

Character displacement in dawn chorusing behaviour of sympatric mountain and black-capped chickadees



Angélique Grava^a, Ken A. Otter^{a,*}, Thibault Grava^a, Stefanie E. LaZerte^a, Angelika Poesel^b, Andrew C. Rush^c

^a Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC, Canada

^b Department of Evolution, Ecology and Organismal Biology and Borror Laboratory of Bioacoustics, The Ohio State University, Columbus, OH, U.S.A.

^c Museum of Vertebrate Zoology, University of California, Berkeley, CA, U.S.A.

ARTICLE INFO

Article history:

Received 20 November 2012
Initial acceptance 2 January 2013
Final acceptance 22 April 2013
Available online 18 June 2013
MS. number: A12-00871R

Keywords:

acoustic competition
black-capped chickadee
character displacement
interspecific interaction
mountain chickadee
Poecile atricapillus
Poecile gambeli
song

Signals of closely related species tend to be more distinct when occurring in sympatry than in allopatry. Such differences allow species-specific identification and presumably reduce interspecific mating. Among chickadees, dawn chorus behaviour affects female mate choice. Within our sympatric study population of black-capped chickadees, *Poecile atricapillus*, and mountain chickadees, *Poecile gambeli*, directional hybridization occurs via extrapair matings between female mountain chickadees (the subordinate species) and male black-capped chickadees (the dominant species). In this study, we compared dawn singing from this sympatric population with dawn recordings from allopatric populations of each species. Mountain chickadees used more chick-a-dee calls than songs during the dawn chorus when they co-occurred with black-capped chickadees in the sympatric population, but used similar proportions of calls and songs in the allopatric populations. We also found differences in the fine structure of the song; both species typically had a descending first note in their song (glissando), but mountain chickadees in the sympatric population used an ascending first note. The internote ratio between the first two notes of the song of the sympatric mountain chickadees lacked a characteristic frequency drop found in the allopatric mountain chickadee population and in the allopatric and sympatric populations of black-capped chickadees. Geographical analysis of songs of mountain chickadees across western North America revealed consistent differences in song features among sympatric/allopatric populations in different regions, but the nature of character shifts were not always parallel among populations. These findings illustrate possible character displacement in a subordinate species (mountain chickadee) to reduce acoustic overlap with a dominant heterospecific (black-capped chickadee).

© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Populations of closely related species are often more easily differentiated (e.g. morphologically or behaviourally) when they occur in sympatry than when they occur in allopatry (Brown & Wilson 1956). When closely related species co-occur in sympatry, individuals may fail to discriminate species-specific signals, which could both increase interspecific competition and lower individual fitness through the potential for interspecific mating (Grant 1994). Therefore, one would expect selection to favour evolution of enhanced differences in species-specific signals to increase discrimination when species coexist (i.e. divergent character displacement: Grant 1972; Schluter 1994; Grant & Grant 2010; Pfennig & Pfennig 2010), which may or may not be as pronounced

in allopatric populations of the same species (Brown & Wilson 1956; Loftus-Hills & Littlejohn 1992; Noor 1999; Pfennig & Pfennig 2010). However, character displacement does not necessarily occur symmetrically among the two species involved; when competitive interactions between species are, themselves, asymmetric, character shifts are predicted to be greater in the subordinate species (Miller 1968; Grant 1972; Doutrelant et al. 2000b; Grant & Grant 2010; Dhondt 2012).

Situations of asymmetry in interspecific competitive ability are common within the Paridae (titmice and chickadees), where several species often overlap in distribution and interact over common resources (Dhondt 1989, 2012; Curry 2005). Many of these overlapping species have asymmetries in their competitive abilities, which might result in asymmetrical character shifts, such as song (e.g. Doutrelant et al. 2000b; Gorissen et al. 2006). Among North American species, black-capped chickadees, *Poecile atricapillus*, and mountain chickadees, *Poecile gambeli*, co-occur in western populations, and interspecific competition between these

* Correspondence: K. A. Otter, Ecosystem Science & Management Program/Natural Resources & Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada.
E-mail address: otterk@unbc.ca (K. A. Otter).

species has been noted (Hill & Lein 1989; Martin & Norris 2007; Grava et al. 2012a).

Black-capped and mountain chickadees are typically considered sister-species among the North American chickadees (Gill et al. 1993, 2005). Although their breeding ranges overlap significantly, these species often have locally allopatric distributions due to ecological segregation. Sympatry does occur, however, along an altitudinal gradient where deciduous patches (black-capped-like habitat) abut coniferous forests (mountain-like habitat). One such overlap zone occurs at the John Prince Research Forest (JPRF) near Fort St James in central British Columbia, Canada; in this population, black-capped chickadees are the socially dominant species in interspecific interactions (Grava et al. 2012b). Furthermore, hybridization occurs in this population, resulting from female mountain chickadees engaging in extrapair copulations with male black-capped chickadees (Grava et al. 2012b). Thus, in this sympatric population, there may be selective pressure for the subordinate species (mountain chickadees) to alter intraspecific signals, such as singing behaviour, to avoid acoustic overlap with the more dominant black-capped chickadees.

Dawn singing is a common signalling behaviour among chickadees, where males vocalize using songs, calls or a mix of both (depending on the species) during the female fertility period in the early spring (Mennill & Otter 2007). Males begin vocalizing before sunrise and sing/call nearly continuously for 15–90 min in the vicinity of their nest cavity (Otter & Ratcliffe 1993; Otter et al. 1997; Gammon 2004; Mennill & Otter 2007). Usually, males stop singing or calling when females leave the nest or their roosting spot (e.g. Smith 1991; McCallum et al. 1999; Gammon 2004), at which point the pair often copulates (e.g. Otter & Ratcliffe 1993; Gammon 2004; A. Grava & K. A. Otter, personal observations). In some species, females use songs not only in species recognition, but also to assess male quality and extrapair partners (e.g. Hasselquist et al. 1996; Kempnaers et al. 1997; Otter et al. 1997; Mennill et al. 2003; Searcy & Nowicki 2005; Seddon & Tobias 2010). Furthermore, interspecific interactions may promote the subordinate species to shift to songs that have lower overlap with, and thus elicit less aggression from, the dominant species (Doutrelant et al. 2000a, b; Gorissen et al. 2006). One might, therefore, expect greater divergence in vocal behaviour among sympatric compared to allopatric populations of these two chickadee species (Pfennig & Pfennig 2010).

Lohr (2008) explored this possibility in one sympatric mountain/black-capped chickadee population (southwestern Alberta, Canada), comparing song structure of the two species. For black-capped chickadees, the dominant vocalization during the chorus is the two-note fee-bee song, which has highly stereotyped frequency ratios both within and between notes across most of the species' range (Hailman 1989; Kroodsmas et al. 1995; Mennill & Otter 2007; Lohr 2008). Mountain chickadees use a mix of whistled songs and chick-a-dee calls during dawn vocalization (McCallum et al. 1999). Mountain chickadee songs have a more variable number of notes (three to five, typically), but often include similar frequency modulations within and between notes as occur in black-capped chickadees (McCallum et al. 1999; Wiebe & Lein 1999; Lohr 2008). In his comparative study, Lohr (2008) found that songs of the two species in this sympatric population were sufficiently distinct in absolute pitch to allow differentiation, but found little evidence for character displacement in relative frequency ratios within songs. However, both the nature of the character shifts and the selective pressure for displacement in the subordinate species may differ among isolated sympatric populations (Pfennig & Pfennig 2010). The known directional hybridization and highly asymmetric competitive interactions among wintering birds in our study population at JPRF (Grava et al. 2012b) might predict pressure for mountain chickadees in our study area

to alter acoustic signals away from dominant heterospecifics. Furthermore, while several studies have documented song variation and fine details of note structure in mountain chickadees (Wiebe & Lein 1999; Lohr 2008), little research has investigated the differential use of calls and songs during dawn chorus behaviour in mountain chickadees, particularly between populations sympatric and allopatric with black-capped chickadees.

We investigated mountain chickadee dawn chorus behaviour and song characteristics for indications of character displacement. We recorded the dawn choruses of both mountain and black-capped chickadees with a sympatric population and compared both the use of calls/songs and the composition of notes within songs to an allopatric population of each species. We then compared spectral characteristics of the mountain chickadee songs within our sympatric population to songs over a broader geographical area, using local knowledge and species sighting catalogues to determine whether mountain chickadees were allopatric or sympatric with black-capped chickadees in each location. Our goal was to determine whether the structure of mountain chickadee dawn signalling, or the songs themselves, differ among individuals that co-occur in sympatry with black-capped chickadees compared to those that occur in allopatry.

