

Pitch-related cues in the songs of sympatric mountain and black-capped chickadees

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Abstract

Acoustic frequency (pitch) cues are known to be important in the recognition of conspecific song in a number of songbird species. Mountain chickadees (*Poecile gambeli*) and black-capped chickadees (*Poecile atricapillus*) are sympatric over parts of their ranges and their species-typical songs share many features. I examined the acoustic characteristics of song of these two congeners in a region of sympatry in southern Alberta, Canada. As reported for other populations in allopatry, black-capped chickadees emphasized relative frequency cues in song production. In particular, variation in the ratios between note frequencies was significantly less than variation in the note frequencies themselves. In contrast, songs of mountain chickadees did not have constant frequency ratios and contained an introductory acoustic element absent in black-capped chickadee song. Both species may rely on song note frequency or the presence of this introductory acoustic element when differentiating between conspecific song and heterospecific song. Song measures for chickadees in sympatry were similar to measures in allopatry, providing little evidence for character displacement in song production.

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1. Introduction

Pitch is known to play a prominent role in song recognition in a number of bird species (Becker, 1982; Dabelsteen and Pedersen, 1985; Hurly et al., 1990; Nelson, 1988, 1989; Weary, 1996; Weisman and Ratcliffe, 1989, 2004). Pitch- or frequency-related information may involve absolute or relative cues. These two classes of cues have been studied principally in the context of human music perception, but also have proved useful in an analysis of frequency information in birdsong (Weary, 1996; Weisman et al., 1990; Weisman and Ratcliffe, 2004). Absolute frequency perception refers to the ability to identify a single sound, such as a song note, based on its frequency or frequency bandwidth (pitch range) (Ward and Burns, 1982). Relative frequency perception, on the other hand, depends on the ability to recognize relationships between the frequencies of two or more song notes. This may involve simply identifying the direction of frequency change (i.e. increasing or decreasing frequency from one note to the next; in music, ascending or descending

“contour”) (Deutsch, 1982; Dowling, 1978; White, 1960). In a more specialized sense, it may involve the ability to identify constant mathematical ratios between the frequencies of successive notes (in music, identifying the “pitch interval”) (Deutsch, 1969; Shepard, 1982). Human listeners use such abilities, in part, to recognize musical melodies that have been shifted in frequency, or transposed in “key” (Deutsch, 1982; Dowling, 1982; Dowling and Fujitani, 1971).

It is not yet clear whether absolute or relative frequency cues by themselves may be responsible for the recognition or discrimination of song by songbirds. Field and laboratory studies in some birds have shown that constant ratios between adjacent note frequencies play at least some role in conspecific song recognition in several species, including black-capped chickadees (*Poecile atricapillus*), white-throated sparrows (*Zonotrichia albicollis*), and veeries (*Catharus fuscescens*) (Hurly et al., 1990; Weary et al., 1991; Weisman et al., 1990). On the other hand, Lohr et al. (1991, 1994) demonstrated that the Carolina chickadee (*Poecile carolinensis*), a closely related congener of the black-capped chickadee, does not produce simple ratios between note frequencies in song, and song recognition in this species involves predominantly absolute rather than relative frequency-related cues. In laboratory studies involving starlings

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(*Sturnus vulgaris*), brown-headed cowbirds (*Molothrus ater*), and mockingbirds (*Mimus polyglottos*), absolute frequency cues were shown to take precedence over relative cues in tone sequence recognition tasks (Hulse and Cynx, 1985; Page et al., 1989). Additionally, several studies with at least a dozen different species have suggested that birds cease responding to conspecific song when it is moved outside its normal frequency range (Bremond, 1976; Dabelsteen and Pedersen, 1985; Emlen, 1972; Falls, 1963; Nelson, 1989; Thompson, 1969; Weisman and Ratcliffe, 1989; Wunderle, 1979), but see Aubin and Bremond (1983). A potentially ideal setting for examining the importance of relative and absolute cues in the species-specific recognition of birdsong would be found in habitats where closely related species coexist and a number of song characteristics are similar.

Mountain chickadees (*Poecile gambeli*) are also closely related congeners of black-capped chickadees, and occur in some of the same habitats in western North America (McCallum et al., 1999). These two species, along with the Carolina chickadee, form a closely related subgroup of the North American Paridae, and have similar pure-toned songs that are used in territorial interactions (Gill et al., 1989, 1993; McCallum et al., 1999; Mostrom et al., 2002; Smith, 1993). While the geographic ranges of black-capped and Carolina chickadees are largely distinct, with an intervening hybrid zone, the ranges of black-capped and mountain chickadees overlap broadly (McCallum et al., 1999). In areas of sympatry, territories of mountain and black-capped chickadees may overlap (Hill and Lein, 1989b). In such areas individuals respond predominantly to playbacks of conspecific

song and not heterospecific song (Hill and Lein, 1989a). Given the distances over which chickadees vocalize in these habitats, they often cannot see the broadcasting source (Hill and Lein, 1989a; pers. obs.), suggesting that acoustic cues alone are sufficient for eliciting an appropriate, species-typical territorial response. Mountain and black-capped chickadees present a compelling case for the study of sensory mechanisms in species identification. Because hybridization is rare between these two closely related congeners living in some of the same habitats (McCallum et al., 1999), both species must be able to discriminate reliably and consistently between conspecific and heterospecific signals.

