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University of Alberta

Multiple frequency range discriminations in Chickadees (*Poecile atricapillus* and *P. gambeli*) and Finches (*Taeniopygia guttata*)

by

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Abstract

The pitch, or frequency, of many songbird vocalizations plays an integral role in species recognition. Two species of chickadees (*Poecile atricapillus* and *P. gambeli*) along with zebra finches (*Taeniopygia guttata*) were trained to sort frequencies ranging from 980 Hz to 5660 Hz, arranged into contiguous rewarded and non-rewarded ranges, in a GO/NOGO operant conditioning task. To assess whether the birds memorized or categorized frequency by range, a transfer test was also conducted. Results replicated those previously reported in that zebra finches performed at a high level of accuracy and outperformed both species of chickadees. Interestingly, male and female chickadees did not differ in their absolute pitch perception abilities. This is in contrast to previous work showing a marked sex difference in zebra finches with males outperforming females. Furthermore, results of the transfer suggest that all three species were able to categorize novel stimuli by the contingency placed on the ranges during training. The relatively poor performance and lack of sex differences in chickadees may be due to a combination of ecological, developmental, evolutionary and neurobiological factors.

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List of Abbreviations

BCCH   Black-capped chickadee

CI   Stimuli responded to above the 95% confidence interval

DR   Discrimination ratio = average percentage of response to S+ tones divided by the sum of the average percentage of response to S+ and S- tones

MOCH   Mountain Chickadee

TRCRIT   Trials to criterion

S+   Rewarded stimuli

S-   Unrewarded stimuli

ZB   Zebra finch

Acoustic communication plays a crucial role in the survival of oscine birds (i.e., true songbirds). So crucial is acoustic communication, in fact, that songbirds have evolved specialized perceptual processes that facilitate the recognition and discrimination of acoustic signals such as calls and songs. Catchpole and Slater (1995) differentiate between songs and calls by context in which the vocalization is produced and its complexity – though these are not rigid criterion. They describe calls as shorter, simpler contact vocalizations that are produced year round (e.g. alarm of predators) by both sexes of a species. On the other hand, songs are defined as longer, more complex vocalizations often produced by males during aggressive interactions and mate attraction. These descriptions, while generally accurate of temperate birds, do not fit as well with tropical species in which females commonly produce songs and are comparable to complexity of male song (Morton, 1996). While these bioacoustical definitions are not accurate of all species, the terms are still used in the literature, making the distinction useful to understand.

These perceptual processes mentioned above aid in the discrimination of individual conspecifics and between con- and heterospecifics. Ultimately, these abilities are pivotal in allowing songbirds to acquire and defend a territory, select a mate and engage in conspecific communication. Among the many species of songbirds (~ 5000), chickadees (e.g., black-capped chickadees, *Poecile atricapillus* and mountain chickadees, *P. gambeli*) belong to a genus whose vocalizations

and behaviours are well studied (for a reviews see Hailman, 1989; Hailman & Ficken, 1996). This, combined with the fact that they are amenable to perceptual testing in a laboratory setting, makes them ideal species to study the mechanisms involved in pitch perception.

The black-capped chickadee is a common songbird found extensively across North America, inhabiting deciduous and mixed deciduous/coniferous regions (Smith, 1993). In contrast, the black-capped chickadee's closest relative (Gill, Mostrom & Mack, 1993), the mountain chickadee, is far less widespread in its distribution, preferring coniferous and mixed coniferous/deciduous areas in alpine regions (McCallum, Grundel & Dahiston, 1999). Further, there are unique geographical regions (e.g., areas in the Rocky Mountains) where black-capped and mountain chickadees live sympatrically, thus making it crucial for each species to discriminate conspecifics from heterospecifics. The need for accurate species discrimination in these regions of sympatry is enhanced due to the acoustic similarity in congeners' calls and songs (Hill & Lein, 1987, 1989; Lohr, 1995).

Black-capped and mountain chickadees produce a chick-a-dee call that is relatively more complex in structure than their songs. In both species, calls are generally used for signaling alarm and coordinating flock activities (Ficken, Ficken & Witken, 1978). Structurally, the black-capped chickadee call contains four note-types (A, B, C and D), and that always produced in the same order (A →B→C→D), though some notes can be

omitted or repeated within a given call (Ficken et al., 1978; Charrier, Bloomfield & Sturdy, 2004). Mountain chickadees, however, possess six different note types (A, A/B, B, C, D_h, and D), again following a similar order as the black-capped chick-a-dee call (Bloomfield, Charrier & Sturdy, 2004).

Perhaps even more relevant to this study than the species-specific chick-a-dee calls, are the songs of the two chickadees species. Black-capped chickadees and mountain chickadees produce songs that are highly tonal in nature (i.e., cover a narrow frequency bandwidth; Figure 1). Black-capped chickadee song characteristically contains two notes ("fee bee") that are separated by a constant frequency ratio (but see Kroodsma et al., 1995 and Gammon & Baker, 2004 for examples of populations of black-capped chickadees that have multiple song types), independent of the absolute frequency of the first note sung (average frequency of "fee": in normal song = 3900 Hz; Ratcliffe & Weisman, 1985; Weisman, Ratcliffe, Johnsrude & Hurly, 1990; Shackleton & Ratcliffe, 1994). That is, when an individual produces the "fee" note at a higher frequency of their species-typical vocalization range, the "bee" note will be produced at a constant frequency ratio to that of a "fee bee" song produced at a lower pitch. Black-capped chickadees also produce a *shifted* fee bee song that is lower in absolute frequency than the normal fee bee song, but still maintains the same frequency ratio between the two notes (average frequency of first note of shifted song = 3700 Hz; Ratcliffe & Weisman,

Figure 1. Representative spectrogram samples of black-capped and
mountain chickadee song

Male Black-capped chickadee song

Male Mountain Chickadee Song
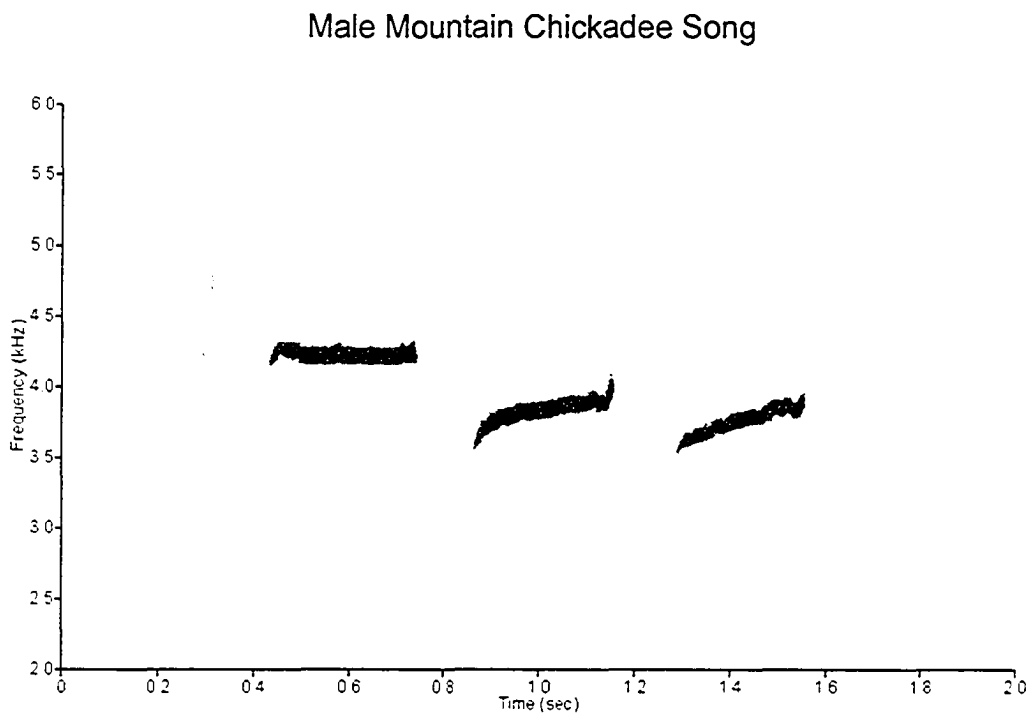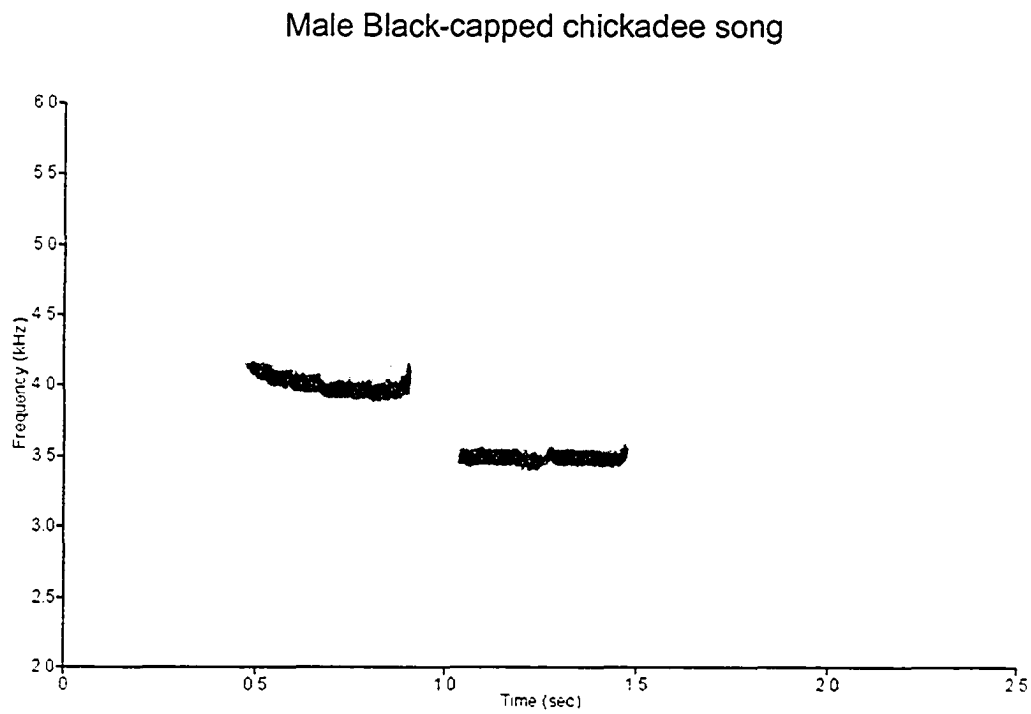
1985).