METHODS

Primary Study Sites

We sampled black-capped (BCCH) and mountain chickadees (MOCH) at the JPRF (hereafter 'sympatric-BCCH' and 'sympatric-MOCH' populations, respectively). We sampled one additional population occupied by black-capped chickadees (Prince George, BC, 'allopatric-BCCH') and one occupied by mountain chickadees (Riske Creek, BC, 'allopatric-MOCH'): 95% of the chickadees in each of these two allopatric populations were from one species only, with few incidental occurrences of the other species. These totals are based upon at least 5 years of population monitoring in both populations (Otter et al. 2007; K. Martin, personal communication).

Dawn Chorus Recording

The peak in dawn signalling among males (dawn chorus) occurs during the early breeding season, in late April to early May depending on the year, site and species. This corresponds to the female fertile period, as dawn singing peaks during the period of nest cavity excavation and egg laying and drops dramatically as females begin incubation. The first songs/calls of a male's dawn singing bout begin before sunrise, and individual males vocalize with a consistent cadence of 12–20 songs or calls/min for up to 1 h (Mennill & Otter 2007). A complete recording of one morning's dawn singing is enough to cover the size of an individual's repertoire (Doutrelant et al. 2000a; Mennill & Otter 2007). We recorded all dawn chorus bouts from a male's first vocalization (chick-a-dee call or song) until the bird stopped vocalizing for at least 5 consecutive minutes. We used a Marantz PMD671 digital recorder with either a Sennheiser ME67 microphone/K6 power supply or a Sennheiser MKH70 microphone/MZA14 power supply to record the mountain chickadees from the sympatric-MOCH ($N = 10$) and allopatric-MOCH ($N = 8$) populations in 2010. Comparison choruses from black-capped chickadees were drawn randomly from recordings associated with other studies in the allopatric-BCCH population (van Oort et al. 2006) and the sympatric-BCCH population (Grava et al. 2009); similar criteria were used in these studies for defining the start and end of the chorus. A total of 12 choruses were selected from the sympatric-BCCH population evenly distributed from recordings made in 2006, 2008 and 2009 using the same recording equipment

as noted above. A total of 10 choruses from black-capped chickadees in the allopatric-BCCH population were selected from recordings made in 2000, 2002 and 2003. These latter recordings were made with Marantz PMD430 audio-cassette recorders in conjunction with one of the following directional microphones: a Sennheiser ME 67 with a K6 power supply, a Sennheiser MKH 70 with a MZA14 power supply or an Audio-Technica AT815b.

Analysis of General Chorus Pattern

We transcribed dawn chorus recordings of black-capped and mountain chickadees to determine the proportion of time that an individual used calls versus songs. As chickadees vocalized continuously during the dawn chorus, we analysed choruses in 1 min segments. Birds typically sing one vocalization or the other in string sequences (many songs with no chick-a-dee calls, followed by strings of chick-a-dee calls with no songs). We calculated the proportion of time in each minute that the birds spent producing either songs or chick-a-dee calls (this included the time of the vocalization itself and the intervalization space).

Spectral Analysis of Songs and Calls in Focal Populations

We randomly isolated nine songs from the recordings evenly distributed across the chorus for detailed spectral analysis, using the methodology similar to Christie et al. (2004). Using the sound analysis package Seewave (Sueur et al. 2008) with R 2.8.1 (R Development Core Team 2008), we extracted frequency values at the start and end of each note within each of the nine songs (Fig. 1). As in Lohr (2008), the notes for mountain chickadee songs were numbered sequentially as N1, N2, N3, et cetera, to account for the greater interindividual and interpopulation variation in note number among mountain versus black-capped chickadee songs (Fig. 1b). For comparison, 'N1' and 'N2' in a black-capped chickadee

would correspond to the fee and bee notes, respectively, in their two-note fee-bee song (Fig. 1a). Mountain, but not black-capped, chickadees often introduce a variable number of short syllables (introductory syllables) at the start of their song. These notes are very short (approximately 1/10 the duration of the major notes), but similar in pitch to the N1 note of the song. As these do not occur in black-capped chickadees, we excluded them in the detailed analysis of chorus singing between black-capped and mountain chickadees in our focal populations, focusing on those elements common to both species. These introductory notes were included in the geographical analysis of variation in mountain chickadee songs (see below).

We conducted acoustic analyses of songs by comparing the absolute frequency and frequency ratios within songs for each of the four study populations (Fig. 1). Previous research used the internote ratio (ratio between the frequency at the end of the first note and the frequency at the start of the second note) and the glissando (ratio between the frequency at the start and the frequency at the end of the first note) to describe the acoustic structure of black-capped chickadee dawn chorus (Christie et al. 2004). Although we calculated the glissando of the first note for both mountain and black-capped chickadees (frequency $N1_{start}/N1_{end}$), the second note of the mountain chickadee song has a highly variable ascending start among males and between populations (A. Grava & K. A. Otter, personal observations) that does not reflect the dominant frequency of the note. To account for this, we used the ratio between the frequency at the end of the first note and the dominant frequency at the end of second note ($N1_{end}/N2_{dom}$) to calculate the 'internote ratio' (Fig. 1).

We conducted spectral analysis of 30 chick-a-dee calls, evenly distributed across the chorus, to determine whether call note composition and/or syntax differed between sympatric and allopatric populations. Analysis was conducted with SASLab-Pro software (Avisoft Bioacoustics, Berlin). Mountain chickadee call note

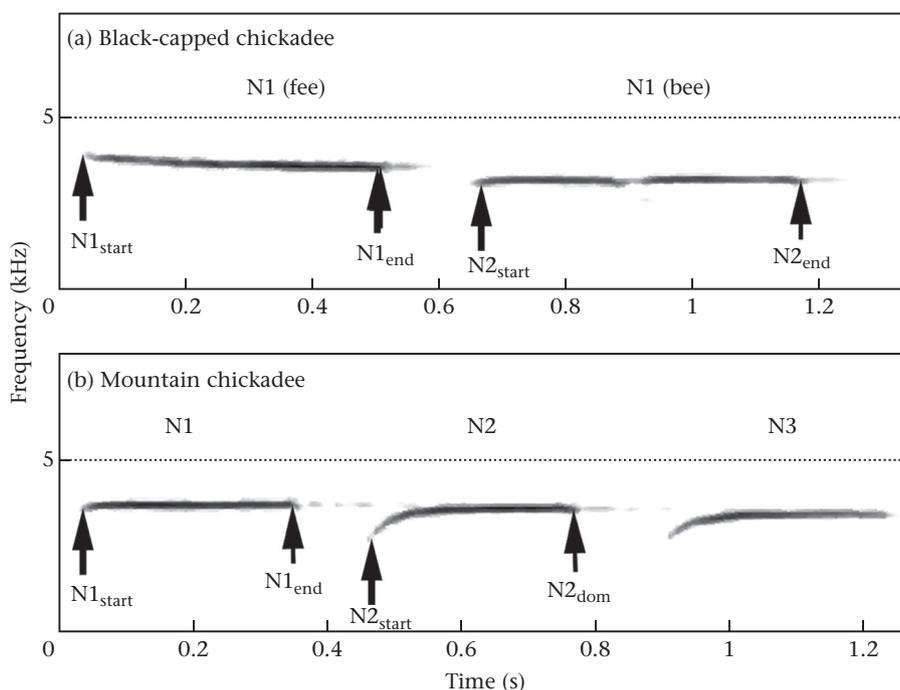


Figure 1. Song spectrograms from the sympatric population of (a) black-capped and (b) mountain chickadees at the John Prince Research Forest (JPRF) near Fort St James, British Columbia, Canada. Notes were numbered sequentially (N1, N2, etc.) following the convention used by Lohr (2008). N1 and N2 in black-capped chickadees correspond to the fee and bee notes (Foote et al. 2010), respectively. For comparisons between mountain and black-capped chickadee songs, we measured dominant frequencies and frequencies at the start (e.g. $N1_{start}$, $N2_{start}$) and end ($N1_{end}$, $N2_{end}$) of each song, and used these measures to calculate the following standardized frequency ratios: glissando ($N1_{start}/N1_{end}$) and internote ratio ($N1_{end}/N2_{end}$). For broader geographical studies among mountain chickadee populations, we also measured note lengths, number of notes per song and presence of introductory syllables (not shown).

types have been described by Bloomfield et al. (2004). These authors differentiated six note types: A, A/B, B, C, Dh and D (Fig. 2). Because there is a constant gradient from note A to A/B to B, we classified those three note types as being note A-B.

Statistical analysis was conducted using Statistica (10.0, Statsoft, Tulsa, OK, U.S.A.). We used nonparametric analyses for proportional data (proportion of chorus spent producing songs versus calls) or when the data did not meet assumptions of normality (geographical comparisons of internote ratio and glissando). We used general linear ANOVA models when the data were continuous and met assumptions of normality.

