University of Alberta

Intra- and Inter-specific Vocal Perception in Black-capped (*Poecile atricapillus*) and Mountain (*P. gambeli*) Chickadees

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Psychology

Edmonton, Alberta
Fall 2007

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Your file Votre référence
ISBN: 978-0-494-32920-7
Our file Notre référence
ISBN: 978-0-494-32920-7

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Abstract

In their natural habitat, songbirds (order Passeriformes, suborder oscines) produce vocal signals to convey a variety of information to conspecific listeners. While songs are used mainly by males during the reproductive period to convey their status and advertise their territory, calls are used by both males and females during non-reproductive periods. All chickadee species (genus *Poecile*) produce a variant of the 'chick-a-dee' call, putatively to co-ordinate flock activity with, and to convey mild alarm to, conspecifics. In some regions both black-capped (*P. atricapillus*) and mountain chickadees (*P. gambeli*) occupy overlapping ranges, yet how chickadees perceive their own and other species chick-a-dee calls in unknown. While there is very little interaction between the two species during the reproductive period, inter-specific interactions during other times may be beneficial. In this thesis, a bioacoustic analysis of the chick-a-dee call and call notes of mountain chickadees (Chapter 2) revealed 2 note types not observed in the call of black-capped chickadees. A subsequent operant conditioning task determined that black-capped and mountain chickadees perceived the calls as belonging to two separate, species-defined categories into which novel calls were classified (Chapter 3). When portions of each species' calls (e.g., 'chick-a' and 'dee') were presented in a variety of manners in the operant chamber, responding by birds indicated that the terminal 'dee' portion conveyed species identity (Chapter 4). In nature, vocal and behavioural responses by black-capped chickadees suggested that birds utilized either the first half ('chick-a') or the second half ('dee') of the call for species discriminations (Chapter 5). Finally, the ontogenetic experience of an individual did not affect species' discrimination,

categorization, or memorization abilities, as performance of adult chickadees in an operant task were similar to the performance of black-capped chickadees reared in the laboratory among either black-capped or mountain chickadees (Chapter 6). To summarize, differences in the two species' chick-a-dee calls, including the terminal 'dee' portions, may contribute to species recognition. Finally, irrespective of the previous experience of birds, the calls are perceived as belonging to two separate open-ended categories, a skill once thought to be uniquely human.

Acknowledgements

The successful completion of this dissertation is due in part to the contributions of colleagues, friends, and family, who I wish to thank here.

First and foremost, I am indebted to Dr. Christopher Sturdy for working tirelessly to teach me the finer details of being a scientist, a teacher, and a mentor. I look forward to a lifetime of conversations and collaborations with you. I would also like to extend my sincere gratitude to Drs. Marcia Spetch and Clayton Dickson for providing valuable input to the dissertation in all of its stages.

Many fellow students have contributed in many helpful ways. Although they all deserve recognition, I would especially like to thank Tiffany Lee, Isabelle Charrier, Marc Avey, and Tara Farrell for providing much needed help, friendship, and support.

Much of this research could not have been possible without the contributions of: Ron Weisman for providing research equipment; Lou Omerzu, Isaac Lank, and Harold Tischer for equipment maintenance; Judy, Dave, and Gary for help at the Kananaskis Field Research Station; and Simmone Kerswell and staff for animal care.

My parents, Judie and Allan Bloomfield, and my immediate and extended family members have supported every decision that I have made throughout my educational career, and I thank them for giving me the opportunity to make them proud.

And lastly, I will forever be grateful to Richard, who has remained by my side throughout every step of this process. I thank him for his love and continual faith in me, without which this might not have been possible.

This dissertation is written in loving memory of my wonderful uncle, Mel Harris, who would have loved to celebrate the completion of my journey.

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Chapter 1: General Introduction

Communication, both visual and auditory, is essential for many vertebrate species existing in complex social organizations (see Bertram, 1978). Furthermore, vocal communication is especially important for maintaining contact with conspecifics when distance or naturally occurring obstructions such as vegetation prevent visual contact. Vocalizations can provide nearby listeners with particular information such as the presence of a predator, food, or of invading con- or heterospecifics. Thus, vocal communication can provide animals with environmental and contextual information necessary for fitness and survival. This is certainly true for songbirds (the oscine Passeriformes).

Songbird Vocal Learning

It is perhaps important to begin by differentiating between songs and calls. As typically prescribed in the literature, songs are complex and learned while calls are simple and innate. Songs can be long and elaborate vocalizations, produced (mostly) by males during the breeding season to attract females, repel rivals, and advertise territory ownership (but see Spector, 1994 for a discussion). Alternatively, calls are described as simple vocalizations, used by both males and females for communicating with conspecifics regarding, for example, food sources and approaching predators. These descriptions have resulted in a plethora of empirical research investigating song learning and production. However, it is becoming evident that calls can be neither simple, nor innate. For example, Zann (1984) documented a sex difference in the complex distance call produced by male and female zebra finches (*Taeniopygia gutatta*) that is dependent on learning in males. In addition, several finch species (*Carduelis pinus* and *C. tristis*) also exhibit call modification potentially related to pair-bond formation occurring later in life, suggesting that social and environmental factors are involved (Mundinger, 1970). Thus, although the descriptions of songs and calls were compatible with the knowledge at the time, evidence for call learning is becoming increasingly more prevalent, rendering the former descriptions unreliable.

Songbirds are one of 7 groups of animals that must have exposure to conspecific adults and their vocalizations in order to memorize, practice, and ultimately produce their species-specific sounds (others include humans, parrots, hummingbirds, bats, cetaceans, and elephants). One of the first empirical investigations into songbird vocal learning occurred nearly a half century ago (Thorpe, 1958). This seminal work found that chaffinches (*Fingilla ceolebs*), reared in isolation from normally singing adults, produced abnormal song. Further, birds rejected heterospecific vocalizations over conspecific vocalizations (see also Marler, 1970). However, Immelmann (1969) found that zebra finches (*Taeniopygia guttata*) would learn heterospecific vocalizations, but only when raised by (i.e., had direct social interaction with) heterospecific foster-parents. Therefore the ontogenetic experience of an individual can impact the learning process, and Thorpe was the first to describe this learning process in songbirds: birds first learn *what* to sing, and subsequently learn *how* to sing (see Baptista, 1996 for a review).

Following up on the work of Thorpe, his students found that not only do songbirds require auditory access to a tutor, but this access must occur within a particular time frame (i.e., the 'sensitive' or 'critical' period; Marler, 1970). For most songbird species (e.g., chaffinches, zebra finches), the sensitive period for attending to and memorizing conspecific vocalizations is typically within the first three months of life. However, if birds are reared in complete isolation of singing adults or presented with tape-tutoring, this sensory phase can be extended with exposure to live singing adults (Baptista & Petrinovich, 1984). In some species, the subsequent sensory-motor phase, when birds begin to practice the memorized vocalizations and modify their vocal output, overlaps with the sensory phase (see Brainard & Doupe, 2000 for a review). During the sensory-motor phase, hearing one's own vocal output is necessary; a hearing deficiency incurred during this phase results in atypical vocal production irrespective of any exposure to singing adults during the sensory phase (Konishi, 1965; Nottebohm, 1968). Finally, specialized brain regions are devoted to perceiving and producing conspecific vocalizations, and insults to these brain regions negatively impact vocal learning and production (Nottebohm, Stokes, & Leonard, 1976). Clearly, given the time, effort, and brain regions committed to vocal learning, there is selective pressure for learning to accurately produce the sounds that function to maintain social relationships in nature. In turn, investigation into songbird vocal learning has thrived over the last 50 years in an effort to fully understand and describe the function(s) and mechanism(s) of songbird vocal production and perception.

Vocal Production and Perception

Assuming that the necessary conditions for vocal learning (access to a singing adult during the sensitive period, auditory feedback, and intact brain regions) are in place, young songbirds must attend to the vocalizations of conspecific adults to later produce accurate renditions of these vocalizations. Birds show a preference for conspecific vocalizations pre- and immediately post-hatch via increased heart rate and vocal response (Dooling & Searcy, 1980; Nelson & Marler, 1993). Putatively, particular species-typical features present in the songs of adult males garner the attention of the young. For example, a high-pitched whistle universally produced at the beginning of the song of white-throated sparrows (*Zonotrichia leucophrys*) is reliably learned by young birds. When this whistle is included among the syllables of heterospecific song, the young birds will learn to produce the heterospecific song, an effect not seen when the whistle is excluded (Soha & Marler, 2000). Young birds will also learn a novel (i.e., unnatural) tempo in their song provided that the species-specific song syllables are present (Podos, 1996). Interestingly, when song syllables are presented out of their species-typical syntax, young birds will rearrange the syllables and accurately produce their song with the appropriate syntax (Soha & Marler, 2001). That birds show an innate preference for conspecific vocalizations, and are predisposed to attending to, learning and producing accurate conspecific vocalizations (e.g., see Adret, 2004 for a review) suggests that learning and producing species-specific vocalizations could ultimately impact one's reproductive fitness and survival.

Songbirds spend a large proportion of their time defending territories, attracting mates, foraging, and avoiding predators, and have evolved specialized abilities to recognize species and individuals based on auditory signals (Becker, 1982; Falls, 1982). For example, territory owners must recognize the acoustic signals of their neighbours to avoid unnecessary confrontations with these birds at established territory boundaries (Falls & Brooks, 1975) and mount strong aggressive responses towards invading strangers (see Stoddard, 1996). Furthermore, songbirds must be discriminating when selecting a mate, and can assess the quality of a potential mate based on vocal production (e.g., Nowicki, Peters, & Podos, 1998). In addition, perceiving and interpreting calls conveying information regarding food sources could be critical for foraging conspecifics (e.g., Freeberg & Lucas, 2002). Finally, the ability to recognize calls containing information regarding predators could be critical for survival among conspecifics (e.g., Templeton, Greene, & Davis, 2005), and, potentially, for eavesdropping heterospecifics (e.g., MacDonald & Henderson, 1977). Clearly then, acoustic signals have the potential to provide conspecifics (and possibly heterospecifics) with cues critical to fitness and survival.

Chickadees (order Passeriformes, genus Poecile)

Chickadees provide an excellent model for studying acoustic communication because not only is their song learned (Shackleton & Ratcliffe, 1993), but some of their calls have a learned component as well (e.g., gargle call, Ficken, Ficken, & Apel, 1985; chick-a-dee call, Hughes, Nowicki, & Lohr, 1998). Moreover, chickadees produce more call types compared to song types (see Ficken, Ficken, & Witkin, 1978; Hailman & Ficken, 1996), and some calls are more acoustically complex than their song, allowing for greater possible diversity and complexity in the messages potentially being communicated (see Hailman, Ficken, & Ficken, 1985). Lastly, all members of the genus *Poecile* produce a species-typical variant of the chick-a-dee call (see Ficken, Hailman, & Hailman, 1994; Ficken, McLaren, & Hailman, 1996; Ficken et al., 1978; Gaddis, 1985; Hailman & Ficken, 1996; S.T. Smith, 1972), making chickadees an ideal model for comparative studies of acoustic communication.

The vocal repertoire of the black-capped chickadee is arguably the most well-studied of all the chickadee species. Their chick-a-dee call, associated with mild alarm and flock communication and co-ordination (Ficken et al., 1978; S.M. Smith, 1991), consists of four note types; A, B, C, and D. While maintaining a fixed syntactical ordering of the notes (A through D), any of the notes can be repeated or omitted to produce a seemingly infinite number of call types (Hailman et al., 1985). Black-capped chickadees perceive their chick-a-dee calls and their constituent note types as belonging to natural, open-ended categories (Bloomfield, Sturdy, Phillmore, & Weisman, 2003; Sturdy, Phillmore, & Weisman, 2000), providing evidence of a perceptual hierarchy of (at least) individual calls comprised of call notes. In addition to using features present in songs to discriminate among individual conspecifics (Phillmore, Sturdy, & Weisman, 2003), black-capped chickadees also perceive differences among chick-a-dee calls to discriminate between flock members and non-flock members (Mammen & Nowicki, 1981). Thus both the black-capped chickadee song and chick-a-dee call contain features which aid in individual and flock recognition.

Most closely related to the black-capped chickadee is the mountain chickadee (Gill, Mostrom, & Mack, 1993). While the black-capped chickadee inhabits the northern United States and most of Canada, the mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (McCallum, Grundel, & Dahlsten, 1999; S.M. Smith, 1993). In some regions the two species occupy overlapping regions (i.e., live sympatrically) and engage in interspecific activities such as foraging (pers. obs.). Both species respond weakly to playback of heterospecific song within their (sympatric) ranges (Hill & Lein, 1989), indicating that the song of both black-capped and mountain chickadees contains information specific to each species. However, the species-specific and individual-specific features in the vocal repertoire of the mountain chickadee, including its chick-a-dee call, are not known.

The chick-a-dee call of the mountain chickadee is acoustically similar to the black-capped chick-a-dee call and is used is similar contexts (Gaddis, 1985). Gaddis (1985) describes the call notes using some terminology similar to that used to describe the black-capped chickadee call, yet provides little information related to the variability of notes within and between individuals. In light of the fact that this call has received relatively little attention, the note types, syntax, and species- and individual-specific features remain largely unknown (but see McCallum et al., 1999 for adaptations of note type descriptions by Gaddis, 1985).

Attending to the vocalizations and vocal interactions of conspecifics can provide listeners with valuable information such as the social rank and fitness of an individual. Mennill, Ratcliffe and Boag (2002) demonstrated that female chickadees base their reproductive decisions, at least in part, on information gained by attending to male-male singing contests. Similarly, great tits (*Parus major*, European relatives of North American chickadees) assess the quality of their rivals based on overheard vocal interactions (Peake, Terry, McGregor, & Dabelsteen, 2001). In addition to the information gleaned from attending to the vocalizations of conspecifics, attending to the vocalizations of heterospecifics might also be beneficial in some instances. For example, several species of birds (e.g., Hurd, 1996; Rabatsky, 1997; Templeton & Greene, 2007; Thompson & Barnard, 1983) and mammals (e.g., Windfelder, 2001; Zuberbühler, 2000; Shriner, 1998) determine whether a threat is imminent by attending to the vocal output of heterospecifics. Since black-capped and mountain chickadees inhabit overlapping ranges, it remains possible that these two closely-related species may attend and respond to each other's vocalizations in particular contexts. Such vocal interactions among songbirds in general, and among chickadees in particular, may contribute important information pertaining to mating, territory defense, foraging and predation.

Accurate descriptions and analyses of calls and call notes are essential, not only for understanding the behavioural contexts in which the calls are used and the messages they may potentially convey, but also for identifying the particular features of the calls and call notes that provide birds with relevant information, such as when to take action or when to ignore the vocalizations of others (e.g., predator- or non-predator related call), or whether the caller is conspecific or heterospecific, male or female, neighbour or stranger. If such hierarchical classifications can be done quickly and easily, birds will not waste energy mistakenly fleeing upon hearing a non-predator related calls (vocalization-type classification), defending a territory or mate against a heterospecific (species-level classification), courting a male (sex-based classification), or attacking a friend (individual recognition and classification). Once the features of the chick-a-dee call of the mountain chickadee have been described and measured, only then can direct comparisons of chick-a-dee calls across species be conducted, followed by an empirical search to understand the classification strategies of birds and the mechanisms underlying these abilities.

Open-ended Categorization

In order for chickadees (and other songbird species) to know when to ignore and when to take advantage of the surrounding cacophony, recognition and quick identification of the vocalization type, the species of the singer, and in some cases the singer's individual identity, is important. Herrnstein (1990) suggests that that all members or objects within a group have one or more perceptual features in common. If one or more common perceptual features are present, objects may be classified as belonging to the same group; if common features are not present, objects may not be classified as belonging to that group. Once the common features of a group have been identified, novel or unfamiliar objects can quickly and easily be classified based on the extent of their perceptual similarities. In other words, animals can generalize their learning to novel instances, suggesting that the categories are open-ended. Pigeons (*Columba livia*) have provided evidence that hundreds of novel objects can be accurately classified once the common features of a class are identified, (e.g., Astley & Wasserman, 1992; Herrnstein, Loveland, & Cable, 1976; Vaughan & Greene, 1984). Generalization, or transfer of learning to novel stimuli, provides an important piece of evidence to suggest that animals are not simply utilizing a rote memorization strategy. Whereas rote memorization requires experience with each individual exemplar, open-ended categorization does not.

If birds required experience with every individual and its vocalizations in order to memorize and later classify the singer as conspecific or heterospecific, male or female, or friend or foe, precious time and energy could be wasted. Therefore, utilizing a categorization strategy would allow birds to quickly recognize the features of vocalizations that are shared by all members of the group of interest (e.g., conspecifics) and ignore vocalizations that do not contain the relevant features. Evidence of open-ended categorization has previously been reported in many species, including black-capped chickadees. Responding by chickadees in operant-discrimination tasks suggests that the birds use open-ended categorization to classify their chick-a-dee call notes by type (Sturdy et al., 2000) and their chick-a-dee calls by species (conspecific and heterospecific: Carolina chickadee, *P. carolinensis*, Bloomfield et al., 2003). Evidence for category perception is also provided by field playback studies with chickadees (flock-mate and non flock-mate; Nowicki, 1983; species-typical and not species-typical, Charrier & Sturdy, 2005; Shackleton, Ratcliffe, & Weary, 1992; Weisman & Ratcliffe, 1989), and further suggests that chickadees derive some benefit from hierarchical category perception.

Understanding the mechanisms for perceiving stimuli as belonging to categories can provide an indication of the perceptual abilities in animals. However, stimuli can be very complex; therefore determining the mechanisms for discrimination can be a difficult expedition. Category membership likely depends on an object having a number of complex features in common, yet no one feature is either necessary or sufficient for category membership (i.e., are polymorphous, see Lea & Harrison, 1978). For example, although pigeons can discriminate the music of Bach from the music of Stravinsky (Porter & Neuringer, 1984), and the paintings of Monet from the paintings of Picasso (Watanabe, Sakamoto, & Wakita, 1995), the features that differ between each class of stimuli can be quite extensive and numerous. In order to determine the mechanisms for discriminating, replacing or modifying each feature, one at a time, would be necessary. Therefore, given the complexities of these stimuli (classical music and artwork), the methods for determining the mechanisms for discriminating can also be extensive and complex.

Alternatively, a polymorphic rule based on the presence or absence of particular stimulus features may not necessarily be the manner in which animals classify stimuli. Other theories of categorization include an exemplar theory and a prototype theory (see Pearce, 1994 for a review). The former suggests that animals base their decisions regarding category membership on their memory of previously encountered stimuli, whereas the latter suggests that animals create a representation of a 'typical' exemplar based on, perhaps, the mean or mode of previously encountered stimuli. Determining not only which theory explains categorization strategies in animals but also which features (present either in current exemplars, previous exemplars, or most commonly encountered exemplars) are used for discriminating can be a very daunting task considering the complexities inherent in natural stimuli. Thus, most studies of categorization employ simple or artificial stimuli to manipulate or reduce the number of possible features (see Sturdy, Bloomfield, Farrell, Avey, & Weisman, 2007 for a review). Identifying the theory to explain how birds classify conspecific and heterospecific calls is not the focus of the current research. Rather, as a first and necessary step, the current research seeks to determine (a) whether chickadees perceive their own and other chickadee species' complex chick-a-dee calls as belonging to separate, open-ended categories, (b) the possible mechanism(s) for category discrimination, and (c) the effect of experience on category perception.

Summary of Current Studies

Once a vocalization and all is constituent parts have been described and analyzed for variability (via bioacoustic techniques), experimentation (via field playback experiments and laboratory operant-discrimination techniques) can follow. Here I conduct an extensive bioacoustic analysis to describe and quantify the chick-a-dee call and call notes produced by mountain chickadees (Chapter 2). The results of this analysis provide the opportunity to directly compare the chick-a-dee calls of black-capped and mountain chickadees, and further provide putative explanations for the discrimination performances observed in birds in subsequent experiments.

Next, I investigate the perceptual abilities of black-capped and mountain chickadees by examining, via an operant conditioning task, whether birds use an open-ended categorization strategy when confronted with their own calls and the calls of another chickadee species (Chapter 3). Further, this experiment explores the role that experience with the other species' calls may play in a birds' ability to memorize and categorize chick-a-dee calls. This is achieved by including in the study black-capped chickadees from an area shared with mountain chickadees (sympatry) and from an area not shared with mountain chickadees (allopatry). Ultimately this will provide us with a better understanding of how chickadees classify conspecific and highly similar heterospecific chick-a-dee calls.

Subsequently, I examine the mechanism(s) for species' discriminations in black-capped (both sympatric and allopatric) and mountain chickadees (Chapter 4) using an operant conditioning task. By intermittently presenting test calls, including only the first of each species' chick-a-dee calls, only the second half of each species chick-a-dee calls, and hybrid combinations of both species' calls and comparing responses, a better understanding of the salient species-specific features of chick-a-dee calls can be realized.

This is followed by a field playback experiment examining the role of the first and second half of the chick-a-dee calls on behavioural responses of wild chickadees (Chapter 5). Thus, while the purpose of experimentation in Chapter 4 is to determine which portion of their chick-a-dee call birds *can* use to discriminate between the two calls, the purpose of experimentation in Chapter 5 is to determine which portion birds *do* use to discriminate between the two species' calls in their natural habitat.

Finally, I investigate the ability of black-capped chickadees, hand-reared in the presence of either adult black-capped chickadees or adult mountain chickadees, to categorize and memorize chick-a-dee calls (Chapter 6) in an operant discrimination task. Here I examine how nature and nurture interact and contribute to categorization and individual recognition tasks, and whether birds have evolved specialized abilities for the perception of conspecific vocalizations. Ultimately, the culmination of the current dissertation will contribute greatly to our understanding of the vocal discrimination, categorization, and memorization abilities in songbirds in general and chickadees in particular, and how the developmental experience of an individual can affect these higher cognitive abilities.

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Chapter 2: Note types and coding in Parid vocalizations. II: The chick-a-dee call of the mountain chickadee (*Poecile gambeli*)

A version of this chapter has been published. Bloomfield, L.L., Charrier, I., & Sturdy, C.B. (2004). *Canadian Journal of Zoology, 82,* 780-793.

Introduction

In a manner analogous to human vocal learning, songbirds (the oscines) learn the vocalizations essential for communication with conspecifics. For example, males learn to produce song to attract females and repel rivals, and females perceive male song to gauge fitness and ultimately select a mate. Songbirds also learn, produce and perceive species-specific calls, and use these calls in a number of specific, increasingly well-defined behavioural circumstances. As calls are generally defined as being less complex compared to songs, they are frequently overlooked in the study of songbird communication. However, to gain a comprehensive understanding of acoustic communication, analyses must not be limited to the study of learned song. Rather all modes of acoustic signaling, including the mechanisms and function of communication via learned calls, must be considered (see Hailman & Ficken 1996; Hughes, Nowicki, & Lohr, 1998; Vicario, Raksin, Naqvi, Thande, & Simpson, 2002 for others following this broadening of scope).

In their natural habitat, birds must be able to discriminate between conspecifics and heterospecifics based on acoustic signals. This perceptual ability is important because the caller and the listener are often out of view of one another due to naturally occurring obstructions such as trees and foliage. Thus, species-specific characteristics must be present and distinguishable in birds' acoustic signals. Such characteristics can be largely overt. For example, syllables (notes) are often not randomly assembled within songs and calls, but rather are emitted in highly predictable ways that may aid in species-recognition (e.g., white throated sparrows, *Zonotrichia albicollis*, Soha & Marler, 2001). In addition, field sparrow (*Spizella pusilla*) songs played back outside the species' frequency range are largely ignored (Nelson, 1989). The ability to recognize and discriminate conspecifics from heterospecifics is critical for songbirds of both sexes. Males must be selective when deciding against whom they should defend their territory, as agonistic encounters require energy expenditure and could potentially place the bird at risk of being harmed or predated. Females must be selective when choosing a mate, as it would not be prudent to waste valuable time choosing a heterospecific. Clearly, species-specific signals provide both males and females with cues critical to territory defense and mating decisions.

However, the ability to discriminate among vocalizations extends beyond species recognition. Once the caller has been identified as a conspecific, the listener is often required to perform further decisions regarding the source of the vocalizations. For example, recognizing individuals based on vocalizations is critical for many of the same reasons that species recognition is important. Identifying a caller as a neighbour (friend or known foe) and not a trespassing rival will reduce time and energy spent on territory defense (Falls & Brooks, 1975). Recognizing and identifying a caller as a male and not a female will reduce or eliminate the possibility of courting a bird of the wrong sex. Finally, identifying another conspecific as a flockmate member can have many advantages, such as co-operative foraging and prey detection (see Bertram, 1978 for a review of the benefits of group living). Thus, because birds spend a large majority of their lives defending territories, attracting mates, and foraging, they have evolved methods of recognizing species and individuals based on auditory signals. But what are the features present within the signals that enable birds to accomplish this feat? In the present study we seek to examine the acoustic features present in the call of the mountain chickadee (*Poecile gambeli*), the chick-a-dee call, and identify the features that may be used to serve these functions.

The North American chickadees (genus *Poecile*), of which there are six species, are an excellent group for comparative studies of songbird vocal learning, vocal production, and vocal perception. The vocal repertoire of the black-capped chickadee (*P. atricapilla*), including the fee bee song and the chick-a-dee call, has been described in great detail (e.g., Ficken, Ficken, & Witkin, 1978; Hailman, Ficken, & Ficken, 1985; Weisman, Ratcliffe, Johnsrude, & Hurley, 1990). However, chickadees are largely non-conformists when it comes to the central dogma surrounding oscine vocalizations; with songs considered to be more complex than calls. The song of the black-capped chickadee for instance, used primarily to attract mates and repel rivals (S.T. Smith, 1991), is exceedingly simple in comparison to other oscines in that it consists of only two whistled notes: fee and bee. While the absolute pitch at which the two notes are produced can vary within their species-specific range (Ratcliffe & Weisman, 1985), the relative change in pitch between the two notes remains constant across all individuals (Weisman et al., 1990). Black-capped chickadees learn to perceive these relative pitch changes early in life given the presence of a male tutor (Njegovan & Weisman, 1997), and females prefer male songs that include an accurate pitch ratio (Ratcliffe & Otter, 1996). Given these perceptual abilities, the relative pitch ratio may be useful for species recognition.

In stark contrast with the black-capped chickadee song, the chick-a-dee call, associated with mild alarm and flock communication and co-ordination (Ficken et al., 1978; S.T. Smith, 1991), is acoustically complex. In black-capped chickadees it consists of four note types; A, B, C, and D, and while maintaining a fixed syntactical ordering of the notes (A through D), any of the notes can be repeated or omitted to produce a seemingly infinite number of call types (Hailman et al., 1985). Black-capped chickadees perceive their chick-a-dee calls and their constituent note types as natural, open-ended categories (Bloomfield, Sturdy, Phillmore, & Weisman, 2003; Sturdy, Phillmore, & Weisman, 2000), providing evidence of a perceptual hierarchy of individual calls comprised of call notes. In addition to using features present in songs to discriminate among individual conspecifics (Phillmore, Sturdy, & Weisman, 2003), black-capped chickadees also perceive differences among calls to discriminate among flockmates (Mammen & Nowicki, 1981). Thus the black-capped chickadee song and chick-a-dee call both contain features which aid in individual recognition.

Most closely related to the black-capped chickadee is the mountain chickadee (Gill, Mostrom, & Mack, 1993). While the black-capped chickadee inhabits the northern United States and most of Canada, the mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (McCallum, Grundel, & Dahlsten, 1999; Smith, 1993). In some regions the two species live sympatrically and engage in interspecific activities such as foraging (pers. obs.) and interbreeding (Howe, 1985; Martin & Martin, 1996); however birds do not interbreed or exhibit interspecific competition in the regions associated with our study sample. In fact, both species responded weakly to playback of heterospecific song within their (sympatric) territory (Hill & Lein, 1989), indicating that the song of both black-capped and mountain chickadees contains information specific to each species. However, the species-specific and individual-specific features in the vocal repertoire of mountain chickadee, including its chick-a-dee call, are not known.