Mountain chickadees also have a song type similar to the two note song of the black-capped chickadee. Whether the frequency ratios between and within the notes are constant has yet to be shown. In addition to this two note song, they have at least 4 to 6 other song types that consist of between 2-5 notes, all of which descend in frequency from the initial note onward (average start frequency of the first note in mountain chickadee song = 4259 Hz; Lohr, 1995; Wiebe, 1995). Lohr (1995) also describes an introductory element (the vertical line shown in Figure 1 of the mountain chickadee song spectrogram) of the mountain chickadee song that may function as an aid to species discrimination, although this possibility has not been fully tested (B. Lohr, pers. comm.).

Frequency as a cue to species and individual recognition

In many songbird species, song frequency (Hz) is an especially salient cue to species and individual recognition (Nelson, 1988, 1989; Dabelsteen & Pederson, 1985), whether used in an absolute, relative or combined fashion. Absolute pitch perception refers to the capacity to recognize and remember pitches without an external referent (Weisman, Njegovan, Williams, Cohen & Sturdy, 2004). On the other hand, relative pitch perception refers to the capacity to use the relation between two frequencies to recognize and remember pitches (Weisman et al., 2004).

Playback studies conducted in the field have shown that the *absolute* frequency range of songs emerges as the chief species-defining

characteristic superior to all other acoustic features tested in many species. In one such study, field sparrow songs (*Spizella pusilla*) were manipulated to fall outside (i.e., above and below) the species-typical frequency range (Nelson 1988, 1989). Behavioural responses of listening males, such as number of calls and songs and flights over the speaker, were significantly lower following playback of the frequency-altered song (Nelson 1988, 1989).

Other studies investigating *relative* pitch processing have demonstrated greater sensitivity to detecting frequency ratio differences (frequency of note 1 ÷ frequency of note 2) than frequency differences (frequency of note1 − frequency of note 2) in veeries (*Catharus fuscescens*; Weary, Weisman, Lemon, Chin & Mongrain, 1991). In a laboratory study of relative pitch processing, Weisman, Njegovan and Ito (1994) demonstrated that zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*) accurately discriminated pairs of synthetic stimuli of a consistent frequency ratio; however zebra finches also memorized note pairs of varying pitch ratio. Still other studies that investigated both absolute and relative pitch perception simultaneously demonstrated that songbirds possess the ability to process both types of bioacoustic information. When presented with tests including absolute and relative frequency cues, European starlings (*Sturnus vulgaris*) used relative pitch cues to discriminate rising and falling sequences of artificially synthesized tones. When tested with novel stimuli, they correctly discriminated them

(Hulse, Cynx & Humpal, 1984). When faced with novel stimuli only containing absolute pitch cues, however, the birds only accurately discriminated within the frequency range they were initially trained in (Hulse & Cynx, 1985). A subsequent follow-up study with low-ascending and high-descending tone sequences (i.e., absolute and relative pitch cues present), birds quickly learned to discriminate by relative pitch cues after initially using absolute pitch cues (MacDougall-Shackleton & Hulse, 1996). In yet another variation, white-throated sparrows (*Zonotrichia albicollis*) appear to simultaneously attend to both relative and absolute pitch cues in their songs (Hurly, Ratcliffe, Weary & Weisman, 1992) responding differentially to songs that are altered in either relative or absolute pitch characteristics. Taken together, these studies demonstrate that songbirds can learn about both absolute and relative pitch properties, and absolute pitch processing appears to be more dominant, at least for starlings.

Like other songbirds, chickadees also follow this trend of attending to pitch cues in their species song. In fact, Ratcliffe and Weisman (1985) demonstrated that black-capped chickadees are highly sensitive to manipulations of the pitch ratio between the first and second note in their songs. Alterations of the pitch ratio that move it outside species-typical ranges fail to elicit aggressive responses in field playback experiments, reflecting their relative pitch discrimination abilities.

Other evidence that frequency plays a fundamental role in the function of black-capped chickadee song is from studies that measure aggressive interactions. For instance, male chickadees engaged in countersinging contests, communicate aggressiveness and high social rank by producing shifted songs (Hill & Lein, 1987; Mennill, Boag & Ratcliffe, 2003; Weisman & Ratcliffe, 1989). Countersinging contests provide opportunity for: males to evaluate each other (Otter, Ratcliffe, Njegovan & Fotheringham, 2002; Shackleton & Ratcliffe, 1994), gathering of information about neighbouring competitors (Mennill & Ratcliffe, 2004), and females to assess male-reproductive fitness (Mennill et al., 2003).

Despite extensive literature on the production and perception of black-capped chickadee song, little is known about the production and perception of mountain chickadee song. To date, there are no published accounts documenting the behavioural effects, if any, to manipulations of mountain chickadee song. Taken together, songbirds in general and chickadees, in particular, have a specialized perceptual adaptation to facilitate recognition of conspecifics and heterospecifics by vocalizations.

Absolute pitch perception in animals

Most studies in songbird pitch perception used field playback experiments and natural stimuli shifted in pitch. Rather than shifting natural signals, Weisman and colleagues (e.g. 1994, 2004) tested absolute pitch perception using synthetic pure sine wave tones. They demonstrated that two species of songbirds, zebra finches and white-

throated sparrows (*Zontrichia albicollis*), and a parrot species, budgerigars (*Melopsittatus undulatus*), exhibited accurate absolute pitch discrimination performance by the final day of discrimination. On the other hand, humans and rats (*Rattus norvegicus*), were very poor at the same absolute pitch discrimination task (Weisman et al, 2004). The mammalian species did achieve a very modest level of discrimination; however their performance was vastly inferior compared to the avian species. Furthermore, the normally-reared zebra finches exhibited superior performance to all other avian species tested on the final day of performance. In terms of percentage of response on the final day of the task, normally-reared male zebra finches were superior to normally-reared female zebra finches and isolate-reared zebra finches were able to perform the task, though not as accurately as the normally reared zebra finches. Finally, Weisman and colleagues (2004) also demonstrated a significant effect of developmental experience in the finches where normally reared males performed the task with a greater precision than isolated reared males. Normally-reared female zebra finches, however, did not significantly differ from isolate-reared females and males on the final day of the task. These studies of absolute pitch perception across a wide range of species of both sexes, with different experience levels suggest that species, sex and development influence pitch processing abilities.

Since the songs of both black-capped and mountain chickadees are tonal in nature, and black-capped chickadee song contains invariant

relative pitch cues (i.e. the ratio between the frequency of the end of the fee to the start frequency of the bee note and the ratio between the start frequency of the fee and end frequency of the fee are constant), we suggest that frequency may serve as an especially salient feature in recognition of conspecific and heterospecific vocalizations for both species. As a result, these species may be required to have exceptional absolute and relative pitch perception abilities, as has been shown to be the case in other songbird species (Weisman, Njegovan, Sturdy, Phillmore, Coyle & Mewhort, 1998).