Mountain chickadee song is geographically variable (Fig. 1). In contrast, black-capped chickadee song is relatively invariant across most of its range, usually consisting of a single, simple two-note song (Fig. 2B). In some areas, mountain and black-capped chickadee song may be fairly distinct, differing along several acoustic dimensions, and easily distinguishable to human listeners (Figs. 1 and 2) (Gaddis, 1985; Kroodsma et al., 1999; McCallum et al., 1999). In other locations, including one region of sympatry, their songs may be more similar (Fig. 2), and much more difficult for human listeners to distinguish acoustically. However, across most geographic regions, this study has found at least two consistent differences between mountain and black-capped chickadee song: (1) the acoustic frequency (pitch) range of song notes, which is higher in mountain chickadees than in black-capped chickadees and (2) a brief introductory acoustic element in mountain chickadee song that is not typically present

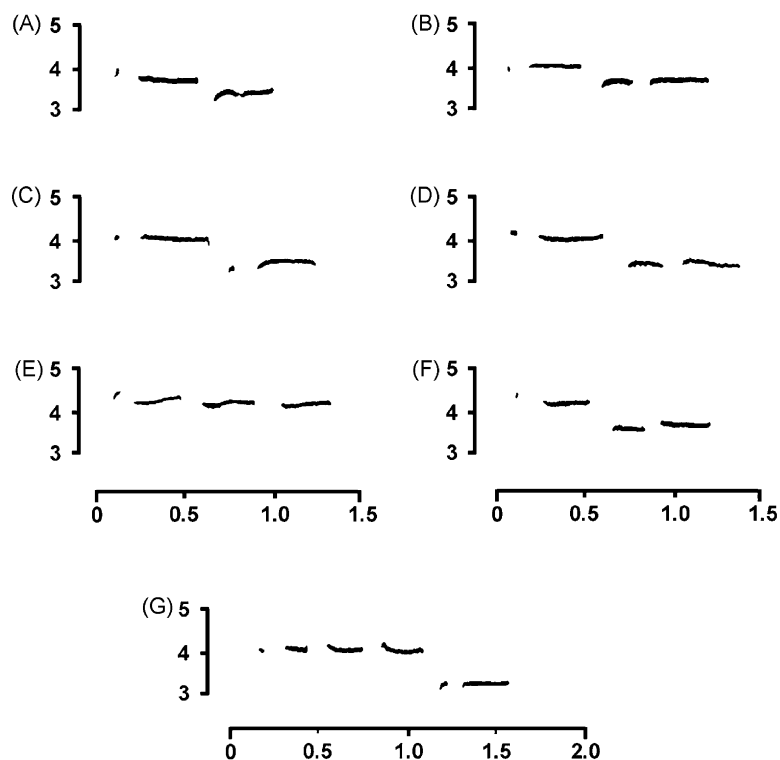


Fig. 1. Sound spectrograms of mountain chickadee song types from single individuals recorded at a number of locations in western North America. Recordings of these songs were obtained from the Macauley Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York (C) (P) All Rights reserved. General location and catalogue numbers for these recordings are provided in Table 3. Sound spectrograms were produced on a Kay Elemetric DSP 5500 Sona-Graph (0–8 kHz analysis range, 59 Hz frequency resolution).

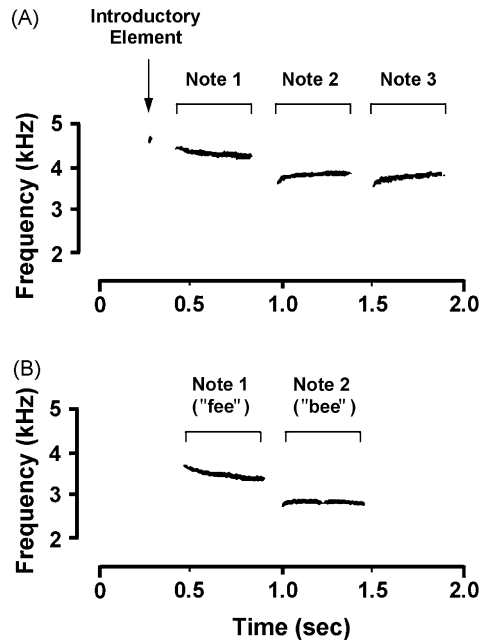


Fig. 2. Sound spectrograms of (A) a mountain chickadee (*Poecile gambeli*) song recorded at the Kananaskis Field Station, 70 km west of Calgary, Alberta. This song consists of a short introductory element followed by three notes. (B) A black-capped chickadee (*Poecile atricapillus*) song recorded at the same site. Sound spectrograms were produced as in Fig. 1.

in black-capped chickadee song (Fig. 1). This introductory element could serve to distinguish mountain from black-capped chickadee song in areas where the two species co-occur, at least over short distances, as it is theoretically a reliable indicator of species identity in song. In addition, black-capped chickadee song contains a brief amplitude break (or absence of acoustic energy) in the middle of the second note in song (Fig. 2B). This amplitude break also could potentially serve as a distinctive feature, again over short distances, though brief temporal gaps may occur in mountain chickadee songs in some areas (Fig. 1).

Here I examine song characteristics in both mountain and black-capped chickadees in an area of sympatry, and compare these to measures of song from the two species in allopatry. I evaluate song measures from the perspective of identifying the absolute and relative frequency relationships that could be used by these birds as potential cues for discriminating between songs of the two species. In particular, I identify the most distinctive song characteristics in an area where songs of the two species are especially similar. I present evidence suggesting an emphasis on absolute note frequencies in song production by mountain chickadees, and I confirm the emphasis on relative frequency relationships in song production shown by black-capped chickadees elsewhere (Hill and Lein, 1987; Weisman et al., 1990).

2. Materials and methods

2.1. Study area

I recorded spontaneous song from mountain chickadees and black-capped chickadees near the Barrier Lake site of the Uni-

versity of Calgary's Kananaskis Field Stations. This field site is located in the Kananaskis valley, 70 km west of Calgary, Alberta, Canada. In this region, territories of both mountain and black-capped chickadees occur at elevations of 1500–2000 m in mixed coniferous-deciduous forest dominated by Lodgepole Pine (*Pinus contorta*), White Spruce (*Picea glauca*), and Quaking Aspen (*Populus tremuloides*). I recorded all birds between 06:00–13:00 MST from 4 April–7 May 1993, and assigned birds to species by song and by visual markings, specifically the presence of a white superciliary stripe that distinguishes mountain chickadees from all other North American parids (McCallum et al., 1999). I identified individuals by territory location and recorded each in a single session, with all territories separated by at least 0.5 km from the nearest bird of the same species to ensure that all recorded birds were different individuals (Hill and Lein, 1989b).

2.2. Recordings

I used a Sony TC-D5M cassette recorder and either a Sennheiser ME88 shotgun microphone or an Audiotechnica 2AX Pro omnidirectional microphone mounted in a Sony PBR 330 parabola to record birds. To standardize measures of song frequency and verify tape speed, I recorded a 512 Hz test tone from a tuning fork at the beginning and end of each song recording session. In addition, I obtained archived recordings of mountain chickadee songs from the Macauley Library of Natural Sounds, Cornell University, for comparison with songs from southern Alberta. Most of these recordings do not contain test frequencies to verify tape speed, precluding the accurate determination of absolute song note frequencies. However, ratios between note frequencies may still be determined for songs from these recordings.

