Character displacement of mountain chickadee song where they co-occur with black-capped chickadees

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Abstract

Mechanisms for species recognition are important when closely related species overlap in their ranges because hybridization (i.e., the interbreeding between two species) can be costly. Hybridization is maladaptive when it results in wasted reproductive effort, inviable offspring, or offspring with reduced fitness. When hybridization is costly, the characters used for species recognition may diverge where species co-occur. In passerine birds, song is an important mechanism of species recognition. The black-capped chickadee (*Poecile atricapillus*) and the mountain chickadee (*Poecile gambeli*) are two closely related species with both geographically isolated (i.e., allopatric) and geographically overlapping (i.e., sympatric) populations; in the latter, hybridization has been observed on numerous occasions. In this study, we compared songs of allopatric and sympatric populations of black-capped and mountain chickadees. We tested whether song divergence is greater in sympatry compared to allopatry given the potential selective pressures for species to avoid hybridization. As such, we predicted that songs of sympatric black-capped and mountain chickadee populations would be more divergent from each other than those of allopatric populations. We found that sympatric mountain chickadees produced more notes per song and were more likely to include an extra introductory note compared to allopatric mountain chickadees. Our findings support our predictions that character displacement should exist in sympatry, potentially so that chickadees avoid maladaptive hybridization.

Introduction

Species utilize a variety of visual, acoustic, and chemical signals to recognize one another (Doherty and Hoy 1985; Rand et al. 1992; Matyjasiak 2005; Wong et al. 2005; Grabenstein and Taylor 2018). Species recognition can fail when closely related species overlap in their ranges if their signals are not divergent enough, which can lead to hybridization (i.e., the interbreeding between two closely-related species; Grabenstein and Taylor 2018). Hybridization can be costly for a number of reasons such as wasted reproductive effort, the production of inviable offspring, or the production of offspring with reduced fitness (Haldane 1922; Burke and Arnold 2001; Lancaster et al. 2007; Muhlfeld et al. 2009). When mechanisms of species recognition fail, hybridization and maladaptive offspring are more likely to occur. In some regions of overlap (i.e., sympatry), mechanisms of species recognition are strengthened through a phenomenon known as character displacement, in which certain phenotypic traits diverge further in sympatry than they do in regions where species do not overlap (i.e., allopatry; Grant and Grant 2006; Kirschel et al. 2009; Grava et al. 2013). Character displacement may therefore be advantageous for preventing costly hybridization.

In passerine birds, song is an important mechanism of species recognition, territory defense, and assortative mating (i.e., preferential mating based on phenotypic similarity; Lynch 2019). Much like human language, bird song in most passerines is learned at a young age through exposure to parents or other neighboring adults (Lynch 2019). Further, juveniles may potentially learn and copy songs even from heterospecific adults of closely related species (Helb et al. 1985). Previous studies have hypothesized that such a scenario may be a driving factor in the observed convergence of song between sympatric populations of the melodious warbler (*Hippolais polyglotta*) and the icterine warbler (*H. icterina*; Secondi et al. 2003), and of the pied flycatcher (*Ficedula hypoleuca*) towards that of the collared flycatcher (*F. albicollis*; Haavie et al. 2004). Interestingly, results from the same flycatcher study showed that the songs of sympatric collared flycatchers simultaneously diverged from pied flycatchers (Haavie et al. 2004), demonstrating another potential outcome for song variation in sympatry: divergence that emphasizes and maintains species boundaries (i.e., character displacement). Acoustic divergence has been observed in the songs of the yellow-throated tinkerbird (*Pogoniulus subsulphureus*) and the yellow-rumped tinkerbird (*P. bilineatus*; Kirschel et al. 2009). In some instances, divergence occurs asymmetrically; that is, where one species' song diverges and the other's remains unchanged. Asymmetric divergence has been observed in the dawn chorusing behavior of sympatric mountain chickadees (*Poecile gambeli*) away from black-capped chickadees (*Poecile atricapillus*; Grava et al. 2013) in terms of alarm call frequency and song structure.

Interspecific dominance relations may be an important predictor in determining instances of asymmetric divergence in sympatry (Grant and Grant 2010; Vokurková et al. 2013). Given the prominent function of birdsong in both mate attraction and territory defense, it would benefit subordinate species to sing songs that are more clearly differentiated from those of the dominant species in order to avoid aggressive interspecific interactions. Thus, one may predict that a morphologically and/or socially subordinate species is more likely to diverge its song in sympatry, while a morphologically and/or socially dominant species will likely make no adjustments. This effect is demonstrated in a study on a sympatric population of the large ground finch (*Geospiza magnirostris*), the medium ground finch (*G. fortis*), and the small cactus finch (*G. scandens*; Grant and Grant 2010). The large ground finch, in addition to being larger in body size than its relatives, is known to bully them for increased access to feeding and nesting sites. And, in agreement with the above prediction, the large ground finch showed little change in its song between allopatric and sympatric populations compared to the medium ground finch and the small cactus finch (Grant and Grant 2010).