We set out to determine the absolute pitch processing abilities in black-capped and mountain chickadees. To do so, we adopted procedures to test absolute pitch perception previously established in human and non-human animals (e.g. Weisman et al., 1998, 2004). We included zebra finches as a control for modifications (new generation set-ups) in equipment and procedures (i.e. food supplementation to maintain health of the chickadees) that we made in the present study. Furthermore, the highly accurate performance of the zebra finches on an absolute pitch perception task also serves as a basis for comparison for the chickadees. In an effort to understand their basic perceptual abilities, we conducted comparative studies of multiple frequency discriminations (as those used in Weisman et al., 1998, 2004) in chickadees to determine the extent of their ability to perceive acoustic stimuli, where differences might emerge according to their degree of phylogenetic relatedness, their ecology, or as

a function of their own distinct vocal repertoires. As a first step, we assessed the chickadees' ability to discriminate absolute pitches. This study was conducted to assess the extent of black-capped chickadee absolute pitch perception, to compare their absolute pitch abilities with a closely related species, the mountain chickadee and finally, to assess the absolute pitch abilities of females (of both species) to males.

<u>Methods</u>

Animals

Sixteen black-capped (8 females and 8 males) and 16 mountain chickadees (8 females and 8 males), in addition to 4 zebra finches (all male) were used. Birds were sexed by blood DNA analysis (Griffiths 2000). All animals were treated in accordance with standards set forth by the Canadian Council on Animal Care and the Biological Sciences Animal Welfare and Policy Committee at the University of Alberta. Chickadees were captured from Kananaskis field station, Alberta, Canada (51° 02'N, 115° 03'W). Black-capped chickadees were also captured on the University of Alberta campus in Edmonton (Alberta, Canada, 53°34'N - 113°25' W). Chickadees were at least second year, as determined assessed by using the shape and colouration of outer retrices (Pyle, 1997). Zebra finches were obtained from a local supplier. Animals were housed in individual cages in the laboratory for at least 1 month. Each species was housed in separate colony rooms and the cages allowed visual and auditory communication but not physical contact between

individuals. All the birds had no prior experience with any of the following experimental procedures or stimuli. The birds were maintained on a light-dark cycle typical for the season in Edmonton, Alberta. The colony room temperatures were maintained at about 20° C.

Birds could access food (Mazuri; Canadian Food Lab diets), grit, cuttle bone, and water (which was treated with vitamin supplements three times a week; Hagen Vitamin Supplement Conditioner for Birds) ad libitum. Once a week, as a nutritional supplement, birds received a small amount of hard-boiled egg mixed with spinach and were given a meal worm three times a week.

During training and testing, however, access to food (Mazuri) was provided only during visits to the automated feeder, and a mealworm provided each day. Additional supplements outlined above were provided on days that birds were not run on the task (i.e. free-feed days between phases of the task).

Apparatus

During training and testing periods, birds were housed in modified budgerigar cages (0.3m wide x 0.4m high x 0.4m deep) with an opening (11 x 16 cm) in the cage aligned to the feeder, allowing access to food. To ensure the birds did not have access to spilled food, a mesh floor was attached to the bottom of the cage. Also, the cages had several perches and dispensers for water and grit. Each cage was housed in a ventilated, sound-attenuating chamber illuminated by a 9-W twin-tube full-spectrum

fluorescent bulb. Infrared cells monitored a motor-driven feeder mounted beside the cage and a perch opposite the feeder entrance monitored the bird's position. A standard CD-ROM interfaced with a PC computer was used to control the experiment and record responses to stimuli. Tone stimuli were played from CD-ROM drives in computers that were attached to either a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or NAD 310 Integrated Amplifier which were flat through the frequency range tested here. Tones were played through a Fostex FE108Σ full-range speaker (frequency range 80-18,000 Hz; Fostex Corp., Japan) located beside the feeder with the centre of the driver at about the height of the bird.

Calibration of stimuli in the operant chambers was individually performed using an Integrating Sound Level Meter Type 2239A (Brüel & Kjær, Denmark). Tones from the stimulus set were played in each operant box and measured periodically on the sound level meter in order to maintain consistency of tones played through the speakers among the operant chambers used for testing.

Stimuli

Pure tone stimuli were synthesized using Signal 4.0 for Windows (Engineering Design, Belmont, Massachusetts) at 44,100 Hz, 16 bit samples per second. In total, 80 tones were synthesized ranging from 980 – 5660 Hz (at 70 and 80 dB SPL; Table 1) for Acquisition. For the Transfer stage, 64 novel tones were synthesized between 1040-5600 Hz (at 70 and

80 dB SPL; Table 2). Only those novel stimuli that fell within a range were tested because those falling between ranges were too ambiguous.

All tones were 440 ms in duration. Each tone was given a 5 ms rise/fall time to avoid transients (i.e. sudden changes in frequency that may cause popping noises). In order to control for possible effects of amplitude cues on the frequency range discriminations, two different amplitudes (70 dB sound pressure level (SPL) and 80 dB SPL) for each frequency were synthesized. Each bird received two different versions of the set of stimuli in which the amplitude of the tones were randomly assigned (half of the tones were 70 dB SPL and the remaining were 80 dB SPL). Therefore, on a given day, birds received a full set of stimuli (40 tones); however, each individual tone was either of the two amplitude sets chosen (i.e. 980 Hz at 70 dB SPL). The following day, the second version of the tone set was presented (i.e., 980 Hz at 80 dB SPL).

Table 1. Frequencies (Hz) of S+ (rewarded) tones and S- (nonrewarded) tones for the S- first and S+ first groups for the Acquisition phase.

Frequency Range	S- First Group	S+ First Group	Frequency (Hz)				
1	S-	S+	980	1100	1220	1340	1460
2	S+	S-	1580	1700	1820	1940	2060
3	S-	S+	2180	2300	2420	2540	2660
4	S+	S-	2780	2900	3020	3140	3260
5	S-	S+	3380	3500	3620	3740	3860
6	S+	S-	3980	4100	4220	4340	4460
7	S-	S+	4580	4700	4820	4940	5060
8	S+	S-	5180	5300	5420	5540	5660

Table 2. Frequencies (Hz) of novel stimuli for the Transfer phase (100%

reinforced) and the range in which they fall based on the tones from the

Acquisition phase

Frequency Range	S- First Group	S+ First Group	Frequency (Hz)			
1	S-	S+	1040	1160	1280	1400
2	S+	S-	1640	1760	1880	2000
3	S-	S+	2240	2360	2480	2600
4	S+	S-	2840	2960	3080	3200
5	S-	S+	3440	3560	3680	3800
6	S+	S-	4040	4160	4280	4400
7	S-	S+	4640	4760	4880	5000
8	S+	S-	5240	5360	5480	5600

Procedure

A standard GO/NOGO procedure (see below) was used to assess the multiple frequency range discrimination abilities of the black-capped and mountain chickadees (e.g., Sturdy et al., 2000). Data were collected daily in 500 trial bins for Training and Acquisition stages and in 816-trial bins for the Transfer phase.

Training

Birds were trained to use the perch to request a stimulus (i.e., to initiate a trial) and then to respond by going to the feeder (GO response) or withhold responding (NOGO response). During a trial, birds waited on a request perch for a randomly selected time interval between 900-1100 milliseconds while the speaker was silent. Following this interval, and when a tone was played, birds flew to the feeder and broke an infrared beam to receive the food reinforcement. However, when no tone was heard, birds had to refrain from responding (the NOGO response) or they would be punished with 30-seconds of lights out. Additionally, to ensure that birds paid attention to the stimuli, a time-out procedure was instituted. If birds flew off the request perch before the stimulus finished playing, they were punished with a 30 second lights out period.

During pre-training, birds were exposed to the two (70 or 80 dB SPL) versions of the stimulus set on alternating days. They received 100% reinforcement for giving the "GO" response to all the tones. This would ensure that the birds would not respond differentially to the tones. Once

birds learned to use the perch and feeder, pre-training began and continued until birds responded to all tones about equally and at least 60% of the time. Once the birds responded to all the tones at a high and consistent level (about 3,000 trials or 3 days), they were then moved on to discrimination training.

Discrimination Training

Discrimination contingencies were then instituted on the same set of stimuli as used during pre-training. Each stimulus was either rewarded (S+) or unrewarded (S-). The stimulus set of 40 frequency tones were broken up into 8 ranges (i.e., 5 consecutive tones per range). Birds were assigned to one of two discrimination groups, S+ first or S- first. The S+ first group received food reinforcement for the first, third, fifth and seventh ranges of five stimuli each while the S- group received food reinforcement for the second, fourth, sixth and eighth ranges (Table 1). All other procedures remained the same as during pre-training.