Geographical Comparisons of Mountain Chickadee Songs

Mountain chickadees are known to have dialectal variation between populations (Lohr 2008). To determine whether the differences in song structure we observed between our focal sympatric/allopatric populations had parallels in different regions where the two species may or may not co-occur, we obtained recordings of mountain chickadees made at other locations in British Columbia, Canada, as well as from recordings obtained from a range of locations throughout the western United States (songs used with permission from the Borror Laboratory of Bioacoustics, The Ohio State University, Columbus, OH, U.S.A.). The locations of song recordings as well as some of the representative variation in song structure are shown in Fig. 3.

For each of the 58 males used in the study, we extracted up to 10 individual songs for analysis (range 1–10, mean \pm SE = 8.5 ± 0.3 , for a total of 494 songs). Within this data set, some recordings occurred within the geographical overlap of the species range for the black-capped chickadee (Foote et al. 2010), while some of the recordings were from populations outside this range. These included recordings from the Borror Laboratory of Bioacoustics, plus personal recordings made by the authors. In total, we obtained recordings of 32 males from British Columbia, Canada (John Prince Research Forest ($N = 13$), Riske Creek ($N = 7$), plus two additional locations, William's Lake ($N = 8$) and Kamloops ($N = 4$)) and 26 males from the United States (California ($N = 15$), New Mexico ($N = 3$), Colorado ($N = 2$), Nevada ($N = 2$), Arizona ($N = 2$), Utah ($N = 1$) and Montana ($N = 1$)). All songs used in the analysis were high-pass filtered (2.8 kHz) to remove background noise. Temporal and frequency measures (note length; start, end and dominant frequency) for each of the major notes (e.g. N1, N2, etc.) in each song, plus a count of the number of any introductory syllables were extracted using Seewave and R 2.8.1 (R Development Core Team 2008), as described above. We calculated the glissando of each major note and the internote ratios between each successive pair of notes for each song. The averaged values of these measures were then calculated for each male across all recorded songs and entered into a principal components analysis, PCA (Statistica 10.0) to compare variation among males and populations. The variables entering the analysis were: number of introductory

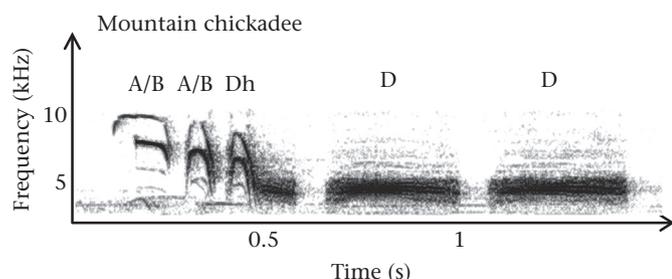


Figure 2. Mountain chickadee chick-a-dee call sonagram. Of the calls used during the chorus, 95% were composed of note types A-B, Dh and D.

syllables; number of major notes (N1, N2, etc.); song length (excluding introductory syllables: (s)); duration of N1, N2 and N3 (s); dominant frequency of N1, N2 and N3; glissando within N1, N2 and N3; internote ratios between each successive pair of notes (end frequency of N_i /dominant frequency of N_{i+1}); and, finally, the largest internote ratio between two successive notes within the whole song. We introduced this last measure because some populations show the major frequency drop between successive notes N2 and N3 rather than between successive notes N1 and N2. Furthermore, males in some populations routinely have four major notes in the song (N1–N4), but as this occurred in only 14 of the 58 males, we excluded frequency/duration measures of this note from the PCA. We accounted for this variability by including these extra notes in the variables 'song length' and 'number of notes in song'.

Due to relative positive/negative loadings of variables, higher values of PC1 represent songs with longer overall song length and longer individual notes for N1, N2 and N3, and more introductory syllables, but smaller internote ratios (between N1 and N2 and also between the two notes with greatest internote ratio) and, smaller glissandos within notes N1, N2 and N3 (Table 1).

Higher values of PC2 correspond to lower dominant frequencies in all three major notes (N1, N2 and N3), shallower glissandos in N1 and N2, a slightly larger internote ratio between N1 and N2, a smaller ratio between N2 and N3, but shorter overall song length and N2 length (Table 1). Finally, higher values of PC3 correspond to fewer notes in the song (excluding introductory syllables), longer note length and dominant frequency for N3, and smaller internote ratio between N2 and N3 (suggesting N2 and N3 are similar in pitch among songs with fewer notes); there is also a lower maximum internote ratio between two successive notes (Table 1).

For each recording site, we then classified the mountain chickadees as either sympatric or allopatric with black-capped chickadees, based on a hierarchy of criteria. As the first level, we used the recordist's local knowledge of the presence of singing black-capped chickadee males within the immediate area of the focal mountain chickadee male. If we lacked this local knowledge (as in many of the songs from recording archives), we identified the point location of the recording from archive notes and surveyed the location using 'ebird' point and range maps (ebird.org, Audubon and Cornell Lab of Ornithology, accessed February 2013). We first surveyed each recording sight for records of mountain chickadees; all ebird maps had point observations of mountain chickadees, confirming that the area had been surveyed. We then surveyed the same area for records of black-capped chickadees. We set an a priori criterion that the region would be considered locally sympatric if there were multiple black-capped chickadee records within 10 km of the recording site. If there were no black-capped records within this distance, the sites were classified as allopatric. In all cases where this criterion was applied, the results were unambiguous: there were either no black-capped chickadee records within >20 km of the site, or multiple black-capped chickadee records within 5 km of the site. Our classification led to 34 mountain chickadee recordings being classified as allopatric and 24 being classified as sympatric with black-capped chickadees (Fig. 3). This sympatry was also broadly spread over the total geographical range of black-capped chickadees (see Foote et al. 2010).

We compared the PC scores across males by region and whether they occurred within allopatric or sympatric regions using ANOVA models (Statistica 10.0).

RESULTS

General Chorus Pattern

Black-capped chickadee dawn choruses were composed almost exclusively of song, both for the sympatric and allopatric populations.