Chickadee song behavior appears to be particularly variable. For example, Grava et al. (2013) reported divergence in dawn chorusing behavior between sympatric and allopatric black-capped and mountain chickadees in British Columbia, Canada. However, another study on song measurements from the same species in Alberta, Canada found no evidence of such divergence (Lohr 2008). These conflicting findings could be a result of insufficient sample size, especially given the subjective nature of song data analysis. Nevertheless, this lack of consistency paired with observations in other sympatric species indicates a gap in our current understanding of sympatric song behavior; that is, why do some songs converge in sympatry while others diverge? Here, we investigate the discrepancy between Grava et al. (2013) and

Lohr (2008) by conducting a study of song variation between allopatric and sympatric black-capped and mountain chickadees, focusing on their Rocky Mountain region of sympatry (Figure 1).

The black-capped chickadee and the mountain chickadee are two closely-related species with both allopatric and sympatric populations (Grava et al. 2012). Black-capped chickadees are typically found in lower-elevation, deciduous forests, while mountain chickadees usually inhabit coniferous forests at higher elevations (Grabenstein et al. 2023). Their differing ecological preferences allow them to occupy separate niches and form allopatric populations. However, areas of sympatry are observed in transitional habitats where their preferences overlap, that is, in the upper elevational range of black-capped chickadees and the lower range of mountain chickadees (Grava et al. 2012; Grabenstein et al. 2023). Observations of interspecific interactions have shown black-capped chickadees as dominant over mountain chickadees (Grava et al. 2012). Furthermore, there appears to be a cost of co-occurrence, where black-capped and mountain chickadees in sympatry both exhibit lower body condition than where they occur in allopatry (Grabenstein et al. 2022). Finally, hybridization, while rare, has been observed on numerous occasions in regions of overlap and results in at least some sterile offspring (Grabenstein et al. 2023).

Both black-capped and mountain chickadees exhibit song variation. Typical mountain chickadee song can consist of anywhere between two and six notes, with individual variation resulting from the presence or absence of brief “introductory” notes (Wiebe and Lein 1999; Grava et al. 2013). Populations of mountain chickadees have also demonstrated geographically- and elevationally-associated variation in song structure (Lohr 2008; Branch and Pravosudov 2015). Typical black-capped chickadee song is usually much less variable, and consists of between two and three notes (Kroodsma et al. 1999). Indeed, while the black-capped chickadee’s notorious *fee-bee* song is popularly reported to be standard in most observed populations, variations from this continental standard have been described in three islands off the coast of Massachusetts, and in discrete patches of suitable habitat along the Poudre River in Fort Collins, CO, an area encompassed by the Rocky Mountain region of sympatry between black-capped and mountain chickadees (Kroodsma et al. 1999; Gammon et al. 2005). Additionally, juvenile black-capped chickadees can imitate tutor tapes of a variety of songs from the related Carolina chickadee (*P. carolinensis*) in laboratory settings (Kroodsma et al. 1995).

Song variation observed in isolated populations of black-capped chickadees might be the result of a decreased selective pressure on individuals to sing like their parents and neighbors when they occur in small populations (Gammon et al. 2005). A decreased selective pressure in small populations could allow for the persistence of “errors” in an individual’s song, and for the increased likelihood of transmission to future generations. Additionally, allopatric populations of black-capped chickadees, who, compared to sympatric populations, face a reduced risk of hybridization and its consequent maladaptive offspring might experience weaker selection against song errors. Sympatric populations of black-capped chickadees should experience an increased selective pressure to sing their established species song due to the potential for song variations to be perceived as heterospecific and lead to hybridization. Following this idea, we hypothesize that the songs of sympatric black-capped and mountain chickadees will be more divergent from each other than songs of allopatric populations. Furthermore, given evidence that mountain chickadees are socially subordinate to black-capped chickadees (Grava et al. 2012), we hypothesize that the degree of song divergence will be greater in mountain chickadees.

Methods

Field sampling

We recorded both black-capped and mountain chickadees in regions of allopatry and sympatry with a PMD660 or PMD661 Marantz digital recorder and a Sennheiser ME-66 unidirectional microphone with a sampling rate of 44,000 Hz and a 16-bit resolution. Sympatric populations were recorded in Boulder County, Colorado (black-capped chickadee *n* = 11; mountain chickadee *n* = 8). Allopatric black-capped chickadees were recorded in Ithaca, New York (*n* = 11), and allopatric mountain chickadees were recorded in Truckee, California (*n* =11; Figure 1). To avoid repeat sampling, we walked at least 500 meters between recordings. We collected a total of 719 songs and an average of 17 songs per individual.