Discrimination criterion was such that birds were required to have a discrimination ratio for rewarded tones equal to or greater than 0.80 over 3,000 consecutive trials (roughly 3 days; see *Response measures and statistical analyses for definition*) or a maximum of 15,000 trials, which ever was achieved first. This maximum number of trials was chosen based on the results of previous research (Weisman et al., 1998), which allowed for 10 days of training (roughly 10,000 trials) for zebra finches to acquire this task. However, in order to ensure that the chickadees were given

adequate opportunity to acquire the task accurately, we increased the maximum time for training to 15,000 trials.

To assess whether the birds were simply memorizing the tones learned during Acquisition or were learning that certain frequency ranges were rewarded and unrewarded (i.e., categorizing tones based on frequency range), we instituted a transfer procedure that exposed the birds to novel stimuli. These stimuli were 60 Hz from each adjacent training stimulus and we only tested birds with unambiguous stimuli, that is, those that were within the rewarded and unrewarded ranges (Table 2). Given that the Weber fraction for several species of songbirds is between 1-2% (Dooling, 1982), it is reasonable to suggest that chickadees would certainly be able to detect frequency differences of 60 Hz through most of the frequency range tested.

Initially, we presented seven of the chickadees with all of the novel stimuli in one day-long session at 100% reinforcement across all of the tones. However, the birds did not appear to respond appropriately to these tones. In some cases, birds very quickly learned that all novel tones were reinforced at 100% and adjusted their behaviour accordingly, responding to all test stimuli at a high rate. By contrast, other birds did not respond at all, withholding all flights to the feeder at presentation of novel tones. Due to these setbacks, we tested all remaining birds using an alternate, more covert, testing regime described below.

Transfer

Once the birds met criterion or reached the maximum 15, 000 trials, we allowed the birds to have two days of free feed. Following this, the bird was returned to discrimination training and then alternated between discrimination training and testing to ensure that they maintained the same level of discrimination through the transfer stage.

In this modified testing procedure, we presented all 80 tones from Acquisition, along with probe trials in which 16 novel stimuli (25% of the 64 novel tones) were given on each of four testing days. Thus, there were four different "sets" of transfer days, interspersed with four days of discrimination tones only. During a transfer day, each discrimination tone was presented 10 times and probe (novel) stimuli were presented once, with 100% reinforcement.

Response measures and statistical analyses

As a gross measure, we tallied the number of trials required for a given bird to reach criterion (TCRIT). Birds that did not achieve criterion were still assigned a value of 15,000 trials for analysis because this was the maximum number of trials allowed.

A general indication of the birds' ability to discriminate the stimuli is known as a discrimination ratio. For our criterion, birds must have had a discrimination ratio (DR) greater than or equal to 0.80. We calculated this value by dividing the average percentage of response to rewarded tones by the total average percentage of response to rewarded and unrewarded

stimuli.

However, it is possible that an individual bird may be able to discriminate a particular S+ stimulus very accurately, but not others. Therefore, we adopted a method used in previous studies (Weisman et al., 1994; Weisman et al., 2004) in which we used the two-tailed 95% confidence interval. This would allow us to determine how many of the S+ tones were discriminable from S- tones. Initially, the 95% confidence interval was calculated from the mean and standard deviations of the percentages of response to the S- tones for each bin (500 trials). We then tallied the number of S+ tones at which the bird's percentage of response was higher than the 95% confidence interval for that bin of trials, then divided that value by 20 (there were 20 S+ tones) to yield a proportion. Since the data were not normally distributed, we calculated the 95% confidence interval based on the data we collected using a bootstrap (R for Windows, version 1.7.1). Thus, all CI data presented here were calculated using a bootstrapping and randomization approach.

Finally, the average percentage of response to each separate tone over the final 1000 trials was calculated for each individual bird. To do this, we used the total number of GO responses to that tone divided by the total number of presentations minus the number of times the bird received a time-out punishment (i.e. when the bird flew to the feeder or away from the feeder before the stimulus finished playing, the lights were extinguished).

For analyses, we used a one-way analysis of variance (ANOVA) to

compare the number of trials to reach criterion for each species, sex, and conditioning procedure (S+ vs. S- first). Following current statistical recommendations (e.g., Moser, Stevens & Watts, 1989; Moser and Stevens 1992), we employed corrections for unequal variances (Welch's correction; Welch 1938) for all one-way ANOVAs, regardless of the results of heteroscedasticity diagnostic tests. For post-hoc analyses, we used the Games-Howell for unequal variances and sample sizes (Toothaker 1993) using SPSS for Windows (Chicago, USA).

Repeated measures ANOVAs and Tukey's HSD were conducted on DRs and CIs using STATISTICA 6.0 (Statsoft, Tulsa, OK). In the case where zebra finches were included in the analysis, a Tukey-Kramer post-hoc test was used for unequal sample sizes. In calculating DRs, the data may not be distributed normally when values are near 0 and 1. Thus, we calculated a parallel analysis of the square root arcsine transform of all measures (DRs and the proportion of stimuli above the 95% CI values). These analyses showed virtually identical results, therefore, we report only the untransformed data.

Results

Number of trials to criterion

In a one-way ANOVA analyzing the TCRIT, there was a significant difference between species ($F_{(2,12)} = 29.052$, $p < 0.001$). Tukey's tests revealed that zebra finches were faster to reach criterion than both chickadee species ($p = 0.023$ for black-capped chickadees; $p = 0.008$ for

mountain chickadees; Figure 2); however, black-capped chickadees did

not differ from mountain chickadees (p=0.66). Given that only male zebra

finches were included in this study, we excluded their data from the

analysis of the effect of sex and instead conducted these analyses for

chickadees only. Furthermore, since there was no significant difference

between chickadee species on TCRIT, we pooled across species in the

analyses, revealing no effect of sex ($F_{(1,33)}$=1.217, p =0.278) and no

differences between the two discrimination training groups, S+ or S- First

($F_{(1,31)}$=0.188, p=0.668).

Figure 2. Trials to criterion during the Acquisition phase for zebra finches,

black-capped and mountain chickadees
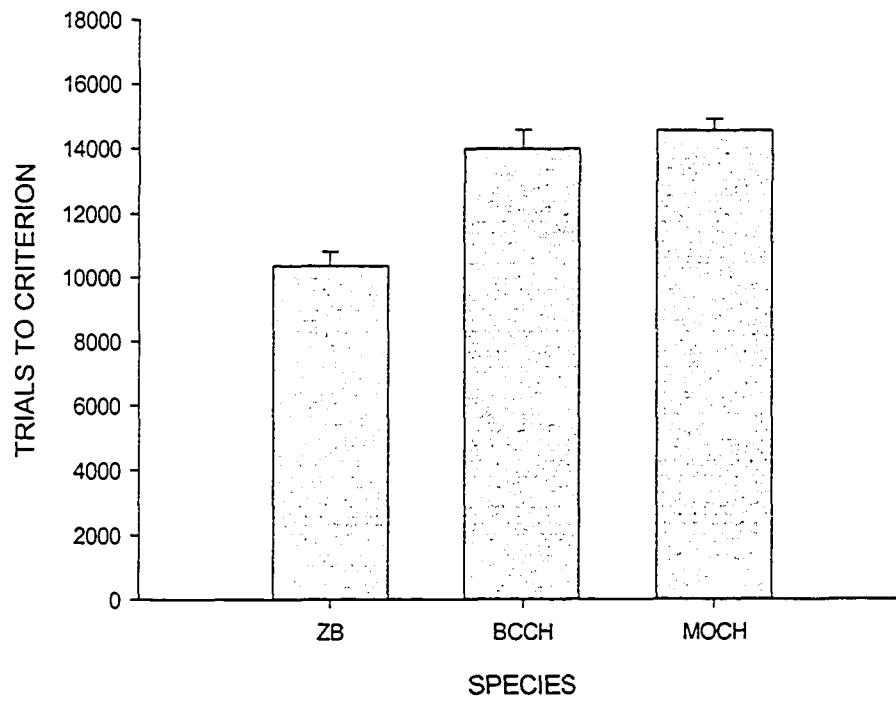
Acquisition

One of the birds, a female black-capped chickadee, reached criterion by 8000 trials of discrimination training. Therefore, analysis of acquisition of DRs and CIs were analyzed only until the 8000th trial. We found a significant interaction of species by trials on DR ($F_{(2,30)}$= 3.464, $\underline{p}$<0.0001; see Figure 3, right panel) and the proportion of stimuli above the 95% CI ($F(2,30)$=3.970, $\underline{p}$<0.0001; see figure 3, left panel). Tukey-Kramer tests showed that all three species did not differ, except with illogical comparisons (e.g. zebra finch at 500 trials versus mountain chickadees at 6000 trials) for DR. Post-hoc analyses on CI data showed only two significant and meaningful comparisons.