The mountain chickadee song repertoire consists of 4-7 song types comprised of 2-6 whistled notes, used to attract females and defend territories (Wiebe & Lein, 1999). In common with black-capped chickadee song, mountain chickadee song contains acoustic information used for species identification (Hill & Lein, 1989). Among the mountain chickadee call repertoire is the chick-a-dee call, acoustically similar to the black-capped chick-a-dee call (see Figure 2-1), used when mildly alarmed and in flock movement (Gaddis, 1985). Gaddis (1985) provides a cursory description of the call notes using some terminology similar to that used to describe the black-capped chickadee call, yet provides no indication of the variability of notes within and between individuals. In light of the fact that the mountain chickadee call has received little attention relative to the black-capped chickadee, the note types, syntax, and species- and individual-specific features are largely unknown (but see McCallum et al., 1999 for adaptations of note type descriptions by Gaddis, 1985).

Accurate descriptions and analyses of calls and call notes are essential to understanding not only the behavioural contexts in which they are used and the messages they may potentially convey, but also to recognize the features in the calls and call notes that provide birds with information as to the identity of the caller; conspecific or heterospecific, male or female, neighbour or stranger. If such hierarchical classification can be done quickly and easily by birds, energy will not be wasted by mistakenly defending a territory or mate against a heterospecific (species-level classification), courting a male (sex-based classification), or attacking a friend (individual recognition and classification).

The purpose of the present study is to gain a broader understanding of the mountain chickadee chick-a-dee call and its constituent notes. In Study 1 we describe and classify the notes into types based on their physical appearance in sound spectrograms; in Study 2 we conduct frequency and temporal measurements on various features of the notes. These descriptive data are then used to compare variation within and among the population, attempting to identify cues present in the calls and call notes that may be useful to mountain chickadees in identifying species, sex, and individuals.

General Methods

Animals

Twenty adult (>1 year of age) male (n =11) and female (n =9) mountain chickadees were captured between January 2002 and March 2003 at the Barrier Lake Field Research Station in Kananaskis Valley, Alberta, Canada (51° 02'N, 115° 03'W). Sex identification was conducted either by visually inspecting their gonads via laparotomy or by DNA analysis (Griffiths, 2000). Birds were housed at the University of Alberta (Edmonton, Alberta) in individual Jupiter Parakeet cages (0.3m wide x 0.4m high x 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada) which allowed visual and auditory communication but not physical contact between birds. Birds had free access to food (composed of a 1:1 mixture of ground, hulled sunflower seeds and Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), water, and grit mixture (Rolf C. Hagen Inc., Montreal QC Canada). Liquid vitamin (Hagen Vitamin Supplement Conditioner for Birds; Rolf C. Hagen Inc., Quebec, Canada) was added to the water 3 times per week. Hard boiled egg and greens were provided once per week and 1 mealworm was provided 3 times per week. The birds were maintained on a light-dark cycle typical for the season in Edmonton, Alberta. The temperature was maintained at about 20° C.

Call Recording

Mountain chickadees were recorded individually from June 2002 to July 2003 between 0900 – 1700h, by placing their home cage in a large (1.83m x 1.83m x 1.83m) sound attenuating chamber (Industrial Acoustics Corporation, Bronx, NY). On occasion, a mirror was attached to the inside of the bird's cage to induce vocalizations. Birds were recorded using a C 1000 S condenser microphone (frequency response: 50-20,000 kHz; AKG Acoustics, Vienna, Austria), an ART Original microphone preamplifier (frequency response: 10-20,000 Hz; Applied Research and Technology, Rochester, NY), and a Sony SME Modified TCM-5000EV cassette recorder (frequency response: 90Hz – 12,000 Hz; Sony, Tokyo, Japan).

Recordings were digitized at 44,100 Hz 16-bit samples per second using DartDisk Direct-to-disk Recorder (Engineering Design, Belmont, MA). All analyses were conducted using Signal 4.0 sound analysis software (Engineering Design, Belmont, MA).

Study 1 - Note Classification

We conducted an extensive visual analysis of sound spectrograms to identify and classify the notes into categories of similar visual appearance. The goal was to provide careful and accurate descriptions and spectrographic examples of note types found in the call. Following the classification, call composition and call syntax (the ordering of notes) was examined.

Methods

Sound Spectrograms and Note Classification

Ten calls from each of 20 birds were randomly chosen for inclusion in both Study 1 and 2 (see below), resulting in a total of 878 individual call notes sampled from 200 calls. In an effort to standardize all analyses, each individual call note was saved as a separate file with a duration of 300 ms (non D-type notes) or 500 ms (D-type notes), by adding leading and trailing silence of equal duration to each individual note file. The sound spectrogram for each note (cut-off amplitude of -35dB relative to peak amplitude, window size: 512 pts) was printed on glossy, high quality photo paper to create a "deck" of mountain chick-a-dee call-note cards, each measuring about 5 cm^2. Each card was labeled with a four-digit code, randomly assigned to individual notes, which allowed us to identify the notes as to singer and position in the call after blind sorting by the observers.

In a preliminary analysis, the first author sorted note cards by visual similarity into an unlimited number of categories. In this process, 6 call-note types were identified (see Figure 2-2). Following this, 2 notes of each type were randomly chosen from the sample and printed in the same manner as were the sorting notes. These 12 call-note cards were labeled with a randomly chosen number from 1-6 and served as examples for sorting by experienced bioacousticians. These examples, along with a written description of each note type (see Note Descriptions below) were provided to the second and third authors for sorting. Percent agreement among sorters was examined to determine the note types present within mountain chickadee chick-a-dee calls.

Results

Call-Note Classification

Six note types (see Figure 2-2) emerged from the classification of the 878 notes.

The percentage of agreement (reliability) of the classification of notes into types was high (> 90% across note types). In 77 instances (8.8% of the 878 notes), the observers disagreed on the classification of notes into types (see Table 1).

To resolve the ambiguity of the 77 multi-classified notes, the observers re-examined the note cards as a group to determine their classification. Following this procedure, observers reached 100% agreement on the classification of the previously disagreed upon notes and sorted them into one of the 6 categories.

Note Descriptions

Descriptions for each of the 6 note types, outlined below, were made available to sorters during their classification sessions. Sorters were also instructed to attend to the main (loudest) frequency band of the note when sorting notes, as some note types contained frequency bands above and/or below the main band. Nomenclature was based upon that for labeling black-capped chickadee chick-a-dee call notes (see Hailman et al., 1985) when appropriate (i.e., when the note types resembled those of the black-capped chickadee chick-a-dee call). Following call-note sorting, note types were separated into two main types based on physical appearance: non D-type notes and D-type notes.

Non D-type Notes

A notes are similar to the A notes seen in the black-capped chick-a-dee call. A notes have a short ascending arm, a peak, and a long descending arm (see Figure 2-2A). The peak of the note remains stable for a small amount of time before descending. In other words, the note appears relatively flat at its highest frequency. Often the notes do not have an ascending arm, but begin at one frequency and maintain this frequency until descending. A notes are longer in duration than the other non D-type notes. Occasionally one or more faint harmonic-like structures appear above (and below) the main frequency band.

A/B notes have the qualities of both mountain chickadee A and B notes (see below), and appear to be an A note in transition to becoming a B note, thus forming a continuum of A→B notes (see Figure 2-2B). These notes appear similar in duration to A notes (between 50-100 msec), but have equal, or near equal length arms, similar to B notes. These notes have an inverted "U" shape, with a very rounded peak between the end of the ascending arm and the beginning of the descending arm (i.e., at the peak of the note). Occasionally one or more faint harmonic-like structures appear above (and below) the main frequency band.

B notes are also similar to the B notes seen in the black-capped chick-a-dee call, and have qualities similar to the A/B note seen in the mountain chick-a-dee call. B notes can have equal ascending and descending arms (see Figure 2-2C), but most often the ascending arm is longer than the descending arm (i.e., opposite to A notes). The peak of the note is very pointed (i.e., an inverted "V" shape) due to the rapid rise (attack) and fall (decay) in frequency. In other words, the peak frequency is maintained for a very brief period of time; this note is short in duration (<50msec). Occasionally one or more faint harmonic-like structures appear above (and below) the main frequency band.

C notes appear similar to C notes seen in the black-capped chick-a-dee call (see Figure 2-2D). C notes have an ascending arm that begins at a low frequency and remains flat for a brief duration (approximately half the total note duration) before ascending and rapidly descending in frequency. The end frequency of the note terminates at a frequency higher than that of the start frequency. Harmonic-like structures are present both above the constant frequency portion of the ascending slope and above the peak frequency and descending slope of the note.

D-type Notes

D notes appear similar to D notes seen in the black-capped chick-a-dee call. They have a harmonic-like structure (consisting of multiple frequency bands) with little frequency modulation (see Figure 2-2E). Occasionally noise flanks both the start and end of the note, leaving only the frequency bands in the middle portion of the note visible. These frequency bands have little to no frequency modulation; they maintain a constant frequency throughout the duration of the note. D notes are often longer in duration and lower in frequency than the other note types.

D_{hybrid} notes (henceforth denoted as D_h) are similar to mountain chick-a-dee D notes however they have 2 distinctly different parts (see Figure 2-2F). The first part of the note is frequency modulated (more tonal in nature); the note begins at a low frequency, quickly ascends, peaks, and descends (similar to an A, A/B, or B note). Once the frequency of the descending arm reaches its minimum frequency, this frequency is maintained across the remaining duration of the note, forming the lowest band of the second part of the note (which appears similar to a harmonic-like D note). Occasionally the lowest band is not visible and therefore it is not obvious that the tonal note is contiguous to the D-portion. Beginning concurrently with the descending portion of the tonal note is the second band (harmonic) of the second portion of the note. It begins at a frequency equal to or higher than the peak of the tonal note, descends to a frequency approximately that of the middle of the tonal note, and then maintains this frequency across time, ending concurrently with the first (lowest frequency) band. This band is generally the loudest band in the note. One or more bands may be seen above the main band, or noise may appear both above and below the main band in the second portion of the note, obscuring the identification of any other bands. Infrequently, an additional tonal note may occur within the second portion of the note (see Figure 2-2F). That is, the second portion of the note does not always maintain a constant frequency across time

Call Composition and Syntax

Once the notes were identified by type, the frequency of note occurrence within calls and the syntax (ordering of the note types) was identified and summarized. We also tallied statistics for the number of birds that sang each note type and how often birds used each note type in their calls.

Mountain chickadee chick-a-dee call durations ranged from 290 ms to 2,091 ms (*M* = 846 ms, *SD* = 379 ms). The number of notes in each call ranged from 2 to 10 (*M* = 4.4, *SD* = 1.4, see Table 2-1), with calls of 3-6 notes constituting 86% of the sample. While D notes were most common in our sample (24% of all notes), D_h notes occurred in more of the sampled calls (93% compared to 69% for D notes). Each of the 200 calls contained at least one D_h note or one D note at the end of the call. A, A/B, and B notes were almost equally as common in our sample of notes (~17%, ~20% and ~11% respectively), within calls (~60%, ~60% and ~45% respectively), and among birds (18, 20, and 18 birds respectively). C notes were the least common, occurring in 7% of our note sample and in 6% of calls by 9 birds. However, when a call contained C notes, these notes occurred at a higher average number per call compared to all other note types. In other words, C notes were either completely omitted from calls or when present, C notes were repeated more frequently than other note types in other calls.

In examining our sample of 200 calls, 32% of calls were composed of a combination of A, D_h, and D note types (e.g., A,D_h,D,D,D, or A,A,A,D_h,D,D, see Table 2-2). As can be observed in Table 2-2, A, A/B, and B notes do not follow a stringent syntax within calls. Twenty-five calls (12.5% of our call sample) produced by 10 birds consisted of one or more A/B notes occurring before B notes within a call (e.g., A,A/B,B,D_h,D,D), while 15 calls (7.5% of our call sample) produced by 8 birds consisted of B notes occurring before A/B notes (e.g., A,B,A/B,D_h,D,D). In addition, 29 calls (14.5% of our sample) produced by 9 birds contained A/B or B notes in more than one location (e.g., A,B,A/B,B,D_h,D or A/B,B,A/B,D_h,D). Among a majority of these mixed syntactical calls, pitch contour (decreasing frequencies across note types within calls) did not hold. In other words, when A/B notes occurred before B notes a descending pitch contour across note types was evident. However, when B notes occurred before A/B notes, the B notes were higher in frequency than the subsequent A/B notes.

Study 2 – Note-Type Analysis

In Study 2 we conducted a comprehensive bioacoustic analysis of mountain chickadee chick-a-dee call-note categories, measuring several frequency and temporal parameters for each note type. Further, we examined the relative variability of these bioacoustic parameters within and among note types and within and among individual birds, in an effort to estimate the potential for note-type coding (PNTC) and potential for individual coding (PIC) in the call notes from our sample (see Statistical Analyses for details on PNTC and PIC rationale and calculations). These analyses were conducted to provide a sound, *a priori*, bioacoustic basis for future operant conditioning and field playback experiments aimed at uncovering the acoustic features used in note-type and individual recognition.

Methods

The same 200 calls used in Study 1 were used for analysis in Study 2. Multiple frequency and temporal measures were obtained for all notes using sound spectrograms (cut-off amplitude = -35 dB) and fast-Fourier Transforms (FFT settings for frequency measures: Hanning window = 1,024 points, precision = 43 Hz; FFT settings for temporal measures: Hanning window = 256 points, precision = 5.8 ms). Given the distinct differences in frequency and temporal parameters between non D-type notes and D-type notes, measurements conducted on the two categories differed slightly (see Figure 2-2).

Non D-type Notes: Each non D-type note (i.e., A, A/B, B, and C) was analyzed in a digital spectrogram for three different frequency measures (start frequency (SF), peak frequency (PF), and end frequency (EF)) and three different temporal measures (ascending duration (AD), descending duration (DD) and total note duration (TD)). Additionally, we measured the note peak frequency (NPF; the loudest frequency in the highest harmonic when additional harmonics occur) as well as the slopes of the ascending (FMasc) and descending (FMdesc) frequency modulations that were calculated using the formulas (PF-SF)/AD and (EF-PF)/DD, respectively. Loudest frequency (Fmax) was measured in a spectrum window (mean window size: A notes = 8,192 pts, A/B, B, C notes = 4,096 pts). Although considered a 'D-type note', each D_h note was also examined in a digital spectrogram for SF, PF, NPF, AD, and FMasc in the tonal portion of the note (see Note Descriptions above). This was done to determine which, if any, of the non D-type notes (A, A/B, and B) the D_h tonal portion most resembled. (DD and FMdesc could not be examined because it was not possible to accurately determine where the tonal portion of the note ended and the harmonic portion of the note began.)

D-type Notes: Each D-type note (i.e., D and D_h) was analyzed in a spectrum window (mean window size: D notes = 16,384 pts, D_h notes = 8,192 pts) for frequency (kHz) of the first visible harmonic (f_0), note peak frequency (NPF), and loudest frequency (Fmax). Total duration (ms, TD) of each note was measured in a digital spectrogram. In D_h type notes, the harmonic portion was analyzed separately from the tonal portion to obtain accurate measurements for f_0, NPF and Fmax.

Statistical Analyses

On the basis that A, A/B, and B notes were misclassified most often in Study 1 (see Table 2-1), we performed univariate analyses of variance (ANOVAs) using SPSS v11.5 (SPSS Inc., 2002) to statistically assess the differences between all non D-type notes. In all instances we used Welch's correction (Welch, 1938) for unequal variances and Games-Howell for unequal sample sizes and unequal variances in the post-hoc analyses. In addition, we reduced the probability of Type I errors by employing a Bonferroni correction (i.e., standard α value divided by the number of planned comparisons/analyses; Keppel, 1991) which results in a more conservative α level.

For the analysis of note-specific acoustic features in the highly similar non D-type notes (i.e., A, A/B, B, C) we examined the potential for note-type coding (PNTC), which may provide an indication of whether one or more features are less variable within note types and can therefore potentially be used for discriminating between note types. The PNTC is the ratio of the coefficient of variation between notes (CV_b) and the mean of the coefficients of variation within notes (mean CV_w). A high PNTC value for a given acoustic feature suggests that the feature is specific to that note type, and therefore, may provide birds with a cue to discriminate between the note types.

For birds to be able to discriminate between individual birds, calls must contain information specific to each individual. Thus one or more acoustic parameters must show high individual stereotypy. In other words, the variation across individuals must be greater than the variation within an individual for any given parameter for it to be a reliable signal. To identify the acoustic parameters that may encode individual identity, we examined the potential for individual coding (PIC) in small samples using the ratio of the coefficient of variation between individuals, $CV_b = (SD/X_{mean}) \times 100$, where X_{mean} and SD is the overall mean and standard deviation for each note type, and the coefficient of variation within individuals, $CV_w = (SD/X_{mean})*(1+1/4n) \times 100$ where X_{mean} is the mean, SD is the standard deviation of the individual means, and n is the number of exemplars/individual (Sokal & Rohlf, 1995). Acoustic features showing PIC > 1 were regarded as parameters that may be useful for individual recognition, since their intra-individual variability is less than their inter-individual variability.

Results

The same 878 notes classified into types in Study 1 were analyzed in Study 2. However, in some instances faint recordings resulted in the inability to obtain some measurements. We measured 143 A notes, 177 A/B notes, 93 B notes, 56 C notes, 181 D_h notes, and 212 D notes. Four D_h notes (2% of all D_h notes in our sample) were excluded immediately from all analyses as a result of a second frequency-modulated portion within the harmonic portion of the notes (see Figure 2-2F for a representative example).

Note-Type Acoustic Features

Independent Welch's t-tests were first conducted on all measurements to determine if differences exist among the chick-a-dee call notes of male and female mountain chickadees. Across all note types there were neither significant temporal nor frequency differences (all p's ≥ 0.044; adjusted $p = 0.005$ for A, A/B, B, C, and D_h notes, and $p = 0.013$ for D notes). Thus, there appear to be no sex differences among chick-a-dee call notes of mountain chickadees in our sample; therefore, sex is pooled across the remaining statistical analyses.

In an attempt to uncover the basis for the misclassifications of A, A/B and B notes in Study 1, we conducted a univariate ANOVA to compare all non D-type notes on all acoustic features (adjusted $p = 0.005$). There were significant differences (all F's ≥ 83.11, all p's ≤ 0.001) between all note types on all acoustic features. Post hoc analyses revealed a greater number of significant differences between A and B notes compared to between A and A/B notes and between A/B and B notes (adjusted $p = 0.008$). In particular, although each of these note types had similar frequency measures among the highest frequency bands (NPF, all p's ≥ 0.02), A and A/B notes shared similar peak frequencies among the main frequency bands (PF; $p = 0.074$), ascending durations (AD; $p = 0.865$), and descending durations (DD; $p = 0.235$), whereas A/B and B notes shared similar end frequencies (EF; $p = 0.982$, see Table 2-3 for descriptive statistics). The PNTC analysis indicated that features TD, PF, and SF were more likely to provide non-D-type note identifying cues.

On the basis that D notes and the harmonic portion of D_h notes appear quite similar to each other (see Figures 2-2E and 2-2F), independent Welch's t-tests were conducted to determine whether any statistically significant differences exist (adjusted p

= 0.016). These note types were found to be significantly different on all measured parameters (see Table 2-4), including Fmax ($t_{361.90} = -3.09, p = 0.002$), NPF ($t_{346.32} = 4.24, p < 0.001$), and f_0 ($t_{305.28} = -4.50, p < 0.001$), indicating that D and D_h note types differ along more features than just the presence of the tonal portion of D_h notes. Similarly, because the tonal portion of D_h notes appeared similar to A, A/B, and B notes, we collected measurements on just the tonal portion of the D_h note and conducted a univariate ANOVA on the measures SF, PF, AD, FMasc, Fmax, and NPF (adjusted p = 0.008). Significant differences were revealed among all note types (A, A/B, B, and D_h tonal) on all measures (all F's $\geq$ 31.512, all p's $\leq$ 0.000). Post-hoc analyses (adjusted p = 0.008) indicated that the tonal D_h note did not differ from B notes in SF (p = 0.639) and AD (p = 0.033), and did not differ from A/B notes in FMasc (p = 0.685).

Individual Coding in Note Types

Univariate ANOVAs (adjusted p = 0.005 for A, A/B, B, C, and D_h notes and p = 0.013 for D notes) conducted on each note type revealed significant differences between individuals on several of the acoustic features (Tables 2-4 and 2-5). Additionally, the coefficients of variation between individual birds (CV_b) were larger than the coefficients of variation within individuals (mean CV_w), resulting in PIC > 1 (Tables 2-4 and 2-5). Among all note types, only A/B and D notes revealed significant differences between individuals on all acoustic features. For each of the remaining note types, approximately half of the acoustic features measured showed significant differences between individuals. The acoustic features potentially containing individualized information in A, A/B, and B notes were SF, PF and DD ($p \leq 0.001$ in all instances). Note peak frequency (NPF) also appeared to be highly individualized in all note types including D notes and both the tonal portion and the harmonic portion of D_h notes ($p \leq 0.001$). Thus, several features within each note type appear to be highly individual-specific and may aid in the individual recognition process. The highest PIC values (≥ 1.5) were those associated with EF (A notes), AD (A/B notes), PF (A/B and B notes), Fmax (B notes), TD (D_h), and f_0 (D notes, see Tables 2-4 and 2-5).

Discussion

In Study 1 of the present work, we classified the various notes in the chick-a-dee call of the mountain chickadee into types and provided an accurate description of each note type. Although a classification had previously been conducted (Gaddis, 1985), the methods used here (several human sorters) provided a more reliable categorization of the multiple variations of note types. Nowicki and Nelson (1990) compared three methods for classifying the chick-a-dee call notes of the black-capped chickadee (human sorting, multi-dimensional scaling, and cluster analyses) and concluded that each method produces similar and accurate results. Finally, this classification provides information necessary for conducting future research with chick-a-dee calls of mountain chickadees, such as the extensive call and call-note analyses conducted in Studies 1 and 2 of the present work.

In Study 2 we conducted detailed bioacoustic analyses of the chick-a-dee call notes of the mountain chickadee, which provide information that has no comparison in the literature. Analyses conducted on the chick-a-dee call of black-capped and Carolina chickadees have concluded that features present within the calls (e.g., occurrence and combinations of note types) and call notes allow birds to convey contextual information (Freeberg & Lucas, 2002) as well as identify flock membership (e.g., Mammen &

Nowicki, 1981) and microgeographic indicators (Freeberg, Lucas, & Clucas, 2003) in conspecifics. However, without the prior availability of a detailed bioacoustic analysis, such evidence in mountain chickadee calls and call notes have yet to be discovered. The current study focuses on the note-type acoustic features, which allowed us to make predictions concerning the parameters that putatively control call and call-note perception in mountain chickadees.

In addition, we examine the potential for note-type coding (PNTC) and the potential for individual coding (PIC), which allowed us to assess the features that are likely to be used by the birds to discriminate between the various note types and between individual conspecifics. By conducting the PNTC, we were better able to explain the difficulties (disagreements) observed among note sorters (Study 1), and therefore, were better able to gain an understanding of the mechanisms used by birds to discriminate among the note types. By conducting the PIC, we were able to suggest which note-type parameters were specific to individuals, and thus, may be used for recognition and identification of particular conspecifics. Such an analysis has never been conducted with the call notes of the chick-a-dee call of the mountain chickadee but has been used successfully in analyzing the variation among the individual vocalizations of Spheniscidae (i.e., penguins; Robisson, Aubin, & Bremond, 1993; Lengagne, Lauga, & Jouventin, 1998), Stercorariidae (i.e., skuas; Charrier, Jouventin, Mathevon, & Aubin, 2001; Mathevon, Charrier, & Jouventin, 2003), and Otariidae (i.e., fur seals; Charrier, Mathevon, & Jouventin, 2002; 2003).

Study 1-Descriptive Analyses of Calls and Call Notes

Using spectrographic exemplars and written descriptions, we developed a classification scheme to sort the 878 sampled notes into one of six note-type categories (A, A/B, B, C, D_h, D). Most calls consisted of 4 notes, which differs from black-capped chick-a-dee calls with an average of 6 notes/call (Hailman et al., 1985) and from Carolina chick-a-dee calls (*Poecile carolinensis*) with an average of 8 notes/call (Bloomfield, Phillmore, Weisman, & Sturdy, 2005). The most commonly occurring call type in chick-a-dee calls of mountain chickadees consisted of note types A, D_h, D. Although D notes are most numerous in our sample, the D_h note appeared once in nearly every call sampled. Although there is evidence to suggest that a hybrid D note occurs in the chick-a-dee calls of the black-capped chickadee (Hailman et al., 1985) and the Carolina chickadee (Bloomfield et al., 2005), the frequency of occurrence in chick-a-dee calls of mountain chickadees is considerably greater and more similar to the occurrence of the hybrid note seen in the chick-a-dee call of the Mexican chickadee (*P. sclateri*, Ficken, Hailman, & Hailman, 1994). The C note was most often repeated in the chick-a-dee calls of mountain chickadees (mean = 4 C notes/call) yet was less common than the remaining note types (i.e., most often omitted from calls). That the C note was the least commonly occurring note type among chick-a-dee call notes of mountain chickadees paralleled the evidence that the C notes were among the least common in the chick-a-dee calls of the black-capped chickadee (Charrier, Bloomfield, & Sturdy, 2004; Nowicki & Nelson, 1990) and of the Carolina chickadee (Bloomfield et al., 2005). Recently, Freeberg and Lucas (2002) suggested that the chick-a-dee calls of the Carolina chickadee, which contain more C notes (i.e., C-rich calls) compared to D notes, may convey information regarding food availability. The fact that the birds recorded in our sample did not produce many C notes may be due to the context of their recording environment. However, there is to date no evidence to suggest that the same or similar information is being conveyed in the chick-a-dee calls of the mountain chickadee with C notes, although this could be tested experimentally.

In contrast to chick-a-dee calls of the black-capped and Carolina chickadees, the syntactical organization of call notes within mountain chick-a-dee calls appeared to be more flexible. While evidence indicated that note types occur in the order of $A \rightarrow B \rightarrow C \rightarrow D$ (black-capped chickadees; Hailman et al., 1985) and $A \rightarrow B_{(1 \rightarrow 2 \rightarrow 3)} \rightarrow C \rightarrow D$ (Carolina chickadees; Bloomfield et al., 2005), the order of mountain chick-a-dee call-note types can be best described as $A \rightarrow (A/B \leftrightarrow B) \rightarrow C \rightarrow D_h \rightarrow D$. In other words, note types A/B and B were often interchangeable within calls. However, it is also important to point out that a D_h note never occurred (in our sample) after a C note. Therefore, if note-type combinations or repetitions vary with the messages being conveyed, as suggested for the chick-a-dee calls of black-capped chickadees (Hailman et al., 1985) and Carolina chickadees (Freeberg & Lucas, 2002), then the amount of information that can potentially be conveyed among mountain chickadees would be greater, given the greater number of note-type permutations possible. However, there is to date no behavioural evidence to suggest this fact and awaits a full Markov chain analysis or similar, as conducted by Hailman et al. (1985) on the chick-a-dee calls of the black-capped chickadee.

Syntax, among other features, may provide birds with species-identifying cues (see Becker, 1982 for a review). Given the differences in note-types and syntax among the black-capped, Carolina, and mountain chickadees discussed herein, it is possible that these differences provide all chickadees with overt cues for species-identification among all chickadee species. Bloomfield et al. (2003) showed that black-capped chickadees perceived conspecific and heterospecific (Carolina) chick-a-dee calls as two distinct categories, and given novel chick-a-dee calls, accurately classified them. Although there is no evidence to date, it is possible that the varying note types and syntax between chickadee species offer sufficient differences for birds to make higher-order (species-level) perceptual discriminations. In the white-crowned sparrow (*Zonotrichia leucophrys*), hand-reared birds presented with individual, species-specific song elements learned and assembled these elements into songs of species-typical sequence (Soha & Marler, 2001). In European tits (relatives of North American chickadees), the presence or absence of a trilled note within the calls altered responses by conspecifics and heterospecifics (Doutrelant, Leitao, Otter, & Lambrechts, 2000). Thus, syntax does appear to be useful for species identification in oscines, and the mountain chickadee is no exception.

Study 2-Bioacoustic Analyses of Note-Specific and Individual-Specific Features

The classification and descriptions provided in Study 1 allowed us to continue our descriptive analysis in Study 2. Without such descriptions, bioacoustic analyses and comparisons across chickadee species would be impossible. Importantly, conducting bioacoustic analyses on these vocalizations can help determine which features most likely control the mechanisms underlying the perceptual differences among note types and among individuals. The present work is the first to report spectral and temporal estimates of variation within and between the six note types and to identify features that differ between individuals.