I used the "SIGNAL/RTSD" sound analysis software (Beeman, 2001) for all song acquisition and analysis. Songs were digitized at a rate of 22,598 Hz (Data Translation DT2821 A/D board). I made measurements of note frequencies from 1024 point FFTs (frequency resolution 22 Hz) calculated at the start, mid-point, and end of each note. For comparisons across species, I averaged measurements from the five highest-quality recordings of song for each individual (recordings having the highest signal-to-noise ratio).

2.3. Measurements

I first analyzed the spectral and temporal properties of song notes within each species, and the introductory song element if present, for both mountain and black-capped chickadees. The goal with these initial descriptive measurements was to gather baseline data for these species in sympatry (and for mountain chickadees as a whole, since detailed quantitative data on song variation have not been reported previously for this species), and to identify potential acoustic cues that could be used to discriminate between songs of these two species.

I then compared the characteristics of mountain and black-capped chickadee song in an absolute/relative framework in several ways. First, I determined the coefficient of variation

for note frequencies and for the ratios between note frequencies. I used this measure to compare variability in the absolute and relative frequency characteristics of adjacent song notes. Second, I examined correlations between note frequencies in song, which provide a measure of the predictability of one note's frequency based on the frequencies of other notes. High correlations between note frequencies suggest an emphasis on relative frequency cues in song production (Lohr et al., 1991; Weisman et al., 1990). Third, I recorded the patterns of increase or decrease in successive note frequencies within songs of mountain and black-capped chickadees. Any differences between species in the directional changes of note frequencies would provide a potential means of differentiating conspecific from heterospecific song. Finally, the occurrence of frequency-shifted versions of a species song, in which note frequencies are altered but directional changes and/or frequency ratios are preserved (in essence, songs in different "keys"), would suggest an emphasis on relative frequency characteristics for encoding species identity in song production.

As an additional comparison, I measured song note duration for both mountain and black-capped chickadees. I wished to determine whether detectable temporal differences were present in the song notes of the two species, and whether such cues might contribute to song discrimination.

2.4. Statistical analysis

I used the Sigmatat and Systat (Wilkinson, 1997) statistical software for performing statistical tests. Values are reported as means \pm S.E. I used repeated measures ANOVAs with Bonferroni-adjusted post hoc comparisons to test for differences in the frequency and duration of song notes within species (for comparisons of three groups Bonferroni probability adjustments = $0.05/3 = 0.0167$). I used independent *t*-tests to test for differences between mountain and black-capped chickadee songs. Sample sizes for tests of frequency measures involved $n = 17$ mountain chickadees and $n = 14$ black-capped chickadees. Recordings for $n = 15$ of the original mountain chickadee subjects and all original black-capped chickadee subjects were high enough in quality to obtain accurate measures of note duration. In absolute/relative frequency comparisons, I tested for associations between note frequencies using Pearson product-moment correlations. I used the coefficient of variation (CV) to examine the relative variability of song note frequencies and frequency ratios. The CV was defined as $(S.D. \times 100)/\text{mean}$ (Sokal and Rohlf, 1995). I tested comparisons of CVs according to Sokal and Rohlf (1995; pp. 146–148).

3. Results

3.1. Within song comparisons

Mountain chickadee song consisted of a brief (<65 ms) introductory element followed by a series of longer notes (Fig. 2A). Hereafter, I refer to the first note following the introductory element as Note 1, the second note following the introductory element as Note 2, etc. Unlike black-capped chickadees, individ-

ual mountain chickadees near the Kananaskis site and elsewhere in southern Alberta (Hill and Lein, 1989a) sang songs having variable numbers of notes, with the most common variant of song consisting of an introductory element followed by 2 or 3 notes (both median and mode = 2 notes/song for this sample). Songs described here correspond to the "common 2-note" and "common 3-note" songs of Wiebe and Lein (1999). Mountain chickadees repeated a song variant with the same number of notes many times before switching to another song variant (i.e. they sang with "eventual variety"). Long bouts of songs containing only two notes were common in all males in this study.

All black-capped chickadees sang one song type consisting of two notes ("fee-bee," or "hey-sweetie") (Fig. 2B), without an introductory element, as is common for the species throughout the majority of its range (Dixon and Stefanski, 1970; Ficken et al., 1978; Kroodsmas et al., 1999; Ratcliffe and Weisman, 1985). The first note contained a downward frequency sweep, while the second note exhibited a brief amplitude break in the approximate middle of the note. This amplitude break is variable in duration across individuals, within an individual across different renditions, and at different distances from the source (Fotheringham and Ratcliffe, 1995; pers. obs.). Black-capped chickadees regularly frequency-shifted their songs, in which the same two notes were sung at higher or lower frequencies, but with a high degree of constancy in the frequency ratio between them (i.e. in musical terms, maintaining "melody," but shifting the "key") (Hill and Lein, 1987; Horn et al., 1992; Ratcliffe and Weisman, 1985).

As in the typical black-capped chickadee song, Note 1 of mountain chickadee song exhibited a downward frequency sweep from beginning to end, with the initial frequency of this note (4259 ± 19 Hz) (mean \pm S.E.) significantly greater than the mid-point (4182 ± 20 Hz) or final frequencies (4157 ± 21 Hz) ($F_{2,32} = 44.2$, $p < 0.001$). Subsequent notes showed a transient increase in frequency at the beginning of each note. In these cases, frequencies within notes also differed ($F_{S_{2,32}} \geq 6.7$, $ps < 0.01$), with post hoc tests showing that initial frequencies were significantly lower than the mid-point or final frequencies, which did not differ significantly (Fig. 2A). In black-capped chickadee song, the initial frequency of Note 1 (3858 ± 75 Hz) was also significantly greater than the mid-point frequency (3735 ± 72 Hz), which in turn was significantly greater than the final frequency (3683 ± 68 Hz) ($F_{2,26} = 54.4$, $p < 0.001$) (Table 1). Measures of frequency in Note 2 of black-capped chickadee song, taken at the mid-point of sections prior to and following the amplitude break of this note, did not differ ($F_{1,13} = 1.4$, ns) (Fig. 2B). Subsequent comparisons are based on averages of the mid- and endpoint frequencies of mountain chickadee song notes, and the average frequency of Note 2 in black-capped chickadee song, since these measurements did not differ significantly for any of those notes.