Again, when analyzing the effect of sex, male zebra finches were excluded. Furthermore, there were no significant differences between the two chickadee species, allowing us to pool the data over species. Repeated measures ANOVA revealed no significant effect of sex on acquisition as measured by DR ($F_{(1,24)}$=0.769, $\underline{p}$=0.389) or CI ($F_{(1,24)}$=0.545, $\underline{p}$=0.467), but there was a significant main effect of trials for both DRs ($F_{(15,360)}$=60.474, $\underline{p}$<0.0001) and CIs ($F_{(15,360)}$=54.369, $\underline{p}$<0.0001).

Finally, there was no significant difference between the two discrimination groups in performance measured either by DRs ($F_{(1,30)}$=0.736, $\underline{p}$=0.398) or CIs ($F_{(1,30)}$=0.808, $\underline{p}$=0.376). Again, there was a significant main effect of trials in which birds achieved higher DRs

Figure 3. Average discrimination ratio (left panels) and proportion of

stimuli that birds responded to above the 95% confidence interval (right

panels) for zebra finches (ZB), black-capped (BCCH) and mountain

chickadees (MOCH) during Acquisition.
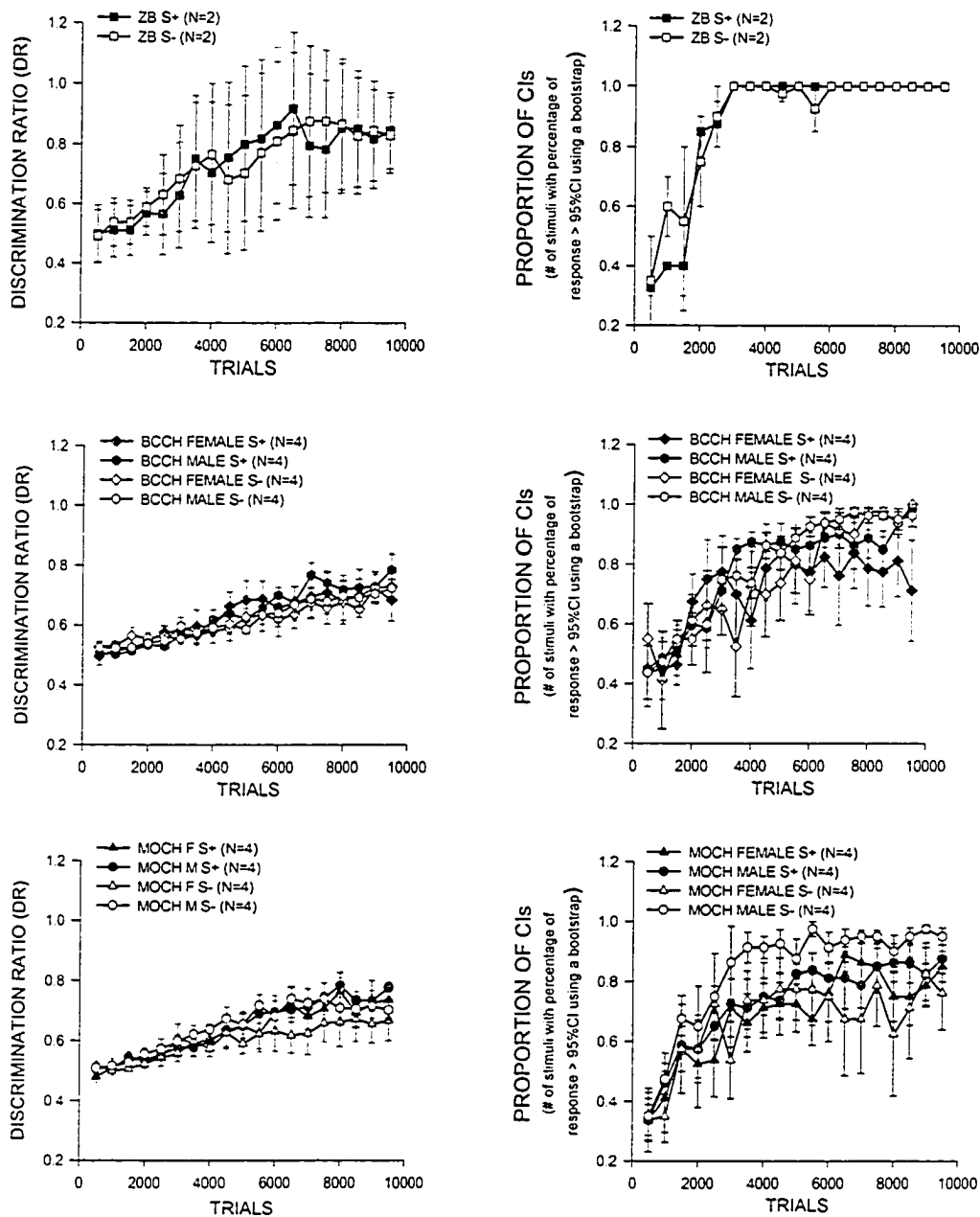
$(F_{(15,450)}=55.06, \underline{p}<0.0001)$ and proportion of CIs $(F_{(15,450)}=63.864,$ $\underline{p}<0.0001)$ across successive trials.

Final 1000 trials of Acquisition

On this measure, the average percentage of response to all S+ tones and S- tones within the final 1000 trials of Acquisition were calculated for each individual bird and then compared across species, sex and training procedure. Percentage response to each of the forty tones on the final 1000 trials by species and training procedure is depicted in Figure 4. Analysis of the average percentage of response to S+ and S- tones showed significant differences between species $(F_{(2,22)}=4.45, \underline{p}=0.024$ and $F_{(2,22)}=4.962, \underline{p}=0.017$ respectively). Games-Howell tests showed that, in general, zebra finches responded about 12% more than mountain chickadees to S+ tones $(\underline{p}=0.041)$, whereas there were no significant differences between black-capped chickadees and zebra finches $(\underline{p}=0.263)$ or mountain chickadees $(\underline{p}=0.729)$. The post-hoc analyses of the average percentage of response to S- tones, however, showed that zebra finches responded about 7.6% less than black-capped chickadees to S- tones $(\underline{p}=0.049)$.

To establish whether there were any differences in responding between males and females, we excluded zebra finch data since only males were tested and focused only on chickadees. We found no significant effect of sex between the two species of chickadee for S+ tones $(F_{(1,24)}=0.649, \underline{p}=0.43)$. However, there was a significant main effect of