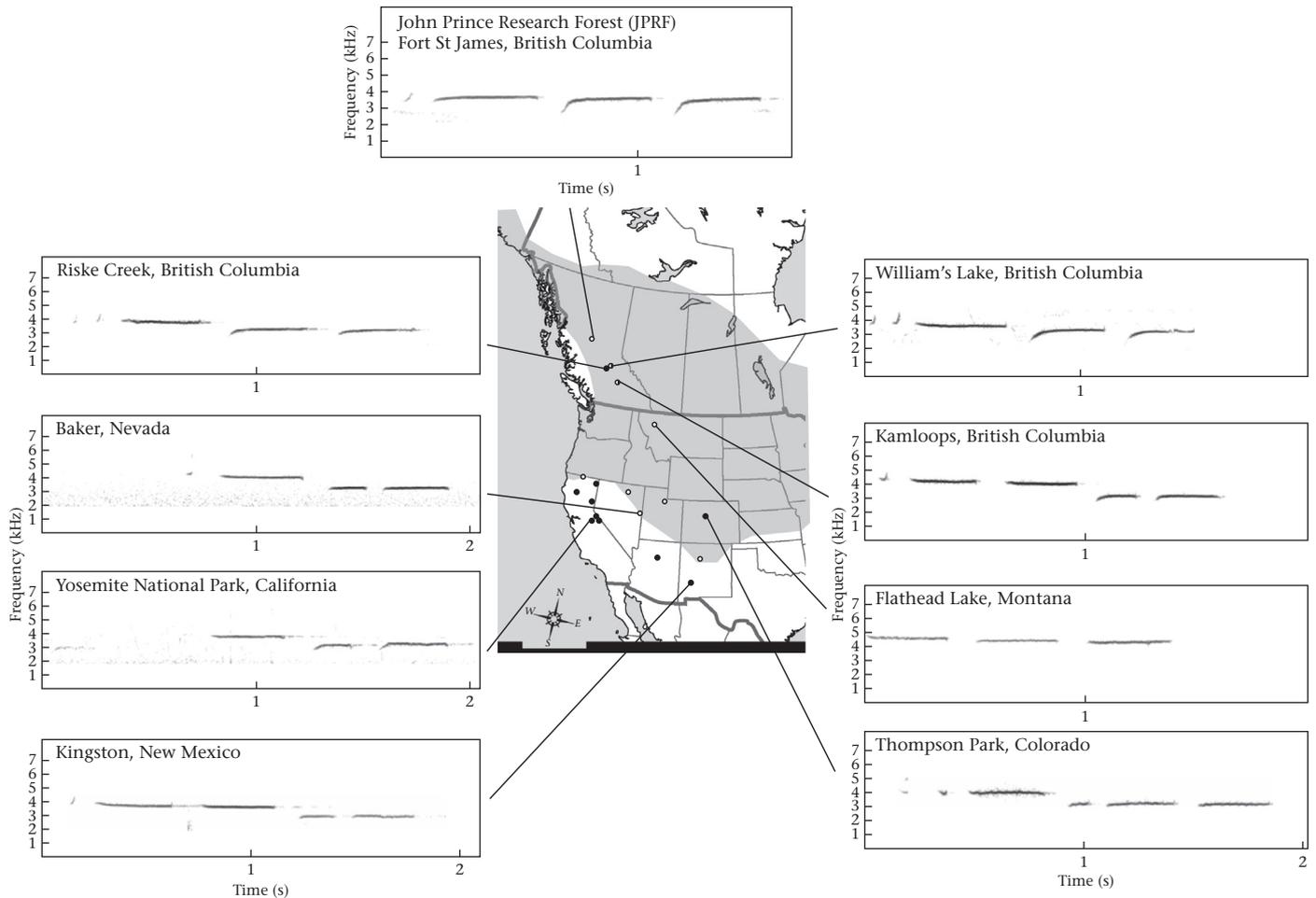


Figure 3. Locations of mountain chickadee calls used in geographical comparisons of song frequency ratios. Grey shading indicates the geographical species range of black-capped chickadees. Recording sites of mountain chickadees were classified as either locally sympatric (open circles) or allopatric (filled circles) based on direct field observation or co-occurrence of species records with ebird point and range maps (ebird.org, Audubon and Cornell University Lab of Ornithology, accessed February 2013). Sites that had both allopatric and sympatric local populations are denoted in half-filled circles. Spectrograms depict some of the variability in mountain chickadee songs from across these sites. Map source: <http://www.zonu.com/fullsize-en/2009-11-08-10949/North-America-Political-Outline-Map.html>.

During an entire chorus, black-capped chickadees from the sympatric-BCCH population used songs 94% of the time when vocalizing (Wilcoxon signed-ranks test: time spent singing versus calling: $T = 0$, $N = 12$, $P = 0.002$) and those from the allopatric-BCCH population used songs 92% of the time ($T = 0$, $N = 10$, $P = 0.005$). The proportion of the total time during the dawn chorus that black-capped chickadees used songs did not differ significantly between allopatric-BCCH and sympatric-BCCH populations (Mann–Whitney U test: $U = 58$, $N_1 = 10$, $N_2 = 12$, $P = 0.89$).

The dawn chorus of the mountain chickadee was a mix of songs and chick-a-dee calls. In the allopatric-MOCH population, there was no significant difference between the proportion of time spent producing songs (45% of the time) versus chick-a-dee calls (55%) during the chorus (Wilcoxon test: $T = 14$, $N = 8$, $P = 1.0$). In contrast, birds from the sympatric-MOCH population spent significantly more time producing chick-a-dee calls (80% of the time) than songs (20% of the time; Wilcoxon test: $T = 1.0$, $N = 9$, $P = 0.01$; Fig. 4). Birds from the sympatric-MOCH population used significantly more chick-a-dee calls than did individuals from the allopatric-MOCH population (Mann–Whitney U test: $U = 16.5$, $N_1 = 8$, $N_2 = 9$, $P = 0.05$).

Chick-a-dee Call Analysis

Chick-a-dee calls used by mountain chickadees during the dawn chorus were highly stereotyped: among the 30 calls per bird that

we randomly extracted from the chorus, 95% were composed of note types A-B, Dh and D (Fig. 2). Half of the calls were either A-B A-B A-B Dh D D (21% at the sympatric-MOCH population, 30% at the allopatric-MOCH population) or A-B A-B Dh D D (29% at the sympatric-MOCH population, 20% at the allopatric-MOCH population).

Song Analysis

In both the allopatric-MOCH and the sympatric-MOCH populations, mountain chickadees used songs that were primarily composed of three notes. We observed a somewhat higher amount of two-, four- and five-note songs among the sympatric-MOCH population (32%), even though three-note songs were still the most common (68%). By comparison, the allopatric-MOCH population used three-note songs more consistently (92% of all songs). However, this variation in number of notes per song did not differ significantly between the two sites (Mann–Whitney U test: $U = 13.5$, $N_1 = 7$, $N_2 = 7$, $P = 0.16$).

There was no significant difference in the frequency at the end of the first note between birds in the four comparison groups (allopatric-MOCH, allopatric-BCCH, sympatric-BCCH and sympatric-MOCH; ANOVA: $F_{3,32} = 0.95$, $P = 0.43$). However, we found significant differences between populations in the frequency at the end of the second note ($F_{3,32} = 3.299$, $P = 0.03$). Post hoc

Table 1
Results of a principal component analysis on multiple song measures from 58 mountain chickadees in different populations throughout western North America

Variable	Principal component		
	PC1	PC2	PC3
Number of introductory syllables	0.44	0.11	0.071
Number of notes in songs (excluding introductory phrase)	0.16	-0.26	-0.78
Song length	0.73	-0.40	-0.29
Note length, N1	0.74	0.19	0.0041
Note length, N2	0.76	-0.39	-0.18
Note length, N3	0.52	0.010	0.70
Dominant frequency, N1	-0.52	-0.72	0.22
Dominant frequency, N2	0.088	-0.97	0.077
Dominant frequency, N3	0.060	-0.71	0.66
Glissando, N1	-0.45	-0.25	-0.33
Glissando, N2	-0.65	-0.59	-0.0060
Glissando, N3	-0.73	-0.43	0.22
Internote ratio ($N1_{end}/N2_{dom}$)	-0.68	0.55	0.14
Internote ratio ($N2_{end}/N3_{dom}$)	0.093	-0.45	-0.82
Max. internote ratio between two successive notes (N_{iend}/N_{i+1dom})	-0.75	0.29	-0.43
% Total variance explained by factor	30.87	23.88	18.33

The first three principal axes of the analysis explained more of the variation across males than expected by chance alone, using the broken-stick method of factor significance (Jackson 1993; Legendre & Legendre 1998). Variables with individual contributions to the principal factor of 0.33 or higher were considered to be contributing significantly to the individual principal component measure (Ho 2006) and are indicated in bold: those above 0.60 were considered to be contributing most strongly.

analysis showed that this difference occurred between the two populations at the contact zone site with the sympatric-MOCHs' second note being higher pitch than the sympatric-BCCHs' second note (Tukey HSD test: $df = 32, N = 36, P = 0.01$). There was no difference in the absolute frequency of the second note between black-capped chickadees from the allopatric-BCCH and the sympatric-BCCH populations ($P = 0.40$). The absolute frequency of the second note did not differ between the songs of mountain

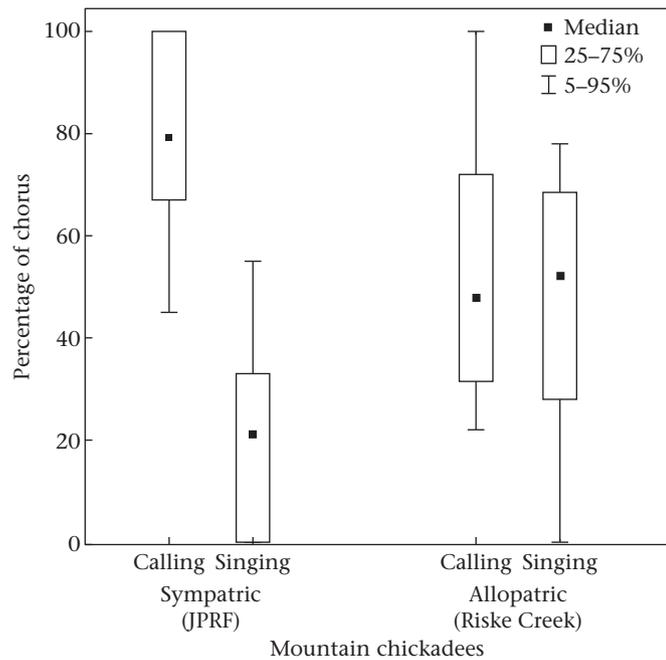


Figure 4. Percentage of time that mountain chickadees from the sympatric (with black-capped chickadees) population (sympatric-MOCH; Wilcoxon test: $P = 0.01$) and the allopatric population (allopatric-MOCH; Wilcoxon test: $P = 1$) spent calling versus singing during the dawn chorus.

chickadees in the allopatric-MOCH or sympatric-MOCH population ($P = 0.37$). However, examination of the internote ratio revealed that the mountain chickadees from the sympatric-MOCH population had a significantly lower internote ratio than the three other studied populations ($F_{3,32} = 47.54, P < 0.001$; Fig. 5a). Post hoc analysis revealed significant differences in internote ratio between the sympatric-MOCH population and the allopatric-MOCH population (Tukey HSD test: $df = 32, N = 36, P < 0.001$), the sympatric-BCCH population ($df = 32, N = 36, P < 0.001$) and the allopatric-BCCH population ($df = 32, N = 36, P < 0.001$). There were no significant differences in internote frequency ratios among the other three populations (sympatric-BCCH, allopatric-BCCH and allopatric-MOCH; all $P > 0.1$).

