance rank. Since chickadees are year-round residents, generally disperse short distances, and usually remain in the same overwintering flock each year (Smith, 1991), the average number of conspecifics an individual is likely to encounter within its lifespan is relatively small (e.g., typical flocks contain 2-12 individuals; Smith, 1991). For chickadees in the wild, memorizing the dominance rank and songs produced by each individual that is encountered may be a sufficient

strategy for recognition, and may be one reason the current results do not provide conclusive evidence for the use of open-ended categorization.

There was evidence for differences in responding depending on which category of songs was rewarded; specifically, birds rewarded for subordinate songs had higher DRs compared to birds rewarded for dominant songs. This indicates that birds in the subordinate song group were performing more accurately across trials (i.e., responding to proportionally more of the rewarded songs versus the unrewarded songs) compared to birds in the dominant song group. However, by the final day of discrimination, there was no difference in the DRs for birds in the dominant song and subordinate song groups, indicating that by the final day of training all birds were performing similarly. One explanation for the lower performance accuracy by birds in the dominant song group is the biological relevance of the response to the signal. In this task, we required birds to fly to the feeder following a certain category of songs to obtain food; however, in the wild, dominant males have preferential access to a food source and will chase away or supplant lower ranking males at these food sources (Smith, 1991). It is possible that birds may have had more difficulty going to a food source following a signal that typically indicates that a bird risks being chased away from food, thus leading a bird to not enter the feeder as often following dominant songs. In line with this, we also found that males in the dominant song group required more trials to reach training criterion than males in the subordinate song group. In a similar go/no-go discrimination task, Bloomfield, Sturdy, Phillmore, & Weisman (2003) found that chickadees had more difficulty inhibiting their response (i.e., not flying to the feeder) following conspecific *chick-a-dee* calls, a signal that can be used in the wild to indicate a food source (Ficken, 1981).

Acoustic mechanisms

Another indication that animals are using open-ended categorization is examining how birds respond to novel song exemplars; if birds continue to respond to novel song exemplars based on the contingencies from training, it is a strong indicator that birds were using open-ended categorization. Birds did not demonstrate generalization when presented with test songs from University of Northern British Columbia, the same region that the songs they had been trained on were recorded from; however, the lack of generalization may have been due to the small number of transfer stimuli (i.e., five dominant songs and three subordinate songs). In general, chickadees respond less to novel songs presented in generalization (Bloomfield et al., 2008, Hahn et al., 2015) and responding may not generalize without a larger sample of novel song exemplars. In contrast, when presented with songs from Ontario, birds in both true category groups continued to respond based on the contingencies during discrimination training (see Figure 6), suggesting that there was acoustic similarity based on dominance rank in the songs from these two geographic locations. More work is needed to determine the specific acoustic feature(s) that birds used during the discrimination. Dominance-based categorization was not evident when birds were tested on songs from John Prince Research Forest, suggesting that acoustic similarity within the songs produced by males of similar rank may only persist across some geographic locations.

Previous bioacoustic analyses and playback studies suggest that the relative amplitude varies between dominant and subordinate male songs, indicating that this acoustic feature may be used when distinguishing a male's dominance rank (Hahn et al., 2013; Hoeschele et al., 2010). In the current study, we tested this feature as a possible acoustic mechanism by manipulating this song feature in dominant and subordinate songs. Overall, birds responded significantly less to all

manipulated test songs compared to the rewarded training songs, suggesting that the rewarded songs from discrimination training achieved a high degree of stimulus control over the birds' responding. Chickadees did not respond to songs with manipulated relative amplitude in a way that would be predicted based solely on variation in relative amplitude between dominant and subordinate songs.