Figure 4. Average percentage of response to individual tones during

Acquisition for zebra finches (ZB), black-capped (BCCH) and mountain

chickadees (MOCH).
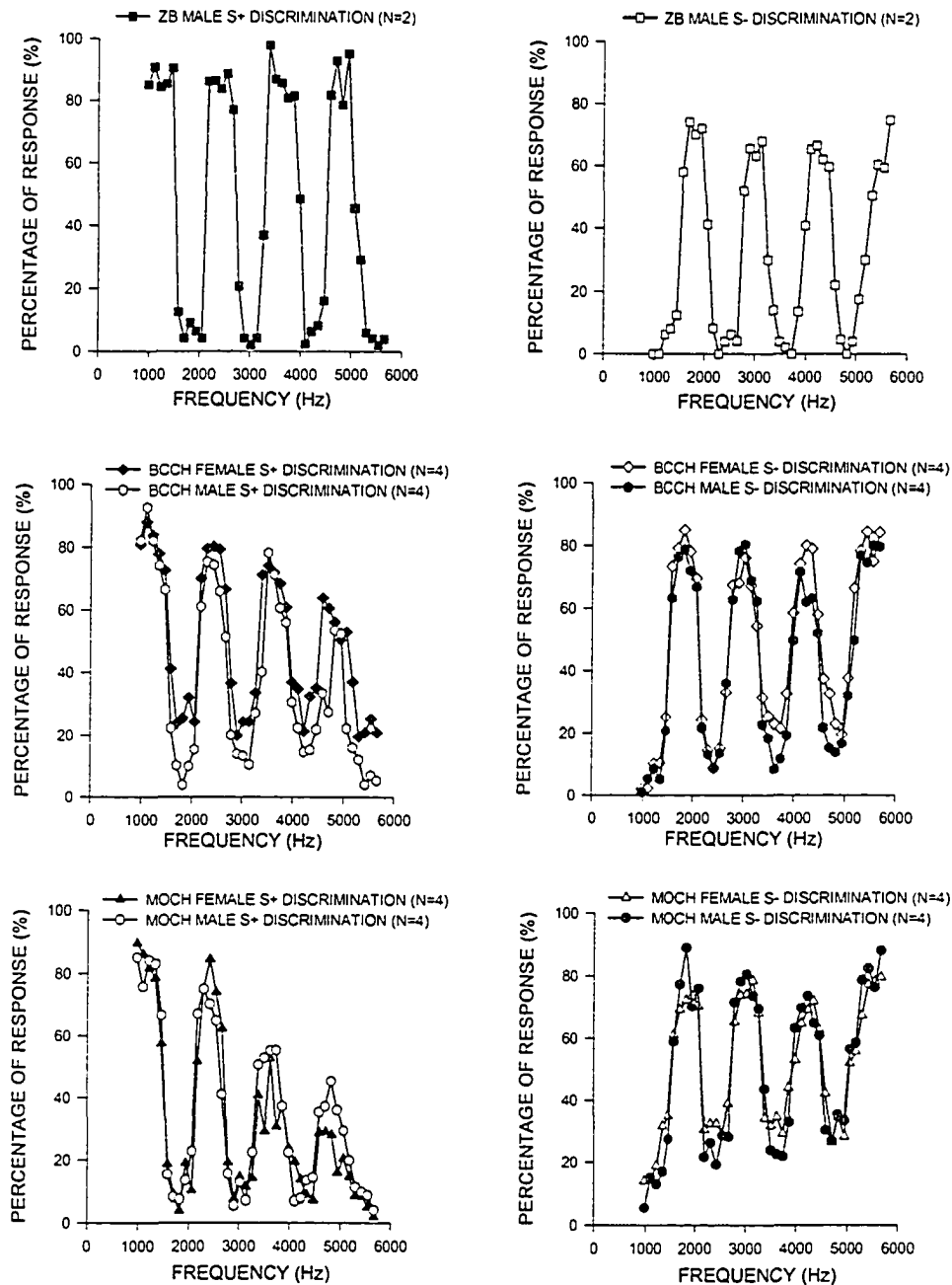
sex for the average percentage of response to S- tones in which females tended to respond to S- tones about 8% more than males ($F_{(1,24)}=6.28$, $\underline{p}<0.05$).

Closer investigation of the average percentage of response over each individual frequency range, again, conducted for chickadees only, revealed no significant differences between species ($F_{(16,26)}=0.89$, $\underline{p}=0.589$) or sex ($F_{(8,15)}=0.705$, $\underline{p}=0.684$) over any of the ranges.

Transfer

We compared the average percentage of responses to novel stimuli that fell into ranges of the training S+ tones and S- tones using a repeated measures ANOVA. For this analysis, we had to exclude the first 7 birds that were run through the initial transfer procedure and birds that we were unable to run in the transfer stage (3 birds that completed discrimination training while still in good health died prior to the completion of transfer training). Thus, eleven black-capped chickadees (4 females and 1 male removed) and eleven mountain chickadees (3 males and 2 females removed) were included for comparison (Figure 5). We found that there were no species differences in average percentage of response to novel tones in the S+ range for species ($F_{(2,23)}=1.025$, $\underline{p}=0.374$) or phase (i.e. acquisition or transfer; $F_{(1,23)}=1.56$, $\underline{p}=0.231$). There was also no significant differences between species ($F_{(2,23)}=0.604$, $\underline{p}=0.550$) or phase ($F_{(1,23)}=0.023$, $\underline{p}=0.879$) for tones in the S- range.

We then compared the average percentage of responses to S+ and

Figure 5. Comparison of the average percentage of response to novel stimuli during Transfer and training tones during Acquisition for zebra finches (ZB), black-capped (BCCH) and mountain chickadees (MOCH)
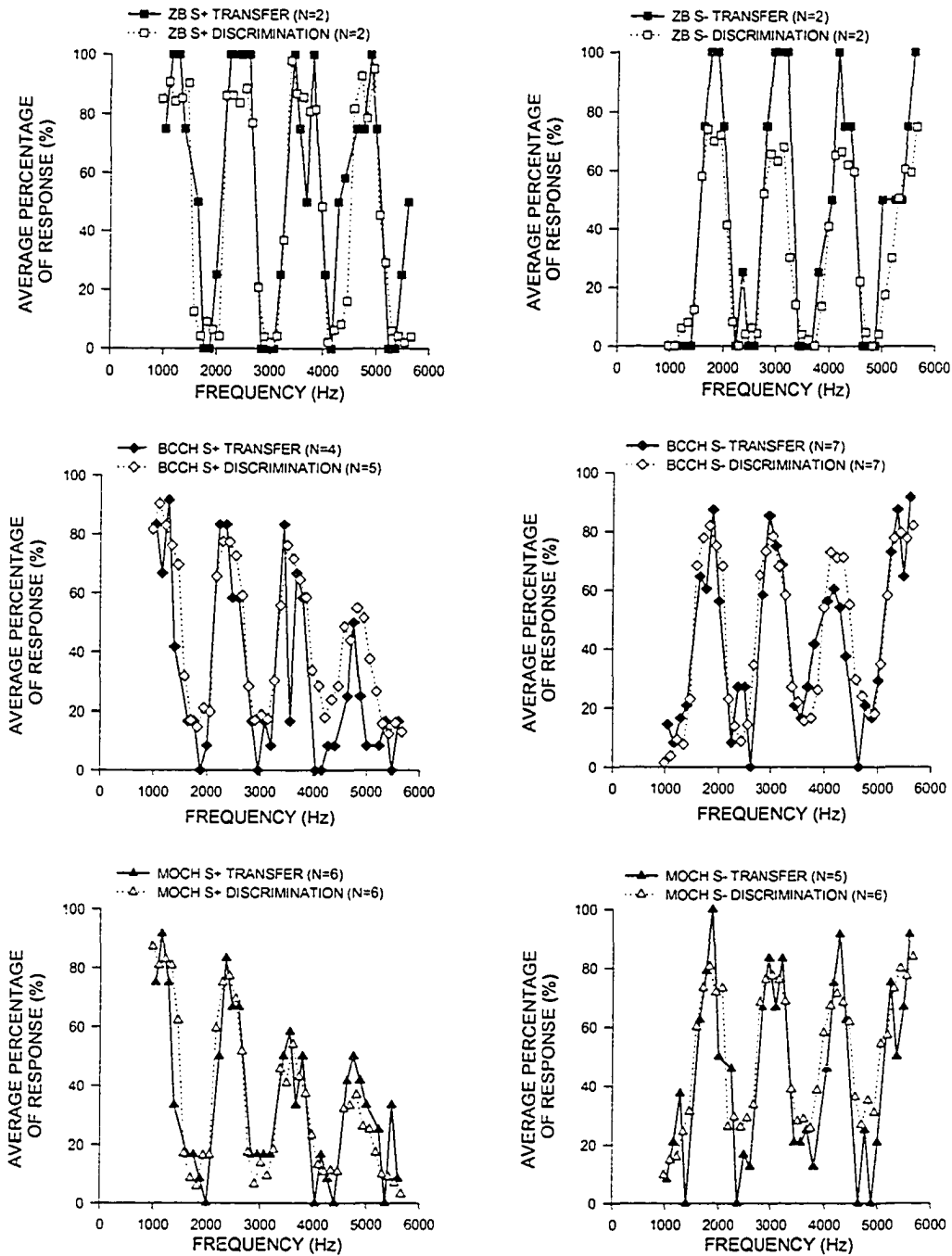
S- tones (during discrimination) with the novel tones that fell within each corresponding range (during the transfer). In this analysis, there were no significant effects of species ($F_{(16,26)}=1.52$, $p=0.167$) or phase ($F_{(8,11)}=1.78$, $p=0.19$). Finally, to investigate the effect of sex on the chickadees, we excluded the zebra finch data and pooled over species for analysis. We found no main effect of sex ($F_{(8,11)}=1.89$, $p=0.162$) or phase ($F_{(8,11)}=2.35$, $p=0.10$).

Discussion

Weisman and colleagues have conducted several studies on absolute pitch perception in several animals, showing that songbirds and parrots are superior to two mammalian species. Here, we report on a comparative study aimed at uncovering absolute pitch processing abilities in two closely-related species of chickadees, black-capped and mountain chickadees compared with zebra finches. These results contribute to Weisman and colleague's studies because, together, it appears that birds in general have superior absolute pitch perception than mammals tested thus far. Furthermore, we include new information demonstrating that the species tested here can transfer what they have learned about pitch ranges to novel stimuli, which has not been previously reported.