We also found that black-capped chickadees differed from mountain chickadees in the glissando of the first note ($F_{3,32} = 32.53, P < 0.001$; Fig. 5b). Post hoc analysis revealed that the glissando of the first note for the allopatric-MOCH population was statistically smaller than that of the sympatric-BCCH (Tukey HSD test: $df = 32, N = 36, P < 0.001$) and allopatric-BCCH ($df = 32,$

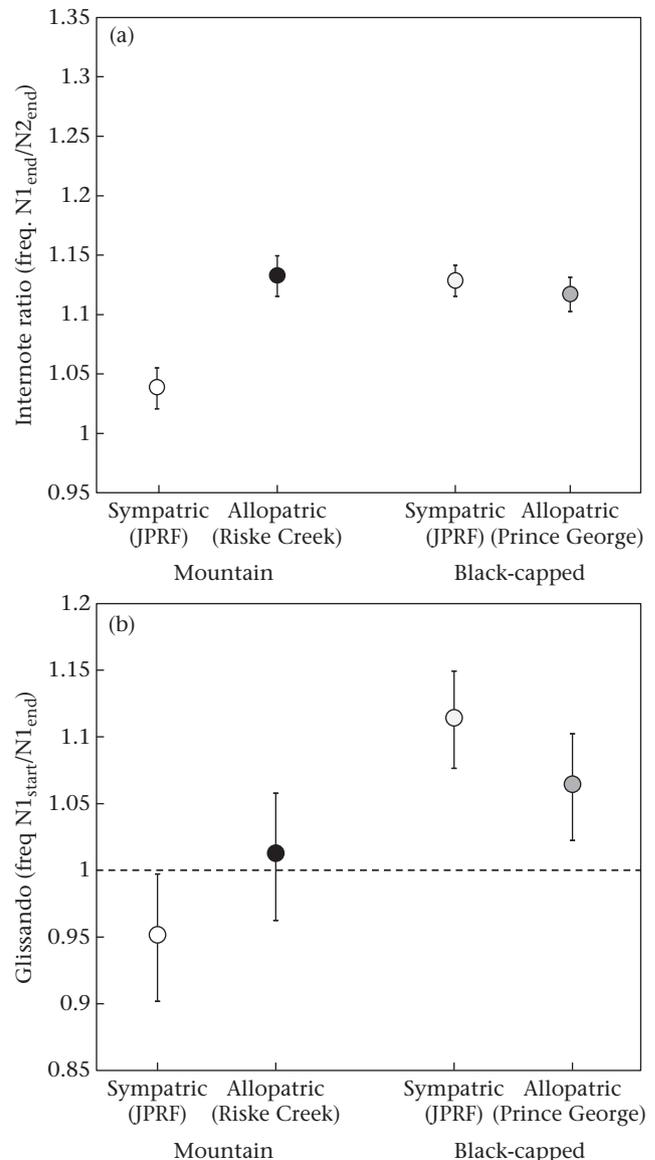


Figure 5. (a) Internote ratio and (b) glissando of sympatric and allopatric black-capped and mountain chickadees. Values are means \pm SE.

$N = 36$, $P = 0.005$) populations. The glissando of the sympatric-MOCH population was also significantly smaller than that of the allopatric-BCCH ($df = 32$, $N = 36$, $P < 0.001$) and sympatric-BCCH ($df = 32$, $N = 36$, $P < 0.001$) populations, but was also significantly smaller than that of the allopatric-MOCH population ($df = 32$, $N = 36$, $P = 0.003$). All studied populations except the sympatric-MOCH had a glissando with a ratio > 1 . This indicated a descending first note, whereas the sympatric-MOCH glissando was less than one, illustrating a slightly ascending first note (Fig. 5b).

Broader Geographical Comparisons of Mountain Chickadees in Allopatric/Sympatric Populations

Mountain chickadee songs from recording locations sympatric with black-capped chickadee populations had significantly higher PC1 scores than those from allopatric recording sites ($F_{1,56} = 12.12$, $P = 0.001$), suggesting that the songs of sympatric birds had smaller glissandos in individual notes and smaller internote ratios, but they were longer and had more introductory notes. There was no difference in PC2 ($F_{1,56} = 2.74$, $P = 0.10$) or PC3 ($F_{1,56} = 0.047$, $P = 0.83$) scores between sympatric and allopatric sites. This result, however, may have been driven by regional variation in song structure. Indeed, we found significant differences in PC1 ($F_{7,50} = 10.22$, $P < 0.00001$), PC2 ($F_{7,50} = 4.26$, $P = 0.001$) and PC3 ($F_{7,50} = 3.94$, $P = 0.002$) scores between states or province of mountain chickadee recordings. In particular, British Columbia populations (which had 16 sympatric and 16 allopatric recordings) and California populations (which had three sympatric and 12 allopatric population recordings) had regional differences in PC1 scores that mirrored the overall differences between allopatric and sympatric populations (i.e. the populations in California had lower PC1 scores than those in British Columbia).

As we had a large number of recordings from these two regions and from both allopatric and sympatric sites, we conducted a two-factor ANOVA with region (British Columbia versus California) and sympatric versus allopatric categorical predictors on the PC analyses to determine the relative influence of geographical variation versus interactions with heterospecifics. For PC1, we found a significant effect of region, with British Columbia having significantly higher principal component scores than California ($F_{1,43} = 81.07$, $P < 0.0001$), but the effect of allopatry/sympatry was diminished ($F_{1,43} = 3.13$, $P = 0.084$). However, the interaction between region and sympatry was significant ($F_{1,43} = 13.74$, $P = 0.0006$; Fig. 6a); in British Columbia, sympatric populations had significantly higher PC1 scores (songs had lower glissandos within notes and smaller internote ratios, but were longer overall with more introductory syllables) than allopatric populations ($P = 0.00002$), but the effect was opposite in California. While there was still a difference between sympatric and allopatric populations, allopatric populations tended to have higher PC1 scores ($P = 0.08$).

We found both a significant effect of region ($F_{1,43} = 5.09$, $P = 0.03$) and sympatry/allopatry ($F_{1,43} = 5.40$, $P = 0.025$) for PC2 scores when comparing mountain chickadees in California and British Columbia. There was no interaction effect ($F_{1,43} = 0.0021$, $P = 0.96$), and the results for each region appeared to be in parallel (Fig. 6b). This suggests that sympatric birds had songs with lower dominant frequencies in all major notes, but also had shorter N2 notes and slightly shorter songs. The same pattern of difference was found in British Columbia versus California birds.

Birds from British Columbia tended to have higher values in PC3 than those from California ($F_{1,43} = 3.78$, $P = 0.06$). However, there was no effect of allopatry/sympatry ($F_{1,43} = 0.058$, $P = 0.81$) and no significant interaction effect between region and allopatry/sympatry ($F_{1,43} = 2.88$, $P = 0.10$).

DISCUSSION

Mountain chickadee dawn chorus behaviour varied between our focal populations that were either sympatric or allopatric with black-capped chickadees. There was a significant increase in the proportion of chick-a-dee calls in the sympatric-MOCH population compared to chorusing behaviour of mountain chickadees in the allopatric-MOCH population. The chorusing behaviour of the more dominant black-capped chickadee, however, did not differ between allopatric-BCCH and sympatric-BCCH populations and was consistent with dawn chorus patterns reported throughout the majority of this species' distribution range (Gammon 2007).

Interestingly, mountain chickadees in the focal allopatric-MOCH population had internote ratios similar to those of black-capped chickadees from both sampled populations. The mountain chickadees from the sympatric-MOCH population, however, had significantly lower internote ratios than any other focal population, showing a shift in the structure of their song away from the observed pattern of black-capped chickadee song. Black-capped chickadees do not appear to modify their internote ratios whether they co-occur with mountain chickadees (sympatric-BCCH) or not (allopatric-BCCH). Furthermore, the internote ratios for both our black-capped populations were similar to those reported in Alberta (Lohr 2008) and Ontario, Canada (Christie et al. 2004).