Sex differences

During the instrumental learning task, females reached criterion faster compared to males; however, this difference appears to be mostly driven by males in the dominant song group and pseudo category group (see Figure 4). Go/no-go discrimination tasks using *chick-a-dee* calls, which are produced by both sexes throughout the year, have reported no sex difference in responding (e.g., Bloomfield et al., 2008; Charrier, Lee, Bloomfield, & Sturdy, 2005; Guillette, Redden, Hurd, & Sturdy, 2009). However, go/no-go discrimination tasks using *fee-bee* songs as stimuli (like in the current study) have found differences in responses by male and female subjects (e.g., female chickadees discriminate more accurately compared to males by responding to more rewarded songs, Hahn et al., 2015, and attaining higher DRs; Hoeschele et al., 2012) and sex differences in learning speed have also been reported in other songbird species (e.g., zebra finches; *Taeniopygia guttata*) performing auditory discrimination tasks (see Kriengwatana, Spierings, ten Cate, 2016).

Songs are signals used in intersexual and intrasexual communication; in species in which the same song types function in both types of communication, there may be differing levels of costs or benefits associated with responding to certain songs that vary with the sex of the

receiver. For example, male songs are a signal for intersexual attraction and females may choose high-quality mates in order to gain direct (e.g., better nesting territory; more parental care) or indirect (e.g., better genetic fitness for young) benefits. For females, mating with a male that is less-than-ideal can be a costly mistake (e.g., it may affect her outcome for the entire breeding season). In comparison, male songs are also used for intrasexual competition, but if a male makes a territorial response to another male who was not a threat, the costs are relatively low (e.g., wasted time or energy responding to a non-rival; Ratcliffe & Otter, 1996). If the costs associated with mistakenly responding to a song are higher for females, females should be more expert discriminators. The results from the current study support this idea; females may have learned the discrimination faster because they are more expert at distinguishing between male signals that vary with male quality or dominance rank. Additionally, the relative dominance rank of each subject may have influenced how the bird performed during the discrimination task. Males generally have a higher dominance rank compared to females (Smith, 1991), so it seems likely that differences in dominance rank between the sexes may have also influenced the sex differences in discrimination performance.

Acoustic preference and performance accuracy

In the current study, we tested chickadees with songs that were recorded from other geographic locations (i.e., chickadees originating in Alberta were tested with songs recorded in British Columbia and Ontario). There are discriminable geographic differences in the songs that chickadees attend to (Hahn et al., 2016), and there are also acoustic differences indicating a male's dominance rank that vary with geographic location (Hahn et al., 2013). Using a passive

playback experimental design (i.e., birds are presented with different playback stimuli but do not actively choose what they hear) Hoeschele et al. (2010) found that female chickadees that originated from the same locations as the birds tested in the current study and tested with songs from one of the two locations used in the current study (i.e., the University of Northern British Columbia) vocalized more when presented with dominant male songs compared to subordinate male songs. The rationale for using a choice preference task in the current study is that the birds actively select which songs to listen to as opposed to measuring responses to song playback. Overall, we found that birds preferred to spend more time on the silent perch compared to the acoustic perches; however, birds visited the three perches a similar number of times. This suggests that birds may have been more likely to visit the acoustic perches and fly away, while visit and remain perched on the silent perch; however, further work is needed to examine why birds may have preferred spending more time on the silent perch.

Individual differences can influence responding in chickadees, for example, Grava, Grava, and Otter (2013) found that songs produced by socially dominant males are perceived differently depending on the habitat-of-origin of the singer and the song receiver. In mountain chickadees (*Poecile gambeli*), females show a preference for males from their same habitat elevation, suggesting that females have a preference for locally-adapted males (Branch, Kozlovsky, & Pravosudov, 2015). Further investigation is required to understand how acoustic variation in songs relates to dominance rank in the population of chickadees from which our subjects came (i.e., central Alberta) and the extent to which acoustic similarity with local songs may have influenced responding during the tasks.

In black-capped chickadees, individual variation in exploration style correlates with cognitive abilities such as information acquisition (learning speed) and information use

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(performance accuracy) on an instrumental discrimination task (Guillette, Hahn, Hoeschele, Przyslupski, & Sturdy, 2015; Guillette, Reddon, Hoeschele, & Sturdy, 2011; Guillette, et al., 2009). Here we find that preference strength is related to information use: performance accuracy was a significant predictor of a bird's preference strength during the choice preference task. Chickadees with stronger pre-existing preference had lower performance accuracy when the probability of reinforcement for making a correct response was decreased (from p = 1.0 to p = 0.85). Taken together these results suggest that performance on cognitive tasks is related to non-cognitive abilities such as personality and initial preference for novel acoustic stimuli (Griffin, Guillette, & Healy, 2015).