We had several objectives to this study. First, we wanted to determine the extent of absolute pitch processing abilities of black-capped chickadees. This species relies extensively on relative pitch cues to recognize their species-specific vocal signals (Ratcliffe & Weisman, 1989;

Weisman et al., 1990). However, black-capped chickadees also shift the absolute pitch of their song (while maintaining the pitch ratio) within their species typical frequency range, which could encode information about the identity of an individual (Weisman et al., 1990), even indicating relative social status of the singer (Christie, Mennill & Ratcliffe, 2004). Determining the absolute pitch processing abilities of black-capped chickadees is the first step in understanding how they may be able to discriminate between species and individuals.

Second, we wanted to further determine whether the closest-living congener to the black-capped chickadee, the mountain chickadee, possessed comparable absolute pitch processing abilities. These two species often overlap in territory and share many commonalities in vocal production, yet hybridize very rarely. How then, is species discrimination accomplished?

Thirdly, we wanted to investigate the absolute pitch perception abilities of female black-capped and mountain chickadees. These comparisons were important to make since female chickadees also learn (Hughes, Nowicki & Lohr, 1998) and produce several vocalizations (Smith, 1991) and have comparable sized song control nuclei (MacDougall-Shackleton, Hernandez, Valyear & Clark, 2003). It is thus reasonable to suspect that if the song system plays any role in our absolute pitch discrimination task, that female songbirds (which learn and produce vocalizations) should show less of a deficit, if any, compared to males.

This is in contrast to the case of more sexually dimorphic species, such as zebra finches, that show differences between the sexes in absolute pitch discrimination performance.

Species differences in Acquisition and final performance

Previous studies have reliably demonstrated that zebra finches possess excellent absolute pitch perceptual abilities that are superior to every animal species, including human musicians (Weisman et al., 1998). Our results support are no exception. Male zebra finches acquired the task faster than both species of chickadees when using the trials to criterion as a measure of discrimination performance. On the other hand, they did not differ from the chickadees on discrimination ratio, proportion of stimuli responded to above the 95% confidence interval, or the average percentage of response to S+ and S- tones on final day performance. It is possible that since the zebra finch group size was two, one bird that performed with high accuracy compared to a bird that performed with a lower accuracy ended up having a larger effect on the overall mean (i.e., of the discrimination ratio or proportion of stimuli above the 95% confidence interval). For instance, the left panels of Figure 3 show that the standard error of the discrimination ratio for zebra finches has a wider range than for the two chickadee species, while the reverse is true for the proportion of confidence intervals in which mountain chickadees have the biggest range. Running four additional zebra finches through this task may help clarify any potential differences between the species. That said, past

results and the inspection of each individual zebra finch's data revealed that by and large all finches excelled at this task, by any measure of performance.

Examination of final day performance (Figure 4) confirms what the analysis of proportion of confidence intervals suggested. In both versions of the discrimination, zebra finches directed a large proportion of their responses towards S+ stimuli in all rewarded ranges and very few responses towards S- tones in any range. In contrast, both chickadee species in the S+ first discrimination tended to direct incrementally fewer responses to each successive range of rewarded stimuli (see Figure 4). It is possible that both mountain and black-capped chickadees' hearing were not as sensitive at these frequencies; however, the S- first groups of both species did not exhibit a parallel deficit in these same ranges, making it unlikely that the S+ first birds could not adequately hear the tones. Furthermore, analysis of each individual range failed to show any differences between species, sex and training procedure. It also makes sense that final day performance would show little differences because at this point, most of the birds had already reached our discrimination criterion, forcing performance levels of all birds to be more accurate. Not only that, Dooling (1980) demonstrated that oscine birds' hearing sensitivity is, on average, from about 2, 000 to 8, 000 Hz. There is no reason to suspect that chickadees are an exception.

Transfer to Novel Tones

Did the birds simply learn the absolute pitch of each individual stimulus? In an attempt to answer this question, we included a phase in which novel pitches of tones were presented. Following completion of discrimination training, we tested whether birds would generalize their discrimination training to novel tones not previously heard. In general, all birds tested, regardless of species or sex, showed at least some evidence of transfer from the training tones to the novel testing tones (see Figure 5). Moreover, the pattern of responding to transfer tones for all birds followed the patterns of responding towards training stimuli in the last 1000 trials of acquisition. Zebra finches produced testing data that more closely followed that of their final performance than both chickadee species, suggesting that zebra finches are, in fact, better at categorizing absolute pitch by range; however these differences were not statistically significant. *Why are zebra finches so good at absolute pitch tasks?*

We replicate the findings of Weisman and colleagues (1998, 2004) that male zebra finches are excellent at discriminating absolute pitch. In addition, zebra finch superiority in discriminating absolute pitch is further demonstrated in how accurately they discriminate novel stimuli and show higher accuracy compared to the two chickadee species, though not statistically significant, which has not been previously reported. This may be in part, due to behavioural differences. Black-capped and mountain chickadees convincingly demonstrate that they can acquire the task. Any differences in performance by the final day of discrimination are relatively

small when compared to zebra finches. While engaged in daily maintenance of the birds, casual observations suggest that the male zebra finches were relatively calm while the black-capped chickadees were noticeably more active. Mountain chickadees appeared to be somewhere between the behaviour of the zebra finches and black-capped chickadees. Thus, it is these behavioural differences that may have allowed the zebra finches to pay greater attention to the discrimination task than the chickadee species.

Lack of sex differences in absolute pitch discrimination performance

In the current study, female chickadees performed at a similar level to males. In fact, the fastest bird to reach discrimination criterion was a female black-capped chickadee (8000 trials). Why did male and female black-capped and mountain chickadees lack differences in performance of absolute pitch discrimination? The fact that female mountain chickadees exhibited similar performance to males in our absolute pitch discrimination task suggests that they also possess a specialized ability for pitch processing. Currently, there is little research on acoustic production and perception in mountain chickadee song. However, the results of this study suggest that female mountain chickadees may use song in a similar fashion to female black-capped chickadees, though it remains to be studied extensively.

In terms of female black-capped chickadees, previous research determined that females possess measurable song control nuclei

(MacDougall-Shackleton, Hernandez, Valyear & Clark, 2003) and also

produce song themselves (Lee, Charrier & Sturdy, submitted). If the song

control nuclei are involved in pitch processing, it makes sense that

females have abilities for absolute pitch processing that are just as

specialized as males. Mennill, Boag and Ratcliffe (2004) also

demonstrated that female black-capped chickadees' reproductive choices

are at least partly influenced by eavesdropping on countersinging

contests, preferring higher ranked males or lower ranked males when they

were engaged in countersinging with "submissive playback". Female

black-capped chickadees must also pay close attention to song because

quality of the male may be encoded in it (Christie, et al., 2004). Based on

this evidence, it is likely that females are heavily reliant on cues from song

in male selection. In the case of absolute pitch discrimination, female

zebra finches and white-throated sparrows do not perform at the same

level as male zebra finches. Unfortunately, a comparison of absolute pitch

perception abilities between male and female white-throated sparrows has

not been tested to date. There may be several reasons for sex differences

in performance of zebra finches. First, other characteristics may influence

or emphasize what the females pay attention to other than the frequency

of the tones. Burley and Coopersmith (1987) showed that female zebra

finches prefer bright red beaks and even demonstrated that female zebra

finches will show preference for red artificial leg bands over light blue

(Burley, 1986). Another alternative is that other features of species song,

such as duration and rate of song, may be crucial for mate selection. Nolan and Hill (2004) found that captive female house finches (*Carpodacus mexicanus*) preferred songs that were longer in duration and sung at a faster rate, but showed no preference for song repertoire size.

Past absolute pitch discrimination experiments revealed some sex differences in male and female zebra finches, where percentage of response levels to the S+ and S- tones were more similar to a perfect sorter in males (Weisman et al., 2004). However, when taking into account the fact that not only did they respond to S+ stimuli more than females, the same is true of S- tones. It is possible then, that male zebra finches were simply more GO-biased than female zebra finches. Although, the mean percentage of response to individual S+ tones in females was noticeably lower than that of males. It is unfortunate that Weisman and colleagues did not present the acquisition data, which may have yielded sex differences. However, the fact remains that all experiments using the paradigm used here show that male zebra finches have the highest accuracy in discriminating absolute pitch when considering both discrimination ratio and percentage of response on the final day of performance.

Female white throated sparrows, on the other hand, showed a deficit in absolute pitch perception abilities compared to male and female zebra finches. Female white-throated sparrows' percentages of response were lower for S+ tones compared to female zebra finches and at similar

levels to S- tones. However, only females were tested, making it difficult to assess general white-throated sparrow abilities. If male white-throated sparrows were also run through this absolute pitch task, we predict that they would perform at similar levels as females. This is because their song is also relatively tonal in nature and males have been shown to be sensitive to relative pitch changes (Hurly, Ratcliffe, Weary & Weisman, 1992).