There were significant differences among the note frequencies within mountain chickadee song ($F_{2,32} = 241.2$, $p < 0.001$). Pairwise post hoc comparisons showed that Note 1 was significantly higher in frequency than Notes 2 and 3. The frequencies of Notes 2 and 3 did not differ significantly. In black-capped chickadee song, the final frequency of Note 1 was significantly higher

Table 1
Means, standard errors (S.E.s), and coefficients of variation (CVs) for note frequencies (Hz), ratios between note frequencies, and note durations (ms) in song of mountain chickadees ($n = 17$ birds) and black-capped chickadees ($n = 14$ birds) from the Kananaskis field site, southern Alberta (CV = S.D. \times 100/mean)

	Mountain chickadees			Black-capped chickadees	
	Mean \pm S.E.	CV		Mean \pm S.E.	CV
Frequencies					
Note 1 (N1)	4170 \pm 20	2.0	Note 1 start (N1s)	3858 \pm 75	7.2
Note 2 (N2)	3692 \pm 30	3.4	Note 1 end (N1e)	3683 \pm 68	6.9
Note 3 (N3)	3647 \pm 20	2.3	Note 2 (N2)	3215 \pm 49	5.7
Ratios					
N1/N2	1.131 \pm 0.010	3.7	N1s/N1e	1.047 \pm 0.007	2.3
N2/N3	1.012 \pm 0.006	3.0	N1e/N2	1.145 \pm 0.006	1.9
Durations					
Note 1	382 \pm 10	9.8	Note 1	397 \pm 12	11.0
Note 2	370 \pm 8	8.2	Note 2	415 \pm 13	11.4
Note 3	342 \pm 14	15.6			

Mountain chickadee note frequencies are averages of the mid and endpoint frequencies of each note, since these measures did not differ significantly.

than the average frequency of Note 2 ($F_{1,13} = 414.6$, $p < 0.001$). During mountain chickadee song, the mean duration of each note decreased slightly when compared with preceding notes (Table 1). Post hoc comparisons showed that Note 1 was significantly longer in duration than Note 3 ($F_{2,28} = 6.5$, $p < 0.01$). Note 1 of black-capped chickadee song in this population did not differ significantly in duration from Note 2 ($F_{1,13} = 4.5$, ns).

3.2. Comparisons between species

Songs of mountain chickadees and black-capped chickadees do not overlap in frequency as a whole, but rather occupy nearby frequency bands. The frequency of Note 1 differed for the two species ($t = 4.4$, d.f. = 29, $p < 0.001$), as did the frequencies of Notes 2 and 3 in mountain chickadees when compared with the frequency of Note 2 in black-capped chickadees ($t_s > 8.6$, d.f. = 29, $p < 0.001$). The frequencies of Notes 2 and 3 in mountain chickadee song were not significantly different, however, from the midpoint or end frequencies of Note 1 in black-capped chickadee song ($t_s < 1.28$, d.f. = 29, ns).

3.2.1. Variation of frequencies and intervals

In mountain chickadees the CV for the ratio between Notes 2 and 3 was significantly greater than the CV for the frequency of Note 1 ($p < 0.05$), and the CV for the ratio between Notes 1 and 2 was significantly greater than the CVs for the frequencies of both Notes 1 and 3 ($p_s < 0.05$) (Table 1). The ratios between mountain chickadee note frequencies are therefore at least as variable, if not more so, than note frequencies themselves in this population. In contrast, the CVs for ratios between note frequencies in black-capped chickadee song all were significantly smaller than the CVs for individual note frequencies ($p_s < 0.05$) (Table 1), as is characteristic of populations of black-capped chickadees elsewhere (Weisman et al., 1990).

3.2.2. Correlations between note frequencies

Correlations among the notes within song differed between mountain chickadees and black-capped chickadees. As a result,

the ability to predict the frequency of notes based on prior note frequencies differed (Table 2). Only frequencies of Notes 2 and 3 in mountain chickadee song were significantly correlated ($p < 0.05$). For black-capped chickadees at the same site, the strength of correlations was much higher, and correlations among note frequencies all were highly significant (both within the first note and between notes, $r_s > 0.90$, $p_s < 0.001$). This result is similar to that for at least one other black-capped chickadee population, in which correlations among note frequencies also were highly significant (Weisman et al., 1990).

3.2.3. Frequency contour

In this sample, both mountain and black-capped chickadee songs showed a similar directional change in frequency during the progression from one song note to the next. In both species the frequency of each successive note decreased (i.e. exhibited a descending contour; Table 1). Both mountain and black-capped chickadees at the Kananaskis field site had downward frequency sweeps within Note 1. Subsequent notes in mountain chickadee song showed a slight upward sweep in frequency.

Table 2
Correlations among the notes (r) in mountain chickadee song ($n = 17$ birds) and black-capped chickadee song ($n = 14$ birds) from the Kananaskis field site, southern Alberta

	Mountain chickadee song		
	Note 1	Note 2	Note 3
Note 1	1.00		
Note 2	ns	1.00	
Note 3	ns	0.50 ^a	1.00
	Black-capped chickadee song		
	Note 1 start	Note 1 end	Note 2
Note 1 start	1.00		
Note 1 end	0.95 ^b	1.00	
Note 2	0.94 ^b	0.98 ^b	1.00

^a $p = 0.043$.

^b $p < 0.001$.

3.2.4. Shifted song

There were no cases of frequency-shifted song in this sample or any archived recordings of mountain chickadee songs, but more extensive sampling is needed to establish definitively that such songs do not occur in this species. Three of the 14 black-capped chickadees sang frequency-shifted variants of song during recording sessions in this sample.