Among all chick-a-dee call notes of the mountain chickadee, types A, A/B, and B were misclassified most often by sorters. Acoustic analyses indicated that A and A/B notes shared similar peak frequencies (in both the main frequency band, PF, and when present, in the highest frequency band in the note, NPF) and ascending and descending durations (AD and DD), while A/B and B notes shared a similar end frequency (EF). In parallel with Study 1, these results indicated that as the number of similarities between note types increased, the more difficult it became for human sorters, and possibly for conspecific listeners, to distinguish among them. If birds have similar difficulty in identifying these note types, important cues contained within these notes could be missed or confused. Sturdy et al. (2000) revealed that black-capped chickadees can discriminate between the various black-capped chick-a-dee call-note types, and can accurately classify novel exemplars into open-ended categories. Using similar techniques, the ability of mountain chickadees to classify these note types could be understood. Furthermore, identification of the note-specific and individual-specific frequency and temporal ranges provided here is currently being employed in our laboratory to uncover which features contribute the most to the overall perception of note types and the recognition of individuals by mountain chickadees.

Overall there were more differences than similarities across note types, allowing for several, possibly redundant cues to aid birds in their note perception and discrimination. Repetitive or redundant cues within calls may ensure that the listener receives the important information that could otherwise be lost in a noisy environment. However, it is unlikely that these cues are all simultaneously used by birds in the discrimination process. A PNTC analysis was conducted to examine the possibility that a particular feature may be most useful for discriminating among note types. Among the A, A/B, and B note types, most temporal and frequency measures have PNTC values greater than 1. However, AD, EF, FMasc and FMdesc have the lowest values, suggesting that these parameters, although they cannot be completely ruled out, are unlikely candidates for providing note-specific information. Alternatively, TD, PF, and SF (and to a lesser extent, DD and Fmax), are more likely to provide birds with cues for discriminating among the highly similar A-, A/B-, and B-note types.

Among the note-type specific features described above, the descending duration (DD) is similar between A and A/B notes. Therefore, the high PNTC value for DD may indicate that birds could use this parameter to discriminate among A/B and B notes, but not among A and A/B notes. But how reliable are temporal differences, and how capable are birds of using such information? That some A notes are as short as A/B notes, or that A/B notes can be as long as A notes or as short as B notes suggests that this measure is not very reliable. Given these overlaps, and the temporal resolution in birds (10-20% changes, Dooling, 1982), although better than humans (Dooling, Leek, Gleich, & Dent, 2002), it is unlikely that temporal differences alone are sufficient for birds to perceive note-type differences. However, other studies (e.g., Weary, 1991) suggest that temporal features are useful for note and song discriminations. Indeed, verification of the various note-type categories by mountain chickadees is necessary prior to further experimentation seeking to determine which features contribute to their discrimination of these categories.

Frequency measures offer greater promise for note-type discriminations, as birds are 10 times more sensitive to changes in frequency than to changes in duration (Dooling, 1982). Among our sample, SF of non D-note types differed significantly and returned a higher than average PNTC value. This in combination with evidence suggesting that chickadees use pitch cues in other types of discriminations (Lohr, Weisman, & Nowicki, 1994; Otter, Ratcliffe, Njegovan, & Fotheringham, 2002; Ratcliffe & Weisman, 1985; Weisman et al., 1990) gives rise to the possibility that pitch differences may also be important for chick-a-dee call-note discriminations. However, degradation of signals could pose a problem for birds relying on high-pitched acoustic signals and the cues contained within these signals. Recently (Phillmore et al., 2003; Phillmore, Sturdy, Turyk, & Weisman, 2002), it has been shown that despite degradations imposed on conspecific songs, black-capped chickadees were still capable of performing discrimination tasks. In addition, behavioural evidence in black-capped and Carolina chickadees (S.M. Smith, 1991; S.T. Smith, 1972) suggests that the chick-a-dee call is used in close-contact encounters, and thus pitch cues could still be available to birds. Therefore, the possibility remains that differences in frequencies between the mountain chickadee call-notes may in fact largely be responsible for perceptual discriminations.

Acoustic Features for Individual Identification

In the present study, we conducted analyses to compare the mean values for each parameter among each of the 20 birds recorded. In addition, we conducted a PIC analysis to compare the variability of acoustic parameters within birds to that between birds. Thus, the PIC analysis provides us not only with a greater understanding of which cues are most likely used for recognizing individual birds in their natural habitat but also provides us with a narrower range of parameters with which to use in future laboratory and field discrimination tasks.

The PIC analysis returned results similar to the PNTC analysis; all note-type parameters have PIC > 1, with only one exception (SF in A notes). However, some measures are more prominent than others, suggesting that not all parameters are used equally for individual recognition, but perhaps provide redundant cues to ensure their accurate perception. Indeed, among all note types (except D_h), the greater PIC values among frequency parameters suggest that these features are more likely to contain individualized signatures. In fact, PF and Fmax stand out as measures of importance for individual recognition (with values equal to 1.5). Frequency parameters have also been implicated as a fundamental source for individual signatures among several bird species (e.g., *Pygoscelis adeliae* and *P. papua*; Jouventin & Aubin, 2002; *Tachycineta bicolor*; *Zonotrichia querula*; Shackleton, Ratcliffe, Horn, Naugler, 1991; Sharman, Robertson, & Ratcliffe, 1994; *Parus major*; Weary, 1991), as well as mammalian species (e.g., *Arctocephalus tropicalis*; Charrier et al., 2002; *Trichechus inunguis*; Sousa-Lima, Paglia, & da-Fonseca, 2002). Among black-capped chickadees, the D note contains frequency information specific to flock membership (Mammen & Nowicki, 1981) and birds respond differently depending on the presence or absence of this signature (Nowicki, 1983). In mountain chickadee D and D_h note types the largest PIC values were observed (f_0 and TD) compared to all note types. In light of the fact that every call sampled contained at least one D_h or one D note, it is possible that these cues are reliable for identifying the signaler. In summary, given the numerous differences in both frequency and temporal features among the call notes of individual mountain chick-a-dee calls, it is likely that a combination of cues, rather than any one cue alone, lend to individual recognition, thereby decreasing the possibility of missing individual information due to environmental effects.

By providing bioacoustic information for mountain chickadees, further independent analyses on their vocalizations can be conducted. While it is true that this classification scheme is reliable and repeatable with human sorters, it still requires species-specific verification by mountain chickadees themselves, perhaps via operant conditioning as has been used in the past with black-capped chickadees (Sturdy et al., 2000). In addition, knowledge of the various parameter ranges will allow future studies such as manipulating the values of features in an effort to elucidate the feature(s) used by mountain chickadees for note-type, sex, and individual recognition. Finally, by comparing the chick-a-dee calls across various sympatric chickadee species we are able to understand the possible features used for species recognition. Given the similarities between chick-a-dee calls of black-capped and mountain chickadees understanding the ability of these two sympatric species to discriminate between the species' calls, both in the field and in the laboratory will be crucial and the subject of future experimentation. Taken together, these descriptive and bioacoustic data provide (1) an unprecedented understanding of the mountain chick-a-dee call and its constituent call-notes, (2) an indication of the features most salient for the perception of individual call notes and the identity of the caller, and (3) bioacoustic data necessary for continuing research into the mechanisms underlying the perception of chick-a-dee calls by mountain chickadees and other chickadee species. Thus, these results bring us one step closer to understanding the perceptual abilities of mountain chickadees and to conducting comparative studies to increase our understanding of vocal communication among the genus *Poecile* on a whole.

Table 2-1. Percent agreement and occurrence statistics for each note type (*M*=mean).

Note Type	Percent Agreement	Number of Birds	Number Of Calls	Total Notes	Average Note-type Occurrence Per Call
A	75	18	119	150	1.3 ± 0.7
A/B	88	20	120	178	1.5 ± 0.6
B	80	18	90	93	1.0 ± 0.1
C	100	9	12	58	4.8 ± 1.5
D_h	100	20	186	186	1.0 ± 0.0
D	100	19	137	213	1.6 ± 0.7
Total	*M* = 91	20	200	878	4.4 ± 1.4

Table 2-2. Number of calls of each call type (N=24) based on syntax.

Syntax	Number of Calls	Number of Birds
A, A/B, A, D_h	1	1
A, A/B, B, D_h	1	1
A, A/B, D_h	12	5
A, A/B, D_h, D	25	10
A, B, A/B, D_h	6	4
A, B, A/B, D_h, D	9	4
A, B, C, D	1	1
A, B, D_h	7	4
A, B, D_h, D	12	6
A, C, D	2	1
A, D	1	1
A, D_h	10	4
A, D_h, D	32	14
A/B, B, A/B, B, A/B, D_h, D	1	1
A/B, B, A/B, D_h	16	6
A/B, B, A/B, D_h, D	12	6
A/B, B, C, D	1	1
A/B, B, D_h	6	6
A/B, B, D_h, D	17	7
A/B, D_h	4	3
A/B, D_h, D	9	6
B, C, D	1	1
C,D	8	7
D_h, D	6	5

Table 2-3. Potential for note type coding (PNTC) for 9 of the acoustic measures on A, A/B, B and C notes.

Measurement	CV_b	Mean CV_w	**PNTC**
TD	27.0	13.3	**2.0**
AD	43.9	36.4	**1.2**
DD	45.7	27.5	**1.7**
SF	40.5	21.3	**1.9**
PF	19.0	6.8	**2.8**
EF	19.6	14.8	**1.3**
Fmax	12.7	7.4	**1.7**
FMasc	67.9	48.6	**1.4**
FMdesc	-41.3	-39.0	**1.1**

Table 2-5. Potential for individual coding (PIC) values, variation coefficients (CV_b and Mean CV_w), and F values (*see text for significant alpha levels) for each acoustic feature measured on D notes and on whole and harmonic D_h notes.

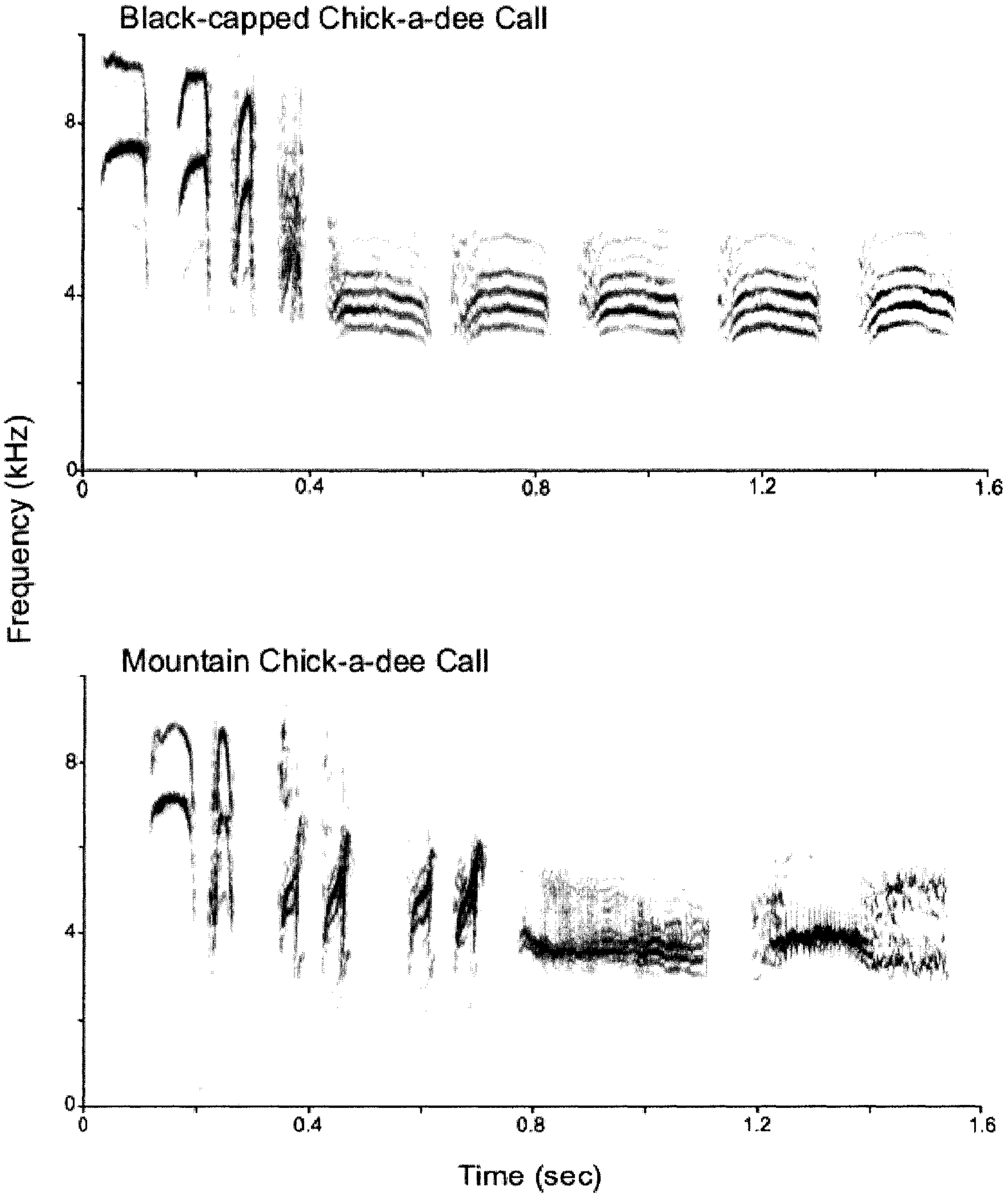
Note Type		TD (ms)	AD (ms)	DD (ms)	SF (Hz)	PF (Hz)	EF (Hz)	FMasc (Hz/ms)	FMdesc (Hz/ms)	Fmax(Hz)	NPF (Hz)
A	Mean	109.8	22.8	26.9	5152	6826	4253	100.5	-100.5	6803	8671
	SD	18.8	11.2	8.6	1322	449	869	80.5	31.8	520	1710
	CV_b	17.1	49.1	31.9	25.7	6.6	20.4	80.2	-31.6	7.6	19.7
	Mean CV_w	12.3	44.5	23.0	28.4	5.9	12.6	73.2	-28.1	6.2	16.6
	PIC	**1.4**	**1.1**	**1.4**	**0.9**	**1.1**	**1.6**	**1.1**	**1.1**	**1.2**	**1.2**
	ANOVA	**0.46**	**2.21**	**5.75***	**5.13***	**3.37***	**5.36***	**1.45**	**1.74**	**1.52**	**3.61***
A/B	Mean	87.9	23.8	25.3	3587	6705	3802	154.0	-121.5	6633	8617
	SD	18.7	10.6	6.5	810	451	452	72.1	36.1	585	1378
	CV_b	21.3	44.7	25.7	22.6	6.7	11.9	46.8	-29.7	8.8	16.0
	Mean CV_w	18.6	29.4	23.1	19.9	4.6	10.9	40.4	-24.8	8.4	11.6
	PIC	**1.1**	**1.5**	**1.1**	**1.1**	**1.5**	**1.1**	**1.2**	**1.2**	**1.1**	**1.4**
	ANOVA	**2.85***	**4.92***	**3.03***	**4.06***	**9.19***	**3.14***	**4.15***	**2.76***	**2.65***	**2.38***
B	Mean	60.5	18.2	16.3	3135	6335	3781	185.5	-160.9	6366	8114
	SD	5.2	5.2	3.3	751	288	435	57.2	37.2	371	1330
	CV_b	8.6	28.4	20.4	24.0	4.5	11.5	30.8	-23.1	5.8	16.4
	Mean CV_w	7.6	22.1	15.8	17.9	3.0	9.2	26.3	-18.6	3.9	9.4
	PIC	**1.1**	**1.3**	**1.3**	**1.3**	**1.5**	**1.2**	**1.2**	**1.2**	**1.5**	**1.7**
	ANOVA	**1.68**	**2.0**	**2.95***	**3.53***	**5.31***	**2.2**	**3.34***	**2.95***	**1.88**	**4.68***
C	Mean	68.5	39.0	9.3	2003	3484	2902	40.3	-61.4	5204	10798
	SD	4.4	9.1	3.0	261	333	441	14.7	44.0	375	936
	CV_{btwn}	6.4	23.4	32.0	13.0	9.5	15.2	36.5	-71.7	7.2	8.7
	Mean CV_w	5.7	18.8	31.5	10.4	7.6	14.2	28.0	-71.4	5.3	6.9
	PIC	**1.1**	**1.2**	**1.0**	**1.3**	**1.3**	**1.1**	**1.3**	**1.0**	**1.4**	**1.3**
	ANOVA	**1.02**	**3.4***	**3.53***	**2.79**	**5.26**	**4.4***	**1.22**	**5.6***	**2.98**	**3.76***
D_h	Mean	-	16.4	-	3024	5517	-	161.4	-	5442	7451
(tonal)	SD		5.2		711	390		53.4		548	2219
	CV_b		31.9		23.5	7.1		33.1		10.1	29.8
	Mean CV_w		27.2		19.0	5.9		28.1		7.6	19.5
	PIC		**1.2**		**1.2**	**1.2**		**1.2**		**1.3**	**1.5**
	ANOVA		**1.83**		**5.83***	**2.98***		**4.39***		**1.94**	**9.25***

Table 5. Potential for individual coding (PIC) values, variation coefficients (CV_b and Mean CV_w), and F values (*see text for significant alpha levels) for each acoustic feature measured on D notes and on whole and harmonic D_h notes.

Note Type		TD (ms)	F_0 (Hz)	Fmax (Hz)	NPF (Hz)
D	Mean	286.2	1945	4080	8732
	SD	57.4	412	384	1563
	CV_b	20.1	21.2	9.4	17.9
	Mean CV_w	17.4	12.7	6.5	13.9
	PIC	**1.2**	**1.7**	**1.5**	**1.3**
	ANOVA	**6.95***	**7.98***	**5.82***	**5.99***
D_h (whole and harmonic)	Mean	192.3 ‡	3951	1804	9502
	SD	40.1 ‡	441	186	1915
	CV_b	20.9 ‡	11.2	10.3	20.2
	Mean CV_w	11.7 ‡	8.7	8.1	17.1
	PIC	**1.8** ‡	**1.3**	**1.3**	**1.2**
	ANOVA	**8.55***	**6.0***	**1.11**	**4.02***

Note: Symbol (‡) represents values for measurements conducted on whole note.

Figure 2-1.



Black-capped Chick-a-dee Call

Mountain Chick-a-dee Call

Figure 2-2.

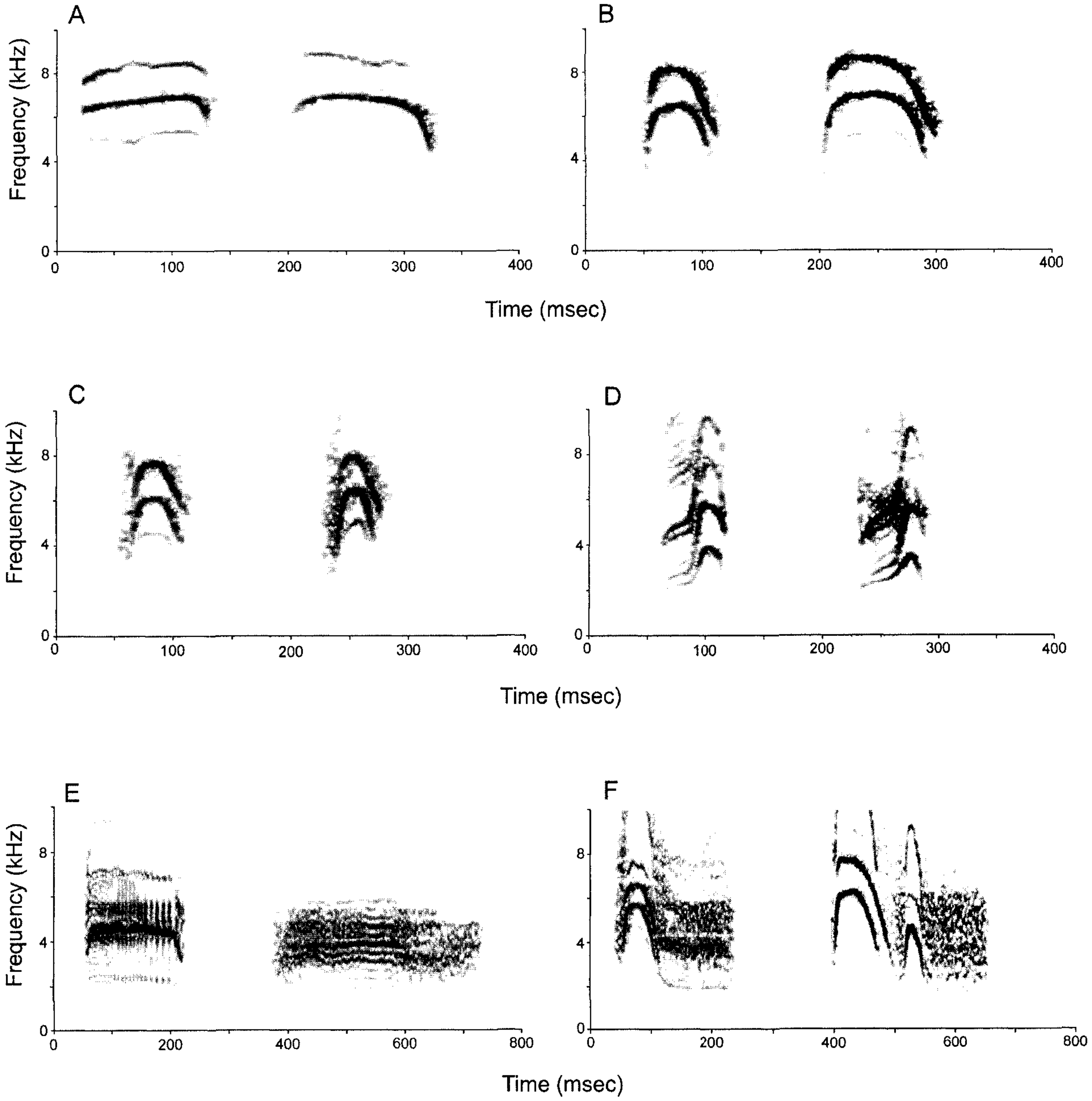
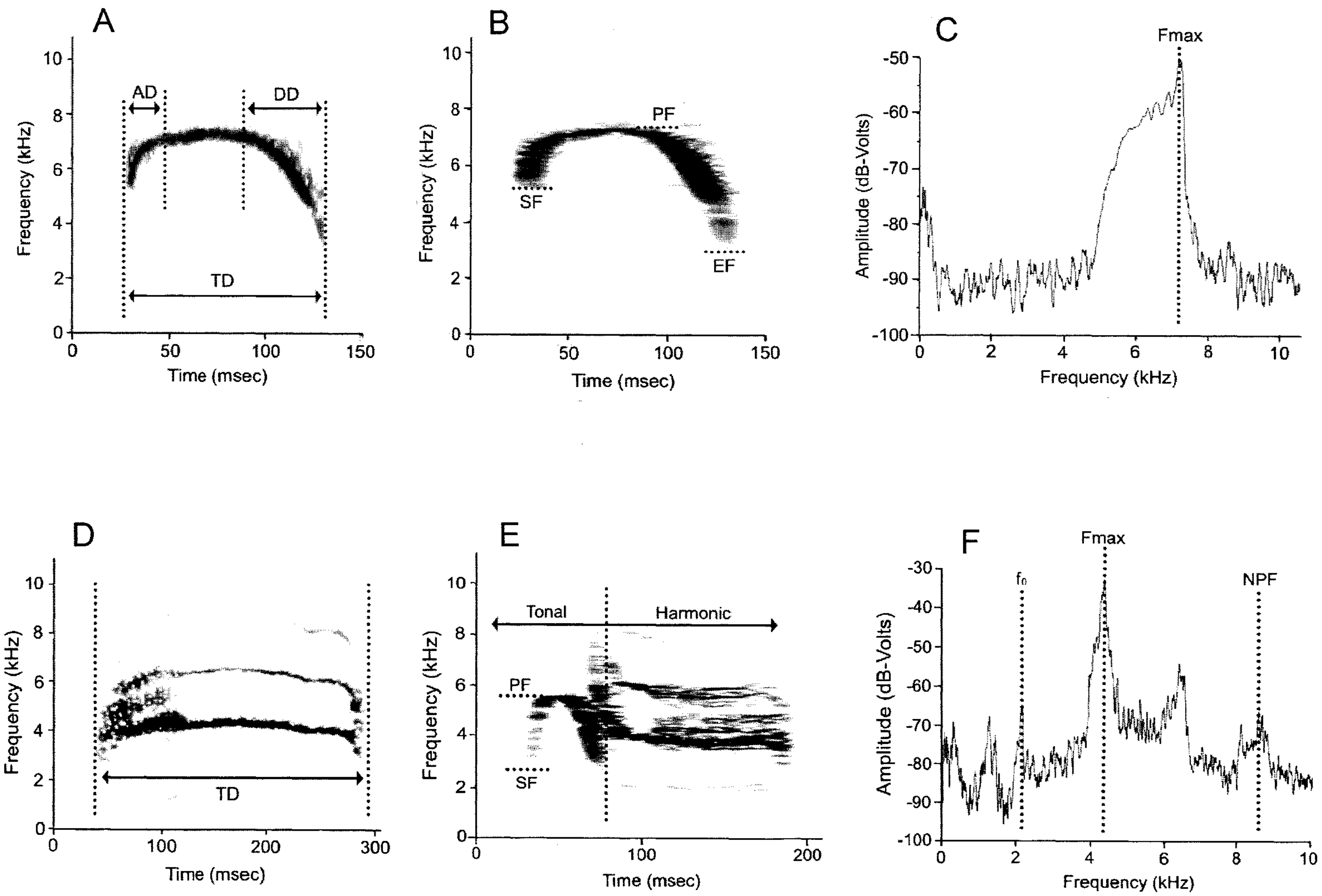

A
B
C
D
E
F
Frequency (kHz)
0
4
8
Time (msec)
0
100
200
300
400
200
400
600
800

Figure 2-3.


A
Frequency (kHz)
Time (msec)
AD
DD
TD
B
Frequency (kHz)
Time (msec)
SF
PF
EF
C
Amplitude (dB-Volts)
Frequency (kHz)
Fmax
D
Frequency (kHz)
Time (msec)
TD
E
Frequency (kHz)
Time (msec)
Tonal
Harmonic
PF
SF
F
Amplitude (dB-Volts)
Frequency (kHz)
f0
Fmax
NPF

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Chapter 3: All "chick-a-dee" calls are not created equally. Part I: Open-ended categorization of chick-a-dee calls by sympatric and allopatric chickadees

A version of this paper is in press. Bloomfield, L.L. & Sturdy, C.B. *Behavioural Processes*.

Introduction

There are over 4,000 species of songbirds (order Passeriformes, suborder oscines; Sibley & Monroe, 1990) that learn to produce their species-typical songs by listening to adult tutors along with their own vocal output while practicing (see Ball & Hulse, 1998 for a review). Learning to accurately produce and perceive their vocalizations allows songbirds to communicate with conspecifics, a necessary skill for social animals (e.g., see Bertram, 1978) that provides several advantages. For example, recognizing a flockmate's song or call can provide the listener with a plethora of information, such as species or individual identity, warning of an approaching predator (in the case of alarm calls) or the location of valuable resources, such as territory and food. In addition to the ability to identify and discriminate among their own species' (i.e., conspecific) vocalizations, it is also crucial for birds to discriminate between conspecific and other species' (i.e., heterospecific) vocalizations. For example, a female songbird that mistakenly selects a heterospecific mate or a male songbird that accidentally courts a heterospecific female based on a misclassified vocalization may result in interspecific breeding, a highly undesirable situation producing nonviable offspring, ultimately reducing one's reproductive fitness.

In some cases, however, it may prove beneficial to actively attend to heterospecific vocalizations. This would be especially true in the case of vocalizations produced by heterospecifics that inhabit the same region and that face similar ecological and environmental challenges, such as predator detection or food availability, a situation common with the subjects of the current set of experiments, the chickadees (genus *Poecile*). Here we examine whether black-capped (*P. atricapillus*) and mountain chickadees (*P. gambeli*) classify their own and other species' chick-a-dee calls as different from one another (species-level categorization) or whether the birds treat all chick-a-dee calls as belonging to one over-arching category (vocalization-type categorization).

