



Discrimination of male black-capped chickadee songs: relationship between acoustic preference and performance accuracy



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Many species form social groups with dominance hierarchies. Often, individuals possess a status signal that indicates dominance rank. Songbirds produce songs that are used to attract mates or repel rivals, and acoustic features within songs can also indicate an individual's quality, including dominance rank. Acoustic status signals have been reported in the songs of male black-capped chickadees, *Poecile atricapillus*, a nonmigratory North American songbird. Here we used two operant conditioning tasks to examine acoustic preference for and discrimination of conspecific songs produced by males varying in dominance rank. We used a choice preference task to examine birds' preferences for listening to dominant or subordinate songs and conducted an instrumental learning task to determine whether chickadees considered dominant and subordinate songs as belonging to separate signal categories based on acoustic features. Overall, our results provide little evidence that birds used open-ended categorization when discriminating, but there is evidence that songs from different geographical regions may contain acoustic similarity based on dominance rank. Consistent with previous song discrimination studies with black-capped chickadees, we found sex differences in discrimination abilities, with females learning the discrimination faster than males. We also found evidence that performance accuracy during the instrumental learning task correlates with acoustic song preference. Overall, these results suggest that when biologically relevant signals (e.g. male songs) are used as stimuli during a perceptual task, the birds' responses may be differentially affected based on individual differences among the subjects performing the task (including sex and underlying preference) and the salience associated with the stimuli (e.g. dominance rank of the singer).

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Dominance ranks were first described by [Schjelderup-Ebbe \(1922/1975\)](#) studying the hierarchical social structure of group-living domestic chickens, *Gallus gallus*. However, dominance ranks and social group interactions have been examined in numerous species ([Allee, 1942/1975](#); [Dewsbury, 1982](#)). Dominance ranks are often established through quantifying behavioural dyadic

interactions, with these interactions usually occurring during disputes focused around access to resources. Although dominance is a relative trait (i.e. an individual may be dominant over another individual, while also being subordinate to a third individual; [Drews, 1993](#)), within social groups with consistent membership over time, dominance hierarchies are usually stable ([Wiley, Steadman, Chadwick, & Wollerman, 1999](#)). When the social hierarchy is stable, individuals do not need to engage in constant confrontations to assert their dominance over other individuals. In the case of chickens, for example, the dominant individual does not need to continue to act aggressively towards lower-ranking individuals once the dominance hierarchy is established ([Schjelderup-Ebbe, 1922/1975](#)). Instead, once the dominance rank is established, few confrontations occur, and time and energy can be spent on other activities that are necessary for survival (e.g. foraging).

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Although familiarity with opponents can facilitate rank stability (Archawaranon, Dove, & Wiley, 1991; Wiley et al., 1999), the formation and maintenance of dominance hierarchies does not imply individual recognition is necessary. Instead, individuals may possess a status signal that allows others to characterize that individual's dominance rank in the absence of individual recognition. If there is a status signal that varies with dominance rank, animals that live in large social groups could make rank discriminations without repeated confrontations with another individual (Cummins, 1996).

A status signal may be a visual trait that indicates dominance status (e.g. antler size in woodland caribou, *Rangifer tarandus caribou*, Barrette & Vandal, 1986; badge size in house sparrows, *Passer domesticus*, Møller, 1987; plumage coloration in black-capped chickadees, *Poecile atricapillus*, Mennill, Doucet, Montgomerie, & Ratcliffe, 2003), or an acoustic feature in an auditory signal (e.g. spotted hyaena, *Crocuta crocuta*, Mathevon, Koralek, Weldele, Glickman, & Theunissen, 2010; rock hyrax, *Procavia capensis*, Koren & Geffen, 2009; fallow deer, *Dama dama*, Vannoni & McElligott, 2008). A behavioural trait can also indicate status, such as dominant individuals vocalizing more frequently compared to subordinates (domestic chicken, Leonard & Horn, 1995; black-capped chickadee, Otter, Chruszcz, & Ratcliffe, 1997).

If a signal indicates an individual's dominance status, how that signal is perceived will depend on who is receiving the signal. Traits that indicate an individual's fighting ability or quality, such as birdsong, can act as a signal of territoriality when directed at other males, or as a signal of mate quality when directed at females. Furthermore, male birdsong often contains additional information regarding the individual that is signalling and, for species that live in social groups with dominance hierarchies, songs can contain information regarding a male's dominance status. In some species, such as brown-headed cowbirds, *Molothrus ater*, song is essential for the establishment of dominance relationships (Dufty, 1986); while subordinate brown-headed cowbird males are capable of singing the song preferred by females, only the dominant male sings these preferred songs (West, King, & Eastzer, 1981). If information regarding a male's dominance rank means something different for a listening female compared to a listening male, how the sexes respond to the signal should also vary. In addition, the type of signal produced by an individual may also vary depending on what audience is present (Dalziell & Cockburn, 2008).

