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Sympatric song variant in mountain chickadees *Poecile gambeli* does not reduce aggression from black-capped chickadees *Poecile atricapillus*

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ABSTRACT

When habitats overlap and species compete for resources, negative interactions frequently occur. Character displacement in the form of behavioural, social or morphological divergences between closely related species can act to reduce negative interactions and often arise in regions of geographic overlap. Mountain chickadees *Poecile gambeli* have an altered song structure in regions of geographic overlap with the behaviourally dominant black-capped chickadee *Poecile atricapillus*. Similar to European and Asian tits, altered song in mountain chickadees may decrease aggression from black-capped chickadees. To test this hypothesis, we conducted a playback study in Prince George, BC, Canada, to examine how black-capped chickadees responded to the songs of mountain chickadees recorded in regions where the two species were either sympatric or allopatric. We used principal component analysis (PCA) to collapse behavioural response variables into a single 'approach' variable and a single 'vocalisation' variable. We then used mixed-model analysis to determine whether there was a difference in approach or vocalisation response to the two types of mountain chickadee songs (allopatric songs and variant sympatric songs). Black-capped chickadees responded with equal intensity to both types of mountain chickadee songs, suggesting that the variant mountain chickadee songs from regions of sympatry with black-capped chickadees do not reduce heterospecific aggression. To our knowledge, this is the only instance of a character shift unassociated with reduced aggression in the family Paridae and raises interesting questions about the selective pressures leading to the evolution of this song divergence.

KEYWORDS

Poecile atricapillus, *Poecile gambeli*, chickadee, song, playback, aggression

INTRODUCTION

When species compete for resources, negative interactions frequently occur. This is particularly true amongst closely related species, which often inhabit similar ecological niches and have similar life history traits, and can lead to high levels of interspecific competition (Dhondt 2012). Character displacement – divergences in ecological, behavioural, morphological or physiological traits between closely related species in regions of geographic overlap – can act to differentiate closely related competitors and reduce interspecific competition (Brown & Wilson 1956). Character displacement has been observed across a range of taxa including several species in the order Carnivora (Davies et al. 2007) as well as salamanders (Adams 2004), lizards (Huey 1974; Melville 2002), fish (Schluter & McPhail 1992) and birds (Grant 1972; Doutrelant et al. 2000; Grava et al. 2013a; Hamao et al. 2015).

In birds, studies on closely related species pairs, such as great tits *Parus major* versus Eurasian blue tits *Cyanistes caeruleus*, mountain chickadees *Poecile gambeli* versus black-capped chickadees *Poecile atricapillus* and varied tits *Poecile varius* versus Japanese tits *Parus minor*, reveal that when these species pairs live in sympatry, the subordinate species diverges in expression of shared traits from the dominant species, undergoing a character displacement (Doutrelant et al. 2000; Grava et al. 2013a; Hamao et al. 2015). For example, Eurasian blue tits that inhabit regions where few or no dominant great tits are present produce songs that are similar to those of great tits (Doutrelant et al. 2000). In regions of sympatry, however, Eurasian blue tits, which are the subordinate species, add a trill to the end of their song. Great tits react less aggressively to the altered Eurasian blue tit trilled songs than they do to either untrilled Eurasian blue tit song or the song of conspecific great tits; the character shift in Eurasian blue tit song acts to reduce aggression from great tits (Doutrelant et al. 2000). A study by Hamao et al. (2015) on Japanese tits and varied tits also revealed a similar pattern. In regions where the two species live in sympatry, subordinate Japanese tits sing at a lower frequency, acoustically diverging from the songs of varied tits as well as from the songs of Japanese tits living in regions where varied tits are not present. These results suggest that the subordinate Japanese tit alters its song characteristics to avoid harassment by the dominant varied tit (Hamao et al. 2015); however, playback studies are needed to confirm that this results in reduced aggression.

In North America, the black-capped chickadee is socially dominant to the mountain chickadee (Grava et al. 2012a; Grava et al. 2012b; Grava et al. 2013a). Typically, the two species segregate because of different preferences in habitat and elevation, but historically zones of overlap exist throughout their ranges. With the onset of forestry practices that create abrupt transitions between remnant coniferous forests and second-growth deciduous forest, the potential for habitat-related isolation has decreased (Grava et al. 2012a).