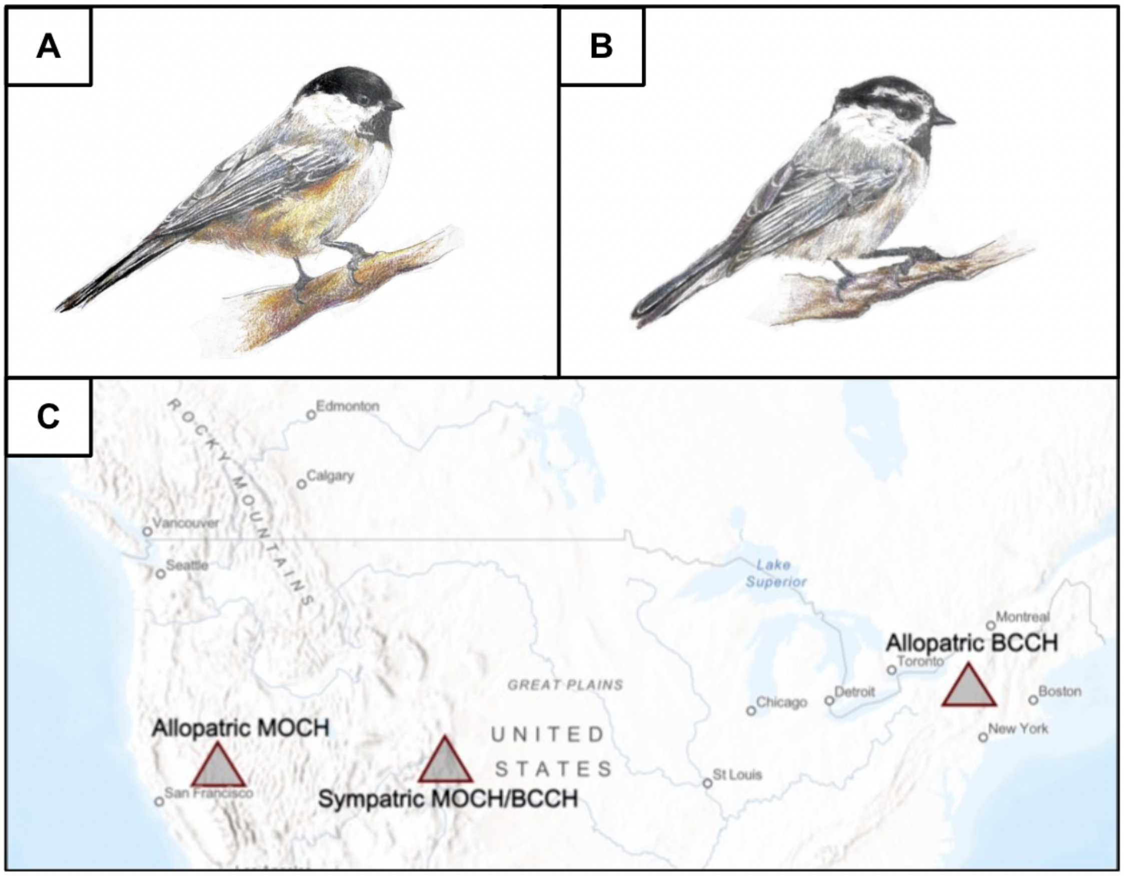

Figure 1. Geographic context of the study. (A) Black-capped chickadee, (B) mountain chickadee, (C) Sampling locations for sympatric and allopatric chickadee populations. Allopatric mountain chickadees (MOCH) were sampled in Truckee, California. Allopatric black-capped chickadees (BCCH) were sampled in Ithaca, New York. Sympatric MOCH/BCCH were sampled in Boulder County, Colorado.

Song analysis

We analyzed songs using the bioacoustics software Raven Pro 1.6.3. We formatted spectrograms in the color scheme "Jet" with the x-axis scaled at 0.1 second intervals and the y-axis scaled at 0.5 kHz intervals. Because the distance and noise levels at which we recorded each bird vary from individual to individual, we adjusted contrast and brightness on each recording to estimate consistency. We measured delta frequency, delta time, frequency 5%, and frequency 95%; internote interval was calculated post hoc (Table 1). We selected our measures based on previous research on black-capped and mountain chickadee song (Branch and Pravosudov 2015; Branch and Pravosudov 2019). For each recording, we annotated song number, note number, and whether or not a selection was an introductory note. We annotated selections as introductory notes if they were shorter than 0.15 seconds. No recordings contained songs with more than three introductory notes. Notes were demarcated by complete amplitude breaks. Faint notes or "wisps" at the beginnings and ends of notes were omitted (Figure 2).

Table 1. A list of song measures included in the statistical analyses and their descriptions.

Song measure	**Description**
Number of notes	The number of notes per song
Introductory notes	The proportion of songs per individual with *n* introductory notes present; *n* = 1-3
Song duration (s)	The total length of each song
Note duration (s)	The length of each note, excluding intro notes
Frequency shift (Hz)	The major frequency shift per song; calculated as the first note of the song divided by the second note, excluding intro notes
Delta frequency (Hz)	The difference between the highest and lowest frequencies per note; recorded for the first and second notes of the

	song, excluding intro notes
Internote interval (s)	The length between each note
Frequency 5% (Hz)	From Raven Pro: the frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection (Charif et al. 2010)
Frequency 95% (Hz)	From Raven Pro: the frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection (Charif et al. 2010)