Pretesting was the first stage in which the reinforcement probability of the rewarded songs was reduced. The current study provides evidence that a bird's preference strength for a category of songs was inversely related to its performance accuracy once this change in reinforcement probability was introduced. This suggests that for birds that were being food reinforced for songs that they preferred, when the preferred songs were presented with a lower probability of reinforcement (i.e., rewarded songs are reinforced on 85% of trials), birds start responding with more variability (i.e., start responding to rewarded and unrewarded songs at a proportionally similar level). When the probability of reinforcement is decreased during pretesting, the 15% of rewarded song trials that do not result in reward are presented under extinction (i.e., the response is made but no reinforcement is provided). Our results are consistent with previous findings suggesting that variability in responding often occurs after extinction is implemented (Neuringer, 2002) and when the probability of reward decreases (Gharib, Gade, & Roberts, 2004).

The results from the current choice preference task are also consistent with previous findings demonstrating that hearing conspecific vocalizations can be rewarding to some individuals, but not rewarding to others (e.g., Riters et al., 2013), suggesting that the incentive salience associated with song is highly individualized. However, instrumental learning tasks are mediated by a different type of incentive (termed 'cognitive incentive', see Berridge & Robinson, 2003). Often incentive salience and cognitive incentive act together and motivate behavior (e.g., motivation to obtain reward) in the same direction (Berridge & Robinson, 2003); however, each is controlled by distinct neural mechanisms (Berridge, 2007), which may be differentially affected when reward probability is altered (Berridge & Robinson, 2003). In the current study, it is possible that different neuromodulatory processes were controlling behavior depending on a bird's initial underlying preference (i.e., incentive salience associated with the vocalization category). While the different neural processes lead to similar behavioral responding during acquisition training, distinct behavioral differences, depending on a bird's initial underlying preference, were evident once the reward probability was altered (i.e., during pretesting). Additional work is needed to further examine this possibility, but our results are consistent with other evidence suggesting that incentive salience and learning paradigms can interact and influence performance on a learning task (see Maney, 2013). Specifically, our results suggest that response variability associated with decreased reward probability differentially affects the responding by individuals depending on the individual's underlying acoustic preference.

In other Parids, exploration style correlates with dominance status measured in captive individuals (mountain chickadees, Fox, Ladage, Roth, & Pravosudov, 2009; great tits, *Parus major*, Verbeek, Boon, & Drent, 1996; Verbeek, de Goede, Drent, & Wiepkema, 1999) and wild

populations (great tits, Dingemanse & de Goede, 2004). Taken together, previous studies examining individual differences in dominance status, acoustic preference, learning speed and performance accuracy suggest that there is a relationship between these measures and cognitive performance of the individual, including how they respond during operant tasks similar to the tasks used in the current study. We did not know the relative dominance rank of each subject; however, each subject's relative dominance rank may have influenced their acoustic preference and their performance during the instrumental learning task. For example, a low-ranking male tested with songs produced by high-ranking and low-ranking males (similar to the current study) may perform differently compared to a high-ranking male tested with the same stimuli. The possible effects of individual characteristics should be considered in future tasks examining the perception of biologically relevant signals.

Conclusions

In the current study, we used two operant conditioning tasks to examine acoustic preference, ability to discriminate, and discrimination mechanisms of conspecific songs that varied with male dominance rank. Results from the test sessions during the instrumental learning task suggest that songs may belong to open-ended categories based on dominance rank; however, results from discrimination training did not demonstrate a benefit of using open-ended categorization over rote memorization, possibly due to the salience of the signal or the efficiency of using rote memorization as a recognition strategy. Results from the choice preference task indicate that acoustic song preference is individualized. In examining the relationship between the preference and instrumental learning task, we found that a bird's acoustic preference

correlates with its performance accuracy when the reinforcement probability is decreased. Given the increasing number of studies reporting individual differences in various cognitive processes, including, acoustic preferences, learning speed, and performance accuracy, the results of the current study suggest that the relationship between all three of these measures need careful consideration in future work.