The song of mountain chickadee is similar to that of black-capped chickadees in containing whistled notes, typically starting with a single high note followed by one to two lower notes (Lohr 2008, Grava et al. 2013a). Whilst the internal syntax, number of notes and frequency ratios within and between notes of black-capped chickadees are highly stereotyped across their distributional range (see review in Mennill and Otter 2007), mountain chickadees exhibit greater range-wide variation in number of notes and frequency changes between notes in their song than do the black-capped chickadees (Lohr 2008). This variation may be driven by dominance-mediated character displacement. Grava et al. (2013a) found differences in mountain chickadee song structure between regions of co-occurrence and isolation, whereas black-capped chickadees have a consistent song throughout North America. In areas of contact between mountain chickadees and black-capped chickadees, the mountain chickadee song exhibited structural differences (i.e. differences in frequency ratios within and between notes) from those of the black-capped song, though the form of these song variants were not consistent across the range (Grava et al. 2013a).

Whilst research by Grava et al. (2012a, 2013a) suggests that mountain chickadees alter song variants in areas of sympatry with black-capped chickadees, no studies have examined whether these sympatric song variants result in fewer negative interactions with dominant black-capped chickadees, as seen in European and Asian tits (Doutrelant et al. 2000; Hamao et al. 2015). Following the study design of Doutrelant et al. (2000), which examined the behavioural response of great tits to Eurasian blue tit vocalisations recorded in areas of sympatry and allopatry, we tested the hypothesis that mountain chickadees alter their vocalisations to minimise the negative interactions from black-capped chickadees. We predicted that black-capped chickadees unfamiliar with mountain chickadee song would respond less aggressively to the mountain chickadee songs recorded in areas of sympatry (sympatric songs) than to allopatric mountain chickadee songs (allopatric song variants).

1. METHODS AND MATERIALS

Playback Construction. We created a series of 10 playback dyads (paired playbacks, one playback with sympatric songs and one with allopatric songs) using mountain chickadee songs from populations across British Columbia and the western United States. Stimuli were obtained from the study by Grava et al. (2013a). 'Allopatric' playbacks consisted of mountain chickadee songs taken from a region where black-capped chickadees were not present whilst 'sympatric' playbacks consisted of mountain chickadee songs recorded from areas where both chickadee species coexist. For each pair of stimuli, songs were taken from allopatric/sympatric populations within a similar region (e.g. sympatric populations from northern California vs. allopatric populations in central and southern California, or known sympatric or allopatric populations within British Columbia). Stimuli were chosen from recordings that had high signal-to-noise ratios; from these, three or four high-quality songs were extracted and used to make each playback stimuli in the dyadic pairs. Each playback consisted of 12 songs per minute, with the three or four exemplar songs randomly interspersed in the sequence. Songs were spaced approximately 5–6 s apart, for a total of 24 songs over a total of 2 min. Each song used in creating the playbacks was standardised for amplitude using Avisoft SASLab Pro software (Specht 2012). We used Audacity software (Audacity Team 2008) to sequence the three to four exemplar songs into each playback stimulus, either allopatric or sympatric, to create variation whilst still representing successive songs of a single stimulus male. Low levels of Brownian noise (1% amplitude) were added to the playbacks with Audacity to diminish noises introduced during the editing process. The completed stimulus included a 30-s blank intro followed by 2 min of stimulus broadcast. Unique dyads were created by randomly pairing one 'allopatric' stimulus with a 'sympatric' stimulus, matched per region of stimulus origins. Four dyadic pairs were made from recordings from the western United States, and six stimulus pairs were made from recordings made throughout British Columbia, Canada. All dyads were loaded onto an Apple iPod Touch for field playback and broadcast through a Logitech X100 Bluetooth speaker. Each dyadic playback set was calibrated to a sound level of 75 dB at 1 m during playback, measured with a Goldline SPL-162 Sound Pressure Level Meter.

Field Methods. Playback experiments were conducted in Prince George, BC, Canada (53°54'40.1"N 122°45'18.6"W), from 21–29 April, 2015, following the methods of Doutrelant et al. (2000). We conducted playback experiments on a total of 22 unbanded black-capped chickadees in an allopatric population, at 22 separated locations around the University of Northern British Columbia campus, the outskirts of Prince George and within the Prince George city park, Forests for the World.