Within the genus *Poecile* there are several chickadee species, such as the closely related black-capped and mountain chickadees, that occupy overlapping ranges (i.e., are sympatric) and are often observed foraging in the same vicinity (e.g., within 2m of one another in the same tree; Hill & Lein, 1988). Due to this range overlap and the similarities in ecology between these chickadee species, it is possible that chickadees in these areas attend to all chickadee vocalizations, regardless of the particular species of the caller, to aide in self-preservation activities such as foraging and predator detection and evasion. If this were the case, upon hearing any chickadee vocalization, a bird may need to only classify it to a broad category such as "chickadee", and not more specifically as a conspecific (or heterospecific) chickadee in order to utilize the vocalization to find the food source or take defensive action. Alternatively, chickadees in these areas may in fact classify chickadee vocalizations based on the species of the caller, suggesting that particular acoustic features in the songs and calls convey species identity.

One of the more common and most recognizable chickadee vocalizations is the "chick-a-dee" call (Ficken, Ficken, & Witkin, 1978, see Figure 3-1), which has a learned component. For example, some chick-a-dee call-note types do not develop under abnormal rearing conditions (Hughes, Nowicki, & Lohr, 1998), and fine spectral features of D notes can be modified during flock formation and cohesion (Nowicki, 1989). This call is produced by males and females of all chickadee species (see Hailman & Ficken,

1996) throughout the year and in similar contexts, such as when mildly alarmed and when coordinating flock movements (Ficken et al., 1996; Gaddis, 1985; S.M. Smith, 1991; S.T. Smith, 1972). Bioacoustic analyses reveal that there are both similarities as well as differences among the chick-a-dee calls of the species studied to date (black-capped chickadees, Charrier, Bloomfield, & Sturdy, 2004; mountain chickadees, Bloomfield, Charrier, & Sturdy, 2004; Carolina chickadees, *P. carolinensis*, Bloomfield, Phillmore, Weisman, & Sturdy, 2005; boreal chickadees, *P. hudsonicus*, Bloomfield, Modanu, Charrier, Ficken, & Sturdy, unpublished manuscript, respectively). Each call consists of a string of notes widely recognized as A-, B-, C-, and D-note types (black-capped chick-a-dee call; Ficken et al., 1978), and in some chickadee species, note-type variants, such as the mountain chick-a-dee A/B and D-hybrid note, are also included. Given that all chickadees produce a variant of the chick-a-dee call, it may serve as a useful species marker for discriminating among chickadee species. While it is likely that chickadees are capable of discriminating the chick-a-dee calls of the various chickadee species, it is not known whether the birds classify the calls of each species as belonging to separate vocal categories, and whether these categories are open-ended, allowing birds to quickly and accurately generalize to and classify novel or unfamiliar calls.

Our current hypotheses of chick-a-dee call perception are based on previous studies of visual category discrimination (see Herrnstein, 1990; Wasserman, 1995) and our own research (Bloomfield, Sturdy, Phillmore, & Weisman, 2003; Sturdy, Phillmore, & Weisman, 2000). Previous studies have shown that pigeons (*Columba livia*) can classify hundreds of visual images, and that the categories into which the images were classified were in fact open-ended in that novel images could also be accurately categorized (e.g., Astley & Wasserman, 1992; Herrnstein, Loveland, & Cable, 1976). Using more biologically relevant stimuli, Sturdy, Phillmore and Weisman (1999b; 2000) have shown that zebra finches (*Taeniopygia guttata*) and black-capped chickadees classify their song and call notes (respectively) into open-ended song and call-note categories defined by bioacousticians (Ficken et al., 1978; Sturdy, Phillmore, Price, & Weisman, 1999a), and that this learning transferred to novel notes of the same types.

In an example more directly related to the aims of the current study, Bloomfield and colleagues (2003) have shown that black-capped chickadees accurately classify conspecific and heterospecific (Carolina chickadee) chick-a-dee calls into their appropriate species-specific categories in an open-ended manner, an ability that preceded any operant discrimination training. That is, in a simultaneous within- and between-category discrimination task, black-capped chickadees responded to rewarded (S+) within-category calls and more quickly learned to withhold responding to unrewarded (S-) between-category calls compared to unrewarded (S-) within-category calls, and continued to do so when presented with novel, unfamiliar between-category calls. Therefore, this suggests that chickadees perceive the acoustic differences between species' calls, and this allows them to quickly respond (i.e., to categorize the calls) without the need for rote memorization of the particular call and the associated contingency. This 2003 study, however, only examined the abilities of allopatric black-capped chickadees, and therefore neither investigated the potential role of familiarity or experience with the heterospecific (Carolina chickadee) vocalizations in their categorizations (as in some regions these two species also share overlapping ranges, Mostrom, Curry, & Lohr, 2002), nor drew direct comparisons with the abilities of the Carolina chickadees.

In the current study we further contribute to our current understanding of open-ended vocal categorization in chickadees by examining the abilities of mountain chickadees and two groups of black-capped chickadees to classify black-capped and mountain chickadee chick-a-dee calls. One group of black-capped chickadees originates from a region where there are no mountain chickadees and is referred to throughout as the allopatric group. The other group of black-capped chickadees originates from the same region as the mountain chickadees in this study and is referred to throughout as the sympatric group. Here we will gain a greater understanding of the role that experience with each species' chick-a-dee calls plays in categorization by examining whether (a) both groups perceive the calls as belonging to two separate species-level categories and use an open-ended categorization strategy to quickly and accurately respond to the two species' calls, (b) both groups perceive the calls as belonging to one vocalization-type category and not as two separate species' categories, or (c) only one of the two groups perceives the calls as belonging to separate species-level categories and uses an open-ended categorization strategy to perform the current task.

Here we can predict several possible outcomes of the current study. First, sympatric black-capped chickadees may only need to respond upon hearing the call of a chickadee, and not necessarily need to discriminate their own from mountain chick-a-dee calls, which could be an advantageous strategy in their natural habitat for finding food and avoiding predators. In contrast, allopatric black-capped chickadees may be more likely to discriminate between conspecific and heterospecific chick-a-dee calls and therefore treat the calls as belonging to two separate categories. This may in part be due to the fact that they have extensive experience with only their own species calls, and any variant that departs from their own species' calls may be more perceptible. However, the alternative to this may in fact occur. That is, sympatric black-capped chickadees, having extensive experience with the chick-a-dee calls of mountain chickadees, may prove to be more skilled in discriminating both among individual mountain chick-a-dee calls (the within-category discrimination) and between the calls of the two species (the between-category discrimination), whereas allopatric black-capped chickadees, having no previous experience with the chick-a-dee calls of mountain chickadees, may in fact treat all chick-a-dee calls as chickadee-like without initially treating them as belonging to separate (species-level) categories.

The extent to which natural stimuli in an animal's environment constitute open-ended categories is the focus of the current study. In Experiment 1 we analyze the speed and the accuracy of performing simultaneous within- and between-category discriminations of black-capped and mountain chick-a-dee calls, and whether there is a species-specific or experiential advantage to these discriminations. In Experiment 2 we test for generalization of learning by introducing novel between-category chick-a-dee calls, and in Experiment 3 we rule out the possibility of rote memorization as an explanation of the results of the first two experiments by reintroducing familiar chick-a-dee calls following a reversal of the category contingency. Taken together, the results will provide us with a better understanding of the categorization skills of chickadees when confronted with salient communication signals, and whether black-capped chickadees perform differently depending on the extent of their experience with mountain chickadee calls.

General Methods

Animals

A total of 36 birds (24 black-capped chickadees and 12 mountain chickadees) at least one year of age (determined by the shape and coloring of the outer tail retrices, Pyle, 1997) and naïve to the experimental stimuli and procedures served in Experiments 1-3. All birds were captured between December 2003 and February 2005. Twelve black-capped chickadees were caught in several locations in and around the city of Edmonton, Alberta, Canada (53° 06'N, 113° 04'W) had no prior exposure to mountain chickadees (as chickadees are non-migratory and mountain chickadees do not naturally occur in these areas), and are referred to as the *allopatric* group. Twelve black-capped chickadees and 12 mountain chickadees were caught from several locations in the sympatric region of Kananaskis Country, Alberta, Canada (51° 02'N, 115° 03'W). In contrast to the black-capped chickadees captured in Edmonton, these latter 12 black-capped chickadees had prior exposure to mountain chickadees, as both mountain and black-capped chickadees are prolific in this area (pers. obs.), and are referred to as the *sympatric* group. Sex identification was conducted by DNA analysis (Griffiths, 2000).

Each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages (0.3m wide x 0.4m high x 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada) for a minimum of 1 month prior to the commencement of the experiments. The housing conditions allowed for auditory and visual but not physical contact among birds of the same species. Birds were maintained on a day-light cycle approximating the natural cycle for Edmonton throughout the duration of training and testing (January – July).

Prior to experimentation, birds were given *ad libitum* access to standard rations (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), cuttle bone, grit, and water (with added vitamin supplement on alternate days; Hagen, Rolf C. Hagen, Inc., Montreal Canada). Birds were also given 1 meal worm three times per week and hard-boiled egg and spinach mixture twice a week.

During Experiments 1-3, standard rations were only available when an appropriate operant response was produced. Birds were given *ad libitum* access to cuttle bone, grit and water (vitamin-supplemented on alternate days). Two meal worms were provided daily to ensure good health throughout the course of the three experiments.

Apparatus

Modified budgerigar cages (0.3 m wide × 0.4 m high × 0.4 m deep) provided continuous housing for the birds during training and testing periods. To ensure the birds did not have access to spilled food, a plastic mesh floor was attached near the bottom of the cage. Each cage was contained in a ventilated, sound-attenuated chamber illuminated by a 9-W, twin-tube, full-spectrum fluorescent bulb and each cage had several perches and dispensers for water and grit. Infrared cells monitored a motor-driven feeder (Njegovan, Hilhorst, Ferguson, & Weisman, 1994) mounted beside the cage, and a perch opposite the feeder entrance monitored the bird's position. Access to the feeder was made possible by an opening (11 cm wide × 16 cm high) in the cage. A single-board computer (Palya & Walter, 2001) interfaced to a personal computer controlled a standard CD-ROM, scheduled the experiment and recorded responses to stimuli. Stimuli were played at 75-85 dB (A weighting, slow response, measured using a Radio Shack Sound Level Meter) from a CD via either a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or a NAD 310 Integrated Amplifier (NAD Electronics, London, England) and then through to a Fostex FE108Σ full-range speaker (Fostex Corp., Japan) located beside the feeder (effective frequency response 200-16,000 Hz). The center of the speaker was positioned at the height of the bird's head when the bird stood on the request perch.

Stimuli Preparation

A total of 60 high-quality chick-a-dee calls (30 black-capped and 30 mountain), recorded using a variety of microphone and recorder types, were randomly selected from our own database of recordings, commercially available compact disks, and bioacoustics libraries. All recorded chick-a-dee calls were unfamiliar to the experimental subjects as they originated from birds recorded in regions at least 120km from the locations of capture. Using GoldWave Version 5.12 (Goldwave, Inc., St. John's, NF), calls were bandpass filtered (1,000 – 10,000 Hz; GoldWave) to remove background noise. Using SIGNAL 4.0 sound analysis software (Engineering Design, CA) the leading and trailing 5-ms of silence were tapered to remove transients, amplitude was equalized, and each call was saved as an individual 2-s sound file. All 60 calls were then transferred to compact discs, one call per track.

Procedure

Nondifferential Training. Nondifferential training began after a bird had learned to use the perch and feeder. When a bird landed on the perch, breaking an infrared beam, the within-trial sequence began. Remaining on the perch for 1-s on average (range 900-

1,100 ms) resulted in a single call being randomly selected and played once. If the bird flew or hopped to the feeder within 1-s after the stimulus was played, breaking another infrared beam, it was rewarded with 1-s access to food (i.e., reinforcement), followed by a 30-s inter-trial interval (ITI). If the bird left the perch without entering the feeder, the trial ended after 1-s. If the bird did not leave the perch, the trial ended after 1-s; a 60-s ITI followed. The 60-s ITI was used to increase the probability of the bird leaving the perch on all trials. Leaving the perch before the stimulus had finished playing (i.e., interrupted trial) resulted in the trial ending and the chamber lights turning off during a 30-s ITI. These procedures helped us to ensure that birds heard and attended to the calls and subsequently left the perch. During nondifferential training, we presented all the calls in the stimulus pool. The purpose of nondifferential training was to ensure that the birds heard and responded to all the calls and to gather similar percentages of responses to each call as a baseline for the evaluation of training in Experiments 1–3. Nondifferential training continued until a bird approached the feeder on a minimum of 60% of the trials (similar to the level of responding observed during discrimination by Bloomfield et al., 2003), an appropriate level considering birds are able to trigger a stimulus for every perch-landing and receive reinforcement for every feeder approach. Birds typically approached the feeder on about 80% of the trials and on average triggered about 1,000 – 2,000 total stimuli per day.

Discrimination Training. Discrimination training began after nondifferential training in Experiment 1 and continued in Experiments 2 and 3. During discrimination training, visits to the feeder after S+ (positive, or reinforced) calls were rewarded with access to food, but visits to the feeder after S– (negative, or nonreinforced) calls resulted in no reward and a 30-s ITI with the chamber lights off (i.e., punishment). Other contingencies and procedures initiated during nondifferential training remained in effect during discrimination training. Further details about the stimulus calls used are presented in the *Method*s sections for each experiment. Typically, each daylong session generated about 1,000 trials.

Response Measures and Statistical Analyses. We calculated a percentage of response measure for each stimulus (whether S+ or S–) using the following formula: (R+/(N trials – N interrupted trials)) × 100, where R+ is the number of trials on which the bird flew or hopped to the feeder, N trials is the total number of trial presentations for that stimulus, and N interrupted trials is the number of trials in which the lights were extinguished for the bird leaving the perch before the stimulus was played in its entirety. We conducted analyses of variance (ANOVAs) on percentages of responses among the discrimination groups using STATISTICA (Version 6, StatSoft, Inc., 2003). When percentages of responses are near 0% or 100%, sample values may not be normally distributed. We therefore conducted parallel ANOVAs using arcsine square-root transformations of the percentages of responses. Analysis of transformed data yielded the same pattern of results with virtually the same levels of significance as untransformed data. Therefore, only results for ANOVAs of the untransformed data are reported here.

Experiment 1: Within- and Between-Category Discrimination

Experiment 1 was designed to examine whether birds more quickly discriminate between the calls of the two chickadee species (between-category, or species' discrimination) or among the calls within one species (within-category, or individual discrimination). Discriminating among the calls of one species requires the rote memorization of each stimulus, and based on this, should require more time to master than discriminating between the two species' calls, which could be accomplished via categorization. If a difference in the speed of acquisition such as this were observed, it would suggest that there is greater similarity among the calls within one species compared to between the two species. Here we hypothesized that birds would discriminate between the calls of the two categories (species' discrimination) faster than they would among the calls within a category (individual discrimination), suggesting that there is indeed greater perceptual similarity within a category of chick-a-dee calls compared to between the two categories, a necessary feature for the use of a categorization strategy. The alternative is that birds would not respond differentially to the two between-category exemplar sets, suggesting that they perceive the calls of the two species as belonging to one vocalization-type category.

Methods

Black-capped and mountain chickadees were randomly assigned to one of two groups; black-capped chick-a-dee S+ (within-category) group (referred to throughout as BCCH-S+ group) or mountain chick-a-dee S+ (within-category) group (referred to throughout as MOCH-S+ group). Birds in the BCCH-S+ group (*n* = 6 allopatric (3 male and 3 female) and 6 sympatric (3 male and 3 female) black-capped chickadees, and 6 (3 male and 3 female) mountain chickadees) were presented randomly with 15 S+ black-capped chick-a-dee calls, 15 S- black-capped chick-a-dee calls (within-category discrimination), and 15 S- mountain chick-a-dee calls (between-category discrimination). Birds in the MOCH-S+ group (*n*=6 allopatric (3 male and 3 female) and 6 sympatric (3 male and 3 female) black-capped chickadees, and 6 (3 male and 3 female) mountain chickadees) were presented randomly with 15 S+ mountain chick-a-dee calls, 15 S- mountain chickadee calls (within-category discrimination) and 15 S- black-capped chick-a-dee calls (between-category discrimination). Notice here that only 15 of the 30 between-category stimuli are used (and are referred to as the *original* stimuli throughout) while the remaining 15 between-category stimuli are reserved for Experiment 2 (and are referred to as the *transfer* stimuli throughout).

Results

Nondifferential Training. We tested for differences in the percentages of responses among the four exemplar sets (including the set reserved for the transfer test in Experiment 2) during nondifferential training prior to discrimination training. We conducted a mixed model Birds (sympatric black-capped chickadees, allopatric black-capped chickadees, mountain chickadees) × S+ Group (BCCH-S+, MOCH-S+) × Sex (male, female) × Exemplar Set (S+, S- within-category, S- between-category) ANOVA and found no significant main effects or higher-order interactions for Birds, S+ Group, or Sex (p's > 0.168) however there was a significant effect of Exemplar Set, $F(3, 72) = 4.5014$, $p = 0.006$. Tukey's post hoc comparisons ($p < 0.05$) revealed that birds responded slightly more to the between-category (transfer) Exemplar Set reserved for Experiment 2 compared to responding to the S+ Exemplar Set and the original S- between-category Exemplar Sets (*M's* = 79%, 75%, 75% respectively).

During discrimination training chickadees in both the BCCH-S+ group and the MOCH-S+ group learned to fly to the feeder following S+ calls and to withhold flying to the feeder following both within- and between-category S- calls (see Figure 3-2). The pattern of responses in Figure 3-2 also suggests that the within-category discrimination was more difficult to learn than the between-category discrimination.

To determine whether there were any overall differences among birds in learning the within- and the between-category discrimination, we conducted a mixed model Birds (sympatric black-capped chickadees, allopatric black-capped chickadees, mountain chickadees) × S+ Group (BCCH-S+, MOCH-S+) × Sex (male, female) × Exemplar Set (S+, S- within-category, S- between-category) × Blocks (1-20) ANOVA on the percentages of responses averaged within each 500-trial block. There was a main effect of Birds, $F(2, 24) = 4.79, p = 0.018$, as mountain chickadees responded significantly less than sympatric black-capped chickadees ($p = 0.024$) and marginally less than allopatric black-capped chickadees ($p = 0.051$). There were no main effects of S+ Group or Sex, *p*s > 0.341. There was a main effect of Blocks, $F(19, 456) = 47.36, p < 0.001$, of Exemplar Set, $F(2, 48) = 729.61, p < 0.001$, a Blocks × Exemplar Set interaction, $F(38, 912) = 133.02, p < 0.001$, and several other higher-order interactions which indicated that birds learned to respond appropriately to the three exemplar sets over blocks of trials, and the three groups of birds assigned to the two different S+ groups performed differently over trials.

To further compare learning rates among groups and to test our *a priori* predictions we conducted planned comparisons (Tukey's, $p < 0.05$) on percentages of responses to S+, S- within- and S- between-category exemplar sets at each 500-trial block. To further facilitate comparisons we present the results below based on group assignment.

BCCH-S+ group

All birds in the black-capped chick-a-dee S+ group more quickly learned to withhold responding to S- between-category exemplars than to S- within-category exemplars. This suggests that compared to the S- within-category exemplars, birds could more easily discriminate the between-category S- exemplars from the S+ exemplars. Further, sympatric and allopatric black-capped chickadees and mountain chickadees learned at about the same rate (i.e., after 1,500 trials) to withhold responding to the S- between-category exemplars (see Figures 3-2A, 3-2C, 3-2E), however at this stage allopatric birds responded significantly less to S- between- compared to responding to S- within-category exemplars. Sympatric birds were the first to discriminate among exemplars within a category (after 2,500 trials) by responding significantly less to S- within-category exemplars compared to responding to S+ exemplars. By 3,000 trials all birds were successfully discriminating within and between categories.

MOCH-S+ group

Birds in the mountain chick-a-dee S+ group also learned more quickly to withhold responding to S- between-category exemplars than to S- within-category exemplars. After 1,500 trials allopatric birds responded significantly less to the S- between-category chick-a-dee calls compared to responding to both the S+ and S- within-category exemplar sets (see Figure 3-2D). By 2,000 trials sympatric and mountain chickadees also responded significantly less to S- between-category chick-a-dee calls compared to responding to S+ calls (see Figures 3-2A, 3-2F). Similar to the sympatric birds in the BCCH-S+ group, sympatric birds in the MOCH-S+ group were the first to discriminate among heterospecific S+ and S- chick-a-dee calls. However these birds required 500 additional trials compared to the sympatric birds in the BCCH-S+ group discriminating among conspecific S+ and S- chick-a-dee calls. Mountain chickadees required the greatest number of trials to perform the within-category discrimination, successfully discriminating among exemplars after 4,500 trials, 1,500 more trials compared to mountain chickadees in the black-capped chick-a-dee S+ group.

Experiment 2: Transfer of Inhibition

In Experiment 2 we replaced the 15 original between-category calls from Experiment 1 with 15 between-category transfer calls. In addition, we reversed the contingency for this stimulus set from unrewarded (S-) to rewarded (S+) to test for transfer of inhibition from the original stimuli to the transfer stimuli. These transfer calls were not presented during discrimination training in Experiment 1 but were presented during nondifferential training prior to Experiment 1. We hypothesized that response inhibition acquired to the between-category stimulus set in Experiment 1 would generalize (i.e., transfer) to these introduced calls in Experiment 2, and subsequently hinder the acquisition of operant responses to these stimuli, a second important feature of open-ended categorization.

Methods

Immediately following Experiment 1, transfer of inhibition testing began and continued for 5,000 trials. During the transfer test, the S+ and within-category S-discrimination exemplar sets remained as in Experiment 1, but the original unrewarded (S-) between-category exemplars from Experiment 1 were replaced with different, rewarded (S+) between-category exemplars.

Results

Figure 3-3 shows percentages of response to the S+, within-category S-, and transfer between-category S+ exemplar sets for each species in each group. During the first 1,000 trials of the transfer test, birds responded to between-category S+ transfer calls at about the same level as within-category S- calls, and at much lower levels than seen for within-category S+ calls or rates of responding to these calls during pretraining sessions. Thereafter, responding to the transfer call set rose to almost the level of responding to the S+ call set.

To determine whether birds maintained their within- and between-category discriminations when novel between-category calls were introduced, we conducted a mixed model Birds (sympatric black-capped chickadee, allopatric black-capped chickadee, mountain chickadee) × S+ Group (BCCH-S+, MOCH-S+) × Sex (male, female) × Exemplar Set (S+, S- within-category, S- between-category) × Blocks (1-10) ANOVA on the percentages of responses averaged within each 500-trial block. There continued to be a main effect of Birds, $F(2, 24) = 4.34$, $p = 0.025$, as mountain chickadees responded at lower levels overall compared to sympatric black-capped chickadees ($p = 0.02$) and main effects of Blocks, $F(9, 216) = 22.42$, $p < 0.001$, and Exemplar Set, $F(2, 48) = 238.12$, $p < 0.001$. There were several higher-order interactions as well, including a Blocks × Exemplar Set interaction, $F(18, 432) = 42.33$, $p < 0.001$. To further explore the responding by birds to the between-category transfer exemplars we conducted planned comparisons (Tukey's, $p < 0.05$) on each 500-trial block.

BCCH-S+ group

After the first 1,000 trials of Experiment 2, all birds continued to respond most to S+ black-capped chick-a-dee calls and significantly less to both S- within-category black-capped chick-a-dee calls and between-category mountain chick-a-dee calls After 2,000 trials responding to S+ and between-category exemplars was not significantly different among sympatric birds, as levels of responding to the now-rewarded between-category calls began to increase (see Figure 3-3A). After 4,500 trials responding to S+ and between-category exemplars among allopatric birds was not significantly different (see Figure 3-3C), and by 5,000 trials mountain chickadees continued to withhold responding to the between-category exemplars (see Figure 3-3E).

MOCH-S+ group

After the first 1,500 trials of Experiment 2, all birds continued to respond most to S+ mountain chick-a-dee calls and significantly less to S- within-category mountain chick-a-dee calls and between-category black-capped chick-a-dee calls. After 2,000 trials responding to S+ and between-category exemplars was not significantly different among sympatric birds, as levels of responding to the now-rewarded between-category calls began to increase (see Figure 3-3B). After 2,500 trials mountain chickadees responded about equally to S+ and between-category calls (see Figure 3-3F). After 3,000 trials allopatric birds also increased their responding to between-category calls to levels about equal to responding observed to S+ exemplars (see Figure 3-3D).

In summary, all three groups of birds in both S+ groups initially withheld responding to between-category transfer calls in Experiment 2 despite the fact that an operant response to calls in this exemplar set would provide reward. Sympatric birds in the BCCH-S+ group required 2,000 trials to respond about equally to S+ black-capped chick-a-dee calls and between-category mountain chick-a-dee calls whereas allopatric birds required 4,500 trials. Mountain chickadees in the BCCH-S+ group continued to show response inhibition throughout the duration of Experiment 2 by withholding responses to between-category mountain chick-a-dee calls. Birds in the MOCH-S+ groups responded in a similar manner as birds in the BCCH-S+ group by withholding their responses to between-category transfer calls during the initial trials of Experiment 2. Sympatric birds were the first to respond about equally to the S+ and between-category calls (2,000 trials), mountain chickadees required 2,500 trials, and allopatric birds required 3,000 trials.

Therefore, by removing the original between-category exemplars used in Experiment 1 and replacing them with different between-category exemplars in Experiment 2, we were able to provide further evidence that birds perceive their own and the other species' calls as belonging to separate categories. That birds continued to respond at low levels to the between-category exemplars despite the fact that (1) they had not been explicitly trained to do so and (2) they had responded at high levels during nondifferential training, indicated that the birds responded according to the most recently learned contingency associated with that category of calls, that is, nonreward.

One might suggest, however, that birds continued to withhold responding to transfer between-category exemplars not because they considered these stimuli as belonging to the same category as the between-category stimuli in Experiment 1, but rather because they were unable to perceive a change in (1) the stimulus set, or (2) the associated contingency. To determine whether the level of responding observed was a result of the birds not detecting a change, we compared the percentages of responses to the original between-category exemplar set during the last 500 trials of Experiment 1 with the percentages of responses to the between-category transfer set during the first 500 trials of Experiment 2 using a mixed model Birds × S+ Group × Experiment ANOVA. There was a main effect of Experiment, $F(1, 30) = 18.36, p < 0.001$, revealing that birds responded slightly but significantly more to the between-category transfer exemplars presented in Experiment 2 ($M = 15\%$) compared to responding to the original between-category exemplars presented in Experiment 1 ($M = 4\%$, see Figure 3-3). These findings suggest that although chickadees transferred their discrimination of the original between-category exemplars to the transfer exemplars, they nonetheless discriminated between the two exemplar sets (by responding slightly but significantly more to the transfer exemplars in Experiment 2). We are therefore confident that the transfer of inhibition observed at the beginning of Experiment 2 was not a failure by birds to discriminate original between-category exemplars from between-category transfer exemplars, but rather as evidence that birds perceived these novel exemplars as belonging to the same category as those between-category exemplars encountered in Experiment 1, and thus responded according to the most recently learned contingency for that category.

Experiment 3: Propagation

The between-category transfer calls used in Experiment 2 were replaced in Experiment 3 with the original, between-category calls used in Experiment 1. If the calls of the two species are perceived as each belonging to a distinct category, training to the between-category transfer stimuli in Experiment 2 should propagate back to the original between-category stimuli, despite their initial contingency association during Experiment 1. If birds continue to respond to the original (S-) between-category stimuli as they had learned to in Experiment 1 (and not based on the new contingency (S+) learned in Experiment 2) this would indicate that they are using rote-memorization and not open-ended categorization as the strategy for responding.

Methods

After the 5,000 trials of Experiment 2, 7 black-capped chickadees (4 female and 3 male) and 6 mountain chickadees (3 male and 3 female) continued to respond at low levels (0 % to 44.3 % in the last 500 trials) to the novel rewarded between-category transfer calls. These birds were given about 2,500 trials of pre-training at the start of Experiment 3, where only the rewarded transfer call set used in Experiment 2 was presented. The purpose of this training was to release the transfer calls from inhibition generalized from the original calls used in Experiment 1. Once birds responded to the transfer calls at a rate approximately equal to the rate of responding to the S+ calls observed during the last 500 trials of Experiment 2, they were put back on Experiment 2 for a minimum of 500 trials prior to the propagation test to ensure that their within- and between-category discriminations were maintained (see Figure 3-3). This training was important because the level of responding to the rewarded transfer calls provides a logical baseline for the propagation test.