3.2.5. Note duration

Note duration differed between mountain and black-capped chickadee song. When considering the first two notes of song, the average duration of mountain chickadee song notes (376 ms), is slightly shorter than that of black-capped chickadee song notes (406 ms) ($F_{1,27} = 4.8, p < 0.05$). However, while significant, this difference between black-capped and mountain chickadees represents an average change in note duration of only 8.0%. When comparing just the first note of song in each of the two species, this difference is reduced to 3.9%, and is not significant ($F_{1,27} = 1.0, ns$).

3.3. Comparisons with other populations

Across populations, the frequency, positioning, and duration of song notes is more variable in mountain chickadees than in black-capped chickadees. Fig. 1 and Table 3 show sound spectrograms and average note frequency ratios, respectively, for songs obtained from single individuals of other mountain chickadee populations. Songs in these geographically distinct populations may have significantly larger note frequency ratios or significantly smaller ratios than songs of the Kananaskis population. Values for song note ratios of these single individuals from many of the other populations lie outside two standard deviations from the mean value for the Kananaskis population, in particular for the ratio between Notes 1 and 2. This comparison should be viewed with some caution as a larger sample of individuals is needed to confirm an accurate contrast with the Kananaskis population. This range of variation in general, however, contrasts with the much smaller range of variation in the largest frequency interval, and the relative positioning of intervals, in black-capped chickadee song across its geographic range (Horn et al., 1992; Kroodsma et al., 1999; Weisman et al., 1990).

Frequency contour characteristics were also more variable across populations in mountain chickadees than in black-capped chickadees. Mountain chickadees in some populations sang songs with Note 3 slightly higher in frequency than Note 2 (Fig. 1 and Table 3). While not all mountain chickadee songs across the species' range contained a downward sweep within the first note, songs from many populations did (Fig. 1). Subsequent notes in different populations of mountain chickadees might be produced with initial upward sweeps in frequency, initial downward sweeps, or neither (as in black-capped chickadees). Thus, within-note frequency characteristics in mountain chickadee songs are also not universally distinct.

In black-capped chickadees, results for frequency measures including the variation in frequency at the start and end of Note 1 (“fee”) and Note 2 (“bee”), and the frequency ratios between these points, are very similar to results obtained previously for other populations (Dixon and Stefanski, 1970; Ficken et al., 1978; Hill and Lein, 1987; Ratcliffe and Weisman, 1985; Weisman et al., 1990). All measures for black-capped chickadees in this sample, including CV, fall well within one standard deviation for these same measures in a geographically distinct population in Ontario, Canada (Weisman et al., 1990). This result suggests that the variation in song frequency characteristics normally present in populations of this species was captured for the Kananaskis population in the present sample.

Mountain chickadee songs contained an introductory acoustic element while black-capped chickadee songs did not (Figs. 1 and 2). I averaged measurements from the Kananaskis population (recordings of $n = 6$ birds were of sufficiently high quality to obtain accurate measurements) for comparison with measurements taken for archived recordings from the seven other sites listed in Table 3. The frequency of this element was always nearly equal to the initial frequency of Note 1. The ratio of average frequency of the introductory element to the initial frequency of Note 1 was 1.003 ± 0.006 for all eight sites; 1.014 ± 0.003 for the Kananaskis population. The average duration of this element across all eight sites was 45.7 ± 4.1 ms; average duration for the six individuals at the Kananaskis site was 33.9 ± 2.0 ms. The introductory element in mountain chickadee song averaged 11.49 ± 1.12 dB lower in

Table 3

Mean values for the frequency ratio of N1/N2 and N2/N3 in song for a single male in each of seven different mountain chickadee populations in western North America as shown in Fig. 1 ($n = 5$ songs each)

Song	Ratio N1/N2	Ratio N2/N3	Introductory element (dB relative to Note 1)	Location	Recordist	Cut
(A)	1.141		−14.98	Wyoming	R.S. Little	2/14696
(B)	1.116	0.993	−13.71	California	R.C. Stein	3/14697
(C)	1.205		−12.64	Oregon	G. Keller	10/44913
(D)	1.165	1.001	−4.74	Oregon	G. Keller	11/44916
(E)	1.031	1.010	−12.25	California	D.S. Herr	14/47548
(F)	1.181	0.981	−12.35	Colorado	G. Keller	17/50220
(G)	1.008	1.004	−9.24	California	K. Colver	21/48828
(G)	(Third interval)	1.286				

Introductory element (dB relative to Note 1) refers to the average reduction in RMS (root-mean-squared) amplitude of the introductory element when compared with the RMS amplitude of Note 1 in song at each site. Recordings were obtained from the Macauley Library of Natural Sounds, Cornell University, and include location, recordist, and cut number.

RMS (root-mean-squared) amplitude than Note 1 across all eight locations (Table 3).

4. Discussion

Mountain and black-capped chickadee songs share a large number of characteristics, yet these two species respond predominantly to conspecific songs in playback tests (Hill and Lein, 1989a). These two species use different resources within the habitats in which they are sympatric, and therefore need not defend territories against heterospecific individuals (Hill and Lein, 1989b). As a consequence, there is extensive territory overlap, and these birds must have a means of reliable vocal discrimination (Lynch and Baker, 1990). The possibility that these two species could use different sets of cues for production and recognition of song is particularly relevant given differences in cues for song production and perception in black-capped and Carolina chickadees (Lohr et al., 1991, 1994). Considering the greater similarity of song structure in black-capped and mountain chickadees and the occurrence of these two species in some of the same habitats, however, it is even more essential that distinctions be made between songs of these two species.

4.1. Acoustic frequency characteristics

The frequency (pitch) of song notes provides a consistent and reliable means of discriminating mountain from black-capped chickadee songs. Song note frequencies produced by mountain chickadees are significantly less variable than note frequencies produced by black-capped chickadees (Table 1). While distributions of all measured note frequencies overlapped in black-capped chickadee song, there was no overlap between the frequency of the first note and frequencies of the second or third note in mountain chickadee songs. Importantly, there was also no overlap in the frequency of Note 1 in mountain chickadee song with the frequencies of any notes in black-capped chickadee song (Table 1). Both passerine and non-passerine birds are capable of detecting about a 1% change in the frequency of tones in the range of 1–4 kHz (Dooling et al., 2000; Fay, 1988). This ability suggests that they are fully capable of discriminating between the first note frequencies of mountain and black-capped chickadee song (a difference in frequency of over 7%). Furthermore, zebra finches (*Taeniopygia guttata*) have been shown to possess the ability to memorize, categorize, and classify tones in frequency ranges as narrow as 480 Hz, with sharply defined 120 Hz frequency boundaries (Njegovan et al., 1995; Weisman et al., 1998). Human subjects trained in an identical procedure were unable to perform this classification task, suggesting that small passerines have an unusually refined ability to recognize and respond to tones in very narrow frequency ranges. Absolute frequency cues therefore may play an important role in song discrimination by mountain chickadees.