The glissando (ratio of the frequency at the start and at the end of the first note) also varied between the four studied populations; mountain chickadees had significantly lower glissando in the first note of the song than did black-capped chickadees. The glissando in both our black-capped chickadee populations did not differ and fell within the same range found by Christie et al. (2004) in Ontario, Canada, and by Lohr (2008) in Alberta, Canada. However, mountain chickadees from the sympatric-MOCH population at the JPRF had significantly lower glissando ratios than mountain chickadees from the allopatric-MOCH population in Riske Creek. As a result, in mountain chickadees in our overlap zone, the first note ascended slightly in frequency from start to end, whereas in the other populations of mountain and black-capped chickadees studied in detail, the first note descended in frequency.

In our broader geographical analysis, PC1 scores best paralleled both of these components of song, with larger values having lower glissandos within the first three notes and smaller internote intervals between notes. This factor varied significantly between regions, but also between allopatry and sympatry. In our comparisons of allopatric/sympatric populations in both British Columbia and California, we found that this pattern of divergence (higher PC1 scores in sympatry) was consistent in all sampled populations in British Columbia (including two additional populations for which we had both locally sympatric and locally allopatric mountain chickadee recordings). Interestingly, though, this pattern was reversed between the two sympatric recording sites in northern California compared to the other recordings from mountain chickadees in areas south of the distribution range of black-capped chickadees. This suggests an effect of sympatry, but that the divergence in song structure when overlapping with the more dominant heterospecific may differ between isolated sympatric populations. Conversely, other aspects of song shifts in sympatry may be similar among the compared regions, as occurred with parallel influence of sympatry/allopatry on PC2 factor scores between California and British Columbia. This factor is largely influenced by dominant frequency within notes and may suggest a shift away from overlap with songs of black-capped chickadees in areas of sympatry, similar to that found by Lohr (2008) in Alberta, Canada.

Taken together, the changes to both the general chorus patterns of songs/call use and the note structure of songs used in the chorus

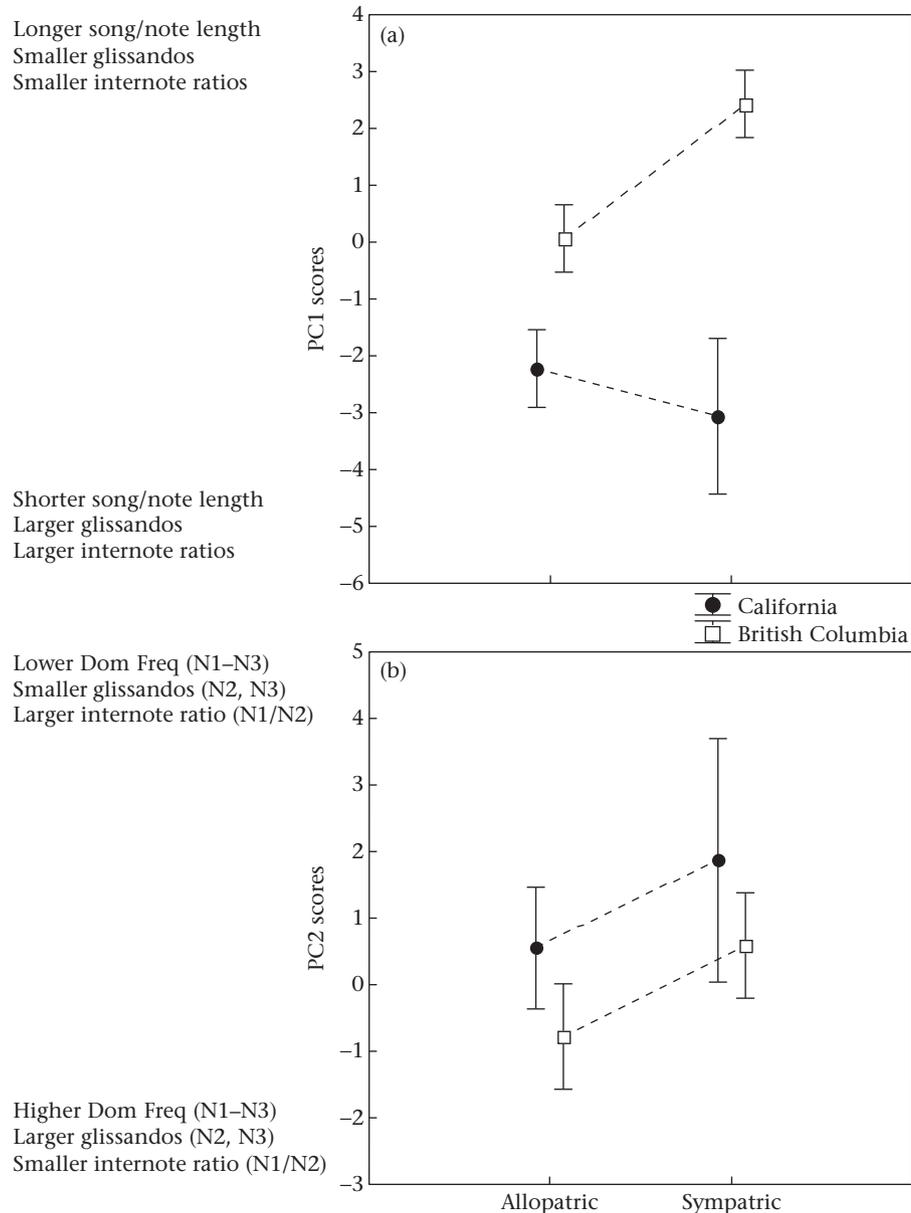


Figure 6. Variation in the songs of sympatric and allopatric mountain chickadees in California, U.S.A. (black circles) and British Columbia, Canada (open squares). We assessed measures of note duration, dominant frequency, internal frequency ratios within and between notes and other measures using principal component analysis, and compared significant variation between region (British Columbia versus California) and sympatry/allopatry with two-factor ANOVA. (a) PC1 (primarily a measure of frequency ratios within and between notes) scores of sympatric and allopatric populations for each region. (b) PC2 (primarily a measure of dominant frequency of the notes within a song) scores of sympatric and allopatric populations for each region.

support the character shift hypothesis; mountain chickadees altered their songs and singing behaviour when they co-occurred with a closely related species (black-capped chickadees). Accentuated differences have also been reported in songs of other sympatric species: pied flycatchers, *Ficedula hypoleuca*, and collared flycatchers, *Ficedula alibicollis* (Wallin 1986); blue tits, *Cyanites caeruleus*, and great tits, *Parus major* (Doutrelant & Lambrecht 2001); yellow-rumped tinkerbirds, *Pogoniulus bilineatus*, and yellow-throated tinkerbirds, *Pogoniulus subsulphure* (Kirschel et al. 2009); and large ground finches, *Geospiza magnirostris*, and either medium ground finches, *Geospiza fortis*, or cactus finches, *Geospiza scandens* (Grant & Grant 2010). Furthermore, our results also support the idea that character shifts occur predominantly within the subordinate species, as observed between great tits and blue tits (Doutrelant et al. 2000a; Doutrelant & Lambrecht 2001; Gorissen

et al. 2006) and among Darwin's finches (Grant & Grant 2010). Black-capped chickadee song is highly stereotyped throughout the species range (Gammon 2007; Mennill & Otter 2007; Lohr 2008; this study). The internal frequency structures, both within and between notes, are similar to those measured from mountain chickadee songs from our allopatric population (allopatric-MOCH) in Riske Creek. However, the mountain chickadees within the overlap zone (sympatric-MOCH) at the JPRF showed significant modification of these ratios away from those associated with black-capped chickadees. Within this contact population, black-capped chickadees are dominant to mountain chickadees, and there is directional hybridization through extrapair copulations, which decrease the potential reproductive output of male mountain chickadees (Grava et al. 2012b). Thus, there may be selective pressure for mountain chickadees in this population to differentiate

their songs from heterospecifics, either to avoid unwanted aggression from the dominant heterospecifics (e.g. Gorissen et al. 2006), or to distinguish themselves to females assessing males for mate choice.

Mountain chickadees in our sympatric-MOCH population used a greater proportion of chick-a-dee calls during their chorus than did mountain chickadees in our allopatric-MOCH population. Previous authors have suggested that the calls of mountain chickadees during the chorus may be directed primarily towards females, while their song is directed towards males (McCallum et al. 1999). Because of the lower social rank of mountain chickadees and hybridization through directional extrapair copulations in our studied sympatric zone (Grava et al. 2012b), mountain chickadee males might increase their proportion of chick-a-dee calls in an attempt to direct more of their chorus to their own mates to limit interspecific extrapair mating. This could also have a secondary benefit of reducing aggression from heterospecific males. However, chick-a-dee calls transmit shorter distances than whistled song, so modifying songs to be distinguishable from heterospecifics may also allow assessment of signallers by neighbouring females, as appears to occur in black-capped chickadees (Mennill et al. 2003).

