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

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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).

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

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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; Kempenaers 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; Kroodsma 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