Males were equally distributed amongst four main sites that were separated by a minimum of 3 km and a maximum of 7 km. Within sites, males tested on the same day were separated by at least 250 m to avoid testing neighbours who might have been eavesdropping on the playbacks (McGregor 1992, 2002; McGregor et al. 1992). Natural song perches were used to determine locations of territory centroids, from which we conducted playbacks.

Playbacks were performed in the morning (07:00 to 12:00 am). Two to four 10-m long ropes, with 5 m markers, were set up equal distances apart radiating out from the middle of each focal bird's location, with a Logitech X100 Bluetooth speaker hanging in the centre, approximately 1 m off the ground. The speaker faced the direction of the focal bird and was connected via Bluetooth or using a plug-in adapter directly to the iPod.

Each focal chickadee was given a randomly selected playback stimulus (either allopatric or sympatric), followed by a second playback stimulus of the alternative type 1–2 h later at the same location, resulting in a total of two behavioural recordings per bird. The next focal bird was given a set of playback stimuli in the opposite order to randomise trials and avoid playback bias resulting from order effects (McGregor 1992, 2002; McGregor et al. 1992). In each playback trial, focal birds were first called in with a 'primer' call (a short playback of mobbing black-capped *chick-a-dee* calls) and were then given the selected playback recording. Behavioural responses were observed and recorded vocally using an Audiotechnica AT8015 microphone and a Marantz PMD661 MKII Professional Portable Flash Field Recorder. We verbally dictated the focal male's distance from the speaker at all points during the trials, noting each instant the male moved to a new location. We noted all movement flights as either short (<5 m) or long (>5 m). Further, we indicated whether or not the mate was present and her position relative to the subject male. Finally, we recorded all vocalisations made (*gargles*, *chick-a-dee* calls or songs) throughout the trials. Each playback dyad was played to either two (N = 8) or three (N = 2) males only, in reversed order, as recommended by McGregor et al. (1992) to avoid issues of pseudoreplication.

Audio Analysis. Recordings were individually annotated using Avisoft SASLab Pro bioacoustics software, taking note of focal bird's location and behaviours mentioned earlier throughout the playback trial. These annotations were then exported into text files. The observations noted in the text files were processed and summarised using R v3.3 statistical software (R Core Team 2016). Specifically, we extracted information on the focal male's distance from the speaker playback, time spent at each distance, how many vocalisations were made and the level of aggressiveness with relation to the stimuli they were exposed to (whether the focal male song was non-overlapping, overlapping or overlapped in relation to the playback stimuli) and time spent within 10 m of the speaker after the playback ended. Only birds with complete recording files of the trial were used in the analysis; incomplete or interrupted recordings were excluded from analysis ($n_{incomplete}$ = 2).

Statistical Analysis. We used R v.3.3 statistical software to conduct iterative principal component analysis (PCA) to collapse the variables into two holistic measures, one describing approach behaviour and the other describing vocal response. Next, we constructed generalised mixed models in JMP 12 (SAS Institute 2015) to determine whether approach response or vocal responses varied with respect to the playback presented (allopatric/sympatric). We included playback order and starting distance (as well as an interaction term) as covariates. Male ID was included as a random effect to account for the paired design.

2. RESULTS

Principal Component Analysis. For each trial, we tested combinations of behaviours associated with both individual approach and vocal responses to playback within PCA. Variables that were intercorrelated, or did not explain much variance, were removed so that we could make a parsimonious model that explained variation in male response with the most concise number of contributing variables. We collapsed time spent within several distinct radii of the playback speaker (e.g. distance from 0 to 5 m and distance from 5 to 10 m were collapsed to distance from 0 to 10 m) to derive a total of six variables, for which the first two principal components (PCs) explained 70% of the variance (Table 1). Both PC1 and PC2 met the broken stick criteria of components that explained a greater proportion of the variation than that explained by chance alone (Legendre and Legendre 1998). PC1 (hereafter called 'approach response') was most strongly associated with variables related to focal male distance from speaker during the playback period, with negative weightings for minimum distance (i.e. higher PC1 values indicate that birds were approached more closely; Table 1), and time spent at >20 m from the speaker, but positively weighted for time spent close to the speaker (time spent at 0–10 m). Also, there was a weak negative weighting on singing fewer overlapping songs. Thus, higher values of PC1 indicate close and sustained approaches to the speaker. PC2 was negatively associated with variables related to focal male vocalisation responses to the stimuli during the playback period (i.e. singing and overlapping songs more; Table 1) and positively with time greater than 20 m from the speaker; so high values of PC2 represent birds being distant and singing and overlapping little in response to playback. We subsequently multiplied the PC2 values by −1 to reverse the axis, so that greater values of PC2 indicate a more 'aggressive' singing response.