If sympatric male mountain chickadees shift to signals during the choruses that are easily distinguishable (composed mainly of chick-a-dee calls rather than fee-bee songs) from the black-capped chickadees to avoid acoustic competition, this difference could be further accentuated by altering the note structure of those songs that are included during the chorus. The differences observed during the dawn chorus between the sympatric mountain chickadees and the three other populations studied in detail (sympatric-BCCH, allopatric-BCCH and allopatric-MOCH) might illustrate an attempt to avoid overlapping the acoustic space used by the dominant black-capped chickadee (see also Lohr 2008). As individuals expressing dominant signals are challenged more often (Gil & Gahr 2002), this change in both the structure of the song, as well as the use of fewer songs overall during the chorus, might also limit aggression from the dominant heterospecifics. When great tits are present, repertoires of the socially subordinate blue tit are smaller (Doutrelant et al. 2000a) and contain more trilled songs (Doutrelant & Lambrecht 2001); trilled songs of the blue tit are the most dissimilar to songs of great tits. Great tits respond less to trilled songs of blue tits (Doutrelant et al. 2000b) and are also less likely to song-match or closely approach trilled songs of blue tits (Gorissen et al. 2006), suggesting that trilled songs may have evolved to avoid interspecific interactions, which is consistent with the character shift hypothesis. Interspecific interactions between sympatric black-capped and mountain chickadees during the breeding season are uncommon, despite these species having overlapping breeding territories (Hill & Lein 1989; Grava 2012), and this lack of interactions may be aided by these character shifts. Playback experiments to test whether sympatric versus allopatric black-capped chickadees have lowered aggression towards divergent mountain chickadee songs are still needed, similar to those conducted in great tits/blue tits (Doutrelant et al. 2000b; Gorissen et al. 2006).

Our results have some contrasts to data on other chickadee hybrid zones. Curry et al. (2007) showed that males in the black-capped chickadee/Carolina chickadee, *Poecile carolinensis*, hybrid zone are often bilingual; members of each species incorporate songs of heterospecifics within their own repertoires instead of changing the acoustic parameters of their own songs. Furthermore, Lohr (2008) found that songs of mountain chickadees in another contact zone with black-capped chickadees were distinguishable by overall note pitch, but still maintained internote ratios similar to the median for other mountain chickadee populations. The absolute frequency of the first notes in the songs of our sympatric-

MOCH versus allopatric-MOCH populations did not differ, but the frequency of the N2 notes did, resulting in highly contrasting internote ratios in the sympatric-MOCH population compared to the allopatric-MOCH population. Furthermore, we found parallel shifts between sympatric/allopatric populations in PC2 among British Columbia versus California mountain chickadees; this principal component was heavily influenced by the dominant frequency of the three major notes of the song, suggesting a general shift in song frequency among sympatric populations. However, sympatric populations in California and British Columbia diverged in opposing directions for PC1 factor scores, which were associated predominantly with glissando and internote ratios in songs. Combined with Lohr's results, this suggests that different sympatric populations may undergo character displacement away from the dominant heterospecific, but the nature of this character displacement may differ between populations. As mountain and black-capped chickadees tend to segregate by habitat type within their overlapping geographical range, contact zones tend to occur in isolated, discrete pockets rather than as a continuous, overlapping hybrid zone, such as that found between Carolina and black-capped chickadees. This may result in independent character shifts occurring in different sympatric populations.

It is interesting that divergence in song characters appears to be occurring in the black-capped/mountain contact populations, whereas in the Carolina/black-capped contact zone there is strong evidence for convergence among song characters (Curry et al. 2007). Other differences between these contact zones may shed light on these patterns. Many individuals in the contact zone between Carolina and black-capped chickadees have hybrid DNA profiles, and pairing appears to be nonassortative with respect to the parental species (Bronson et al. 2005; Curry 2005; Reudink et al. 2005). By comparison, all social pairings in our sympatric population were assortative, with mountain/mountain and black-capped/black-capped social mates; hybrids were found primarily as extrapair young within nests of mountain chickadee pairs or among wintering birds that failed to breed within our study areas (Grava et al. 2012b). While black-capped and Carolina chickadees are ecologically similar, they are largely allopatric across the majority of their geographical ranges. In contrast, mountain and black-capped chickadees have extensive range overlap and are often ecologically segregated where they co-occur locally (Curry 2005). Although hybrid Carolina/black-capped pairs do appear to suffer some reduction in reproductive success relative to the parental species (Bronson et al. 2005), perhaps the niche differences between black-capped and mountain chickadees have a sufficiently deleterious effect on mixed pairs to explain the more assortative matings that we and others have noted (Hill & Lein 1989; Grava et al. 2012a, b) and may explain the apparent greater character displacement in chorus signals.

An alternate explanation for the observed acoustic variation between our four focal populations might be based upon transmission differences due to the habitat structure. The habitat at the sympatric-MOCH/BCCH and the allopatric-BCCH sites are similar (both sites are mature forests within the subboreal spruce zone), but the allopatric-MOCH site was more open with mature forest stands surrounded by grassland within the Interior Douglas fir biogeoclimatic zone. Marten & Marler (1977) found that sound transmission decreases with increasing vegetation density. As a result, acoustic variations enhanced by habitat structure should lead individuals in less open areas (such as in the sympatric-MOCH/sympatric-BCCH site) to use more songs than calls, as pure tonal notes (such as fee-bee songs) tend to transmit better than vocalizations with broader frequency sweeps (such as chick-a-dee calls). In this study, we observed the opposite, which suggests that habitat structure is unlikely to be the cause of the observed differences.

Furthermore, in our broad geographical analysis, we found effects of allopatry/sympatry on song structure in widely disparate locations that also differed in dominant vegetation. This finding reinforces the idea that character displacement among closely related species in sympatric populations may best explain the signals observed in this study.

Acknowledgments

We thank Harry van Oort, Kevin Fort, Carmen Holschuh, Ingebjorg Hansen, Kara Hunter, Zoe McDonnell, Regis Didier, Eileen Brunsch and Samantha Krause for assistance in recording chickadees. Additional song recordings were kindly provided from the Borror Laboratory of Bioacoustics, The Ohio State University, Columbus, OH (all rights reserved). We also thank Andrea Norris and Kathy Martin for access to their mountain chickadee population at Riske Creek and for their logistic support during the study. Comments on the manuscript were kindly provided by D. Gammon and an anonymous referee. Funding for this work was provided by Natural Sciences and Engineering Research Council of Canada, the University of Northern British Columbia (UNBC) and the John Prince Research Station. All work was carried out under permissions from the UNBC Animal Care and Use Committee and conformed to the guidelines for use of animals in research in Canada and by ASAB/ABS.