Absolute and Relative Pitch Perception in Chickadees

A wide body of evidence demonstrates that the black-capped chickadees in nature and in the laboratory use absolute pitch and relative pitch in perception. Two laboratory studies have previously investigated absolute and relative pitch discriminations. The first of these investigated how male black-capped chickadees discriminate relative and absolute pitch cues in both natural and synthetic songs that altered in absolute and relative frequencies using operant conditioning (Weary & Weisman, 1991). This series of studies yielded interesting results in that when tested on novel "songs", they responded more to stimuli that were similar to the positively reinforced training songs in absolute pitch, rather than in the frequency ratio between the two notes.

Furthermore, Njegovan and Weisman (1997) conducted a similar study of absolute and relative pitch perception comparing isolation- and field-reared black-capped chickadees. In this case, they found that the effect of experience with adult song during the development was crucial to

pitch discriminations. Isolation-reared chickadees could learn the tasks; however, these chickadees required four times as many trials to acquire the task as the field-reared chickadees. Instead, it appeared that the isolates attempted to use absolute pitch cues to discriminate the stimuli, but eventually learned to discriminate by relative pitch cues (the frequency ratio between the two pure tone stimuli). Isolation-reared chickadees in Njegovan and Weisman's (1997) relative pitch study initially used a strategy based on absolute pitch for discrimination suggests that absolute pitch may be a more fundamental process. However, exposure to adult tutors may aid in the development of relative pitch processing so that both processes may be used in species and individual recognition.

As mentioned previously, black-capped chickadees often engage in aggressive exchanges through countersinging contests. It has been shown in the field that frequency and temporal matching of songs allows individual chickadees to signal aggressiveness in a graded manner (Otter et al., 2002). In an aggressive encounter, the receiver of the song must be able to accurately assess the absolute frequency of the signal in order to match its own song should it choose to escalate the interaction. Furthermore, individual variations in the ratio between the fee and bee notes associated with pitch shifting in the dawn chorus may indicate the quality of the singer (Christie et al., 2004). In this study, black-capped chickadee song was recorded during the dawn chorus. Findings showed that higher ranking males exhibited less variation in the pitch ratio of their

song despite absolute pitch changes. On the other hand, lower ranking males tended to have a smaller pitch ratio while shifting their song higher in frequency.

Processing Conflict?

It appears that absolute pitch and relative pitch processing may conflict with each other. However, it makes sense that species that rely a great deal on acoustic communication for purposes like flock cohesion, mate attraction and territorial defense have more than one perceptual adaptation in place. Another bioacoustical cue that songbirds use is temporal information. Ratcliffe and Weisman (1986) demonstrated that male black-capped chickadees are also sensitive to note order and number in song. Additionally, Cynx (1993) trained male and female zebra finches to discriminate conspecific songs on two features: absence of individual song syllables and the temporal order of the notes in song. Indeed, the birds could detect the difference as evidenced by a disruption in performance.

Therefore, it is reasonable that vocalizations carry more than one type of information. For instance, the black-capped chickadee song may have to have an absolute pitch that falls within a relatively narrow frequency band as well as a constant frequency ratio between the fee and bee notes to be considered a black-capped chickadee song in addition to potentially giving the listener information about the social status of the singer. That way, if a singer is vocalizing from a distance or in a noisy

environment and part of the song is lost, then the listener may have been able to rely on other cues that aid in conspecific and heterospecific discrimination.

Generality of absolute pitch perception in birds

In several studies of absolute pitch processing, male zebra finches have clearly demonstrated their superiority in absolute pitch discrimination (Weisman et al., 1998, 2004). On the other end of the spectrum, mammalian species such as humans and rats are relatively poor at this task, while a parrot species, budgerigars, are just as accurate as the finches (Weisman et al., 2004). Other species of songbirds such white-throated sparrows (Weisman et al., 2004) and now, black-capped and mountain chickadees demonstrate accurate absolute pitch discrimination as well; however, they do not appear to match male zebra finch levels.

Future Directions

There are several lines of research that may stem from the series of studies already conducted and this study. First, it would be interesting to investigate how male white-throated sparrows discriminate absolute pitch in this task. This would provide a nice comparison to the females already tested (Weisman et al., 2004). Additionally, testing more zebra finches, both male and female, in this discrimination task and more importantly, with the novel stimuli phase may also add valuable information about how songbirds discriminate absolute pitch. It may also serve as another resource to compare males against females.

In the interest of comparative research, it would be informative to test Boreal chickadees (*P. hudsonica*) in this absolute pitch discrimination task. To date, there are no reports of boreal chickadee whistled song (Mclaren, 1976; Ficken, Mclaren & Hailman, 1996). Given that they lack this whistled song then, it may be possible for us to gain a further understanding of general chickadee pitch processing and whether the fact that the other chickadee species do have a whistled song might influence pitch processing abilities. In addition, testing a non-songbird (i.e. a non vocal learner such as a pigeon, *Columba livia*) may also aid in our understanding of whether pitch processing is a specialized adaptation for songbirds only, or extends to avian species in general.

Another species for comparison is the Carolina chickadee (*P. carolinensis*). This closely related species to black-capped chickadees also sings tonal songs that typically alternates high and low frequency notes and have 2-3 different song types (Ward, 1966; Lohr, Nowicki & Weisman, 1991). Carolina chickadees occupy the lower south eastern portion of the United States, at lower elevations. Where the lower, warmer regions, meet with mid- to higher regions of elevation, black-capped and Carolina chickadee populations overlap, which is also an area in which these two species have been reported to interbreed (Brewer, 1963). How then, can Carolina chickadees distinguish conspecifics from black-capped chickadees?

In a series of playback studies conducted on Carolina chickadees,

Lohr (1995) found that Carolina chickadees have two species-typical frequency ranges for song. If individual notes were shifted outside of the normal frequency range, Lohr observed a marked decrease in responding, despite maintaining the species typical pitch ratios and contour between notes. Another experiment showed that the contour of the song also contributes to species recognition, however, is secondary to the absolute pitch of each note type (Lohr, Weisman & Nowicki, 1994; Lohr, 1995). Thus, given that Carolina chickadees show extreme sensitivity to absolute pitch of song notes and are not as selective for relative pitch, these birds may prove to be even greater at absolute pitch discrimination tasks than black-capped or mountain chickadees.

A second direction of this study can lead to tests of relative pitch processing. Would black-capped chickadees perform at a higher level than mountain chickadees given that their songs consistently maintain a frequency ratio between its two notes, while the latter does not?

Another interesting line of research might be to investigate the underlying neural correlates of pitch processing. As previously mentioned, female black-capped chickadees possess song control nuclei while zebra finch females do not. Would electrophysiological or immunohistochemical techniques reveal whether song nuclei are involved in relative or absolute pitch processing?

Conclusions

Black-capped chickadees are a well studied species. Here, we

investigated the extent of their ability to perceive absolute pitch, and that of a closely related species, the mountain chickadee. We show that these two chickadee species have similar absolute pitch processing abilities and that these abilities do not statistically differ to those of male zebra finches. Given that there are alpine regions in which these two species live sympatrically and given that their vocalizations have similar bioacoustical characteristics, it is reasonable to assume that they may also require similar abilities to discriminate conspecifics from heterospecifics. Further to that, males and females may both require the ability to accurately perceive absolute pitch not only to identify species, but also to identify individuals, especially in the cases of mate selection and territorial defense.

Our results show that pitch processing abilities in male and female chickadees do not differ significantly, which is in contrast to findings that male zebra finches are superior to female zebra finches in absolute pitch discrimination. In addition to the present study, previous studies of song perception indicate that both absolute and relative pitch perception can each contribute to species recognition in some songbird species. Thus, absolute and relative pitch perception provide redundant cues for recognition so that if one is degraded, an individual may still use the other to discriminate conspecific from heterospecific, as well as to determine individual identity.

This study demonstrates that both male and female black-capped

and mountain chickadees can accurately discriminate absolute pitch and that both species and sexes do so equally well and to a lesser degree than zebra finch males on measures such as trials to criterion and average percentage of response on the final day of performance. Further, chickadees and finches appear to solve the discrimination by categorizing pitches based on experimenter-imposed frequency range contingencies. Future investigations of absolute pitch perception will need to uncover the specific ecological, neurobiological and phylogenetic factors responsible for our results and that ultimately, will help us to better understand the evolution of absolute pitch perception in animals.

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