PC1 – Approach Response. We analysed paired responses from 20 individuals (40 observations total). Black-capped chickadees did not differ in approach response when presented with allopatric versus sympatric mountain chickadee song ($F_{1,19}$ = 0.34, p = 0.57; Fig. 1). Because the approach response may have been influenced by the initial starting location of the black-capped chickadee, we included starting distance

Table 1. *Principal component analysis results of measures of distance from the speaker and song response variables. PC1 was most strongly associated with the approach variables, whilst PC2 was most associated with vocal responses. Bolded values reflect variables with contributions of greater than 0.33 or less than −0.33, which are considered to make a substantial contribution to the axis (Ho 2006). Note that for PC2, the values were subsequently multiplied by −1 to create an index of increasing song response.*

Variable	PC1 Factor Loading	PC2 Factor Loading
Minimum distance to speaker	**−0.55**	0.21
Distance 0–10 m	0.55	−0.08
Distance 10–20 m	−0.24	−0.24
Distance >20 m	**−0.45**	0.36
Total number of song responses	−0.12	**−0.69**
Total overlapping song responses	**−0.34**	**−0.54**
Total variance explained	0.44	0.26

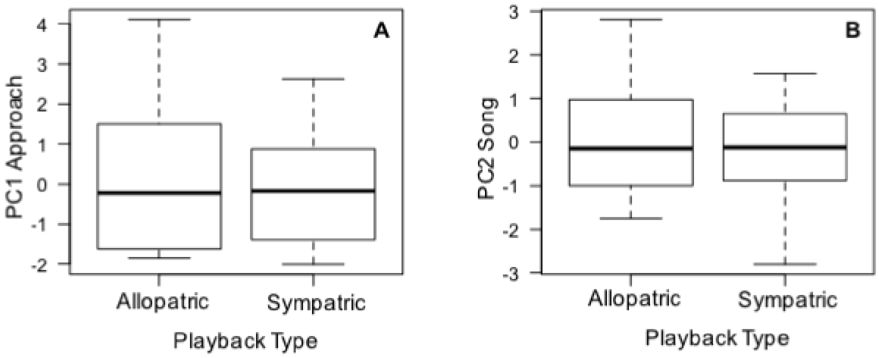

Figure 1. *Response of black-capped to chickadees to allopatric and sympatric mountain chickadee songs. Neither black-capped chickadee PC1 approach (A) nor PC2 song (B) differed between allopatric and sympatric playback trials.*

as a covariate and an interaction between starting distance and playback in the model. As anticipated, starting distance had a strong effect, but there remained no effect of playback type, nor was there an interaction between starting distance and playback type (starting distance: $F_{1,28.1} = 51.73$, $p < 0.0001$; playback type: $F_{1,17.3} = 0.03$, $p = 0.85$; starting distance*playback type: $F_{1,28.3} = 1.57$, $p = 0.22$). Because the interaction term was not significant, it was removed from the model. Starting distance remained significant, but there was no significant effect of playback type (starting distance: $F_{1,27.9} = 59.64$, $p < 0.0001$; playback type: $F_{1,18.3} = 0.03$, $p = 0.87$).

Next, we generated a model with an additional effect of playback order (i.e. whether allopatric was presented first or second) and an interaction term to determine whether there was an order effect (i.e. whether the song played first [allopatric or sympatric] influenced the black-capped chickadee responses). Neither the interaction term nor the order effect were significant (first trial: $F_{1,18} = 0.19$, $p = 0.67$; playback type: $t_{1,18} = 0.32$, $p = 0.58$; first trial*playback type: $F_{1,18} = 0.24$, $p = 0.63$). Upon removal of the interaction term, there was still no effect of either playback order or playback type (first trial: $F_{1,18} = 0.19$, $p = 0.67$; playback type: $F_{1,19} = 0.34$, $p = 0.57$). When we included starting distance in the model, there was a significant effect of starting distance; however, playback trial and order were not significant (first trial: $F_{1,16.6} = 0.26$, $p = 0.62$; playback type: $F_{1,18.3} = 0.03$, $p = 0.87$; starting distance: $F_{1,26.9} = 55.52$, $p = < 0.0001$).