Black-capped chickadees are common North American songbirds that live in winter flocks where social interactions are influenced by stable linear dominance hierarchies. Within a flock, males will usually dominate females, and once the winter flocks break up, birds mate assortatively (i.e. the highest-ranked male mates with the highest-ranked female, and vice versa for the lower-ranked pairs; Smith, 1991). The dominant male in the winter flock has preferential access to food resources (Smith, 1991). Once flock break-up occurs, dominant males more easily obtain a territory during the breeding season (Desrochers, Hannon, & Nordin, 1988) and obtain larger territories with more resources (Mennill, Ramsay, Boag, & Ratcliffe, 2004). Dominant males have higher lifetime reproductive success (Schubert et al., 2007) in part because they are preferred by females seeking extrapair copulations (Mennill et al., 2004; Otter, Ratcliffe, Michaud, & Boag, 1998; Smith, 1988).

Black-capped chickadees produce two-note fee-bee songs. The song's first note (fee note) is produced at a higher frequency compared to the second note (bee note), and the frequency relationship between the two notes remains relatively consistent across song renditions (Horn, Leonard, Ratcliffe, Shackleton, & Weisman, 1992; Weisman, Ratcliffe, Johnsrude, & Hurly, 1990). Males (Mennill & Ratcliffe, 2004) and females (Mennill, Ratcliffe, & Boag, 2002) eavesdrop on male song contests, and male dominance

cues are contained within the songs (Christie, Mennill, & Ratcliffe, 2004; Hahn et al., 2013; Hoeschele et al., 2010). As males sing, they will shift the absolute frequency of their songs (Hill & Lein, 1987; Ratcliffe & Weisman, 1985); however, dominant males are more likely to maintain a consistent frequency relationship between the two notes compared to subordinate males (Christie et al., 2004). Dominant males also produce songs in which the relative amplitude between the two song notes is more consistent compared to the songs produced by subordinate males (Hoeschele et al., 2010). Dominance-related acoustic cues in black-capped chickadee songs also vary between geographical regions. Specifically, the relative amplitude between the two song notes is a signal of dominance status in the songs produced by birds in northern British Columbia, but the relative amplitude between the two notes does not vary with dominance status for birds in eastern Ontario (Hahn et al., 2013). Since dominance-related cues in black-capped chickadee songs vary with geographical location, it allows us to test how birds from distant locations respond to songs produced by unfamiliar males from different geographical locations. For example, Hoeschele et al. (2010) found that females from one geographical location (i.e. central Alberta) responded differentially to dominance-related variation in songs produced by males that were the highest ranked within a flock compared to males that were the lowest ranked within a flock. In that study, the songs were produced by males from a distant geographical location (i.e. northern British Columbia), suggesting that the females perceived acoustic variation relative to dominance in these songs despite the fact that the stimuli were produced by males from a different population.

Subsequent bioacoustic analyses and playback studies of songs produced by dominant and subordinate males have confirmed that male chickadee songs contain dominance cues (e.g. consistency of the relative amplitude between the two song notes, Hoeschele et al., 2010). This raises the possibility that receivers might use open-ended categorization to assess dominance rank without previous experience with the singing individual. With open-ended categorization, individuals classify signals by means of perceptual similarity (Herrnstein, 1990). For example, if dominant individuals produce status signals with similar features, animals could identify a dominant individual by learning a general 'category' rule based on those similarities. If an individual's signal contains those features, the individual is considered to belong to that category (in this example the individual is classified as 'dominant'). If perceptual categories for a status signal do not exist, open-ended categorization is not possible; however, animals could still discriminate using rote memorization. In contrast to open-ended categorization, rote memorization requires an individual to have prior experience with and memorize each signal (e.g. for an acoustic status signal, an individual would need to have prior experience with the vocalizing individual, evaluate the individual's dominance rank and recognize the individual's vocalization). Open-ended categorization of dominance signals may be a more useful cognitive mechanism, and therefore selected for, compared to rote memorization, because open-ended categorization does not require an animal to recognize and remember each individual and their social status, which increases cognitive load as the number of individuals within the social group increases. Furthermore, this could allow classifications of individuals from neighbouring social groups, with whom a receiver may have had more limited social interactions, a phenomenon common when chickadees interact with or settle near members of other wintering flocks.

In addition to the ability to categorize songs based on acoustic dominance cues, birds may also have a preference for listening to dominant or subordinate songs. Preference tests using conspecific song as the reinforcer have demonstrated in other songbird species

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