References

- Bloomfield, L. L., Charrier, I. & Sturdy, C. B. 2004. Note-types and coding in parid vocalizations. II. The chick-a-dee call of the mountain chickadee (*Poecile gambeli*). *Canadian Journal of Zoology*, **82**, 780–793.
- Bronson, C. L., Grubb, T. C., Jr., Sattler, G. D. & Braun, M. J. 2005. Reproductive success across the black-capped chickadee (*Poecile atricapillus*) and Carolina chickadee (*P. carolinensis*) hybrid zone in Ohio. *Auk*, **122**, 759–772.
- Brown, J. R. & Wilson, E. O. 1956. Character displacement. *Systematic Zoology*, **5**, 49–64.
- Christie, P. J., Mennill, D. J. & Ratcliffe, L. M. 2004. Chickadee song structure is individually distinctive over long broadcast distances. *Behaviour*, **141**, 101–124.
- Curry, R. L. 2005. Hybridization in chickadees: much to learn from familiar birds. *Auk*, **122**, 747–758.
- Curry, R. L., Rossano, L. M. & Reudink, M. W. 2007. Behavioral aspects of chickadee hybridization. In: *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach* (Ed. by K. A. Otter), pp. 95–110. Oxford: Oxford University Press.
- Dhondt, A. A. 1989. Ecological and evolutionary effects of interspecific competition in tits. *Wilson Bulletin*, **101**, 198–216.
- Dhondt, A. A. 2012. *Interspecific Competition in Birds*. Oxford: Oxford University Press.
- Doutrelant, C. & Lambrecht, M. M. 2001. Macrogeographic variation in song: a test of competition and habitat effect in blue tits. *Ethology*, **107**, 533–544.
- Doutrelant, C., Blondel, J., Perret, P. & Lambrechts, M. M. 2000a. Blue tit song repertoire size, male quality and interspecific competition. *Journal of Avian Biology*, **31**, 360–366.
- Doutrelant, C., Leita, A., Otter, K. A. & Lambrechts, M. M. 2000b. Effect of blue tit song syntax on great tit territorial responsiveness: an experimental test of the character shift hypothesis. *Behavioral Ecology and Sociobiology*, **48**, 119–124.
- Footo, J. R., Mennill, D. J., Ratcliffe, L. M. & Smith, S. M. 2010. Black-capped chickadee (*Parus atricapillus*). In: *The Birds of North America Online*. No. 39 (Ed. by A. Poole). Ithaca, New York: Cornell Lab of Ornithology. <http://bna.birds.cornell.edu/bna/species/039>.
- Gammon, D. E. 2004. Black-capped chickadee dawn chorus and subsequent sexual activity. *Wilson Bulletin*, **116**, 252–256.
- Gammon, D. E. 2007. How postdispersal social environment may influence acoustic variation in birdsong. In: *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach* (Ed. by K. A. Otter), pp. 183–198. Oxford: Oxford University Press.
- Gil, D. & Gahr, M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, **17**, 133–141.
- Gill, F. B., Mostrom, A. M. & Mack, A. L. 1993. Speciation in North American chickadees: I. Patterns of mtDNA genetic divergence. *Evolution*, **47**, 192–212.
- Gill, F. B., Slikas, B. & Sheldon, F. H. 2005. Phylogeny of titmice (Paridae): II. Species relationships based on sequences of the mitochondrial *cytochrome-b* gene. *Auk*, **122**, 121–143.
- Gorissen, L., Gorissen, M. & Eens, M. 2006. Heterospecific song matching in two closely related songbirds (*Parus major* and *P. caeruleus*): great tits match blue tits but not vice versa. *Behavioral Ecology and Sociobiology*, **60**, 260–269.
- Grant, P. R. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society*, **4**, 39–68.
- Grant, P. R. 1994. Ecological character displacement. *Science*, **266**, 746–747.
- Grant, B. R. & Grant, P. R. 2010. Songs of Darwin's finches diverge when a new species enters the community. *Proceedings of the National Academy of Sciences, U.S.A.*, **107**, 20156–20163.
- Grava, A. 2012. Interspecific interactions between mountain and black-capped chickadees within a contact zone. Ph.D. thesis, University of Northern British Columbia, Canada.
- Grava, A., Grava, T. & Otter, K. A. 2012a. Differential response to interspecific and intraspecific signals amongst chickadees. *Ethology*, **118**, 711–720.
- Grava, A., Grava, T., Didier, R., Lait, L., Koran, E., Dosso, J., Burg, T. & Otter, K. A. 2012b. Interspecific dominance relationships and hybridization between black-capped and mountain chickadees. *Behavioural Ecology*, **23**, 566–572.
- Grava, T., Grava, A. & Otter, K. A. 2009. Supplemental feeding and dawn singing in black-capped chickadees. *Condor*, **111**, 560–564.
- Hailman, J. P. 1989. The organisation of the major vocalizations in the Paridae. *Wilson Bulletin*, **101**, 305–343.
- Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, **381**, 229–232.
- Hill, B. G. & Leim, M. R. 1989. Territory overlap and habitat use of sympatric chickadees. *Auk*, **106**, 259–268.
- Ho, R. 2006. *Handbook of Univariate and Multivariate Data Analysis and Interpretation with SPSS*. Boca Raton, Florida: Chapman & Hall/CRC.
- Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology*, **74**, 2204–2214.
- Kempnaers, B., Verheyen, R. F. & Dhondt, A. A. 1997. Extrajury paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behavioral Ecology*, **8**, 481–492.
- Kirschel, A. N. G., Blumstein, D. T., Smith, T. B. & Schluter, D. 2009. Character displacement of song and morphology in African tinkerbirds. *Proceedings of the National Academy of Sciences, U.S.A.*, **106**, 8256–8261.
- Kroodsmma, D. E., Albano, D. J., Houlihan, P. W. & Wells, J. A. 1995. Song development by black-capped chickadee (*Parus atricapillus*) and Carolina chickadee (*P. carolinensis*). *Auk*, **112**, 29–43.
- Legendre, P. & Legendre, L. (Eds). 1998. *Numerical Ecology: Developments in Environmental Modelling*. 2nd edn. Amsterdam: Elsevier Science.
- Lohr, B. 2008. Pitch-related cues in the songs of sympatric mountain and black-capped chickadees. *Behavioural Processes*, **77**, 156–165.
- Loftus-Hills, J. J. & Littlejohn, M. J. 1992. Reinforcement and reproductive character displacement in *Gastrophyrne carolinensis* and *Gastrophyrne olivacea* (Anura: Microhylidae): a reexamination. *Evolution*, **46**, 896–906.
- McCallum, D. A., Grunzel, R. & Dahlsten, D. L. 1999. Mountain chickadee. In: *The Birds of North America*. No. 453 (Ed. by A. Poole & F. B. Gill), pp. 1–28. Philadelphia/Washington, D.C.: Academy of Natural Sciences/American Ornithologists' Union.
- Marten, K. & Marler, P. 1977. Sound transmission and its significance for animal vocalisation: I. Temperate habitats. *Behavioral Ecology and Sociobiology*, **2**, 271–290.
- Martin, K. & Norris, A. R. 2007. Life in the small-bodied cavity-nester guild: demography of sympatric mountain and black-capped chickadees within nest web communities under changing habitat conditions. In: *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach* (Ed. by K. A. Otter), pp. 111–130. Oxford: Oxford University Press.
- Mennill, D. J. & Otter, K. A. 2007. Status signalling and communication networks in chickadees: complex communication with a simple song. In: *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach* (Ed. by K. A. Otter), pp. 215–240. Oxford: Oxford University Press.
- Mennill, D. J., Boag, P. T. & Ratcliffe, L. M. 2003. The reproductive choices of eavesdropping female black-capped chickadees, *Poecile atricapillus*. *Naturwissenschaften*, **90**, 577–582.
- Miller, R. S. 1968. Condition of competition between redwings and yellow-headed blackbirds. *Journal of Animal Ecology*, **37**, 43–62.
- Noor, M. A. F. 1999. Reinforcement and other consequences of sympatry. *Heredity*, **83**, 503–508.
- van Oort, H., Otter, K. A., Fort, K. & Holschuh, C. I. 2006. Habitat quality affects the reliability of a condition-dependant signal in black-capped chickadees. *Ethology*, **112**, 772–778.
- Otter, K. A. & Ratcliffe, L. M. 1993. Changes in the singing behaviour of male black-capped chickadees (*Parus atricapillus*) following mate removal. *Behavioral Ecology and Sociobiology*, **33**, 409–414.
- Otter, K. A., Chruszcz, B. & Ratcliffe, L. M. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees, *Parus atricapillus*. *Behavioral Ecology*, **8**, 167–173.
- Otter, K. A., van Oort, H. & Fort, K. T. 2007. Habitat quality and reproductive behaviour in chickadees and tits; potential for habitat matrix use in forest generalists. In: *Ecology and Behavior of Chickadees and Titmice: an Integrated Approach* (Ed. by K. A. Otter), pp. 277–291. Oxford: Oxford University Press.
- Pfennig, D. W. & Pfennig, K. S. 2010. Character displacement and the origins of diversity. *American Naturalist, Supplement*, **176**, S26–S44.
- R Development Core Team 2008. *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.

- Reudink, M. W., Mech, S. G. & Curry, R. L.** 2005. Extrapair paternity and mate choice in a chickadee hybrid zone. *Behavioral Ecology*, **17**, 56–62.
- Schluter, D.** 1994. Experimental evidence that competition promotes divergence in adaptive radiation. *Science*, **266**, 798–801.
- Searcy, W. A. & Nowicki, S.** 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton, New Jersey: Princeton University Press.
- Seddon, N. & Tobias, J. A.** 2010. Character displacement from the receiver's perspective: species and mate recognition despite convergent signals in suboscine birds. *Proceedings of the Royal Society B*, **277**, 2475–2483.
- Smith, S. M.** 1991. *The Black-capped Chickadee: Behavioural Ecology and Natural History*. Ithaca, New York: Comstock.
- Sueur, J., Aubin, T. & Simonis, C.** 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics*, **18**, 213–226.
- Wallin, L.** 1986. Divergent character displacement in the song of two allospecies: the pied flycatcher *Ficedula hypoleuca*, and the collared flycatcher *Ficedula albicollis*. *Ibis*, **128**, 251–259.
- Wiebe, M. O. & Lein, M. R.** 1999. Use of song types by mountain chickadees (*Poecile gambeli*). *Wilson Bulletin*, **111**, 368–375.