PC2 – Song Response. We found no difference in song response to the type of playback presented to black-capped chickadees (allopatric vs. sympatric; $t_{1,19} = 0.68$, $p = 0.42$; Fig. 1). As with approach response, we included starting distance as a covariate and an interaction between starting distance and playback type in the model. There was no effect of starting distance, playback type, or the interaction term (starting distance: $F_{1,24.8} = 1.97$, $p = 0.17$; playback type: $F_{1,18.4} = 0.85$, $p = 0.37$; playback type*starting distance: $F_{1,33.3} = 1.16$, $p = 0.29$). Consequently, the interaction term was removed from the model. There remained no effect of either starting distance or playback type (starting distance: $F_{1,24.7} = 1.46$, $p = 0.24$; playback type: $F_{1,19.0} = 0.79$, $p = 0.39$).

Next, we produced models that included playback order and an interaction term. Playback order, playback type, and the interaction term were all not significant (first trial: $F_{1,18} = 0.49$, $p = 0.49$; playback type: $F_{1,18} = 0.65$, $p = 0.43$; first trial*starting distance: $F_{1,18} = 0.12$, $p = 0.74$) and remained non-significant after the removal of the interaction term (first trial: $F_{1,18} = -0.49$, $p = 0.49$; playback type: $F_{1,19} = 0.68$, $p = 0.42$). An additional model was created to examine playback order as well as starting distance; however, there were still no significant effects (first trial: $F_{1,17.3} = 0.42$, $p = 0.53$; playback type: $F_{1,19.1} = 0.78$, $p = 0.39$; starting distance: $F_{1,23.6} = 1.34$, $p = 0.26$).

3. DISCUSSION

In contrast to studies on European and Asian tits, we did not observe that the song variants of mountain chickadees used in regions of sympatry reduced aggressive responses from naïve black-capped chickadees more than the songs from allopatric populations. Black-capped chickadees in our study area did not appear to differentiate between sympatric and allopatric mountain chickadee songs in any of their behavioural responses. During both sympatric and allopatric playback trials, black-capped chickadees reacted by approaching the speaker and vocalising during the trial. Although we did not include a conspecific stimulus in this study – for fear of inducing habituation to too many stimuli – the responses of subject males in this study were qualitatively similar in approach distance and time spent close to the speakers as seen in previous studies when black-capped chickadee males were presented conspecific song in non-interactive playbacks (Shackleton et al. 1992; Otter et al. 2002; Mennill and Ratcliffe 2004; Grava et al. 2013b). Thus, our results suggest that black-capped chickadees recognise both types of mountain chickadee song stimuli and respond to them as a potential threat. The song variants, or character-shifted songs, exhibited by mountain chickadees in populations where the two species are sympatric (Grava et al. 2013a) did not appear to minimise the responses of naïve black-capped chickadee males. This result is unexpected because of the findings of studies on pairs of other Parid species in which the subordinate species do display character shifts that reduce negative interactions with the more dominant form (Doutrelant et al. 2000).

Black-capped chickadees respond less aggressively to heterospecific calls than to conspecific *chick-a-dee* calls (Grava et al. 2012b). However, when we presented black-capped chickadees with only heterospecific mountain chickadee songs, there was an equal reaction to both the allopatric and sympatric versions of this song. One possibility is that the sympatric populations of mountain chickadees from which we obtained stimuli are in the early stages of character displacement; the structure of their songs may still be very similar to that of mountain chickadees in allopatric populations. It may continue to change until it becomes less recognisable to black-capped chickadees, and at that point, it may be perceived as less of a threat.