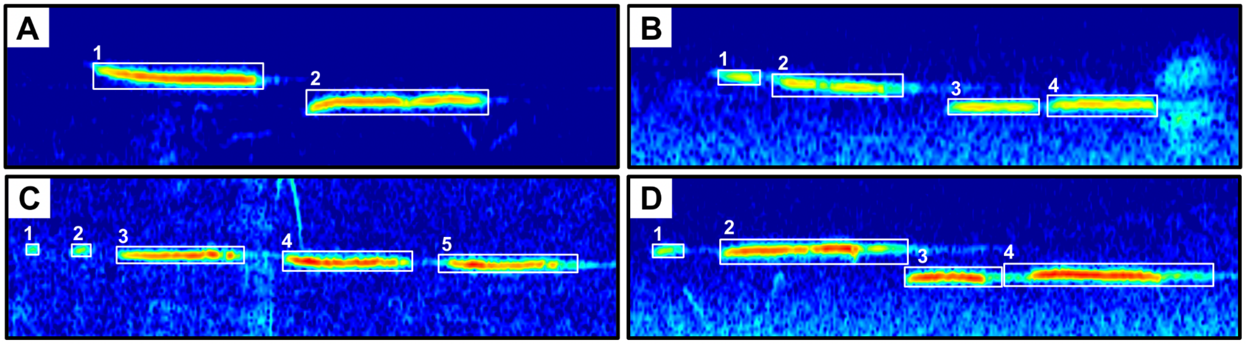

Figure 2. Example selections on song spectrograms made in Raven Pro. Note the faint wisps omitted and the demarcation of notes based on complete amplitude breaks. (A) Song from a sympatric black-capped chickadee. (B) Song from an allopatric black-capped chickadee with one introductory note. (C) Song from a sympatric mountain-chickadee with two introductory notes. (D) Song from an allopatric mountain chickadee with one introductory note.

Statistical analysis

We ran all statistical analyses in R version 4.0.3 (R Core Team 2020). To avoid pseudoreplication, we analyzed the means of each song measure per individual (Branch and Pravosudov 2015; Table 2). We included these means as variables in a principal component analysis (PCA). We used the results of the PCA to inform which measures to include in subsequent linear models, which we ran on each PC axis that had a loading stronger than 0.3, with population as the dependent variable. To assess variation between populations, we ran analyses of variances (ANOVAs) on each linear model. We followed each ANOVA with a Tukey HSD test to quantify differences between populations and their significance.

Table 2. Means and standard deviations for song measures by population.

Song measure	**Allopatric BCCH**	**Sympatric BCCH**	**Allopatric MOCH**	**Sympatric MOCH**
Number of notes	2.66 ± 0.55	2.48 ± 0.37	3.90 ± 0.34	5.33 ± 0.53
Presence of 1 intro note	0.50 ± 0.48	0.12 ± 0.18	0.91 ± 0.30	0.96 ± 0.7
Presence of 2 intro notes	0.00 ± 0.00	0.00 ± 0.01	0.02 ± 0.08	0.71 ± 0.35
Presence of 3 intro notes	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.08	0.17 ± 0.35
Song duration (s)	0.95 ± 0.04	0.90 ± 0.06	1.28 ± 0.12	1.57 ± 0.22
Note duration (s)	0.38 ± 0.08	0.30 ± 0.05	0.32 ± 0.05	0.33 ± 0.04
Frequency shift (Hz)	1.14 ± 0.02	1.15 ± 0.02	1.20 ± 0.02	1.03 ± 0.01
Delta frequency N1 (Hz)	613.47 ± 113.33	580.71 ± 107.05	563.18 ± 135.86	492.74 ± 46.19
Delta frequency N2 (Hz)	490.06 ± 76.47	455.90 ± 43.19	525.91 ± 122.72	531.34 ± 66.22
Internote interval (s)	613.47 ± 113.33	580.71 ± 107.05	563.18 ± 135.86	492.74 ± 46.19
Frequency 5% N1 (Hz)	3848.38 ± 240.09	3752.82 ± 244.11	4214.00 ± 97.68	4511.59 ± 88.21
Frequency 5% N2 (Hz)	3361.99 ± 177.57	3261.80 ± 207.13	3489.52 ± 64.85	4381.75 ± 88.81
Frequency 95% N1 (Hz)	4044.00 ± 254.34	3987.80 ± 252.37	4376.87 ± 91.57	4674.60 ± 89.91
Frequency 95% N2 (Hz)	3525.44 ± 174.81	3434.44 ± 204.10	3642.43 ± 67.93	4547.57 ± 86.44

Results

Principal component (PC) analyses revealed sympatric mountain chickadees to be strongly separated from all other populations by PC1 (61.37%), which primarily loads presence of one introductory note (0.58), number of notes (0.54), and presence of two introductory notes (0.37; Figure 3). Allopatric black-capped chickadees show considerable within-species variation by PC1 (Figure 3). Allopatric mountain chickadees show considerable within-species variation by PC2 (26.1%), which primarily loads delta frequency for note 1 (-0.66), presence of one introductory note (-0.44), delta frequency for note 2 (-0.43), and presence of two introductory notes (0.36; Figure 3). Overall, ANOVAs for PC1 and PC2 were both statistically significant (PC1: $F_{3,37} = 57.77$, $p < 0.001$; PC2: $F_{3,37} = 4.32$, $p_{PC2} = 0.01$) with large effect sizes ($\eta^2_{PC1} = 0.82$, $\eta^2_{PC2} = 0.26$). The ANOVA for PC1 identified statistically significant differences between all populations ($p < 0.05$) except between sympatric and allopatric black-capped chickadees ($p = 0.13$). The ANOVA for PC2 identified statistically significant differences between allopatric mountain chickadees and sympatric black-capped chickadees ($p = 0.053$) and sympatric and allopatric mountain chickadees ($p = 0.03$).