Both mountain and black-capped chickadees produce songs containing notes that decrease in frequency from one note to the next, or have a descending contour. Frequency change across notes, and within a note, may play some role and indeed may be a necessary cue in song recognition, particularly for black-capped

chickadees in which decreasing frequency is characteristic of song throughout the species' range (Shackleton et al., 1992). However, because it is a common characteristic of mountain and black-capped chickadee songs at the Kananaskis field site, a descending contour cannot by itself be a direct means of discriminating between songs of the two species. Furthermore, some mountain chickadees, both at the Kananaskis site and in some other areas, may sing songs with notes all at nearly the same frequency (Gaddis, 1985). In other cases birds may produce songs that show an increase in frequency either between notes, or within notes (Fig. 1 and Table 3), making a descending contour neither a reliable nor consistent characteristic for song recognition in mountain chickadees.

Instances in which notes are shifted significantly upward or downward in frequency, yet precise ratios maintained between note frequencies over the course of a singing bout, are common in black-capped chickadee song (Hill and Lein, 1987; Horn et al., 1992; Weisman et al., 1990). Such songs suggest an emphasis on constant note frequency ratios, at least in song production. Frequency-shifted songs have never been reported for mountain chickadees. Furthermore, in at least several populations, the largest ratio between the frequencies of song notes in one species is very similar to the largest ratio in the other species (Tables 1 and 3). The frequency ratio between Notes 1 and 2 for both mountain and black-capped chickadees at the Kananaskis field site is nearly identical, making this an unlikely means of discriminating song. Moreover, since values for note frequency ratios differ considerably among mountain chickadee populations (Table 3), note frequency ratios are unlikely to play a species-universal role in song recognition in mountain chickadees.

A high correlation between notes indicates a high degree of predictability of one note frequency based on another, and suggests an emphasis on relative frequency characteristics (such as constant mathematical ratios between notes) in song production. Note frequencies in black-capped chickadee song were highly predictable from other note frequencies, a result similar to that obtained for other populations (Weisman et al., 1990). Lohr et al. (1991) found that Carolina chickadees, on the other hand, showed considerably less predictability between note frequencies in song production, and that this species did not rely on relative frequency cues for song recognition (Lohr et al., 1994). In the present study, there was only a single instance in which note frequencies were significantly correlated in mountain chickadee song, this correlation occurred between notes at nearly the same frequency, and the strength of correlation was not as high as those between black-capped chickadee notes (Table 2). Frequencies of notes in mountain chickadee song therefore are not highly predictable based on the frequencies of other notes in song, as would be expected if mountain chickadees relied on relative cues such as note frequency ratios for song recognition or discrimination.

4.2. Other song features

An introductory song element, present in mountain chickadee songs but not in most black-capped chickadee song, could potentially facilitate discrimination between songs of the two species

(but see Gammon and Baker, 2004; Kroodsma et al., 1999, for exceptions in isolated populations). However, this element is typically lower in amplitude than the remainder of the song (Table 3), suggesting that it is primarily salient at close range. Song is predominantly a long distance communication signal. If this introductory element plays some role in song discrimination, it likely functions primarily in short distance interactions in some way. At some distance from the broadcasting source, the introductory element will become inaudible while the remaining notes in song are still detectable.

As a consequence of its reduced amplitude relative to the rest of song, the introductory element in mountain chickadee song might also serve as a ranging cue for estimating the distance of a singer. If the distances at which this introductory element become inaudible are relatively short compared to typical territory sizes, it may well serve as a useful ranging cue (but as a less reliable indicator of species identity in song). In a different way, brief amplitude breaks in song notes, such as those in Note 2 of black-capped chickadee song, also might serve as ranging cues. With increasing distance, reverberative echoes in temperate forests can decrease the duration of, or entirely eliminate, brief temporal gaps between sounds (Dabelsteen et al., 1993; Richards and Wiley, 1980; Wiley and Richards, 1978). Reverberation, therefore, has the potential to make brief temporal gaps inaudible to birds, particularly in the case of tones having similar frequencies prior to and subsequent to the amplitude break (Okanoya and Dooling, 1990). The utility with which brief amplitude breaks might serve as ranging cues again would be dependent on the range of distances over which songs are typically heard in the habitat.

Additional song features are unlikely to provide salient cues for discriminating conspecific from heterospecific song in mountain and black-capped chickadees. While mountain chickadees in the Kananaskis valley and other areas may vary the number of notes in song, two-note songs are common during certain stages of the breeding season (Wiebe and Lein, 1999; pers. obs.), and may be sung for extended periods. Note duration in the Kananaskis area is shorter in mountain chickadee songs than in black-capped chickadee songs, but this difference is unlikely to be detectable throughout the habitat, and unlikely to be consistent across geographic locations and regional song types. Note durations in Kananaskis black-capped chickadees are on average 8.0% longer than in mountain chickadees, but thresholds for the detection of changes in tone duration range between 10% and 20% for tones longer than 200 ms in laboratory tests with small birds (Dooling and Haskell, 1978; Fay, 1988; Kinchla, 1970; Maier and Klump, 1990). Furthermore, reverberative echoes in forested habitats can produce considerable temporal smearing and can cause difficulties for accurately estimating the duration of pure tones (Dabelsteen et al., 1993; Richards and Wiley, 1980; Wiley and Richards, 1978).