In Experiment 3, contingencies for within-category S+ and S- exemplars remained unchanged from Experiments 1 and 2, and the original 15 between-category S- exemplars from Experiment 1 were presented, but these exemplars were now rewarded (S+). Experiment 3 concluded after 500 trials (about 11 trials per exemplar).

Results

Figure 3-4 shows the percentages of responses to the original between-category calls during the last 500 trials of Experiment 1 and the 500 trials of Experiment 3. Percentages of responses to the S+ and within-category S- stimuli were maintained across Experiments 1 and 3, but responding to the between-category calls rose from below the level of responding to within-category S- calls in Experiment 1 toward the level of responding to S+ calls in Experiment 3.

We conducted a mixed model Birds × S+ Group × Sex × Experiment ANOVA on the percentages of responses obtained to the between-category exemplar set during the last 500 trials of Experiment 1 (discrimination) and the 500 trials of Experiment 3 (propagation). There were no main effects of Birds, S+ Group, or Sex, or any higher-order interactions, $ps > 0.128$, however there was a main effect of Experiment, $F(1, 24) = 359.00$, $p < 0.001$. Tukey's planned comparisons revealed that sympatric and allopatric black-capped chickadees and mountain chickadees responded significantly more to the between-category calls during Experiment 3 ($M = 67\%$) compared to responding observed in Experiment 1 ($M = 4\%$, see Figures 3-4A-F)

As noted in Experiment 2, one might suggest that the birds maintained a high level of responding to the original between-category stimuli in Experiment 3 because they were unable to perceive a change in stimulus sets from Experiment 2 to Experiment 3. To determine whether the responding observed in Experiment 3 was a result of the birds not detecting a change in the between-category stimulus sets, we compared the percentages of responses to the novel between-category calls during the last 500 trials of Experiment 2 (or following pretraining) with responding to the original between-category calls during the 500-trial block in the propagation test in a mixed model Birds × S+ Group × Experiment ANOVA.

There was a main effect of Experiment, $F(1, 30) = 19.67, p < 0.001$, revealing that birds responded slightly but significantly less to the between-category exemplars at the beginning of Experiment 3 ($M = 67\%$) compared to responding at the end of Experiment 2 ($M = 77\%$), and there were no differences among species or groups. These findings suggest that although levels of responding to the between-category transfer exemplars propagated back to the original exemplars, they nonetheless discriminated between the two exemplar sets.

Discussion

In Experiments 1-3 we investigated whether black-capped and mountain chickadees would use an open-ended categorization strategy to facilitate discriminations between black-capped and mountain chick-a-dee calls. By testing simultaneous within- and between-category discriminations in Experiment 1, transfer to different exemplars in Experiment 2, and propagation back to the original exemplars in Experiment 3, we were able to provide evidence that mountain and black-capped chickadees use open-ended categorization rather than rote memorization to respond appropriately to conspecific and heterospecific chick-a-dee calls.

Experiment 1: Within- and Between-Category Discriminations

In Experiment 1 we sought to determine whether black-capped chickadees that originated from a region inhabited by mountain chickadees (i.e., sympatric chickadees) would be more or less likely to classify the chick-a-dee calls as belonging to two separate categories compared to black-capped chickadees unfamiliar with mountain chickadees (i.e., allopatric chickadees). In other words, originating from the same region as mountain chickadees and having extensive experience with mountain chickadee chick-a-dee calls suggested to us that perhaps the sympatric black-capped chickadees would treat the chick-a-dee calls of both species as belonging to one chick-a-dee call-category rather than belonging to two separate chick-a-dee call species-categories. While sympatric and allopatric birds learned at about equal rates to withhold responding to S- between-category chick-a-dee calls, allopatric birds in both groups responded significantly less to between-category S- exemplars compared to within-category S- exemplars than did sympatric birds. One possible interpretation of this could be that sympatric birds initially treated all S- chick-a-dee calls as belonging to one, in this case, nonrewarded, chick-a-dee call category while allopatric birds treated the S- within- and between-category calls as belonging to two separate species' categories.

Similar to that of sympatric black-capped chickadees, mountain chickadees continued to respond at about equal levels to the S- within-category exemplar set and the S- between-category exemplar set when allopatric black-capped chickadees were responding significantly less to S- between-category calls compared to S- within-category calls. This again could be interpreted as mountain chickadees initially treating conspecific and heterospecific chick-a-dee calls as belonging to one overarching chick-a-dee call category rather than as belonging to two species' call categories. Nonetheless, over blocks of trials all birds learned more quickly to withhold responding to the S- between-category exemplar set compared to the S- within-category exemplar set, the first necessary step for determining that an open-ended categorization strategy is being used.

Experiment 2: Transfer of Inhibition

In order to obtain further evidence for the use of open-ended categorization, we transferred the birds to different, and now rewarded, between-category stimuli in Experiment 2. Here we were interested in the initial responses by the birds, prior to any significant learning of the new exemplars and contingency. Over the first 1,000 trials all birds continued to withhold responding to between-category transfer calls in accordance with the rule learned with the original between-category exemplars in Experiment 1. Further, a significant increase in responding during the initial trials of Experiment 2 compared to responding at the end of Experiment 1 suggests that birds did indeed perceive the differences between the Experiment 1 and Experiment 2 between-category exemplar sets. Moreover, it is unlikely that this observed increase in responding was solely the result of learning of the new contingency, as birds would have only experienced each exemplar a few times during those 500 trials (about 11 presentations of each exemplar). Therefore, we conclude that the initial low levels of responding provide evidence of generalization. In summary, withholding responding during the initial presentations of transfer stimuli suggests that birds perceive the necessary or sufficient features for category membership, an important requirement to conclude that black-capped and mountain chickadees sort their own and the other species' chick-a-dee calls into separate open-ended categories.

Based on their patterns of responding in Experiment 1, we suggested that sympatric and mountain chickadees may perceive the S- within- and between-category chick-a-dee calls as belonging to one 'chick-a-dee' call category, defined by their contingency (S-), rather than to two 'species' call categories. While there was no requirement to respond differentially to the two S- exemplar sets, allopatric chickadees responded significantly less to between-category S- exemplars compared to responding to S- within-category exemplars. In Experiment 2, allopatric birds required more trials to learn to respond to between-category transfer calls whereas sympatric chickadees quickly learned to respond to these calls. This response inhibition following discrimination training in Experiment 1 could further suggest that allopatric birds have more clearly defined species' categories than sympatric chickadees. In other words, if sympatric birds perceived chick-a-dee calls as belonging to contingency-defined (i.e., S+ and S-) categories, then a sharp increase in responding to now rewarded chick-a-dee calls would support this finding. However, further studies would be required to fully examine this possibility.

Experiment 3: Propagation

In Experiment 3 we pitted the learning that had occurred in Experiment 1 with the learning that had occurred in Experiment 2 by reintroducing the original set of 15 between-category calls. However, unlike Experiment 1, in Experiment 3 these calls were now rewarded. Here we asked whether birds would respond to the calls in this exemplar set as they had learned in Experiment 1 (i.e., withhold responding), or would birds respond according to the most recently learned contingency associated with the category from Experiment 2 (i.e., positive, or rewarded). Evidence for the former would suggest that birds had memorized each exemplar and its associated contingency in Experiment 1, while evidence for the latter would suggest that birds had learned a category-associated contingency in Experiment 2 and perceived the calls in this exemplar set as belonging to that same category.

In short, the high level of responding to between-category calls observed in Experiment 3 suggested that birds perceived the original exemplars as belonging to the same category as the between-category transfer exemplars used in Experiment 2, where birds learned that operant responses made to calls of this category were rewarded. Compared to the responding to the original between-category calls in Experiment 1, birds responded significantly more to these same between-category exemplars in Experiment 3, a category-specific response that they had learned in Experiment 2. Further, statistical differences observed during the last 500 trials of Experiment 2 and the first 500 trials of Experiment 3 suggest that indeed birds perceived the two exemplar sets as distinct. To conclude, results from the current experiments provide conclusive evidence that black-capped and mountain chickadees perceive their own and the other species' chick-a-dee calls as belonging to two separate open-ended categories, into which a possible unlimited number of novel chick-a-dee calls of either species, regardless of one's previous experience, can be assigned.

Sex and Species Effects

For several reasons we did not directly assess whether there were any statistical differences between male and female chickadees in their ability to discriminate either within or between call categories. First, we did not detect any main effects of sex in our statistical analyses. Second, our sample sizes became increasingly smaller as we considered other factors (e.g., birds, group assignment). Third, results of previous studies with chickadees (e.g., Charrier, Lee, Bloomfield, & Sturdy, 2005; Lee et al., 2006; Sturdy et al., 2000) and with chick-a-dee calls (Bloomfield et al., 2003) did not detect any differences in the perceptual abilities of male and female chickadees. In nature, both male and female chickadees produce and perceive chick-a-dee calls (e.g., for flock coordination and flock recognition), and therefore it is not surprising that previous studies have found no differences. That said, the possibility remains that one sex may indeed be more adept at categorizing other vocalizations, such as the 'gargle' call, which is produced mostly by male chickadees during male-male aggressive interactions (Ficken, Weise, & Reinartz, 1987).

We examined whether black-capped and mountain chickadees were better at within-category discriminations when exemplar chick-a-dee calls were conspecific or heterospecific. Although all chickadees learned to discriminate among the 30 within-category chick-a-dee calls, a different pattern of results appeared for sympatric, allopatric, and mountain chickadees. Sympatric black-capped chickadees more quickly learned to discriminate among conspecific S+ and S- within-category chick-a-dee calls than did sympatric black-capped chickadees learning to discriminate among heterospecific S+ and S- chick-a-dee calls. Allopatric black-capped chickadees required an additional 500 trials compared to sympatric chickadees to discriminate among conspecific chick-a-dee calls but learned to discriminate among heterospecific chick-a-dee calls in the same number of trials as was required to discriminate among conspecific calls. Finally, mountain chickadees required more trials to discriminate among conspecific chick-a-dee calls compared to mountain chickadees discriminating among heterospecific chick-a-dee calls.

While one might predict that the memorization of conspecific calls and their associated contingencies is easier than the memorization of heterospecific calls and their contingencies, this only appeared to be the case for sympatric chickadees. Further, one might predict that memorizing heterospecific calls and their contingencies would be easier for birds with previous experience with the heterospecific birds, however sympatric and allopatric chickadees mastered this discrimination at about equal rates and in fact, allopatric birds discriminated among 30 heterospecific calls in the same number of trials as allopatric birds discriminating among conspecific calls. Perhaps most intriguing and unexpected was the finding that mountain chickadees had more difficulty learning to discriminate among conspecific S+ and S- calls than among heterospecific S+ and S- calls. These results are in contrast to results obtained for budgerigars (*Melopsittacus undulates*), canaries (*Serinus canaria*), and zebra finches (*Taeniopygia guttata*), where each of these species more quickly discriminated among conspecific than among heterospecific vocalizations, despite their capability to discriminate among the other species' vocalizations as well (Dooling, Brown, Klump, & Okanoya, 1992). However, previous results obtained with chickadees (Phillmore, Sturdy, Turyk, & Weisman, 2002) found that black-capped chickadees did not show a species-specific advantage in individual recognition for conspecific over heterospecific (zebra finches) vocalizations. Further, these results are in line with a previous, similar study which found that black-capped chickadees were slightly faster at discriminating among the calls of Carolina chickadees compared to learning to discriminate among conspecific chick-a-dee calls (Bloomfield et al., 2003). While it is unclear why mountain chickadees in the current study were better at discriminating among the 30 black-capped chick-a-dee calls, future studies, such as a species-specific note-type discrimination task, will help determine whether some note types within the calls of each species are more easily recognized and memorized by con- and heterospecifics.

Future Directions

The results from the current set of experiments suggest several potential avenues for future research. For example, that sympatric and allopatric black-capped chickadees were capable of both within- and between-category discriminations of heterospecific vocalizations, combined with similar evidence from previous studies (e.g., Bloomfield et al., 2003; Dooling et al., 1992), suggests that the ability to perceive conspecific and unfamiliar heterospecific vocalizations as belonging to separate categories may not require prior knowledge or extensive learning, and thus may be innate. Nonetheless, an examination of birds reared in auditory isolation from normal conspecifics (e.g., Dooling, Park, Brown, & Okanoya, 1990), followed by experiments similar to those conducted here, will ultimately help us understand whether animals in general, and chickadees in particular, perceive auditory stimuli as belonging to distinct species-specific categories innately, or whether development and social factors play a role.

In addition, in the current experiments both sympatric and allopatric chickadees perceived the same species-specific categories, however we do not know whether there are any differences in the mechanisms which birds discriminated these perceptual categories. In other words, do the birds from the different regions attend to different portions or features of the call, yet ultimately perform equally? For example, do allopatric chickadees use the terminal 'dee' portion of the mountain chick-a-dee call while sympatric chickadees use the introductory 'chick-a' portion? Related to this, perhaps chickadees from different regions are more adept at discriminating species using individual chick-a-dee call notes. A linear discriminate analysis of black-capped and mountain chick-a-dee call notes accurately sorts species based on the spectral and temporal parameters of the note types (Dawson, Bloomfield, Charrier, & Sturdy, 2006), however we do not know whether birds are capable of using any or all of these features for discrimination. Further, using signal modification techniques in conjunction with field- and laboratory-based experiments, including an analysis of the neural activity involved in their perception, we will ultimately identify the categories, the perceptually relevant features of these categories, and the acoustic limits of these categories.

Natural Categories

Here we contribute to the growing body of evidence of category perception in animals (e.g., see Pearce, 1994 for a review) and suggest that among chickadees, their entire vocal repertoire may consist of a hierarchically-organized and biologically-relevant categories. We know that chickadees perceive as open-ended categories the different chick-a-dee call notes (black-capped chickadees; Sturdy et al., 2000) and entire chick-a-dee calls of their own and other chickadee species (black-capped and Carolina chickadees; Bloomfield et al., 2003; current experiments). Still awaiting investigation is the extent to which other open-ended acoustic categories exist, such as vocalization type (e.g., fee bee songs and chick-a-dee calls as belonging to a different categories of chickadee vocalizations), call variation (e.g., chick-a-dee calls with and without A notes, but see Baker & Becker, 2002; Freeberg & Lucas, 2002; Templeton, Greene, & Davis, 2005), individual (e.g., across different vocalization types), dialect (e.g., own-flock, not-own-flock), social relationship (e.g., dominant, subordinate), or sex. The present collection of experiments, in combination with results of future studies will both elaborate on our knowledge of intra- and inter-specific communication in chickadees, and further implicate the potential for a cognitive link between human and non-human animals in categorization abilities.

Figure 3-1.

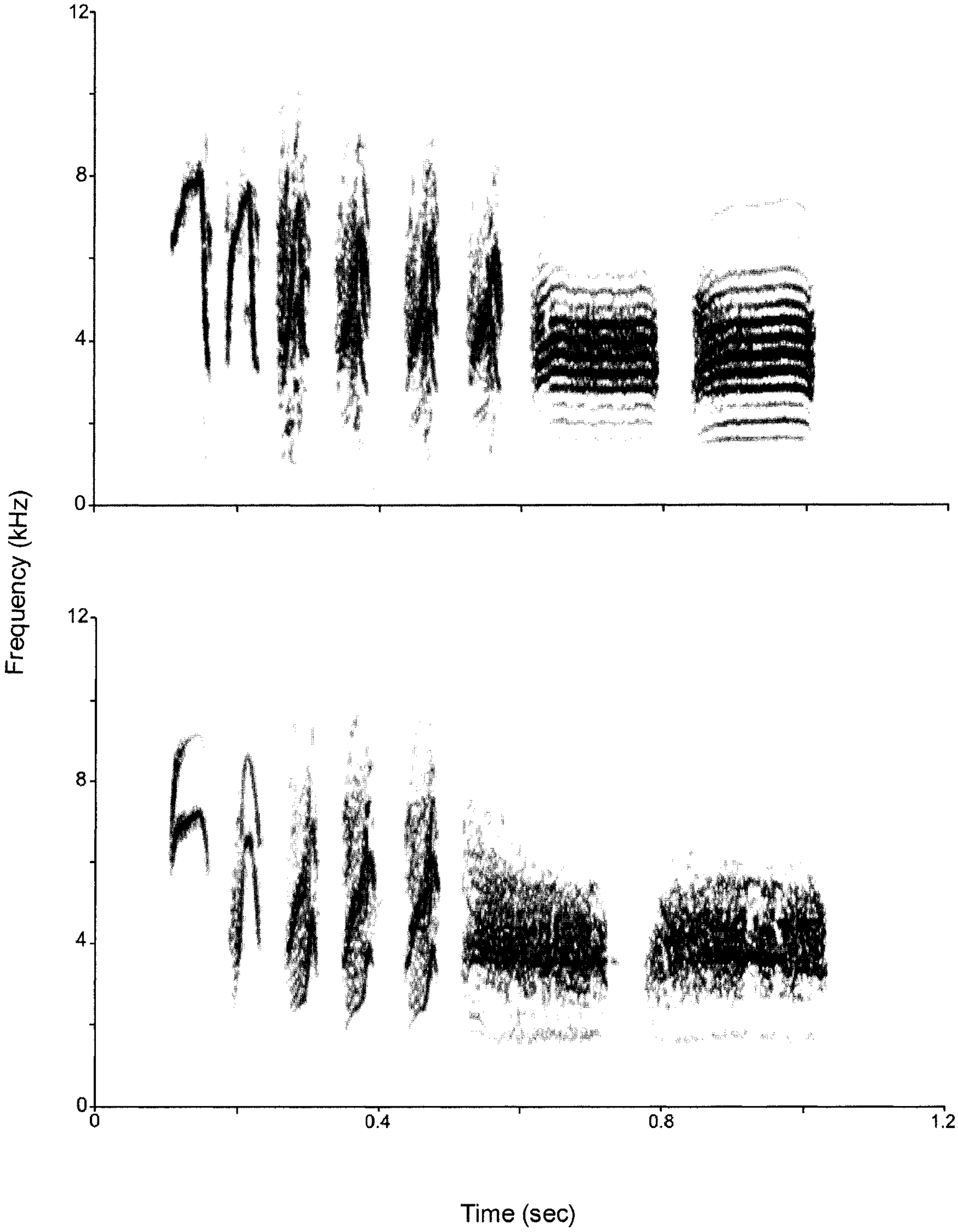

Figure 3-2.

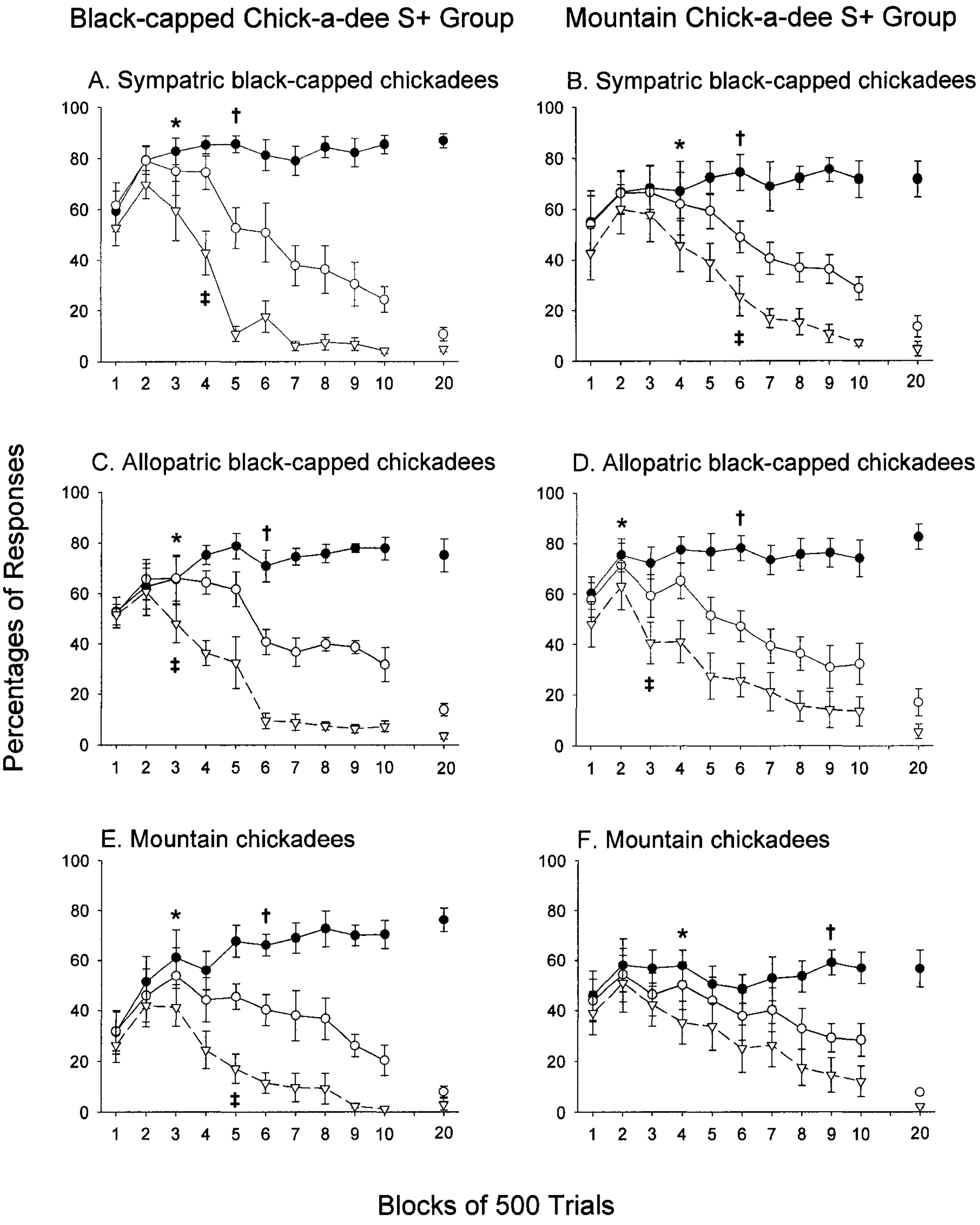
Black-capped Chick-a-dee S+ Group
Mountain Chick-a-dee S+ Group
A. Sympatric black-capped chickadees
B. Sympatric black-capped chickadees
C. Allopatric black-capped chickadees
D. Allopatric black-capped chickadees
E. Mountain chickadees
F. Mountain chickadees
Percentages of Responses
Blocks of 500 Trials
0
20
40
60
80
100
1
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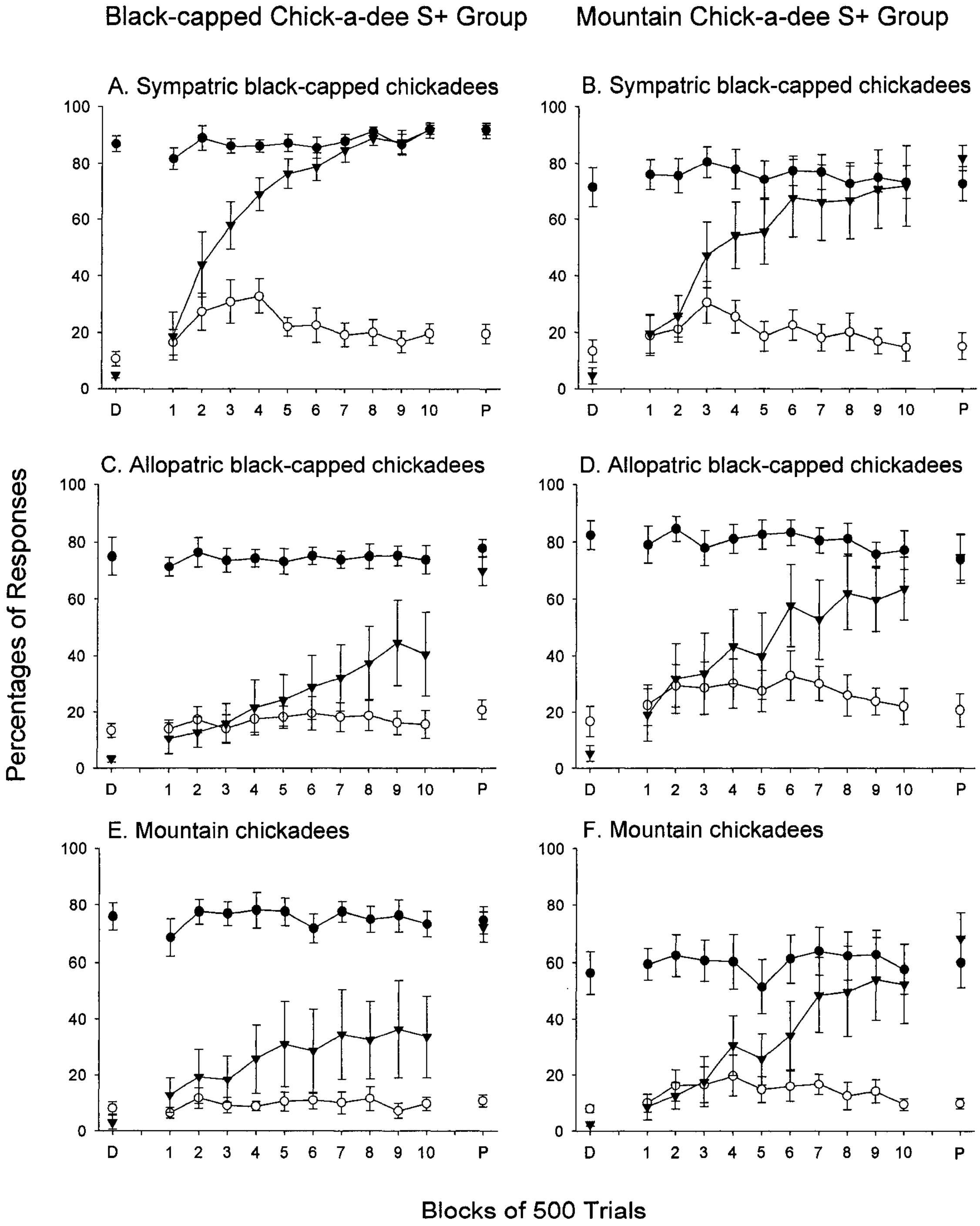
Figure 3-3.


Black-capped Chick-a-dee S+ Group
Mountain Chick-a-dee S+ Group
A. Sympatric black-capped chickadees
B. Sympatric black-capped chickadees
C. Allopatric black-capped chickadees
D. Allopatric black-capped chickadees
E. Mountain chickadees
F. Mountain chickadees
Percentages of Responses
0
20
40
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100
D
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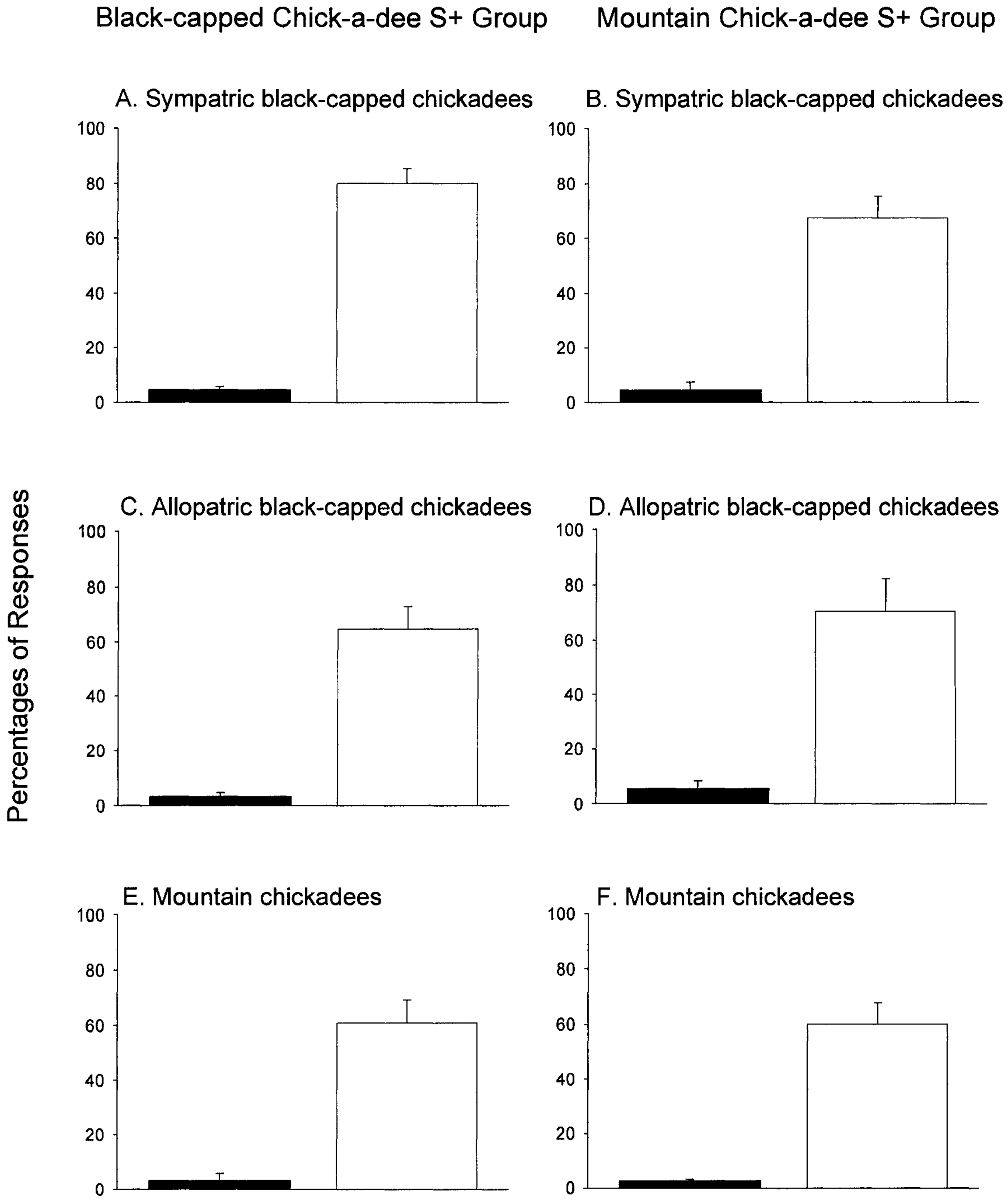
Blocks of 500 Trials

Figure 3-4.