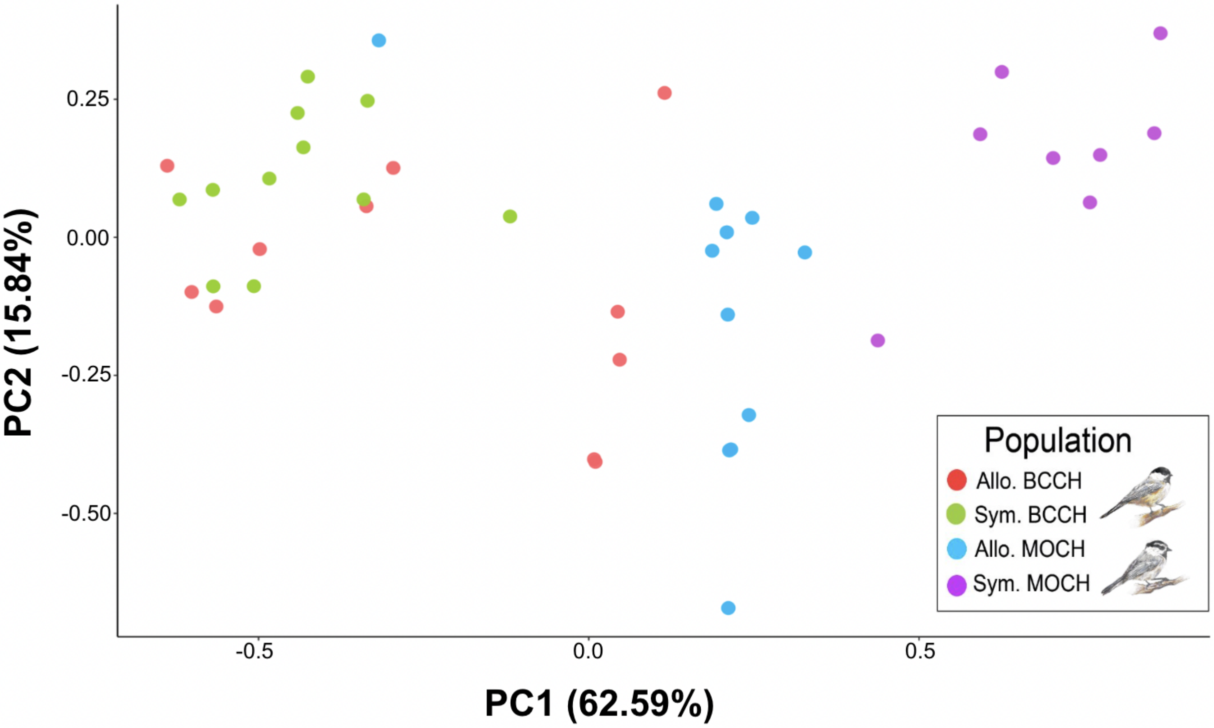

Figure 3. PCA plot showing between-population variation in sympatric mountain chickadees by PC1, within-species variation in allopatric mountain chickadees by PC2, and within-species variation in allopatric black-capped chickadees by PC1 and PC2.

The effects of population on note number per song were statistically significant and large ($F_{3,37} = 78.17$, $p < 0.001$, $\eta^2 = 0.86$; Figure 4). The ANOVA revealed significant differences among all populations except between sympatric and allopatric black-capped chickadees ($p = 0.80$). Allopatric mountain chickadees produced an average of 1.24 more notes than allopatric black-capped chickadees ($p < 0.001$), and an average of 1.41 more notes than sympatric black-capped chickadees ($p < 0.001$). Sympatric mountain chickadees produced an average of 2.67 more notes than allopatric black-capped chickadees ($p < 0.001$) and 2.84 more notes than sympatric black-capped chickadees ($p < 0.001$). Notably, sympatric mountain chickadees also produced an average of 1.43 more notes than allopatric mountain chickadees ($p < 0.001$).