4.3. Song production and discrimination in sympatry

The occurrence of related species with similar songs in some of the same habitats raises the possibility of character displacement in areas of sympatry. However, comparisons of Kananaskis

black-capped chickadee song data with existing data from other populations (Weisman et al., 1990) suggest that song properties in areas of sympatry with mountain chickadees are similar to song properties in regions of allopatry. Song production data suggest an emphasis on relative frequency characteristics for black-capped chickadees in both situations. In mountain chickadees, note frequency ratios and the contour of song note frequencies are extremely variable between populations. Given this broader variation in mountain chickadee song, and the very similar song of mountain and black-capped chickadees in at least one region of sympatry, this study found no evidence for character displacement in song.

Results presented here point to a potential difference in the way in which mountain chickadees and black-capped chickadees both produce and perceive frequency characteristics in song, at least in one area of sympatry. It is curious that black-capped chickadees produce songs with highly stereotyped ratios within and between song notes, when two closely related congeners, the mountain chickadee (this study) and the Carolina chickadee (Lohr et al., 1991, 1994) do not. Black-capped chickadees also have been shown to depend, at least in part, on relative cues such as the ratio between note frequencies for song recognition (Weisman and Ratcliffe, 1989, 2004). One possibility for the origin of this species difference is that stereotyped frequency ratios may be a necessary but insufficient cue for song recognition in black-capped chickadees. Absolute cues, such as the species-typical song frequency range, might also play some role in song recognition, though perhaps a more minor one. Species-typical song or note frequency ranges could play a more dominant role in mountain and Carolina chickadee song recognition, with any tendency to produce specific song note ratios being lost or never acquired as a consequence. In either case, however, for sympatric species whose territories broadly overlap, the discrimination of conspecific from heterospecific song must depend on cues that differ between species. In areas where relative frequency cues are similar between mountain and black-capped chickadees, absolute frequency cues must prevail in discrimination between songs of the two species.

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References

- Aubin, T., Bremond, J.C., 1983. The process of species-specific song recognition in the skylark (*Alauda arvensis*): an experimental study