Black-capped Chick-a-dee S+ Group
Mountain Chick-a-dee S+ Group
A. Sympatric black-capped chickadees
B. Sympatric black-capped chickadees
C. Allopatric black-capped chickadees
D. Allopatric black-capped chickadees
E. Mountain chickadees
F. Mountain chickadees
Percentages of Responses
100
80
60
40
20
0

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Chapter 4: All "chick-a-dee" calls are not created equally. Part II: Mechanisms for discriminations by sympatric and allopatric chickadees

A version of this paper is in press. Bloomfield, L.L., Farrell, T.M., & Sturdy, C.B. *Behavioural Processes*.

Introduction

Acoustic communication is often the primary means by which many songbird species identify conspecifics and discriminate them from heterospecifics (see Becker, 1982), especially when natural obstructions such as vegetation can hinder visual communication. Songbirds spend a large proportion of their time defending territories, attracting mates, and foraging, and have evolved methods of recognizing species and individuals based on their auditory signals (Becker, 1982; Falls, 1982). Territory owners learn to recognize the acoustic signals of their neighbours to avoid unnecessary confrontations with familiar birds and mount strong aggressive responses towards invading strangers (see Stoddard, 1996), thereby increasing the fitness of the individual (McArthur, 1982). Furthermore, songbirds must be discriminating when selecting a mate, and avoid courting heterospecifics (Ratcliffe & Otter, 1996). Clearly, acoustic signals provide conspecifics, and perhaps heterospecifics, with cues critical to fitness and survival.

Chickadees (genus *Poecile*) provide an excellent model system for studying acoustic communication because both their song and some of their calls are learned (Hughes, Nowicki, & Lohr, 1998; Shackleton & Ratcliffe, 1993). Moreover, all members of the genus *Poecile* produce a species-typical variant of the chick-a-dee call (see Ficken, Ficken, & Witkin, 1978; Ficken, Hailman, & Hailman, 1994; Ficken, McLaren, & Hailman, 1996; Gaddis, 1985; Hailman & Ficken, 1996; S.T. Smith, 1972). Finally, in some regions two or more species occupy the same areas, suggesting that both intra- and inter-specific vocal discriminations may occur.

The vocal repertoire of the black-capped chickadee is arguably the most well studied of all the chickadee species. Their chick-a-dee call, associated with mild alarm and flock communication and co-ordination (Ficken et al., 1978; S.M. Smith, 1991), consists of four note types; A, B, and C notes, which constitute the introductory 'chick-a' portion, and D notes, which constitute the terminal 'dee' portion (see Figure 4-1). While maintaining a fixed syntactical ordering of the notes within calls (A through D), any of the notes can be repeated or omitted to produce a seemingly infinite number of call types (Hailman, Ficken, & Ficken, 1985). Black-capped chickadees perceive differences among chick-a-dee calls to discriminate flock mates from non-flock mates (Mammen & Nowicki, 1981), among different chickadee species (Bloomfield & Sturdy, in press; Bloomfield, Sturdy, Phillmore, & Weisman, 2003), and potentially among individuals (Charrier, Bloomfield, & Sturdy, 2004). It therefore seems that chick-a-dee calls have the potential to convey a plethora of information to the conspecific listener.

Most closely related to the black-capped chickadee is the mountain chickadee (Gill, Mostrom, & Mack, 1993). While the black-capped chickadee inhabits the northern United States and most of Canada, the mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (McCallum, Grundel, & Dahlsten, 1999; S.M. Smith, 1993). In some regions the two species live sympatrically and engage in interspecific activities such as foraging (pers. obs.), however in the sympatric regions of the western Rocky Mountains, birds do not appear to interbreed or exhibit interspecific competition (Hill & Lein 1989). In common with the black-capped chick-a-dee call, the chick-a-dee call of the mountain chickadee is used is similar contexts (Gaddis, 1985) and consists of the 'standard' A, B, C and D notes, as well as two unique intermediary notes, A/B notes in the introductory 'chick-a' portion and D-hybrid notes in the terminal 'dee' portion (Bloomfield, Charrier, & Sturdy, 2004). Call notes are produced in a fixed syntactical order of A→ D, and note types may be omitted entirely or repeated. Also in common with black-capped chickadees, mountain chickadees perceive differences between their own chick-a-dee calls and the chick-a-dee calls of heterospecifics (black-capped chickadees, Bloomfield & Sturdy, in press), however the important or salient species-specific features used for these discriminations, and whether different strategies are used by the different species or those from differing geographic origins, are not known.

Here we employ a 'go/nogo' operant discrimination task to gain an understanding of (1) whether chickadees use the introductory 'chick-a' portion or the terminal 'dee' portion of chick-a-dee calls for discriminating conspecific chick-a-dee calls from heterospecific chick-a-dee calls, (2) whether there are differences between black-capped and mountain chickadees in the features used for these discriminations, and (3) whether black-capped chickadees with previous experience with mountain chickadees (i.e., sympatric chickadees) rely on different portions or features of chick-a-dee calls for species' discriminations compared to inexperienced (i.e., allopatric) black-capped chickadees. Our logic here is that given their extensive experience with mountain chickadee's calls, sympatric black-capped chickadees may be more adept at using *either* the introductory *or* terminal portions for discriminating between the calls of the two species. Alternatively, the allopatric chickadees, with no experience with the calls of mountain chickadees, may rely on only the terminal 'dee' portion, the portion that, at least to human ears, is easier to distinguish between the species.

General Methods

Animals

A total of 31 birds (19 black-capped chickadees and 12 mountain chickadees) at least one year of age (determined by the shape and coloring of the outer tail retrices, Pyle, 1997) and naïve to the experimental procedures served in the current set of experiments. All birds were captured between December 2003 and February 2005. Eleven black-capped chickadees were caught in several regions of Edmonton Alberta (53° 06'N, 113° 04'W) and had no prior exposure to mountain chickadees (the *allopatric* group), as chickadees are non-migratory and mountain chickadees do not naturally occur in these areas. Eight black-capped chickadees and 12 mountain chickadees were caught in several regions in Kananaskis Country, Alberta, Canada (51° 02'N, 115° 03'W) and therefore these 8 black-capped chickadees had prior exposure to mountain chickadees (the *sympatric* group), as both species are prolific to these areas (pers. obs.). Sex identification was conducted by DNA analysis (Griffiths, 2000).

Each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages (0.3m wide x 0.4m high x 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada) for a minimum of 1 month prior to the commencement of the experiments. The housing conditions allowed for auditory and visual but not physical contact among birds of the same species. Birds were maintained on a day-light cycle consistent with the natural cycle for the time of year (January – August). Therefore, daylong sessions ranged from about 7.5 hours (January) to a maximum of about 17 hours (June).

Prior to experimentation birds were given *ad libitum* access to lab food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), cuttle bone, grit, and water (vitamin-supplemented on alternate days, Hagen, Rolf C. Hagen, Inc., Montreal Canada).

Birds were also given 1 meal worm three times per week and hard-boiled egg and spinach mixture twice a week.

During the experiment, standard rations were available only when an appropriate operant response was produced. Birds were given *ad libitum* access to cuttle bone, grit and water (vitamin-supplemented on alternate days). Two meal worms were provided daily (morning and evening) to ensure good health throughout the duration of the experiments.

Apparatus

Modified budgerigar cages (0.3 m wide × 0.4 m high × 0.4 m deep) provided continuous housing for the birds during training and testing periods. To ensure the birds did not have access to spilled food, a mesh floor was attached near the bottom of the cage. Each cage was contained in a ventilated, sound-attenuated chamber illuminated by a 9-W twin-tube full-spectrum fluorescent bulb and had several perches and dispensers for water and grit. Infrared cells monitored a motor-driven feeder (Njegovan, Hilhorst, Ferguson, & Weisman, 1994) mounted beside the cage, and a perch opposite the feeder entrance monitored the bird's position. Access to the feeder was made possible by an opening (11 cm wide × 16 cm high) in the cage. A single-board computer (Palya & Walter, 2001) interfaced to a personal computer controlled a standard CD-ROM, scheduled the experiment and recorded responses to stimuli. Stimuli were played at 75-85 dB (A weighting, slow response, measured using a Radio Shack Sound Level Meter) from a CD to either a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or a NAD 310 Integrated Amplifier (NAD Electronics, London, England) and then to a Fostex FE108Σ full-range speaker (Fostex Corp., Japan) located beside the feeder (effective frequency response 200-16,000 Hz). The center of the speaker was at the height of the bird's head when the bird stood on the perch.

Stimuli Preparation

A total of 112 chick-a-dee calls (56 black-capped chick-a-dee calls and 56 mountain chick-a-dee calls, see Fig. 4-1A, 4-1B), recorded using a variety of microphones and recorder types, were randomly selected from several sources (our own database, recordings provided by other researchers, commercially available compact discs, bioacoustics libraries) for use in the current set of experiments. A small proportion of the recorded calls originated from birds that had been captured from the same location as the experimental birds on previous trapping years. That said, because there was at least 12 months between successive trapping events, it is unlikely that birds trapped on successive years would be familiar with previously trapped birds, and certainly not with their particular calls that were recorded in the laboratory and used as stimuli. Further, to reduce any possible influence of familiarity on discrimination, all call stimuli were randomly assigned to the training and testing stimulus sets (see below), and therefore overall performances by the birds in the current study were unlikely to be influenced by potential familiarity with a few of the recorded birds.

Calls were randomly assigned to either one of the 2 training sets or one of the 4 probe stimulus types. The first training set, used during the acquisition phase, consisted of 10 calls of each species (see Figures 4-1A, 4-1B). The second training set, used during the Transfer 1 phase, consisted of 10 different calls of each species. The four probe stimulus types included: (1) Spliced Control calls - 6 calls of each species created using introductory and terminal portions from 12 calls of each species; (2) Multi-Species

Spliced calls - 12 calls created using introductory portions of one species' calls and terminal portions of the other species' calls; (3) Introductory-only calls - 6 introductory 'chick-a' portions of each species calls (terminal portion removed); (4) Terminal-only calls - 6 terminal 'dee' portions of each species calls (introductory portion removed).

All calls were bandpass filtered (1,000 – 10,000 Hz) using GoldWave Version 5.12, (GoldWave, Inc., St. John's, NF) to remove background noise, and using SIGNAL 4.0 sound analysis software (Engineering Design, CA) each call was viewed in a spectrogram (cutoff amplitude -35 dB relative to peak amplitude) to equalize call amplitude and taper the leading and trailing 5-ms of silence to remove transients, and was subsequently saved as an individual 2-s sound file by inserting silence after the end of the call. All calls to be used as probe stimuli (n = 72 calls) were further prepared according to the methods below. It is important to note that none of the recorded chick-a-dee calls was used more than once, either in whole or in part.

Spliced Control calls. Calls (n = 12 of each species) were examined in sound spectrograms to ensure that both the introductory portion of each call (consisting of A-, B-, and C-type notes) and the terminal portion of each call (consisting of D-type notes) contained a minimum of two notes. Any call that did not meet this criterion was randomly exchanged with a call from one of the training sets, ensuring that no call, in whole or in part, was used more than once. Six of the 12 calls were randomly selected for their introductory portion and were randomly paired with the remaining 6 calls in which the terminal portions would be used. The sound spectrogram of each introductory-portion call was opened in SIGNAL 4.0 and the terminal portion of the call was removed at the point of the start of the first D-type note. The leading and trailing 5-ms of silence was tapered and each introductory-portion call was saved as an individual file. Similarly, the sound spectrogram of each of the remaining 6 calls were opened in SIGNAL 4.0 and the introductory portion of the call was removed at the point of the end of the last introductory note (either A, B, or C note). The leading and trailing 5-ms of silence was tapered and each terminal-portion call was saved as an individual file. Subsequently, paired introductory and terminal portions were opened in Signal, spliced together, and each call was saved as an individual 2-s sound file by inserting silence after the end of the manufactured call (see Figures 4-1C, 4-1D).

Multi-Species Spliced calls. Calls (n = 12 of each species) were examined in sound spectrograms to ensure that both the introductory portion of each call (consisting of A, B, and C note types) and the terminal portion of each call (consisting of D note types) contained a minimum of two notes. Any call that did not meet this criterion was randomly exchanged with a call from one of the training sets, ensuring that no call, in whole or in part, was used more than once. Methods for separating introductory portions and terminal portions were identical to methods used for creating Spliced Control calls (above). Six of the 12 black-capped chickadee calls were randomly selected for their introductory portion and the remaining 6 calls would be used for their terminal portions. The same random selection was conducted with the 12 mountain chickadee calls. Once separated, the leading and trailing 5-ms of silence was tapered and each introductory and terminal portion was saved as an individual file. Subsequently, introductory and terminal portions were spliced together in Signal 4.0, resulting in 12 unique calls; 6 calls consisting of black-capped chickadee introductory portions (and mountain chickadee terminal portions), and 6 calls consisting of mountain chickadee introductory portions (and black-capped chickadee terminal portions). Each call was saved as an individual 2-s sound file by inserting silence after the end of the call (see Figures 4-1E, 4-1F)

Introductory- and Terminal-only calls. Calls (n = 6 of each species) were separated into introductory and terminal portions using methods identical to those for creating Spliced Control and Multi-Species Spliced calls (above), however in this case introductory and terminal portions remained separated and only *either* the introductory portion or the terminal portion of each call was retained for use. Each call was saved as an individual 2-s sound file by inserting silence after the end of the call (see Figures 4-1G, 4-1H). The 40 training stimuli and the 48 probe stimuli were then transferred to compact discs, one call per track.

Procedure

Nondifferential Training. Nondifferential training began after a bird had learned to use the perch and feeder. When a bird landed on the perch, breaking an infrared beam, the within-trial sequence began. Remaining on the perch for 1-s on average (range 900-1,100 ms) resulted in a single call being randomly selected and played once (70-80 dB). If the bird flew or hopped to the feeder within 1-s after the stimulus is played, breaking another infrared beam, it was rewarded with 1-s access to food, followed by a 30-s inter-trial interval (ITI). If the bird left the perch without entering the feeder the trial ended after 1-s. If the bird failed to leave the perch the trial ended after 1-s and a 60-s ITI follows. The 60-s ITI was used to increase the probability of the bird leaving the perch on all trials. Leaving the perch before the stimulus had finished playing resulted in the trial ending and the chamber lights turning off during a 30-s ITI. These procedures helped us to ensure that birds heard and attended to the calls and subsequently left the perch.

During nondifferential training, we presented all the calls in the training sets but none of the calls created for the probe sets. The purpose of nondifferential training was to ensure that the birds heard and responded to all the calls and to gather similar percentages of responses to each call as a baseline for the evaluation of training during Probe sessions.

Acquisition Training. Acquisition training began after nondifferential training and continued throughout the experiment. During acquisition training, visits to the feeder after S+ (positive, or reinforced) calls were rewarded with access to food, but visits to the feeder after S- (negative, or nonreinforced) calls resulted in no reward and a 30-s ITI with the chamber lights off. Other procedures initiated during nondifferential training remained in effect during acquisition training. For example, as during nondifferential training, on each trial a single call was selected randomly and without replacement from the stimulus set. Further details about the stimulus calls used are presented in the methods sections for each experiment. Typically, each daylong session generated about 1,000 trials.

Response Measures and Statistical Analyses. We calculated a percentage of response measure for each stimulus (whether S+ or S–) using the following formula: (R+/(N trials – N interrupted trials)) × 100, where R+ is the number of trials on which the bird flew or hopped to the feeder, N trials is the total number of trial presentations for that stimulus, and N interrupted trials is the number of trials in which the lights were extinguished for the bird leaving the perch before the stimulus was played in its entirety. To facilitate comparisons among groups of birds, we scaled the percentages of responses to probe stimuli for each individual subject. Specifically, the highest percentage of response obtained for a probe stimulus was rescaled to 100%, and all other percentages of responses were represented as a ratio of the highest percentage of responding. This method was conducted on the average probe responses for each bird, and ultimately eliminated the problem of individual variation in the overall levels of responding, and allowed for a more critical analysis of the distribution of responses. We conducted analyses of variance (ANOVAs) and planned comparisons (Tukey's) on percentages of responses using STATISTICA (Version 6, StatSoft, Inc., 2003). When percentages of responses are near 0% or 100%, sample values may not be normally distributed. We therefore conducted parallel ANOVAs using arcsine square-root transformations of the percentages of responses. Analysis of transformed data yielded the same pattern of results with the same levels of significance as untransformed data, with two minor exceptions. Therefore, results for ANOVAs of the untransformed data are reported here, as well as the two differing results obtained with the transformed data in the probe analysis.

Training Phase 1: Acquisition

Methods

Prior to testing the putative mechanism(s) used by black-capped and mountain chickadees for discriminating each species' chick-a-dee calls, a baseline for discrimination was established during the initial phase of training (acquisition phase). Birds were presented with 10 black-capped chick-a-dee calls and 10 mountain chick-a-dee calls; calls of one species provided food reinforcement (S+) 100% of the time for flying to the feeder, and calls from the other species did not provide food reinforcement (S-). Birds were randomly assigned to either the black-capped chick-a-dee S+ call group (BCCH-S+ group, *N* = 15, 3 male and 3 female mountain chickadees, 2 male and 2 female sympatric black-capped chickadees, and 3 male and 2 female allopatric black-capped chickadees) or the mountain chick-a-dee S+ call group (MOCH-S+ group, N = 16, 3 male and 3 female mountain chickadees, 2 male and 2 female sympatric black-capped chickadees, and 3 male and 3 female allopatric black-capped chickadees). This phase of training continued until the birds completed a minimum of six 500-trial bins with a discrimination ratio (DR) $\geq$ than 0.80, with the last 2 bins occurring consecutively.

Results

Nondifferential Training. During nondifferential training, birds were presented with all 40 chick-a-dee calls that would be used during training phases 1 and 2 (acquisition and Transfer 1), and were provided with 100% reinforcement for flying to the feeder following each call. This provided us with a consistent level of responding to all calls prior to acquisition/discrimination training. Once birds were responding at least 60% of the time to all calls and no statistical differences in responding occurred between each set of calls (i.e., between black-capped chick-a-dee calls and mountain chick-a-dee calls, examined daily using individual t-tests, $p < 0.05$, see Fig. 4-2), acquisition training began.

Acquisition Training. Chickadees in both S+ groups learned to fly to the feeder following S+ stimuli and learned to withhold flying to the feeder following S- stimuli in a minimum of 4,000 trials (i.e., the fewest number of trials required by some subjects to reach criterion). We conducted a mixed model Birds (sympatric black-capped chickadee, allopatric black-capped chickadee, mountain chickadee) × S+ Group (BCCH-S+, MOCH-S+) × Sex (male, female) × Exemplar Set (black-capped chick-a-dee calls, mountain chick-a-dee calls) × Trial Blocks (1-8) ANOVA on the percentages of responses obtained in each 500-trial block to examine whether there were any differences among black-capped and mountain chickadees in their discrimination abilities. There were no main effects of Species, Sex, or Group, *p*s > 0.266, however there was a main effect of Exemplar Set, $F(1, 19) = 4.93$, $p = 0.039$, of Blocks, $F(7, 133) = 11.30$, $p < 0.001$, and several higher-order interactions, indicating that birds in each group learned over trials to respond to the S+ stimuli and to withhold responding to the S- stimuli.

We further investigated our *a priori* prediction that learning rates may differ between sympatric and allopatric black-capped chickadees and mountain chickadees by conducting planned comparisons (Tukey's, $p < 0.05$). We chose to exclude the Sex factor because (1) there was no main effect of Sex in the omnibus ANOVA, (2) previous studies investigating chick-a-dee call perception in chickadees have yielded no differences in discrimination abilities between males and females (e.g., Bloomfield et al., 2003; in press), and (3) group sizes become increasing smaller (*n*s < 3) when considering the remaining factors (species and group assignment). To further facilitate comparisons we present the results below based on group assignment.

BCCH-S+ group

After the first 500 trials, sympatric, allopatric, and mountain chickadees responded significantly less to the mountain chick-a-dee S- exemplars than to the black-capped chick-a-dee S+ exemplars. All birds continued to discriminate S+ from S- exemplars throughout the duration of Training Phase 1 (i.e., 4,000 trials, see Figures 4-2A, 4-2C, 4-2E).

MOCH-S+ group

After the first 1,500 trials sympatric black-capped chickadees and mountain chickadees responded significantly less to the black-capped chick-a-dee S- exemplars than to the mountain chick-a-dee S+ exemplars. After 2,500 trials all birds successfully discriminated S+ from S- exemplars, and maintained their discriminations throughout the duration of Training Phase 1 (i.e., 4,000 trials, see Figures 4-2B, 4-2D, 4-2F).

Training Phase 2: Transfer 1

Methods

Once birds learned the contingencies associated with the two sets of chick-a-dee calls in the first phase of training, the calls were replaced with 10 novel calls of each species and the same category reinforcement rules established during acquisition were maintained during Transfer 1. The purpose of this phase of training was to ensure that birds understood the rule (i.e., contingency) associated with each stimulus set and were not simply responding based on rote memorization of each stimulus and its related contingency. This phase of training continued until the birds completed a minimum of six 500-trial bins (i.e., 3,000 trials) with a discrimination ratio (DR) ≥ than 0.80, with the last 2 bins occurring consecutively.

Results

Birds in both groups continued to respond according to the category rules learned during acquisition training. To examine our *a priori* prediction that allopatric and sympatric chickadees may differ in their species' discriminations and generalizations, we conducted planned comparisons (Tukey's, $p < 0.05$) on the percentages of responses to S+ and S- exemplar sets during the last 500 trials of acquisition training and the percentages of responses to S+ and S- exemplar sets during the first 500 trials of training in Transfer 1. The logic here is that each stimulus is presented 25 times in a 500-trial bin; however we were interested in determining whether all birds maintained their species' discriminations upon initial exposure to the novel stimuli and not following extensive training with these stimuli.

BCCH-S+ group

After the first 500 trials of Transfer 1, all birds continued to respond at high levels to S+ black-capped chick-a-dee call exemplars and at significantly lower levels to S- mountain chick-a-dee call exemplars (see Figures 4-2A, 4-2C, 4-2E). Allopatric black-capped chickadees responded significantly less to novel S+ calls and significantly more to novel S- calls compared to responding during the last 500 trials of acquisition, however responding to novel S+ and S- exemplars sets remained significantly different (56% and 37% respectively, see Figure 4-2C).

MOCH-S+ group

After the first 500 trials of Transfer 1, all birds continued to respond at high levels to S+ mountain chick-a-dee call exemplars and at significantly lower levels to S- black-capped chick-a-dee call exemplars (see Figures 4-2B, 4-2D, 4-2F). Sympatric and allopatric black-capped chickadees responded slightly but significantly less to novel S+ mountain chick-a-dee calls compared to responding to S+ calls during the last 500 trials of acquisition, however responding to novel S+ and S- exemplars sets remained significantly different for sympatric chickadees (73% and 17% respectively) and for allopatric chickadees (52% and 15% respectively, see Figures 4-2B and 4-2D).

To ensure that birds continued to respond appropriately to S+ and S- exemplar sets throughout the duration of Transfer 1, we conducted planned comparisons (Tukey's, $p < 0.05$) on each 500-trial block of Transfer 1. All birds in both S+ groups continued to respond at high levels to S+ exemplars and at significantly lower levels to S- exemplars (see Figure 4-2).

Training Phase 3: Transfer 2

Methods

Following their training with the novel calls in Transfer 1, birds were required to maintain their levels of responding when presented with all 20 black-capped chick-a-dee calls and all 20 mountain chick-a-dee calls used during acquisition and Transfer 1. Transfer 2 training continued until birds had completed 6 bins of 500 trials with DRs ≥ 0.80.

Results

We compared the percentages of responses to S+ and S- exemplar sets during the last 500 trials of Transfer 1 training with the percentages of responses to S+ and S- exemplar sets during the first 500 trials of Transfer 2 training (Tukey's , $p < 0.05$). All birds, regardless of group assignment, continued to respond at high levels to S+ exemplars and respond at low levels to S- exemplars, as there were no significant differences in responding to the S+ and S- exemplar sets at the end of Transfer 1 and the start of Transfer 2 (see Figure 4-2).

To ensure that birds maintained their species' discriminations throughout the duration of Transfer 2, we conducted planned comparisons (Tukey's, $p < 0.05$) on each

500-trial block. Indeed all birds continued to respond at high levels to S+ exemplars and at significantly lower levels to S- exemplars (see Figure 4-2).

Probe Tests

Methods

Once evidence of category-associated responding to all 20 calls of each species was observed during Transfer 2, all 20 calls of each species were presented for a minimum of 1,000 trials (2 training blocks) with the percentage of reinforcement for S+ stimuli lowered to 85% (Transfer 85). This was done to decrease the notice-ability of differential reinforcement between training and test (probe) stimuli. During the testing phase, birds were required to maintain their species' discriminations of the two sets of 20 chick-a-dee training calls while probe stimuli were intermittently presented. Each probe session (n = 3) consisted of 4 stimuli (2 black-capped chickadee stimuli types and 2 mountain chickadee stimuli types) from each of the 4 probe sets (Spliced Control, Multi-Species Spliced, Introductory-only, and Terminal-only). Each of the 16 probe stimuli in each session was randomly selected without replacement and presented only once in a 416-trial block (10 presentations each of the 40 training stimuli and 1 presentation each of the 16 probe stimuli) with a percentage of reinforcement set at 15%. This low rate of reinforcement was chosen in an effort to maintain responding by birds, but also to avoid the possibility that birds treat probe stimuli as nonrewarded and subsequently withhold responding to them. Once 3 blocks of 416 trials were collected, 1 block of 500 trials of Transfer 85 stimuli (i.e., training stimuli) was interspersed prior to commencing the next probe session. Once all three probe sessions had been presented, the sequence began again, ultimately resulting in each probe session being presented twice, resulting in each of the 48 probe stimuli being presented a total of 6 times. Birds completed, on average, 1-3 blocks of trials per day, and therefore probe sessions were conducted on different days.

Results

To ensure that birds continued to discriminate among the S+ and S- training calls despite the change in reinforcement value from 100% to 85%, we conducted a mixed model Species × Group × Exemplar Set × Training Phase ANOVA on the percentages of responses during the last 500 trials of Transfer 2 and the first 500 trials of Transfer 85 training phases. There were no significant differences in the responding by birds to the S+ and S- exemplars at the end of Transfer 2 and the start of Transfer 85, $F(1, 25) = 0.125, p = 0.726$ (see Figure 4-2). Therefore birds continued to discriminate among black-capped and mountain chick-a-dee calls despite a reduction in the percentage of reinforcement value.