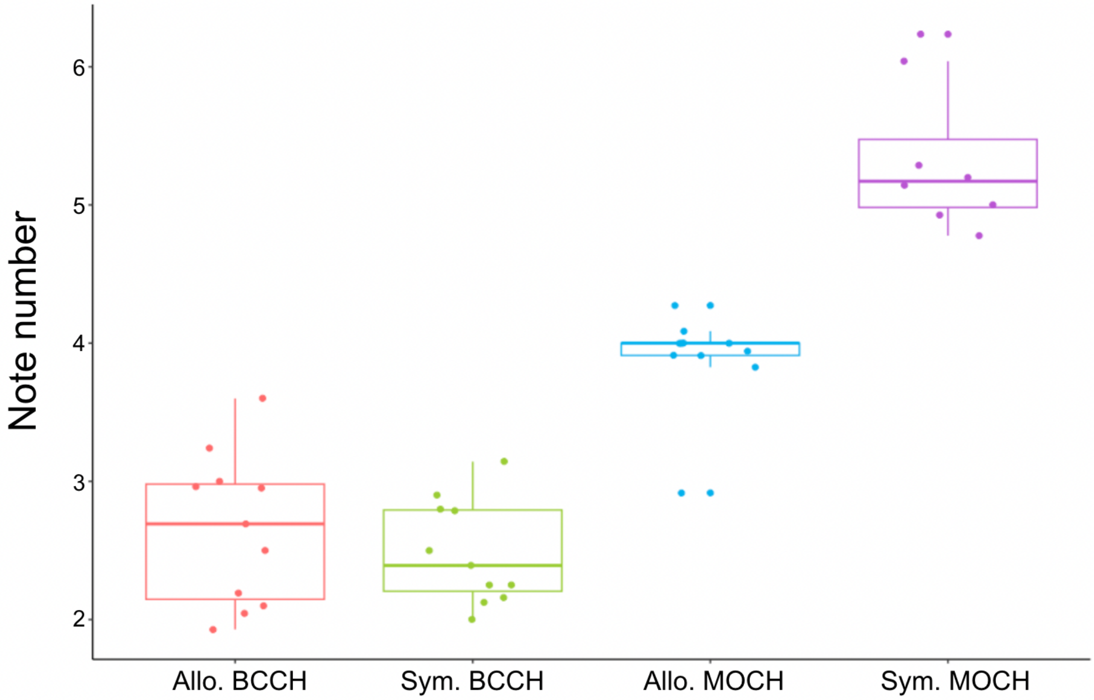

Figure 4. Note number per song by population plotted with individual points. Sympatric mountain chickadees on average have the highest number of notes per song, followed by allopatric mountain chickadees, allopatric black-capped chickadees, and sympatric black-capped chickadees (Table 2).

The effects of population on the presence of one introductory note were statistically significant and large ($F_{3,37} = 16.58$, $p < 0.001$, $\eta^2 = 0.57$; Figure 5). The ANOVA revealed a significant positive difference of 0.79 between allopatric mountain chickadees and sympatric black-capped chickadees ($p < 0.001$), indicating that allopatric mountain chickadees are more likely to produce songs with one introductory note than sympatric black-capped chickadees. There was also a significant positive difference of 0.84 between sympatric mountain and black-capped chickadees ($p < 0.001$), indicating that sympatric mountain chickadees are more likely to produce songs with one introductory note than sympatric black-capped chickadees. Interestingly, five allopatric black-capped chickadee individuals produced a high proportion of songs with introductory notes.

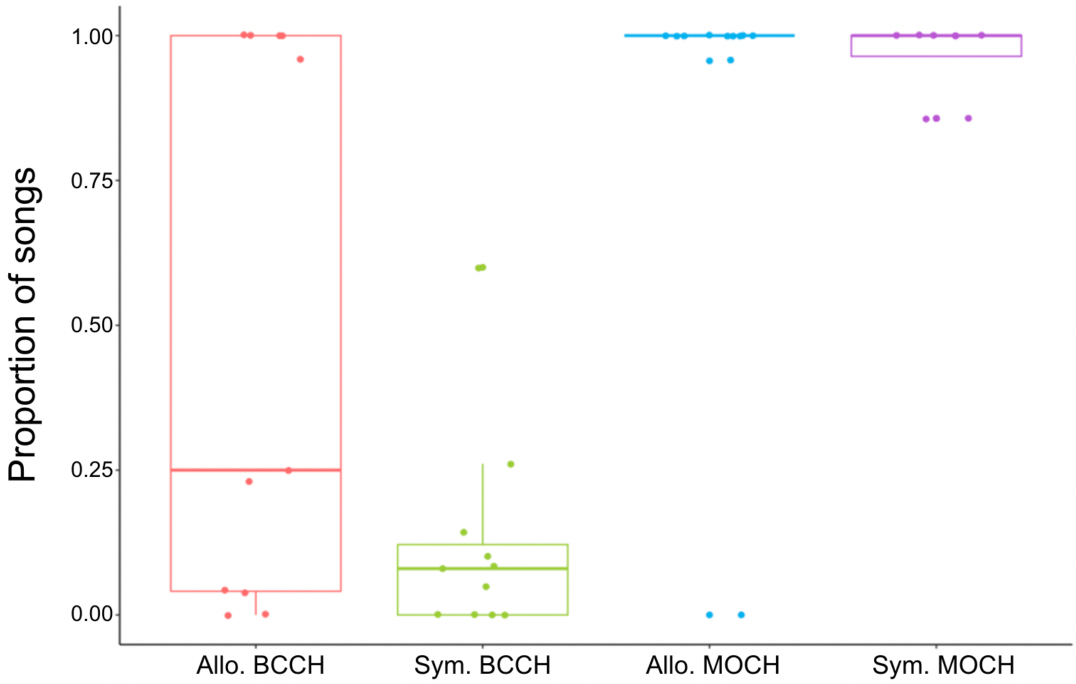

Figure 5. Proportion of songs containing one introductory note by population plotted with individual points. A value of 1.00 indicates that all songs produced by an individual contained an introductory note. A value of 0.00 indicates that no songs produced by an individual contained an introductory note. Sympatric mountain chickadees on average produced the most songs with one introductory note, followed closely by allopatric mountain chickadees. Allopatric black-capped chickadees exhibited the most variation, with some individuals only producing song with an introductory note and others producing none. Sympatric black-capped chickadees produced the least songs with an introductory note (Table 2).