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References

Allee, W.C. (1975). Social dominance and subordination among vertebrates. In, Schein, M.W.

    (Ed.). "Social Hierarchy and Dominance. Benchmark Papers in Animal Behavior,

    Volume 3. Stroudsburg, PA: Dowden, Hutchinson & Ross, Inc., pp. 107-130. (Reprinted

    from *Biological Symposia,* 1942. 8*:* 139-162)

Archawaranon, M., Dove, L., & Wiley, R.H. (1991). Social inertia and hormonal control of

    aggression and dominance in white-throated sparrows. *Behaviour, 118*(1)*,* 43-65.

    doi:10.1163/156853991X00193

Barrette, C., & Vandal, D. (1986). Social rank, dominance, antler size, and access to food in

    snow-bound wild woodland caribou. *Behaviour*, 97(1), 118-145.

    doi:10.1163/156853986X00342

Berridge, K.C. (2007). The debate over dopamine's role in reward: the case for incentive

    salience. *Psychopharmacology, 191,* 391-431. doi: 10.1007/s00213-006-0578-x

Berridge, K.C., & Robinson, T.E. (2003). Parsing reward. *TRENDS in Neurosciences, 26*(9),

    507-513. doi:10.1016/S0166-2236(03)00233-9

Betz, N.E. (1987). Use of discriminant analysis in counseling psychology research. *Journal of*

    Counseling Psychology, 34, 393-403. doi:10.1037/0022-0167.34.4.393

Bloomfield, L.L., Farrell, T.M., & Sturdy, C.B. (2008). All 'chick-a-dee' calls are not created

    equally Part II. Mechanisms for discrimination by sympatric and allopatric chickadees.

    Behavioural Processes, 77(1), 73-86. doi: 10.1016/j.beproc.2007.06.008

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*). *Journal of Comparative Psychology, 117*(3), 290-301. doi:10.1037/0735-7036.117.3.290

Branch, C.L., Kozlovsky, D.Y., & Pravosudov, V.V. (2015). Elevation-related differences in female mate preference in mountain chickadees: are smart chickadees choosier? *Animal Behaviour,* 89-94. doi:10.1016/j.anbehav.2014.10.021

Charrier, I., Lee, T.T.Y., Bloomfield, L.L., & Sturdy, C.B. (2005). Acoustic mechanisms of note-type perception in black-capped chickadee (*Poecile atricapillus*) calls. *Journal of Comparative Psychology, 119*(4), 371-348. doi: 10.1037/0735-7036.119.4.371

Christie, P.J., Mennill, D.J., & Ratcliffe, L.M. (2004). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioural Ecology and Sociobiology. 55*(4)*,* 341-348. doi:10.1007/s00265-003-0711-3

Cohen, B.H. (2008). *Explaining Psychological Statistics*. John Wiley & Sons, Inc, Hoboken, NJ

Cummins, D.D. (1996). Dominance hierarchies and the evolution of human reasoning. *Minds and Machines, 6,* 463-480.

Dalziell, A.H., & Cockburn, A. (2008). Dawn song in superb fairy-wrens: a bird that seeks extrapair copulations during the dawn chorus. *Animal Behaviour, 75,* 489-500. doi:10.1016/j.anbehav.2007.05.014

Desrochers, A., Hannon, S.J., & Nordin, K.E. (1988). Winter survival and territory acquisition in a northern population of black-capped chickadees. *The Auk, 105,* 727-736.

Dewsbury, D.A. (1982). Dominance rank, copulatory behavior, and differential reproduction. *The Quarterly Review of Biology, 57,* 135-159. doi:10.1086/412672

Dingemanse, N.J., & de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology, 15*(6), 1023-1030, doi:10.1093/beheco/arh115

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour, 125*(3), 283-313. doi:.1163/156853993X00290

Dufty, A.M., Jr. (1986). Singing and the establishment and maintenance of dominance hierarchies in captive brown-headed cowbirds. *Behavioral Ecology and Sociobiology, 19,* 49-55

Ficken, M.S. (1981). Food finding in black-capped chickadees: altruistic communication? *The Wilson Bulletin, 93*(3), 393-394