In the following analyses we conducted planned comparisons (Tukey's, $p < 0.05$) on the percentages of responses by chickadees to training calls presented during the last 500 trials of Transfer 85 and the average percentages of responses to the 6 presentations of each of the 8 probe types (4 black-capped chickadee types and 4 mountain chickadee types). One female sympatric black-capped chickadee in the mountain chickadee S+ group was omitted from the following analyses due to an equipment failure that occurred during one of the 6 probe-session presentations.

In general, all 3 groups of birds in both S+ discrimination groups responded significantly less to the probe stimuli compared to responding to the S+ training stimuli, suggesting that birds could indeed discriminate between the training and testing exemplars. To examine the distribution of responses to the 8 probe types (4 S+ associated and 4 S- associated stimulus types) we compared the scaled percentages of responses (see Statistical Analyses above) to each probe type by birds in both S+ discrimination groups. To facilitate comparisons we present the results below based on group assignment.

BCCH-S+ group

Sympatric birds responded most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and both Multi-species Spliced stimuli, with no significant differences among them in levels of responding (see Figure 4-3A). Birds responded significantly less to the black-capped chick-a-dee Introductory-only stimuli and mountain chick-a-dee Spliced Control, Introductory-only, and Terminal-only probe stimuli, (see Figure 4-3A).

Allopatric birds responded in a similar manner to the sympatric black-capped chickadees by responding most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and Multi-species (black-capped terminal) Spliced probe stimuli. However, when the data were transformed, a significant difference in responding to Spliced Control calls and Terminal-only stimuli was observed. Allopatric birds responded significantly less to black-capped chick-a-dee Introductory-only stimuli and all mountain chick-a-dee probe stimuli (see Figure 4-3C).

Mountain chickadees responded most to the black-capped chick-a-dee Spliced Control calls, Terminal-only stimuli, and Multi-species (black-capped terminal) Spliced probe stimuli. However, when the data were transformed, a significant difference in responding to Spliced Control calls and Terminal-only stimuli was observed. Mountain chickadees responded significantly less to black-capped chick-a-dee Introductory-only stimuli and all mountain chick-a-dee probe stimuli (see Figure 4-3E).

MOCH-S+ group

Sympatric birds responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli. Compared to these probe types, sympatric chickadees responded significantly less to mountain chick-a-dee Introductory-only stimuli, Multi-species (mountain terminal) Spliced stimuli, and all black-capped chick-a-dee probe stimulus types.

Allopatric birds responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli, but responded significantly less to the mountain chick-a-dee Introductory-only and Multi-species (mountain terminal) Spliced probe stimuli (see Figure 4-3D). Allopatric birds also responded significantly less to all black-capped chick-a-dee probe types.

Mountain chickadees responded most to the mountain chick-a-dee Spliced Control calls and Terminal-only probe stimuli (see Figure 4-3F), but responded significantly less to the mountain chick-a-dee Introductory-only and Multi-species (mountain terminal) Spliced probe stimuli. Mountain chickadees also responded significantly less to all black-capped chick-a-dee probe types.

We subsequently conducted planned comparisons (Tukey's, $p < 0.05$) to determine whether birds responded differently to each of the probe types. Sympatric black-capped chickadees, allopatric black-capped chickadees, and mountain chickadees responded about equally to each probe type (see Figure 4-4), as there were no significant differences between groups of birds.

Discussion

Here we present the results of an operant discrimination performed by black-capped and mountain chickadees to determine the mechanisms for discriminating black-capped from mountain chick-a-dee calls. In addition, we examined whether experience affected the discriminations of black-capped chickadees and whether the two species of chickadees utilized different portions of the calls for discriminating. By establishing a baseline level of responding to each species' calls we were able to intermittently present experimenter-manipulated chick-a-dee calls and examine the responses by birds.

In a previous set of experiments (Bloomfield & Sturdy, in press) we provided evidence that black-capped and mountain chickadees discriminated their own from the other species' chick-a-dee calls, and perceived each species' calls as belonging to two separate, open-ended, perceptual categories. Further, there appeared to be several differences between sympatric and allopatric black-capped chickadees in their discrimination speed and accuracy. At the outset of the current experiment we hypothesized that black-capped chickadees may discriminate black-capped and mountain chick-a-dee calls differently, depending on their previous histories with mountain chickadees. Given the extensive experience of the sympatric black-capped chickadees with mountain chick-a-dee calls, we predicted that these birds would be better able to discriminate between the species' calls using either the introductory 'chick-a' portion or the terminal 'dee' portion compared to allopatric chickadees.

Sympatric and allopatric black-capped chickadees performed relatively similarly in the current set of experiments. Birds learned to discriminate black-capped from mountain chick-a-dee calls over a minimum of 4,000 trials, taking approximately 200 presentations of each stimulus to master the initial task. Birds in the black-capped chick-a-dee S+ group were the first to acquire the discrimination by responding significantly more to black-capped chick-a-dee calls than to mountain chick-a-dee calls after the first 500 trials whereas sympatric black-capped and mountain chickadees in the mountain chick-a-dee S+ group required 1,500 trials. Allopatric birds in the mountain chick-a-dee S+ group required 2,500 trials to learn to respond to mountain chick-a-dee calls and withhold responding to black-capped chick-a-dee calls. Although the methods were slightly different between the current study and a previous study examining open-ended categorization in chickadees (Bloomfield & Sturdy, in press), similar discrimination results appeared in each study. Specifically, in the previous study sympatric black-capped chickadees and mountain chickadees assigned to the mountain chick-a-dee S+ group required more trials to discriminate S+ mountain chick-a-dee calls from S- black-capped chickadee calls compared to birds in the black-capped chick-a-dee S+ group. While the cause(s) for the differences in speed of acquisition between the two groups is (are) unclear, all birds nonetheless learned the discrimination by 4,000 trials.

Following the acquisition phase, birds were presented with 10 novel calls of each species and were required to maintain their species' discrimination. Allopatric birds in the black-capped chick-a-dee S+ group responded slightly less to novel black-capped chick-a-dee S+ calls and responded slightly more to novel mountain chick-a-dee S- calls. As well, sympatric and allopatric birds in the mountain chick-a-dee S+ group responded slightly less to novel mountain chick-a-dee S+ calls, however all birds continued to respond significantly more to the S+ stimuli compared to the S- stimuli, indicating that they understood the rules of contingency associated with each stimulus set (i.e., each species' category of calls).

Following training we intermittently presented experimenter-manipulated chick-a-dee calls to determine the mechanisms underlying species' discrimination by sympatric and allopatric black-capped chickadees and mountain chickadees. All chickadees performed about equally in the current study. All birds responded most to the S+ Spliced Control calls, created using the 'voice' of one individual for the 'chick-a' portion and the 'voice' of another individual of the same species for the 'dee' portion. However, responding to the Spliced Control calls rarely equaled the level of responding observed for the normal training calls. Similar to the results seen at the beginning of Transfer 1 in the current study, and in other studies with chickadees (Bloomfield & Sturdy, in press; Bloomfield et al., 2003), this could be due to the fact that birds received extensive training with the normal calls and thus were able to detect the difference between the normal and the probe calls. Alternatively, the perception of two voices producing one call may have in fact been perceived by the birds as abnormal, resulting in lower responding.

Sympatric and allopatric black-capped chickadees and mountain chickadees all responded about equally to the S+ associated Spliced Control calls, Terminal-only calls, and the Multi-species calls consisting of the S+ associated terminal portion, suggesting that the terminal 'dee' portion of the call is sufficient for inducing species-specific responses. By comparison, responding to the Introductory-only probe stimuli remained low, indicating that the 'chick-a' portion of the chick-a-dee call may not be a species-indicator. Support for this idea stems from comparing responding to Introductory-only and Terminal-only probe stimuli using post-hoc comparisons ($p < 0.05$); 3 of the 6 groups of birds (sympatric black-capped chickadees in both the BCCH-S+ group and the MOCH-S+ group, and mountain chickadees in the MOCH-S+ group) responded significantly more to Terminal-only stimuli. In addition, sympatric chickadees responded to the Multi-species (black-capped terminal) Spliced probe stimuli. There are two possible explanations for these levels of responding. First, birds may not attend to the introductory portion of chick-a-dee calls for species discriminations when the terminal portion is present. Second, birds may not be able to discriminate between species using only the introductory portion. This second alternative remains a possibility, as all birds responded at low levels to both S+ and S- associated Introductory-only probe stimuli. Experiments currently underway will ultimately determine whether chickadees are capable of discriminating species on the basis of individual introductory and terminal notes of conspecific and heterospecific chick-a-dee calls, as would be suggested by a linear discriminant analysis conducted by Dawson, Bloomfield, Charrier, and Sturdy (2006).

In summary, it appears that the Terminal-only portion of the chick-a-dee call conveys more species-specific information compared to the Introductory-only portion, as birds responded significantly more to the Terminal-only probe type. However, if the birds only used the terminal "dee" portion of the calls for discriminating the calls of black-capped and mountain chickadees, then we might have expected to see higher levels of responding to the Multi-species calls with appropriate S+ terminal 'dee' portions. When the Terminal portion was combined with an Introductory portion of the other species, some differences in responding occurred. In particular, not only did sympatric black-capped chickadees in the BCCH-S+ group respond to the Multi-species Spliced stimuli consisting of the S+ associated Terminal portion, but these birds also responded to the Multi-species Spliced stimuli consisting of the S- associated Terminal portion. Thus perhaps birds were able to detect the S+ associated Introductory portion and responded accordingly. Therefore it remains possible that although birds appeared to mainly rely on the terminal portions of the calls for discriminating, the introductory portions provided some type of species information.

The terminal portions of the calls of black-capped and mountain chickadees are similar in at least one respect: mountain chick-a-dee calls and black-capped chick-a-dee calls almost always contain one or more D notes, and the D notes are similar in structure between the two species (Bloomfield, Charrier, and Sturdy 2004; Charrier, Bloomfield, & Sturdy, 2004). However, the terminal portions of the calls of the two species also differ in at least one respect: mountain chickadees produce an additional note type, the D-hybrid note, present in a majority of their calls (Bloomfield et al., 2004). This note type is more tonal in nature at the outset of the note, appearing more like an introductory A- or B-type note, and quickly transitions to a note that appears more like a typical D note (see Figure 4-1). It remains possible that this is the one main difference that the birds were attending to when discriminating black-capped from mountain chick-a-dee calls. The D-type notes may in fact prove to be reliable species markers, given that they are (1) present in nearly every chick-a-dee call, (2) longer in duration, and therefore may provide the birds with greater opportunity to attend to them and perceive the salient, species-specific information, and (3) lower in frequency compared to all other chick-a-dee call notes, and therefore would be more resistant to degradation in the birds' natural habitats. However further evidence beyond the scope of the current study would be required to determine whether this is in fact the only feature used by the birds for discriminating. It remains possible that micro-acoustic features, such as spectral and temporal differences in these note types, provide birds with species-specific information.

Chickadees are not the only avian species to produce and perceive species-specific markers in their vocalizations. For example, Brenowitz (1982) found that Red-winged Blackbirds (*Agelauis phoeniceus*) can transmit the terminal 'trill' note of their song over 100m in distance, whereas the introductory and higher frequency components of the song were severely attenuated. Further, this portion of the song, in the absence of the introductory components, was both necessary and sufficient for inducing species-specific responses from flock and non-flock members. This trill note is similar in structure to the D notes of black-capped and mountain chickadees, with most of the energy occurring in the 2-4 kHz range, suggesting that perhaps the D notes of chickadees can also be transmitted over long distances without the loss of species-specific information. Brenowitz and others (e.g., Richards, 1981a; 1981b) suggest that the high-frequency introductory notes may act as 'alerting notes', or alternatively function to convey individual identity or information about the distance of the singer. Because the chickadees in the current study did not appear to rely on the introductory notes in the chick-a-dee calls for species' discriminations, it remains possible that these high-frequency notes also function in a manner not related to species-identity.

In American redstarts (*Setophaga ruticilla*) the initial trill of the male song, which is a brief repeated frequency-modulated note, would by itself invoke a species-typical response, however synthetic repetition of the terminal syllable would invoke a similar response, a response not seen when presented only once in the song (Date, Lemon, Weary, & Richter, 1991). This suggests that although a feature may convey less species-specific information than other features, redundancy, for example in the form of repetition, may in turn provide more reliable information than singly presented features. In chickadees, the D notes are often repeated within a call (average 3.4 notes/call in black-capped chickadees, Charrier et al., 2004; average 1.6 notes/call in mountain chickadees, Bloomfield et al., 2004), possibly providing listening birds with redundant, and therefore more reliable, species information. With this in mind, further experimentation is currently underway to determine whether the repetition of any one chick-a-dee call-note type would facilitate species' discrimination by black-capped and mountain chickadees.

Nelson furthered our understanding of species-specific information in the features of songs with the discovery that the relatively invariant feature 'maximum note frequency' was most useful for multivariate discriminations of the songs of the field sparrow (*Spizella pusilla*) and the chipping sparrow (*S. passerine*), and that the frequency of field sparrow song needed to be presented within a species-typical range in order for birds to respond maximally (Nelson, 1988; 1989). Using four features measured in the D notes of black-capped and mountain chickadees, a discriminant analysis clearly indicated that these notes were sufficient for species identification, as the notes were classified according to species with an average accuracy of 94% (Dawson et al., 2006). Apparent differences in the average loudest frequencies (Fmax) of the two species' D notes may have been a significant contributor to this discrimination (see Table 4 in Charrier et al., 2004; Table 5 in Bloomfield et al., 2004).

Taken together, it appears that the D notes in the chick-a-dee calls of (at least) black-capped and mountain chickadees may be suitable for conveying species-specific information. First, they are lower in frequency and longer in duration than all other note types in the chick-a-dee calls of these two species, and are therefore more likely to be resistant to degradation and able to be heard at greater distances. Second, they are present in nearly every single chick-a-dee call produced and are typically repeated within a call, providing greater opportunity for listeners to perceive the pertinent information. Finally, based on only four acoustic measurements (one temporal and three spectral) a linear discriminant analysis was able to accurately classify these note types by species. However we are only beginning to understand the perceptual abilities and limits of songbirds, and therefore it remains possible that human-conducted acoustic measurements do not fully envelope all the possible features that birds may perceive. Therefore birds may in fact acquire more information from these notes than we are able to measure, thereby increasing the number of possible species-specific features in these notes.

It is perhaps important to clarify that the terminal notes in the chick-a-dee calls may not be the only features that can be used by the birds for discriminating. In the current study we provided the birds with one of two options: use the introductory 'chick-a' portion or use the terminal 'dee' portion. This design did not allow us to gain a greater understanding of the potential for each individual note type to convey species information. As a follow-up to the current study we are investigating this possibility by providing the birds with individually- or repeatedly-presented notes of each type and examining their responses. Further, other features, such as absolute and relative pitch (frequency) of the notes and of the whole call, as well as temporal characteristics (such as note duration and call rate) can be manipulated and tested for their potential for species-identifying information. These proposed designs will ultimately answer the question whether birds *rely* on the terminal 'dee' portion of the calls or *depend* on the terminal 'dee' portion of the calls for discriminating black-capped from mountain chick-a-dee calls.

Figure 4-1.

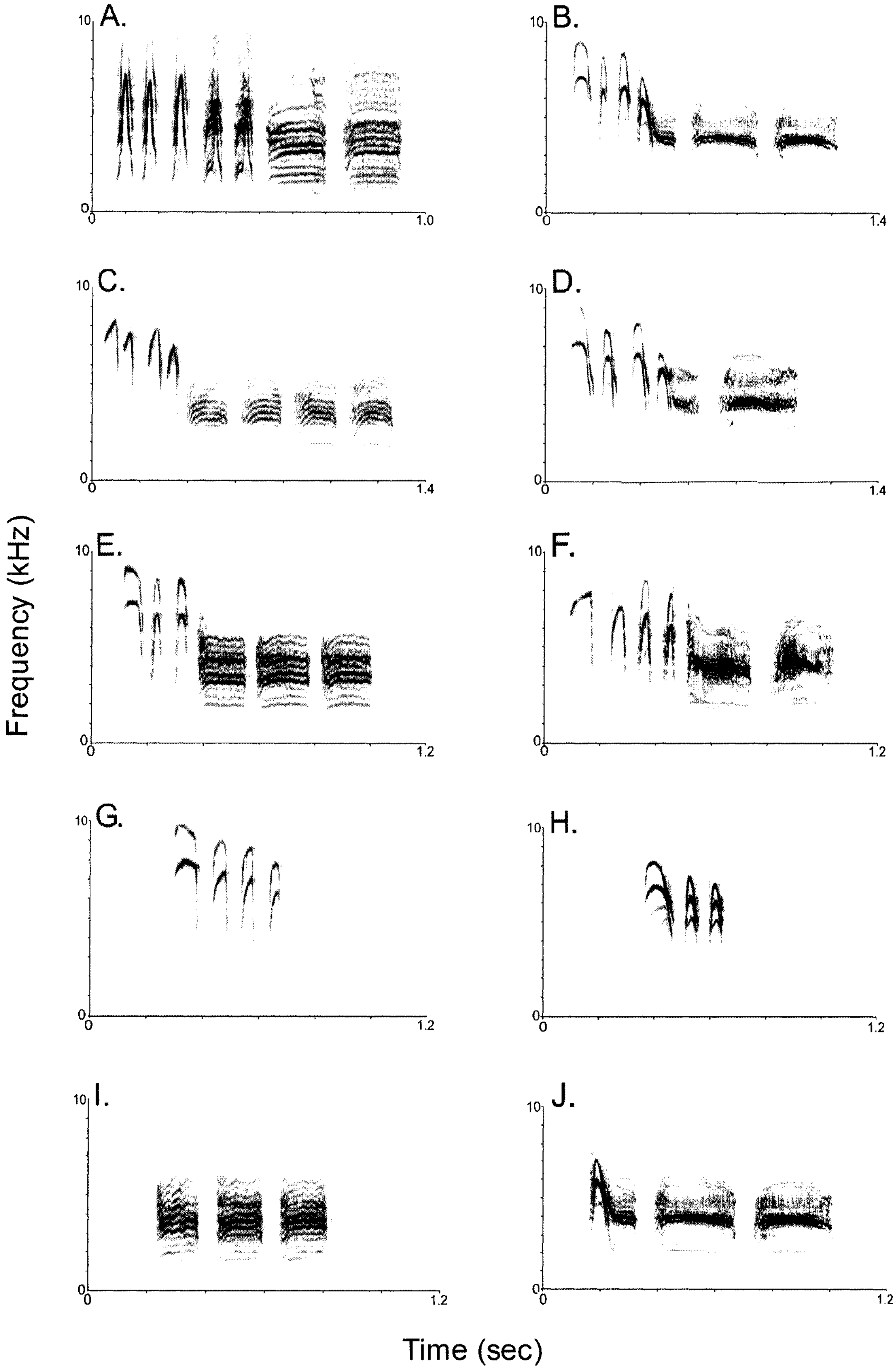


Figure 4-2.

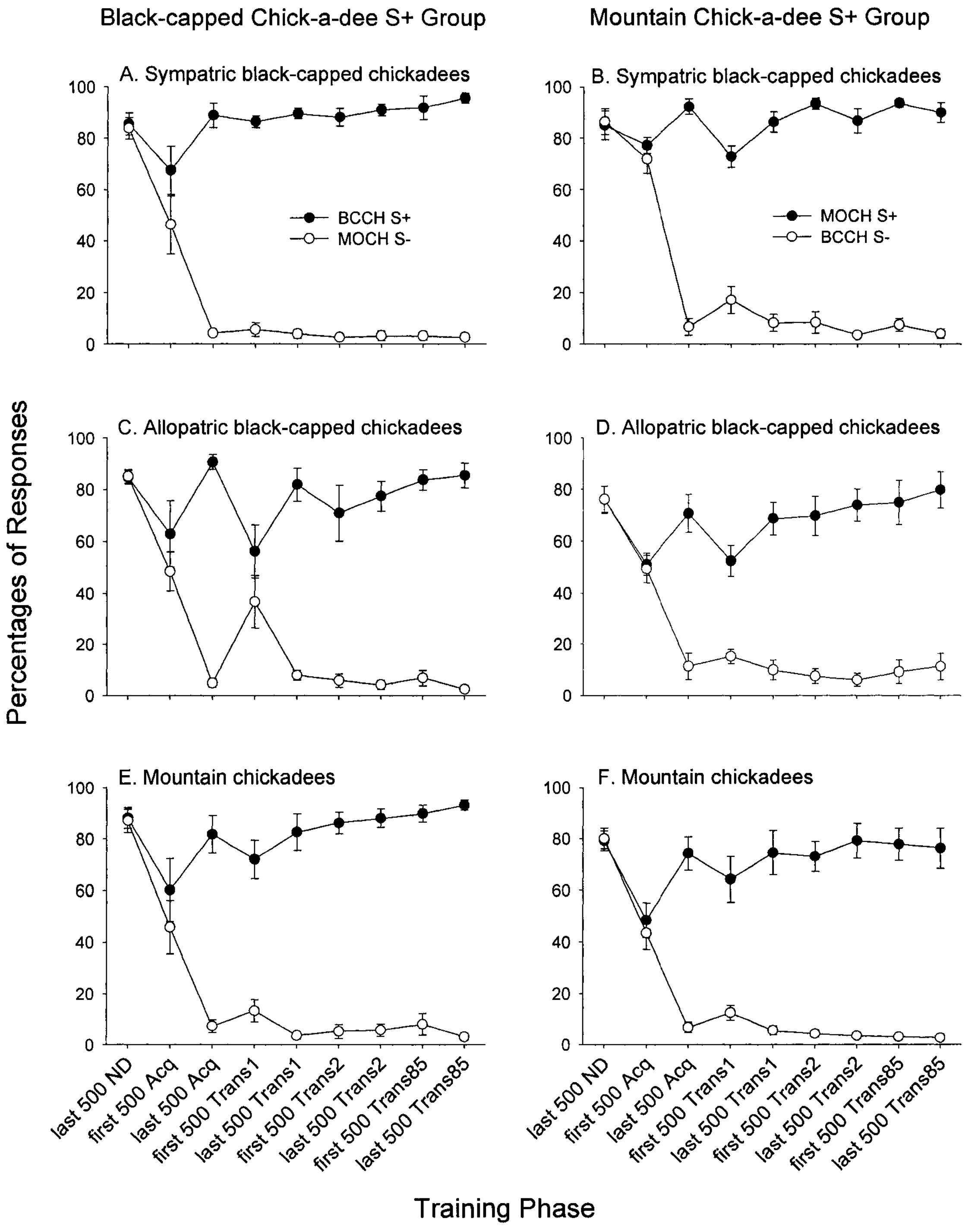

Black-capped Chick-a-dee S+ Group
Mountain Chick-a-dee S+ Group
A. Sympatric black-capped chickadees
BCCH S+
MOCH S-
B. Sympatric black-capped chickadees
MOCH S+
BCCH S-
C. Allopatric black-capped chickadees
D. Allopatric black-capped chickadees
E. Mountain chickadees
F. Mountain chickadees
Percentages of Responses
0
20
40
60
80
100
last 500 ND
first 500 Acq
last 500 Acq
first 500 Trans1
last 500 Trans1
first 500 Trans2
last 500 Trans2
first 500 Trans85
last 500 Trans85
Training Phase

Figure 4-3.

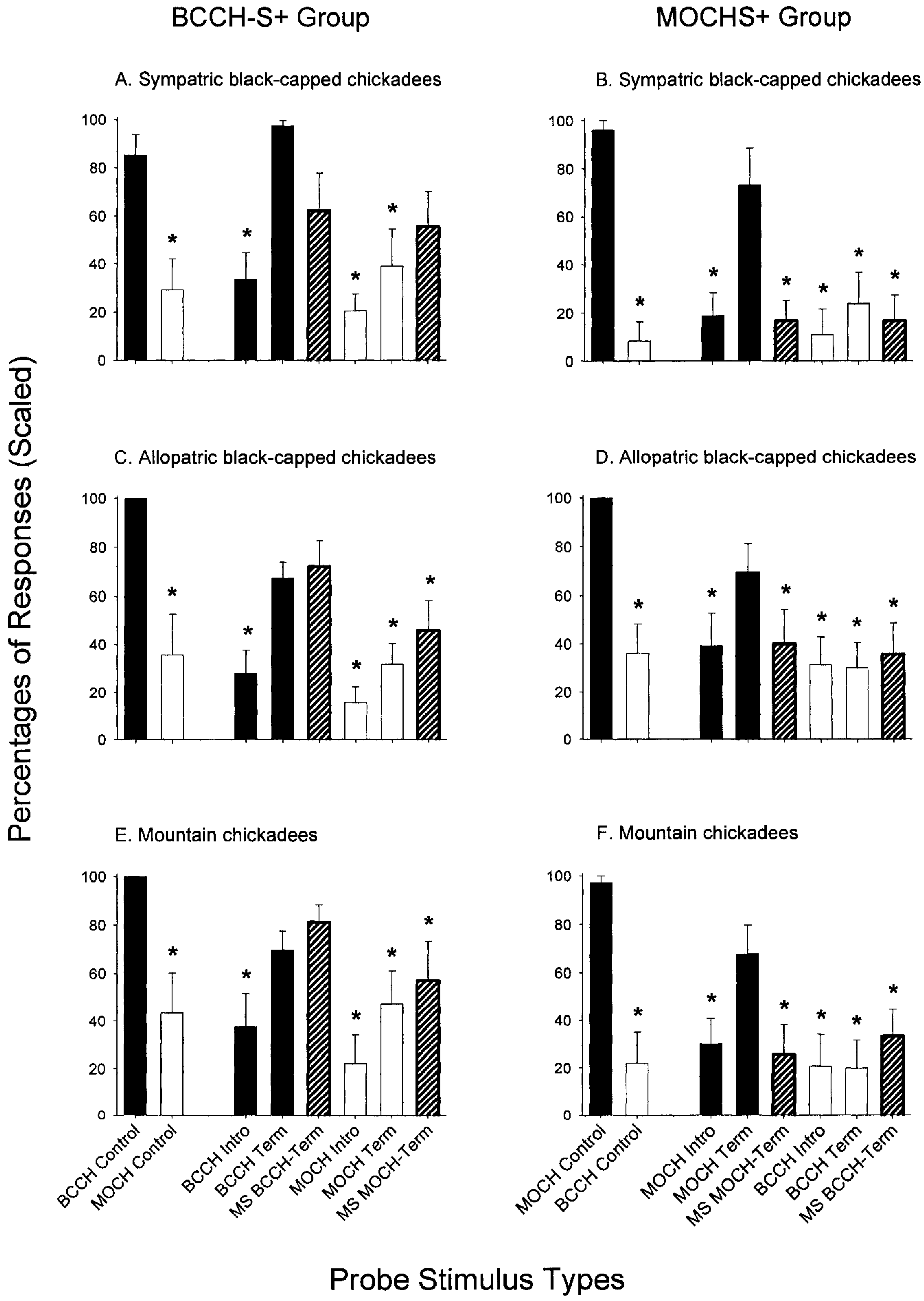
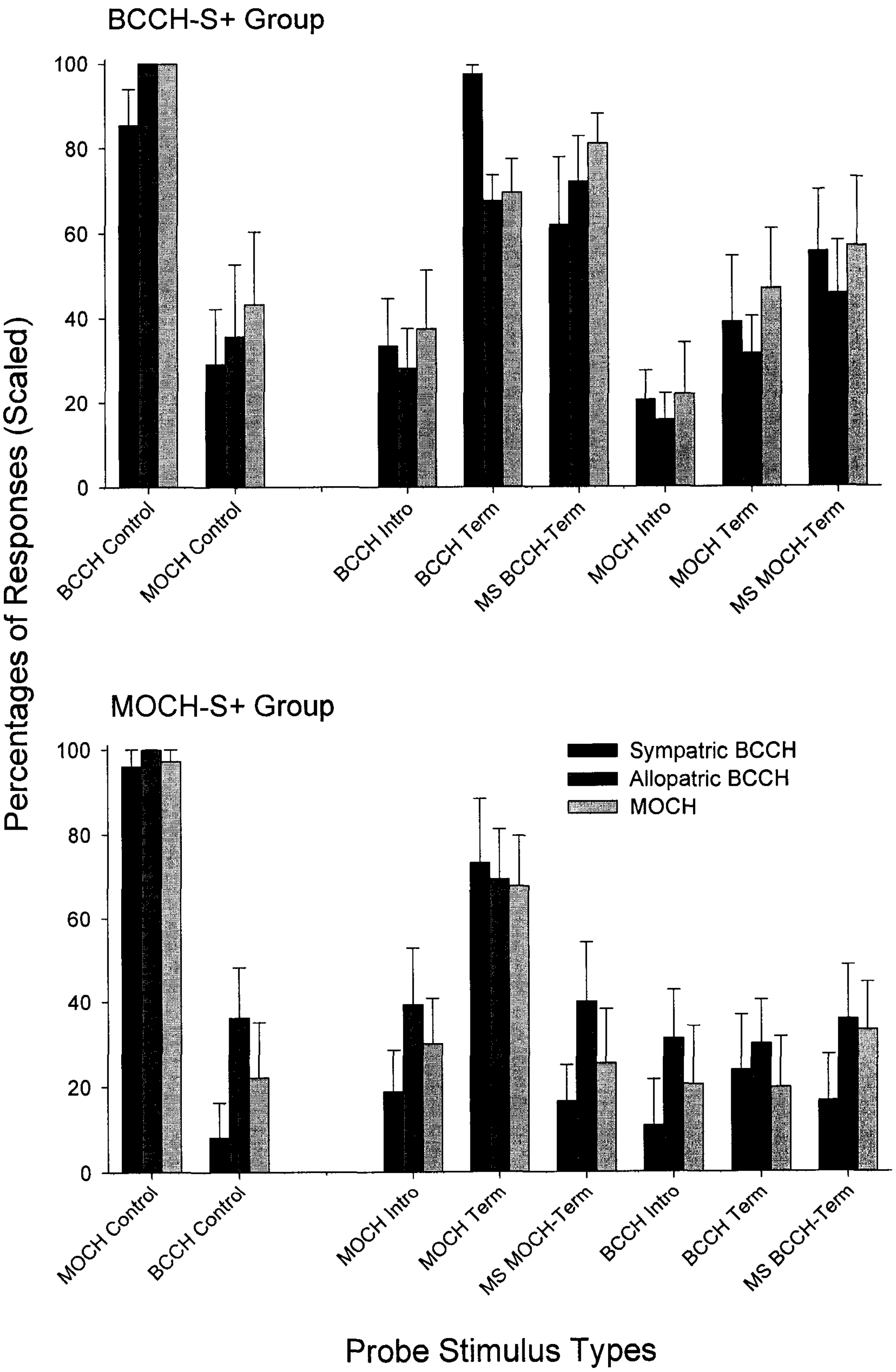

BCCH-S+ Group
MOCHS+ Group
A. Sympatric black-capped chickadees
B. Sympatric black-capped chickadees
C. Allopatric black-capped chickadees
D. Allopatric black-capped chickadees
E. Mountain chickadees
F. Mountain chickadees
Percentages of Responses (Scaled)
0
20
40
60
80
100
*
BCCH Control
MOCH Control
BCCH Intro
BCCH Term
MS BCCH-Term
MOCH Intro
MOCH Term
MS MOCH-Term
MOCH Control
BCCH Control
MOCH Intro
MOCH Term
MS MOCH-Term
BCCH Intro
BCCH Term
MS BCCH-Term
Probe Stimulus Types

Figure 4-4.