The effects of population on the presence of two introductory notes were also statistically significant and large ($F_{3,37}$=40.52, p<0.001, η^2=0.77; Figure 6). The ANOVA revealed a significant positive difference of 0.71 between sympatric mountain chickadees and allopatric black-capped chickadees (p<0.001), and a positive difference of 0.70 between sympatric mountain and black-capped chickadees (p<0.001). Both results indicate that sympatric mountain chickadees are more likely to produce songs with two introductory notes than allopatric and sympatric black-capped chickadees. Notably, results also revealed a significant positive difference of 0.68 between sympatric and allopatric mountain chickadees (p<0.001), indicating that sympatric mountain chickadees are more likely to produce songs with two introductory notes than allopatric mountain chickadees.

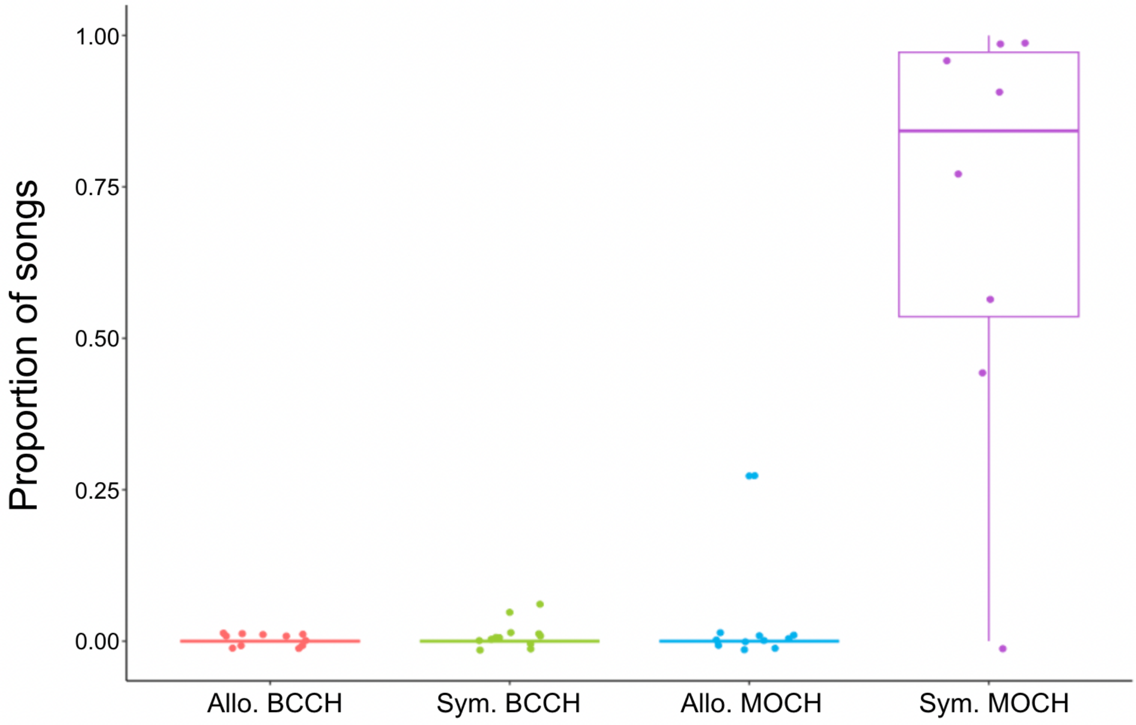

Figure 6. Proportion of songs containing 2 introductory notes by population plotted with individual points. A value of 1.00 indicates that all songs produced by an individual contained two introductory notes. A value of 0.00 indicates that no songs produced by an individual contained two introductory notes. Sympatric mountain chickadees overwhelmingly produced the most songs with 2 introductory notes. Allopatric mountain chickadees rarely produced songs with 2 introductory notes. Allopatric and sympatric black-capped chickadees followed suit (Table 2).

While delta frequencies of notes 1 and 2 loaded strongly on PC2, neither linear model was statistically significant (Note 1: $F_{3,37}$=1.80, P=0.17; Note 2: $F_{3,37}$=1.80, P=0.17). Thus, delta frequency is not a significant predictor of population.