Owing to the natural segregation of both species based on habitat type, there tend to be small areas of overlap rather than large zones. The existence of these isolated areas may result in independent character shifts within each of the distinct sympatric populations (Grava et al. 2013a), that is, a variety of different character-shifted song variants occur amongst disparate sympatric populations. Because chickadees rely on learning for song development, cultural evolution and the rapid emergence of local dialects within sympatric populations of mountain chickadees may limit the ability of black-capped chickadees to recognise and respond to non-local mountain chickadee song variants. LaZerte et al. (2016) demonstrated that male black-capped chickadees required prior exposure to urban noise in order to respond appropriately (shift song upwards in pitch) to playback of experimental noise; it is possible that parallel prior experience with mountain chickadees, and learning the local character-shifted song variant, is required to see reduced responses in male black-capped chickadees. As we tested only black-capped chickadees from an allopatric population, naïve to mountain chickadee song, this may account for the lack of discrimination. Future playbacks on male black-capped chickadees in overlapping populations, testing local sympatric mountain chickadee song variants versus those arising from other sympatric populations, might elucidate this idea.

Alternately, the character-shifted songs seen in sympatric mountain chickadee populations may not have evolved to reduce aggression from black-capped chickadees but rather may arise owing to female mate choice. In black-capped chickadees, females prefer dominant males as social and extra-pair partners (Ramsay et al. 2000) and can learn the relative rank of the male based on non-pitch-based cues in vocalisations and respond more to dominant male songs (Hoeschele et al. 2010). Ratcliffe and Otter (1996) demonstrated that females exhibit reduced response to songs with incorrect internote intervals and flattened within-note frequency ratios in the *fee* note. Additionally, Christie et al. (2003) showed that songs are highly stabilised and that the ability to maintain consistency is a dominance-related characteristic. Because social hierarchies govern social behaviour, interspecific hierarchies could potentially drive hybridisation if females are choosing dominant males as extra-pair partners regardless of species (Grava et al. 2012a). Both black-capped and mountain chickadees are monogamous and form season-long pair-bonds; however, Grava et al. (2012a) found that in regions of overlap, black-capped males sire the majority of mountain chickadee nestlings through extra-pair copulations, rather than through social pairings (Grava et al. 2012a). This pattern can also be seen in hybrid zones between

Carolina chickadees *Poecile carolinensis* and black-capped chickadees, where female black-capped chickadees prefer dominant male Carolina chickadees (Bronson et al. 2003; Reudink et al. 2006). As the subordinate species, male mountain chickadees may have reduced expression of a favoured dominance trait, leading to mating of the female mountain chickadees with the dominant male black-capped chickadees. This could reduce the potential reproductive output of male mountain chickadee (Grava et al. 2012a, 2013a). If variant mountain chickadee songs are perceived as more attractive by females, selection could favour altered vocalisations in regions of sympatry if males expressing this song are better able to attract mates and avoid paternity loss from black-capped chickadees.

Our results do not follow the pattern of character shifts acting to reduce aggression from dominant species, as observed in Asian and European tits, close relatives of North American chickadees. Repeating this study on other black-capped chickadee populations, particularly those already sympatric with mountain chickadees, may prove informative. The form of character displacement in song divergence of mountain chickadees varies across sympatric populations, which may suggest that black-capped chickadees require a period of song learning to recognise local song variants. As such, we would predict that only black-capped chickadees in sympatric populations may exhibit a differentiated response and that black-capped chickadees may only reduce aggression towards the local mountain chickadee variant. In addition, it may be beneficial to control for black-capped chickadee response to black-capped songs (i.e. conspecific song). Presenting a male black-capped chickadee with both a black-capped song (control) and either an allopatric or sympatric mountain chickadee songs would allow black-capped chickadees to compare between conspecific and heterospecific songs, potentially resulting in greater differentiation between sympatric and allopatric songs. Furthermore, incorporation of Carolina chickadee vocalisations, to which black-capped chickadees in western Canada have not been exposed, into a playback presented to black-capped chickadees may allow us to interpret whether black-capped chickadees are merely responding to vocalisations that exhibit 'conspecific-like' attributes or if they do in fact differentiate between species. Finally, mate choice trials in which female mountain chickadees are presented songs from sympatric and allopatric populations could indicate whether song shifts exhibited by mountain chickadees are driven by sexual selection pressures.

Our results demonstrate that mountain chickadee songs with sympatric song variants do not reduce heterospecific aggression from black-capped chickadees. This finding is particularly interesting as, to our knowledge, within the family Paridae, it is the only instance of a character shift being unassociated with reduced aggression. Our results raise interesting questions about the selective pressures leading to the evolution of this song divergence. It is possible that different selective pressures (e.g. social, sexual) may result in similar evolutionary outcomes in the form of altered songs in sympatric populations.

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