Fox, R.A., Ladage, L.D., Roth, T.C. II, Pravosudov, V.V. (2009). Behavioral profile predicts dominance status in mountain chickadees. *Animal Behaviour, 77*(6), 1441-1448. doi:10.1016/j.anbehav.2009.02.022

Gentner, T.Q., & Hulse, S.H. (2000). Female European starling preference and choice for variation in conspecific male song. *Animal Behaviour, 59*(2), 443-458. doi:10.1006/anbe.1999.1313

Gharib, A., Gade, C., & Roberts, S. (2004). Control of variation by reward probability. *Journal of Experimental Psychology: Animal Behavior Processes, 30*(4), 271-282. doi:10.1037/0097-7403.30.4.271

Grava, T., Grava, A., & Otter, K.A. (2013). Habitat-induced changes in song consistency affect

    perception of social status in male chickadees. *Behavioral Ecology and Sociobiology,*

    67(10), 1699-1707. doi:10.1007/s00265-013-1580-z

Griffin, A.S., Guillette, L.M., & Healy, S.D. (2015). Cognition and personality: an analysis of an

    emerging field. *Trends in Ecology & Evolution, 30*(4), 207-214.

    doi:10.1016/j.tree.2015.01.012

Griffiths, R., Double, M.C., Orr, K., & Dawson, R.J.G. (1998). A DNA test to sex most birds.

    Molecular Ecology 7(8), 1071-1075. doi: 10.1046/j.1365-294x.1998.00389.x

Guillette, L.M., Hahn, A.H., Hoeschele, M., Przyslupski, A.M., & Sturdy, C.B. (2015).

    Individual differences in learning speed, performance accuracy and exploratory

    behaviour in black-capped chickadees. *Animal Cognition, 18*(1), 165-178,

    doi:10.1007/s10071-014-0787-3

Guillette, L.M., Reddon, A.R., Hoeschele, M., & Sturdy, C.B. (2011). Sometimes slower is

    better: slow-exploring birds are more sensitive to changes in a vocal discrimination task.

    Proceedings of the Royal Society B: Biological Sciences, 278(1706), 767-773.

    doi:10.1098/rspb.2010.1669

Guillette, L.M., Reddon, A.R., Hurd, P.L., & Sturdy, C.B. (2009). Exploration of a novel space

    is associated with individual differences in learning speed in black-capped chickadees,

    Poecile atricapillus. *Behavioural Processes, 82*(3), 265-270.

    doi:10.1016/j.beproc.2009.07.005

Hahn, A.H., Guillette, L.M., Hoeschele, M., Mennill, D.J., Otter, K.A., Grava, T., Ratcliffe,

L.M., & Sturdy, C.B. (2013). Dominance and geographic information contained within

black-capped chickadee (*Poecile atricapillus*) song. *Behaviour, 150, 1601-1622.*

doi:10.1163/1568539X-00003111

Hahn, A.H., Hoang, J., McMillan, N., Campbell, K., Congdon, J., & Sturdy, C.B. (2015).

Biological salience influences performance and acoustic mechanisms for the

discrimination of male and female songs. *Animal Behaviour, 104,* 213-228.

doi:10.1016/j.anbehav.2015.03.023

Hahn, A.H., Hoeschele, M., Guillette, L.M., Hoang, J., McMillan, N., Congdon, J.V., Campbell,

K.A., Mennill, D.J., Otter, K.A., Grava, T., Ratcliffe, L.M., & Sturdy, C.B. (2016).

Black-capped chickadees categorize songs based on features that vary geographically.