- by means of synthesis. *Zeitschrift für Tierpsychologie* 61, 141–152.
- Becker, P.H., 1982. The coding of species-specific characteristics in bird sounds. In: Kroodsmas, D.E., Miller, E.H. (Eds.), *Acoustic Communication in Birds. I. Production, Perception, and Design Features of Sounds*. Academic Press, New York, pp. 213–252.
- Beeman, K., 2001. *SIGNAL/RTSD User's Guide*. Engineering Design, Belmont, MA.
- Bremond, J.C., 1976. Specific recognition in the song of Bonelli's warbler (*Phylloscopus bonelli*). *Behaviour* 58, 99–116.
- Dabelsteen, T., Larsen, O.N., Pedersen, S.B., 1993. Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *J. Acoustical Soc. Am.* 93, 2206–2220.
- Dabelsteen, T., Pedersen, S.B., 1985. Correspondence between messages in the full song of the blackbird *Turdus merula* and meanings to territorial males, as inferred from responses to computerized modifications of natural song. *Zeitschrift für Tierpsychologie* 69, 149–165.
- Deutsch, D., 1969. Music recognition. *Psychol. Rev.* 76, 300–307.
- Deutsch, D., 1982. The processing of pitch combinations. In: Deutsch, D. (Ed.), *The Psychology of Music*. Academic Press, New York, pp. 271–316.
- Dixon, K.L., Stefanski, R.A., 1970. An appraisal of the song of the black-capped chickadee. *Wilson Bull.* 82, 53–61.
- Dooling, R.J., Haskell, R.J., 1978. Auditory duration discrimination in the parakeet (*Melospittacus undulatus*). *J. Acoustical Soc. Am.* 63, 1640–1642.
- Dooling, R.J., Lohr, B., Dent, M.L., 2000. Hearing in birds and reptiles. In: Dooling, R.J., Popper, A.N., Fay, R.R. (Eds.), *Comparative Hearing: Birds and Reptiles*. Springer-Verlag, New York, pp. 308–359.
- Dowling, W.J., 1978. Scale and contour: two components of a theory of memory for melodies. *Psychol. Rev.* 85, 341–354.
- Dowling, W.J., 1982. Melodic information processing and its development. In: Deutsch, D. (Ed.), *The Psychology of Music*. Academic Press, New York, pp. 413–429.
- Dowling, W.J., Fujitani, D.A., 1971. Contour, interval, and pitch recognition in memory for melodies. *J. Acoustical Soc. Am.* 49, 524–531.
- Emlen, S.T., 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41, 130–171.
- Falls, J.B., 1963. Properties of bird song eliciting responses from territorial males. In: *Proceedings of the XIII International Ornithological Congress*, vol. 13, pp. 259–271.
- Fay, R.R., 1988. *Hearing in Vertebrates: A Psychophysics Databook*. Hill-Fay Associates, Winnetka, IL.
- Ficken, M.S., Ficken, R.W., Witkin, S.R., 1978. Vocal repertoire of the black-capped chickadee. *Auk* 95, 34–48.
- Fotheringham, J.R., Ratcliffe, L., 1995. Song degradation and estimation of acoustic distance in black-capped chickadees (*Parus atricapillus*). *Can. J. Zool.* 73, 858–868.
- Gaddis, P.K., 1985. Structure and variability in the vocal repertoire of the mountain chickadee. *Wilson Bull.* 97, 30–46.
- Gammon, D.E., Baker, M.C., 2004. Song repertoire evolution and acoustic divergence in a population of black-capped chickadees, *Poecile atricapillus*. *Anim. Behav.* 68, 903–913.
- Gill, F.B., Funk, D.H., Silverin, B., 1989. Protein relationships among titmice (*Parus*). *Wilson Bull.* 101, 182–197.
- Gill, F.B., Mstrom, A.M., Mack, A.L., 1993. Speciation in North American chickadees. I. Patterns of mtDNA genetic divergence. *Evolution* 47, 195–212.
- Hill, B.G., Lein, M.R., 1987. Function of frequency-shifted songs of black-capped chickadees. *Condor* 89, 914–915.
- Hill, B.G., Lein, M.R., 1989a. Natural and simulated encounters between sympatric black-capped chickadees and mountain chickadees. *Auk* 106, 645–652.
- Hill, B.G., Lein, M.R., 1989b. Territory overlap and habitat use of sympatric chickadees. *Auk* 106, 259–268.
- 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.
- Hulse, S.H., Cynx, J., 1985. Relative pitch perception is constrained by absolute pitch in songbirds (*Mimus*, *Molothrus*, and *Sturnus*). *J. Comp. Psychol.* 99, 176–196.
- Hurly, T.A., Ratcliffe, L., Weisman, R., 1990. Relative pitch recognition in white-throated sparrows, *Zonotrichia albicollis*. *Anim. Behav.* 40, 176–181.
- Kinchla, J., 1970. Discrimination of two auditory durations by pigeons. *Perception Psychophys.* 8, 299–307.
- Kroodsmas, D.E., Byers, B.E., Halkin, S.L., Hill, C., Minis, D., Bolsinger, J.R., Dawson, J., Donelan, E., Farrington, J., Gill, F.B., Houlihan, P., Innes, D., Keller, G., Macaulay, L., Marantz, C.A., Ortiz, J., Stoddard, P.K., Wilda, K., 1999. Geographic variation in black-capped chickadee songs and singing behavior. *Auk* 116, 387–402.
- Lohr, B., Nowicki, S., Weisman, R., 1991. Pitch production in Carolina chickadee songs. *Condor* 93, 197–199.
- Lohr, B., Weisman, R., Nowicki, S., 1994. The role of pitch cues in song recognition by Carolina chickadees (*Parus carolinensis*). *Behaviour* 130, 1–15.
- Lynch, A., Baker, A.J., 1990. Increased vocal discrimination by learning in sympatry in two species of chaffinches. *Behaviour* 116, 109–126.
- Maier, E.H., Klump, G.M., 1990. Auditory duration discrimination in the European starling (*Sturnus vulgaris*). *J. Acoustical Soc. Am.* 88, 616–621.
- McCallum, D.A., Grundel, R., Dahlsten, D.L., 1999. Mountain chickadee (*Poecile gambeli*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 453. The Birds of North America, Inc., Philadelphia, PA.
- Mstrom, A.M., Curry, R.L., Lohr, B., 2002. Carolina chickadee (*Poecile carolinensis*). In: Poole, A., Gill, F. (Eds.), *The Birds of North America*, No. 636. The Birds of North America, Inc., Philadelphia, PA.
- Nelson, D.A., 1988. Feature weighting in species song recognition by the field sparrow (*Spizella pusilla*). *Behaviour* 106, 158–182.
- Nelson, D.A., 1989. Song frequency as a cue for recognition of species and individuals in the field sparrow (*Spizella pusilla*). *J. Comp. Psychol.* 103, 171–176.
- Njegovan, M., Ito, S., Mewhort, D., Weisman, R., 1995. Classification of frequencies into ranges by songbirds and humans. *J. Exp. Psychol.: Anim. Behav. Process.* 21, 33–42.
- Okanoya, K., Dooling, R.J., 1990. Detection of gaps in noise by budgerigars (*Melospittacus undulatus*) and zebra finches (*Poephila guttata*). *Hearing Res.* 50, 185–192.
- Page, S.C., Hulse, S.H., Cynx, J., 1989. Relative pitch perception in the European starling (*Sturnus vulgaris*): further evidence for an elusive phenomenon. *J. Exp. Psychol.: Anim. Behav. Process.* 15, 137–146.
- Ratcliffe, L., Weisman, R.G., 1985. Frequency shift in the fee bee song of the black-capped chickadee. *Condor* 87, 555–556.
- Richards, D.G., Wiley, R.H., 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Naturalist* 115, 381–399.
- Shackleton, S.A., Ratcliffe, L., Weary, D.M., 1992. Relative frequency parameters and song recognition in black-capped chickadees. *Condor* 94, 782–785.
- Shepard, R.N., 1982. Structural representations of musical pitch. In: Deutsch, D. (Ed.), *The Psychology of Music*. Academic Press, New York, pp. 343–390.
- Smith, S.M., 1993. Black-capped chickadee (*Parus atricapillus*). In: A. Poole, P. Stettenheim, F. Gill (Eds.), *The Birds of North America*, No. 39. Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologist's Union.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, third ed. W.H. Freeman and Company, New York.
- Thompson, W.L., 1969. Song recognition by territorial male buntings (*Passerina*). *Anim. Behav.* 17, 658–663.
- Ward, W.D., Burns, E.M., 1982. Absolute pitch. In: Deutsch, D. (Ed.), *The Psychology of Music*. Academic Press, New York, pp. 431–451.
- Weary, D.M., Weisman, R.G., Lemon, R.E., Chin, T., Mongrain, J., 1991. Use of the relative frequency of notes by veeries in song recognition and production. *Auk* 108, 977–981.
- Weary, D.M., 1996. How birds use frequency to recognize their songs. In: Moss, C.F., Shettleworth, S.J. (Eds.), *Neuroethological Studies of Cognitive and Perceptual Processes*. Westview Press, Boulder, CO, pp. 138–157.
- Weisman, R., Njegovan, M., Sturdy, C., Phillmore, L., Coyle, J., Mewhort, D., 1998. Frequency-range discriminations: special and general abilities in

- zebra finches (*Taeniopygia guttata*) and humans (*Homo sapiens*). *J. Comp. Psychol.* 112, 244–258.
- Weisman, R., Ratcliffe, L., 1989. Absolute and relative pitch processing in black-capped chickadees, *Parus atricapillus*. *Anim. Behav.* 38, 685–692.
- Weisman, R., Ratcliffe, L., 2004. Relative pitch and the song of black-capped chickadees. *Am. Sci.* 92, 532–539.
- Weisman, R., Ratcliffe, L., Johnsrude, I., Hurly, T.A., 1990. Absolute and relative pitch production in the song of the black-capped chickadee. *Condor* 92, 118–124.
- White, B., 1960. Recognition of distorted melodies. *Am. J. Psychol.* 73, 100–107.
- Wiebe, M.O., Lein, M.R., 1999. Use of song types by mountain chickadees (*Poecile gambeli*). *Wilson Bull.* 111, 368–375.
- Wiley, R.H., Richards, D.G., 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3, 69–94.
- Wilkinson, L., 1997. SYSTAT 7.0: Statistics. SPSS Inc., Chicago.
- Wunderle, J.M., 1979. Components of song used for species recognition in the common yellowthroat. *Anim. Behav.* 27, 982–996.