Discussion

We compared 719 songs from 41 individuals of sympatric and allopatric black-capped and mountain chickadees. We found that the songs of allopatric and sympatric mountain chickadees differ significantly by note number, with sympatric individuals singing more notes than allopatric individuals. The increased number of notes may be attributed in part to our finding that sympatric mountain chickadees are also more likely to include an extra introductory note than allopatric mountain chickadees. In general, mountain chickadee songs are distinct from black-capped chickadee songs in that the former typically contains between two and six notes, while the latter typically contains between two and three notes (Kroodsma et al. 1999; Wiebe and Lein 1999). Thus, we present evidence for character displacement where co-occurring mountain chickadees increase the number of notes in their songs potentially because song is used as a mechanism of species recognition to avoid maladaptive hybridization, which we know occurs in this population (Grabenstein et al. in prep). While we also observed that sympatric black-capped chickadees sang fewer notes than allopatric black-capped chickadees, which also follows character displacement theory, the difference in note number between these two populations was smaller than the difference between our two mountain chickadee populations. The greater divergence of mountain chickadees than black-capped chickadees in sympatry versus allopatry supports our prediction that mountain chickadees will diverge their songs to a greater degree as the socially subordinate species to avoid aggressive interspecific interactions (Grava et al. 2012).

Our findings are consistent with Grava et al.'s results showing asymmetric divergence in dawn chorusing behavior by mountain chickadees sympatric with black-capped chickadees (Grava et al. 2012), in addition to divergence documented in Darwin's finches and nightingales (Grant and Grant 2010; Vokurková et al. 2013). However, our results contradict previous studies on song structure between allopatric and sympatric populations of black-capped and mountain chickadees. Lohr (2008) found no evidence of convergence or divergence between the songs of sympatric black-capped and mountain chickadees in Alberta, Canada. Further, Gammon et al. (2005) found atypical black-capped chickadee songs that resemble those of mountain chickadees in Fort Collins, CO. Although this data indicates that black-capped chickadee song converged towards mountain chickadee song, which disagrees with our findings, the results still follow predictions from dominance relations—black-capped chickadees are dominant to mountain chickadees and thus are unlikely to be disadvantaged from interspecific encounters resulting from acoustic misidentification. That being said, one potential explanation for these inconsistencies is that, within the same pair of closely-related species, different regions of sympatry may exhibit different patterns of song behavior. For example, in the aforementioned flycatcher study, the frequency of mixed singers sampled was higher in one sympatric population than the other (Haavie et al. 2004). Therefore, it is unlikely that research on single sympatric populations of closely-related species is uniformly representative of song behavior in all sympatric populations of the same species. As such, our study is constrained by its investigation into single regions of allopatry and sympatry, and we are thus unable to generalize these differences across all sympatric and allopatric populations. To make species-wide conclusions, future research will need to survey allopatric and sympatric populations on a continental scale.

Our observations of introductory notes in allopatric black-capped chickadee song also contradict the popular idea that this species' songs are highly stereotyped across their continental distribution, except for in geographically isolated populations (Kroodsma et al. 1999; Gammon et al. 2005). While our analyses did not reveal statistically significant differences between allopatric and sympatric black-capped chickadees, it is notable that five out of 11 allopatric individuals produced a high proportion of songs with introductory notes (Figure 5). This unusual behavior may be attributed to cultural evolution, which is thought to drive geographic variation under many of the same phenomena as biological evolution: mutation, selection, flow, and drift. Songs of geographically isolated populations may be especially prone to cultural evolution and divergence due to limited contact with individuals from outside populations, which reduces "flow" and enables variation (Lang and Barlow 1997; Kroodsma et al. 1999). It has also been proposed that, because such populations tend to be smaller, there may be decreased selective pressure on individuals to sing their established species song (Gammon et al. 2005). Resulting "errors" in an individual's song may thus be more common in isolated populations, and can subsequently be transmitted to future generations and cause further divergence. However, cultural evolution is an unlikely explanation for the introductory notes we observed in our allopatric black-capped chickadees given that our sample from Ithaca, NY is in continuous habitat. Further research should investigate Ithaca, NY and surrounding areas for more evidence of atypical song behavior in black-capped chickadees.

Our study demonstrates important implications for the role of song as a reproductive barrier between closely related and co-occurring species. Given that hybridization between black-capped and mountain chickadees in sympatry is relatively rare and likely maladaptive (Grabenstein et al. 2023), our findings of character displacement in note number per song offer support for song as a potential reproductive barrier that reduces or prevents maladaptive hybridization. The significance of our study is not limited to bird species, as similar evidence for song as a reproductive barrier has been reported in cicadas and a variety of frog species (Marshall and Cooley 2000; Höbel and Gerhardt 2003; Lemmon 2009; Malone et al. 2014). The ability for species to adjust their signaling behaviors is especially relevant in a period where anthropogenic pressures are increasingly altering species habitats and ranges. Species are not only driven into unprecedented contact with one another due to urbanization (Grabenstein et al. 2023), but they are also facing visual, chemical, and auditory interference due to environmental and noise pollution (Scott and Sloman 2004; Slabbekoorn and Ripmeester 2008; Bird and Parker 2014). As such, understanding mechanisms that allow species to adapt to changing environmental conditions, and to co-occur with one another, are critical in maintaining species diversity.

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