Animal Behaviour, 112, 93-104. doi:10.1016/j.anbehav.2015.11.017

Herrnstein, R.J. (1990). Levels of stimulus control: a function approach. *Cognition, 37,* 133-166.

doi: 10.1016/0010-0277(90)90021-B

Hill, B.G., & Lein, M.R. (1987). Function of frequency-shifted songs of black-capped

chickadees. *Condor, 89,* 914-915. doi:10.2307/1368543

Hoeschele, M., Guillette, L.M., & Sturdy, C.B. (2012). Biological relevance of acoustic signal

affects discrimination performance in a songbird. *Animal Cognition, 15*(4), 677-688. doi:

10.1007/s10071-012-0496-8

Hoeschele, M., Moscicki, M.K., Otter, K.A., van Oort, H., Fort, K.T., Farrell, T.M., Lee, H., Robson, S.W.J., & Sturdy, C.B. (2010). Dominance signaled in an acoustic ornament. *Animal Behaviour, 79*(3), 657-664. doi:10.1016/j.anbehav.2009.12.015

Horn, A.G., Leonard, M.L., Ratcliffe, L., Shackleton, S.A., & Weisman, R.G. (1992). Frequency variation in songs of black-capped chickadees (*Parus atricapillus*). *Auk, 109,* 847-852. doi:10.2307/4088158

Kling, J.W., & Riggs, L.A. (1971). *Woodworth and Scholsberg's experimental psychology.* New York, NY: Holt, Rinehart & Winston

Koren, L., & Geffen, E. (2009). Complex call in male rock hyrax (*Procavia capensis*) a multi-information distributing channel. *Behavioral Ecology and Sociobiology, 63,* 581-590. doi: 10.1007/s00265-008-0693-2

Kriengwatana, B. Spierings, M.J., & ten Cate, C. (2016). Auditory discrimination learning in zebra finches: effects of sex, early life conditions and stimulus characteristics. *Animal Behaviour, 116,* 99-112. doi:10.1016/j.anbehav.2016.03.028

Leitão, A., ten Cate, C., & Riebel, K. (2006). Within-song complexity in a songbird is meaningful to both male and female receivers. *Animal Behaviour, 71,* 1289-1296. doi:10.1016.j.anbehav.2005.08.008

Leonard, M.L., & Horn, A.G. (1995). Crowing in relation to status in roosters. *Animal Behavior, 49*(5)*,* 1283-1290. doi:10.1006/anbe.1995.0160

Maney, D.L. (2013). The incentive salience of courtship vocalizations: Hormone-mediated 'wanting' in the auditory system. *Hearing Research, 305,* 19-30. doi:10.1016/j.heares.2013.04.011

Mathevon, N., Koralek, A., Weldele, M., Glickman, S.E., & Theunissen, F.E. (2010). What the hyena's laugh tells: sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta. BMC Ecology, 10,* 9. doi: 10.1186/1472-6785-10-9

Mennill, D.J., Doucet, S.M., Montgomerie, R., & Ratcliffe, L.M. (2003). Achromatic color variation in black-capped chickadees, *Poecile atricapilla*: black and white signals of sex and rank. *Behavioral Ecology and Sociobiology, 53,* 350-357. doi:10.1007/s00265-003-0581-8

Mennill, D.J., Ramsay, S.M., Boag, P.T., & Ratcliffe, L.M. (2004). Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology. 15.* 757-765. doi:10.1093/beheco/arh076

Mennill, D.J., & Ratcliffe, L.M. (2004). Overlapping and matching in the song contests of black-capped chickadees. *Animal Behaviour, 67*(3)*,* 441-450. doi:10.1016/j.anbehav.2003.04.010

Mennill, D.J., Ratcliffe, L.M., & Boag, P.T. (2002). Female eavesdropping on male song contests in songbirds. *Science, 296,* 873. doi:10.1126/science.296.5569.873

Møller, A.P. (1987). Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signaling. *Animal Behaviour, 35*(6)*,* 1637-1644. doi:10.1016/S0003-3472(87)80056-8

Neuringer, A. (2002). Operant variability: evidence, functions, and theory. *Psychonomic Bulletin & Review, 9*(4), 672-705. doi:10.3758/BF03196324

Njegovan, M., Hilhorst, B., Ferguson, S., & Weisman, R. (1994). A motor-driven feeder for operant training in song birds. *Behavior Research Methods, Instruments, & Computers, 26*(1), 326-27. doi:10.3758/BF03204558

Otter, K.A., Chruszcz, B., & Ratcliffe, L. (1997). Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology, 8*, 167-178. doi:10.1093/beheco/8.2.167

Otter, K., Ratcliffe, L., Michaud, D., & Boag, P.T. (1998). Do female black-capped chickadees prefer high ranking males as extra-pair partners? *Behavioral Ecology and Sociobiology, 43,* 25-36. doi:10.1007/s002650050463

Palya, W.L., & Walter, D.E. (2001). *Document set for the high-performance experiment controller.* http://www.jsu.edu/depart/psychology/sebac/Exp-Ctl.html.

Pyle, P. (1997). *Identification guide to North American birds.* Bolinas, CA: Slate Creek Press

Ratcliffe, L., & Weisman, R.G. (1985). Frequency shift in the *fee bee* song of the black-capped chickadee. *Condor, 87,* 555-556. doi:10.2307/1367963

Ratcliffe, L., & Otter, K. (1996). Sex differences in song recognition. In D.E. Kroodsma & E.H. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds* (pp. 339-356). Ithaca, NY: Cornell University Press

Riters, L.V., Ellis, J.M.S., Angyal, C.S., Borkowski, V.J., Cordes, M.A., & Stevenson, S.A. (2013). Links between breeding readiness, opioid immunolabeling, and the affective state

induced by hearing male courtship song in female European starlings (*Sturnus vulgaris*). *Behavioural Brain Research, 247,* 117-124. doi:10.1016/j.bbr.2013.02.041

Schjelderup-Ebbe, T. (1975). Contributions to the social psychology of the domestic chicken. (M. Schleidt & W.M. Schleidt, Trans.). In, Schein, M.W. (Ed.). "Social Hierarchy and Dominance. Benchmark Papers in Animal Behavior, Volume 3. Stroudsburg, PA: Dowden, Hutchinson & Ross, Inc., pp. 35-49. (Reprinted from *Z. Psychol.,* 1922. 88*:* 225-252)

Schubert, K.A., Mennill, D.J., Ramsay, S.M., Otter, K.A., Boag, P.T., & Ratcliffe, L.M. (2007). Variation in social rank acquisition influences lifetime reproductive success in black-capped chickadees. *Biological Journal of the Linnean Society, 90,* 85-95. doi: 10.1111/j.1095-8312.2007.00713.x

Smith, S.M. (1988). Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour, 107,* 15-23. doi:10.1163/156853988X00160

Smith, S.M. (1991). *The Black-capped Chickadee: Behavioral Ecology and Natural History.* Cornell University Press, Ithaca, NY

Sturdy, C.B., & Weisman, R.G. (2006). Rationale and methodology for testing auditory cognition in songbirds. *Behavioural Processes, 72,* 265-272. doi:10.3758/BF03204558

van Oort, H., Otter, K.A., Fort, K.T., & Holschuh, C.I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. *Ethology, 112,* 772-778. doi:10.1111/j.1439-0310.2006.01228.x

Vannoni, E., & McElligott, A.G. (2008). Low frequency groans indicate larger and more

dominant fallow deer (*Dama dama*) males. *PLoS ONE, 3(9):*e3113.

doi:10.1371/journal.pone.0003113

Verbeek, M.E.M., Boon, A., & Drent, P.J. (1996). Exploration, aggressive behaviour and

dominance in pair-wise confrontations of juvenile male great tits. *Behaviour, 133*(11),

945-963. doi:10.1163/156853996X00314

Verbeek, M.E.M., de Goede, P., Drent, P.J., Wiepkema, P.R. (1999). Individual behavioural

characteristics and dominance in aviary groups of great tits. *Behaviour, 136*(1), 23-48.

doi: 10.1163/156853999500659

Weisman, R.G., Ratcliffe, L.M., Johnsrude, I., & Hurly, T.A. (1990). Absolute and relative pitch

production in the song of the black-capped chickadee. *Condor, 92,* 118-124.

doi:10.2307/1368390

West, M.J., King, A.P., & Eastzer, D.H. (1981). The cowbird: reflections on development from

an unlikely source. *American Scientist, 69,* 56-66

Wiley, R.H., Steadman, L., Chadwick, L., & Wollerman, L. (1999). Social inertia in white-

throated sparrows results from recognition of opponents. *Animal Behaviour, 57,* 453-463.

doi: 10.1006/anbe.1998.0991