BCCH-S+ Group
Percentages of Responses (Scaled)
100
80
60
40
20
0
BCCH Control
MOCH Control
BCCH Intro
BCCH Term
MS BCCH-Term
MOCH Intro
MOCH Term
MS MOCH-Term
MOCH-S+ Group
Sympatric BCCH
Allopatric BCCH
MOCH
MOCH Control
BCCH Control
MOCH Intro
MOCH Term
MS MOCH-Term
BCCH Intro
BCCH Term
MS BCCH-Term
Probe Stimulus Types

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Chapter 5: Responses by black-capped chickadees (*Poecile atricapillus*) to normal and manipulated 'chick-a-dee' calls

A version of this paper has been submitted for publication. Bloomfield, L.L., Proppe, D.S. & Sturdy, C.B. *Canadian Journal of Zoology*.

Introduction

For some species, vocal communication is essential for maintaining contact with conspecifics when distance or naturally occurring obstructions such as vegetation prevent visual contact. Vocalizations are often the primary means by which many songbird species identify conspecifics and discriminate them from heterospecifics (see Becker, 1982). Songbirds must also quickly recognize the acoustic signals of neighbours to avoid unnecessary confrontations with familiar birds and mount strong aggressive responses towards invading strangers (see Stoddard, 1996). Furthermore, songbirds must discriminate within species when selecting a mate, and among species to avoid courting heterospecifics (Ratcliffe & Otter, 1996). Finally, the perception and interpretation of foraging- and predator-related calls could be critical to survival for conspecifics (e.g., Freeburg & Lucas, 2002; Templeton & Greene, 2007; Templeton, Davis, & Greene, 2005).

Chickadees (genus *Poecile*) provide an excellent model for studying acoustic communication because their song and at least some of their calls have a learned component (Hughes, Nowicki, & Lohr, 1998; Mammen & Nowicki, 1983; Shackleton & Ratcliffe, 1993). Moreover, chickadees produce at least as many and typically more call types than song types (see Ficken, Ficken, & Witkin, 1978; Hailman & Ficken, 1996). Some of these calls are more acoustically complex than their songs, allowing for greater possible diversity and complexity in their functions (e.g., the potential 'message' being communicated, see Hailman, Ficken, & Ficken, 1985). In addition, all members of the genus *Poecile* produce a species-typical variant of the chick-a-dee call (see Ficken et al., 1978; Ficken, Hailman, & Hailman, 1994; Ficken, McLaren, & Hailman, 1996; Gaddis, 1985; Hailman & Ficken, 1996; S.T. Smith, 1972), making this call useful for comparing species-specific production and perception. Finally, chickadees will produce chick-a-dee calls in response to perceived chick-a-dee calls in nature, providing researchers with opportunities to draw conclusions regarding chick-a-dee call perception. Taken together, chickadees and their chick-a-dee calls are ideal for comparative studies of acoustic communication.

The black-capped chickadee (*P. atricapillus*) is ubiquitous throughout the northern United States and most of Canada, and their vocal repertoire is arguably the most well studied of all the chickadee species. Their chick-a-dee call, putatively associated with mild alarm and flock communication and co-ordination (S.M. Smith, 1991), consists of four note types; A, B, C, and D (Ficken et al., 1978; see Fig. 5-1A). While maintaining a fixed syntactical ordering of the notes (A through D), the note types can be repeated or omitted within any call to produce a seemingly infinite number of call variants (Hailman et al. 1985), with most black-capped chick-a-dee calls terminating with at least one D note. Black-capped chickadees classify their own chick-a-dee calls and the chick-a-dee calls of other chickadee species into separate open-ended categories (e.g., Carolina chickadees, *P. carolinensis*, Bloomfield, Sturdy, Phillmore, & Weisman, 2003; mountain chickadees, *P. gambeli*, Bloomfield & Sturdy, in press), and bioacoustic analyses suggest that chick-a-dee calls contain individual- and flock-specific features (Charrier, Bloomfield, & Sturdy, 2004; Mammen & Nowicki, 1981). Thus the black-capped chickadee chick-a-dee call has the potential to convey important information.

Most closely related to the black-capped chickadee is the mountain chickadee, (Gill, Mostrom, & Mack, 1993). The mountain chickadee inhabits the western edge of North America, from the Yukon to New Mexico (McCallum, Grundel, & Dahlsten, 1999;

S.M. Smith, 1993). The chick-a-dee call of the mountain chickadee is similar in many respects to the chick-a-dee of the black-capped chickadee (Bloomfield, Charrier, & Sturdy, 2004; see Fig. 5-1). For example, there are 4 main note types, A, B, C and D, and these note types can be repeated or omitted to produce an unlimited number of call combinations. Not present in black-capped chick-a-dee calls are two additional note types, an intermediate A/B note in the introductory 'chick-a' portion and a D-hybrid note in the terminal 'dee' portion. Either of these note types can be completely omitted from a call, however only the A/B note can be repeated within a call. The D-hybrid note, when it occurs, only ever occurs once in a call, although it may be followed by one or more D notes. Nonetheless, and similar to the structure observed in black-capped chick-a-dee calls, in every mountain chick-a-dee call there is at least one D-hybrid note or one D note terminating the call. It is currently not known whether chickadees use these note-type differences among the two species' calls to discriminate black-capped from mountain chick-a-dee calls. However the results of operant discrimination tasks suggest that black-capped and mountain chickadees discriminate their own from the other species' calls (Bloomfield & Sturdy, in press) and that the terminal 'dee' portion provides more species-specific information than the introductory 'chick-a' portion (Bloomfield, Farrell & Sturdy, in press). In the context of the current study, it is not known whether black-capped chickadees, in their natural habitat, discriminate black-capped from mountain chick-a-dee calls and whether one or more particular features of the calls are most useful for discriminating.

Study I

The purpose of Study 1 is to determine whether free-ranging black-capped chickadees, unfamiliar with mountain chickadees, discriminate black-capped chick-a-dee calls from mountain chick-a-dee calls. In the winter of 2005 we played back natural chick-a-dee calls of both black-capped and mountain chickadees (see Fig. 5-1A and 5-1B) and quantified the vocal responses by chickadees to these playbacks. We hypothesized that black-capped chickadees would respond more vigorously to conspecific calls, a behavioural response common among songbirds in the presence of a perceived threat to their territory (e.g., unfamiliar conspecific, see Stoddard, 1996). Alternatively, due to the structural and acoustical similarities of the two species' chick-a-dee calls, and the fact that the experimental subjects had no previous experience with the chick-a-dee calls of mountain chickadees, the null hypothesis was that birds may respond vigorously to both species calls, suggesting that they do not discriminate among black-capped and mountain chick-a-dee calls, but rather treat them both as belonging to one overarching category – chick-a-dee calls.

Methods

Stimulus Preparation

From our collection of recorded chick-a-dee calls we randomly selected 32 black-capped chick-a-dee calls and 32 mountain chick-a-dee calls, each call produced by a different individual chickadee. None of the calls were recorded at or near the playback sites and therefore would not be familiar to the birds exposed to the playback. Chick-a-dee calls originated from several sources using different microphones and recording devices, however in all cases both the equipment used and the calls recorded were high quality (see Fig. 5-1). Calls were resampled at 44,100 Hz (when necessary) and call amplitude was equalised using SIGNAL 4.0 sound analysis software (Engineering Design, Berkeley, CA). Bandpass filtering using Goldwave 4.26 (Goldwave, Inc., 2002, St. John's, Canada) reduced background noise (<1000 Hz and > 10,000 Hz).

The 32 calls of each species were randomly separated into two sets of 16 calls. Each call in the first set of 16 (for each species) was opened separately in SIGNAL and repeated every 10 seconds, resulting in 16 one-minute call-files of each species with 6 call repetitions per minute. One minute of silence was then added to the end of each sound file, resulting in 16 2-minute call-files of each species. Each call in the second set of 16 calls (for each species) was opened separately in SIGNAL and repeated every 10 seconds, and 2 minutes of silence was added to the end of each call-file. Each of the 16 black-capped call-files from the first set was randomly paired with one of the second 16 black-capped call-files from the second set, resulting in 16 sets of paired black-capped chick-a-dee call-files. The same procedure was followed for the mountain calls, resulting in 16 sets of paired mountain chick-a-dee call-files. Once random pairing of calls within species was complete, each of the 16 5-minute (1-min of calling, 1-min of silence, 1-min of calling, 2-mins of silence) black-capped chickadee call-files was randomly paired with one of the 16 5-minute mountain chickadee call files. Some shuffling of call-files ensued to ensure that total call duration and number of occurring note types across species was similar.

Playback Procedure

Playback sessions were conducted in the city of Edmonton Alberta (53.55° N, 113.5° W) during February 2005 between 0800 and 1600 hours. Each trial was played back at a natural sound pressure level (70-80 dB at 1 m from sound source) using a Sony D-SJ301 CD player (Sony, Tokyo, Japan) connected to an Audix PH3s powered speaker (25W, frequency response: 100-20,000 Hz ± 10 dB, Audix USA, Wilsonville, OR) hidden in a tree at approximately 1-2 m above the ground.

Sixteen playback sites in forested areas were chosen based on their distance to the next closest playback location (no less than 1 km) and the presence of chickadees (visual identification and/or audible chick-a-dee calls or other species-specific vocalizations immediately prior to the experimental session). Each site was visited only once and one playback trial of each species' calls was conducted. Each experimental session consisted of a 5 min baseline observation, the first 5-min playback trial, a return-to-baseline period, and the second 5-min playback trial. Determining which paired call-file (of each species) would be played at each site was decided using a random number generator. Determining which species' calls were to be played first was decided by a coin-toss upon arriving at odd-numbered sites (i.e., sites 1, 3, 5 ...15); the opposite order was used at each subsequent site (i.e., sites 2, 4, 6 ...16). During each 5-min baseline trial and each 5-min playback trial we tallied the number of audible chick-a-dee calls.

Statistical Analyses

We conducted a square root transformation of the data ($X = \sqrt{(Y + 0.5)}$, Zar, 1999) and employed the more robust parametric mixed model ANOVA (Rasmussen & Dunlap, 1991) followed by Tukey's post-hoc analysis to examine the quantitative response of number of calls produced by birds during the baseline and playback trials. To facilitate comprehension of the results, all figures are presented using the raw data.

Results

To compare the number of chick-a-dee calls produced during each 5-min baseline trial with the number of calls produced during the subsequent 5-min playback trial of Normal black-capped chick-a-dee calls and the 5-min playback trial of Normal mountain chick-a-dee calls we conducted a mixed model Playback Order (first or second in a session) × Trial (baseline, black-capped chick-a-dee, mountain chick-a-dee) ANOVA. There was a significant main effect of Trial, $F_{2,28} = 15.492, p < 0.001$, and a significant Order × Trial interaction, $F_{2,28} = 4.645, p = 0.018$. Tukey's post-hoc analysis revealed that birds significantly increased their responding above baseline levels to Normal black-capped chick-a-dee calls when these calls were played back first at a site ($p < 0.001$, Fig. 5-2A), but not when they were played back second at a site ($p = 0.338$, Fig. 5-2B). Birds did not significantly increase their responding above baseline to Normal mountain chick-a-dee calls regardless of whether they were played back first ($p = 0.197$) or second ($p = 0.162$) at a site (see Fig. 5-2A and 5-2B).

Study II

The purpose of Study 2 was to investigate whether black-capped chickadees utilize the introductory 'chick-a' portion (e.g., combination of introductory A, B, and C notes) or the terminal 'dee' portion (e.g., combination of terminal D and D-hybrid notes) of chick-a-dee calls to recognize conspecific callers. In the winter of 2007 we returned to the same locations as in Study 1 and played back two different types of experimenter-manipulated chick-a-dee calls of each species. The first type of playback calls were control calls in which the introductory 'chick-a' portion and terminal 'dee' portion of each call was of the same species (i.e., either black-capped or mountain chickadee) but were assembled using the calls of different individuals (see Fig. 5-3A and 5-3B for representative sound spectrograms). The second type of playback calls were multi-species spliced calls in which the introductory 'chick-a' portion originated from either a black-capped or mountain chick-a-dee call, and the terminal 'dee' portion originated from the other species' call (see Fig. 5-3C and 5-3D for representative sound spectrograms). Comparing vocal behaviour of chickadees prior to and following the playback of each of these manipulated calls would determine whether the introductory or terminal portions of chick-a-dee calls are primarily used by chickadees to identify the species of the caller. Based on the results of an operant study from our laboratory suggesting that the terminal 'dee' portion controls species' recognition (Bloomfield, Farrell, & Sturdy, in press), we hypothesized that black-capped chickadees would increase their responding above baseline levels following the playback of conspecific control calls and the multi-species test calls consisting of a black-capped chickadee terminal 'dee' portion.

Methods

Stimulus Preparation

In Experiment 2 we prepared 2 types of call stimuli: Normal Spliced calls and Multi-species Spliced calls. The original set of 64 calls used in Study 1 was also used in Study 2, however, no calls, either in whole or in part, were played back at the same site or at adjacent sites as in Study 1.

Normal Spliced (control) Calls. We randomly selected 32 calls of each species and opened each call separately in SIGNAL. The introductory portion of the calls, consisting of A-, B-, and C-type notes, were randomly spliced together with the terminal portion, consisting of D-type notes, of a different call of the same species, resulting in 16

Normal Spliced calls for each species (see Fig. 5-3A and 5-3B for representative Normal Spliced calls of each species). Each spliced call was repeated every 10 seconds in a 30-s file, resulting in 16 30-s Normal Spliced call-files for each species. There were some exceptions to the random splicing of calls. First, calls previously paired in Study 1 were neither spliced together nor paired in Study 2 (e.g., calls 1 and 2 played at the same site in Study 1 were not spliced together and were not played at the same site in Study 2). Second, a call could not be spliced with the same call twice (e.g., if the introductory notes of call 1 were spliced with terminal notes of call 2, then the introductory notes of call 2 would not be spliced with terminal notes of call 1).

Multi-species Spliced Calls. Each of the remaining 32 calls of each species not used for Normal Spliced calls was opened separately in SIGNAL and the introductory portion of the calls, consisting of A-, B-, and C-type notes, was randomly spliced together with the terminal portion, consisting of D-type notes, of a call of the *other* species. This resulted in 32 Multi-species Spliced calls; 16 calls with black-capped chick-a-dee introductory notes and mountain chick-a-dee terminal notes, and 16 calls with mountain chick-a-dee introductory notes and black-capped chick-a-dee terminal notes (see Fig. 5-3C and 5-3D for representative sound spectrograms). Each call was repeated every 10 seconds in a 30-s file using SIGNAL, resulting in 32 Multi-species Spliced call-files. As noted above, there were some exceptions to the random splicing of introductory and terminal notes. First, calls previously paired in Study 1 (both within a species and across species) were neither spliced together nor played back at the same sites in Study 2. Second, one portion of one call could not be spliced with one portion of another call twice (e.g., if the introductory notes of call 1, species 1 were spliced with terminal notes of call 2, species 2, then the introductory notes of call 2, species 2 would not be spliced with terminal notes of call 1, species 1).

Playback Procedure

Playback sessions were conducted at the same locations as in Study 1 during February 2007 between 0800 and 1600 hours. All equipment used in Study 2 was identical to that in Study 1. Due to the potential order (habituation) effect observed in Study 1 and the increased number of playback trials planned for each site in Study 2, the duration of playback trials in Study 2 was decreased and the number of visits to each site was increased. We therefore visited each site twice, with one day separating the visits. During each visit, one baseline trial and two playback trials were conducted. Playback trials during each visit consisted of presenting either Normal Spliced call-types (black-capped chick-a-dee and mountain chick-a-dee) or Multi-species Spliced call-types (black-capped terminal 'dee' and mountain terminal 'dee'). The order of playbacks was balanced so that call types (e.g., Normal Spliced or Multi-species Spliced) were presented on the first or second site visit an equal number of times, and the order of playback of calls (e.g., black-capped or mountain) of each call type was presented either first or second during each visit an equal number of times.

Upon arriving at each site on each visit, and immediately following the identification of subjects in the area (i.e., species-specific vocalizations heard and/or chickadees observed), the 90-s baseline period began. The first 90-s playback trial, consisting of 30-s of call playback and an additional 60-s of post-playback observation, immediately followed the baseline period. Birds were then allowed to return to baseline activity prior to starting the second 90-s playback trial. During each 90-s trial, chickadee vocal behaviour (i.e., the number of audible chick-a-dee calls produced) was tallied and the latency to the first chick-a-dee vocalization and the first approach by a chickadee within 5 metres of the sound source was also recorded.

Statistical Analyses

To examine the qualitative responses of call latency and approach by birds to each of the four playback types, we conducted nonparametric Cochran's Q tests. To examine the quantitative response of number of calls produced by birds during the baseline and playback trials, we conducted a square root transformation of the data and employed the more robust parametric mixed model ANOVA followed by Tukey's post-hoc analysis. To facilitate comprehension of the results, all figures are presented using the raw data.

Results

For each session, we coded playback trials in which the first vocal response occurred within the first 30-s of playback (=1) and trials in which the first vocal response occurred after the first 30-s of playback (=0), and compared these responses to determine whether birds were more likely to produce a vocal response following the presentation of a particular call. Although not statistically significant, $Q = 3.339$, $N = 16$, $p = 0.342$ (see Fig. 5-4A), birds were more likely to respond within the first 30-s of Normal Spliced black-capped chick-a-dee call playback trials ($X \pm \text{SE} = 25.5 \pm 7.5$ sec, $N = 16$), and less likely to respond within the first 30-s of Multi-species Spliced (black-capped terminal) chick-a-dee call playback trials ($X \pm \text{SE} = 39.1 \pm 7.7$ sec, $N = 16$), Normal Spliced mountain chick-a-dee call playback trials ($X \pm \text{SE} = 39.7 \pm 8.2$ sec, $N = 16$), and Multi-species Spliced (mountain terminal) call playback trials ($X \pm \text{SE} = 44.3 \pm 7.7$ sec, $N = 16$).

Similarly, we compared approach behaviour that occurred following playback of each of the four stimulus types to determine whether birds were more likely to approach and investigate the playback of particular call types. Trials in which a bird approached (within 5m of) the speaker during the 90-s playback trials (=1) and trials in which a bird did not approach the speaker during the 90-s playback trials (=0) were coded. Although not statistically significant, $Q = 5.791$, $N = 16$, $p = 0.122$ (see Fig. 5-4B), birds approached the speaker on 75% of Multi-species Spliced (black-capped terminal) call trials (latency to approach: $X \pm \mathrm{SE} = 24.7 \pm 7.3$ sec, $N = 12$), on 50% of Multi-species Spliced (mountain terminal) call trials (latency to approach: $X \pm \mathrm{SE} = 37.9 \pm 8.6$ sec, $N = 8$), on 44% of Normal Spliced mountain chick-a-dee call trials (latency to approach: $X \pm \mathrm{SE} = 23.75 \pm 9.0$ sec, $N = 7$), and on 38% of Normal Spliced black-capped chick-a-dee call trials (latency to approach: $X \pm \mathrm{SE} = 24.0 \pm 8.1$ sec, $N = 6$).

Next, we compared the number of chick-a-dee calls produced during each 90-s baseline trial with the number of chick-a-dee calls produced during the subsequent 90-s playback trial of Normal Spliced black-capped chick-a-dee calls and 90-s playback trial of Normal Spliced mountain chick-a-dee calls in a mixed model Session Number (first or second session at each site) × Playback Order (first or second trial during each session) × Playback Trial (baseline, black-capped chick-a-dee calls, mountain chick-a-dee calls) ANOVA and Tukey's post-hoc analysis ($p < 0.05$). There was a significant main effect of Trials, $F_{2,24} = 6.935$, $p = 0.004$. Tukey's post hoc analysis revealed that responding was significantly greater than baseline following playback of Normal Spliced black-capped chick-a-dee calls ($p = 0.003$) but not following playback of Normal Spliced mountain chick-a-dee calls ($p = 0.065$). These effects did not interact with either the Session Number or Playback Order, Fs < 1.383, ps > 0.270 (see Fig. 5-5).

Finally, we compared the number of chick-a-dee calls produced during each 90-s baseline trial with the number of chick-a-dee calls produced during the subsequent 90-s playback trial of Multi-species' calls consisting of a black-capped chick-a-dee terminal 'dee' portion and 90-s playback trial of Multi-species' calls consisting of a mountain chick-a-dee terminal 'dee' portion in a mixed model Session Number × Playback Order × Playback Trial and Tukey's post-hoc analysis ($p < 0.05$). There was a significant main effect of Playback Trial, $F_{2,24} = 13.033$ $p < 0.001$. Tukey's post hoc analysis revealed that responding was significantly greater than baseline following playback of chick-a-dee calls consisting of black-capped chickadee terminal 'dee' portions ($p < 0.001$) and following playback of chick-a-dee calls consisting of mountain chickadee terminal 'dee' portions ($p = 0.006$). These effects did not interact with either the order of playback (first or second in a session) or the session number (first or second at each site), Fs < 1.352, ps > 0.278 (see Fig. 5-5).

Discussion

Study I: Black-capped Chick-a-dee Vs. Mountain Chick-a-dee Call Playback

In Study 1 the chick-a-dee calls of both black-capped and mountain chickadees were played back at each site. We reduced the possibility of pseudoreplication (see Kroodsm, Byers, Goodale, Johnson, & Liu, 2001) by creating 16 unique sets of black-capped and mountain Normal Spliced and Multi-species Spliced chick-a-dee calls, and using each set only once. In addition, the minimum distance between each playback site was maintained at 1km to ensure independence of playback sessions. Black-capped chickadees increased their calling behaviour following the playback of black-capped chick-a-dee calls (when played first at a site, $n = 8$ sites), but not following the playback of mountain chick-a-dee calls (when played first at a site, $n = 8$ sites). An order effect was observed by the lack of increased calling behaviour when black-capped chick-a-dee calls were played following the playback of mountain chick-a-dee calls at a site. It is possible that the length of each playback trial within a session (5min each) resulted in this effect, as chickadees often approached within a few metres of the sound source immediately following the first playback, and without observing the calling bird, the chickadees would typically leave the area. Nonetheless, our prediction that black-capped chickadees would increase their calling behaviour following playback of conspecific, but not heterospecific chick-a-dee calls, was confirmed. This suggests that the birds, without prior experience with the chick-a-dee calls of mountain chickadees, discriminated between the structurally similar chick-a-dee calls of the two species.

Birds in the current study most likely perceived the conspecific chick-a-dee call playbacks as originating from territory invaders, and vocally responded to indicate their presence and resource-ownership, and in turn mobilize their flock and initiate aggressive resource-defensive interactions (e.g., Nowicki, 1983). Many previous studies have shown that birds respond defensively to territory-encroaching conspecifics (e.g., non-flockmates and non-neighbours; Falls & Brooks, 1975), however most studies are conducted using song in their playback designs. Here we further contribute to the understanding of songbird communication by providing evidence that birds will respond similarly to conspecific calls. These results are in line with those previous studies (e.g., Charrier & Sturdy, 2005; Nowicki, 1983) and suggest that chickadees up-regulate their calling behaviour in response to unfamiliar conspecific calls and ignore the calls of heterospecifics. How black-capped chickadees perform this discrimination is unknown, and therefore Study 2 was conducted to further examine the discriminating abilities of black-capped chickadees by comparing their responses to various experimenter-manipulated chick-a-dee calls.

Study II: Same-Species Calls Vs. Multi-Species Calls

In Study 2 we conducted two playback trials on each of two days to determine whether black-capped chickadees attend more to the introductory 'chick-a' portion of chick-a-dee calls or the terminal 'dee' portion of chick-a-dee calls when performing species discriminations. To accomplish this we constructed spliced control calls that consisted of two 'voices' of the same species, and spliced multi-species calls that consisted of two 'voices', either a black-capped 'chick-a' combined with a mountain 'dee' or vice versa. Calling behaviour to each of the playback trials was compared with calling behaviour during baseline trials to determine which playback type resulted in an up-regulation of calling behaviour.

Based on the results of Study 1, we predicted that black-capped chickadees would increase their responding following playback of conspecific black-capped chickadee spliced control calls, but not following playback of heterospecific mountain chickadee spliced control calls. In addition, and based on a previous operant conditioning task (Bloomfield, Farrell, & Sturdy, in press), we further predicted that the multi-species calls consisting of the black-capped chickadee terminal 'dee' portion would induce greater responding compared to multi-species calls consisting of the mountain chickadee terminal 'dee' portion.

Regardless of whether spliced control black-capped chick-a-dee calls were played first or second during the playback session, or on the first or second session at a site, birds significantly increased their responding above baseline levels to these calls (see Figure 5-5). In comparison, birds did not significantly increase their responding above baseline level to spliced control mountain chick-a-dee calls. That said, the pattern of responding was highly similar to that observed following playback of black-capped chick-a-dee calls and was bordering on statistical significance. These results replicated those obtained in Study 1, and more importantly, suggested that the manipulations employed (i.e., splicing together of call portions from 2 individuals) did not alter the natural responses by birds to these call types. In addition, and regardless of playback order or day of playback, birds increased their responding above baseline levels to calls consisting of a black-capped chickadee terminal 'dee' portion *and* to calls consisting of the mountain chickadee terminal 'dee' portion. This, we believe, is the first evidence provided by wild chickadees that both the introductory 'chick-a' portion and the terminal 'dee' portion of chick-a-dee calls can be used as a species-identifying cue. These results are in line with linear discriminant analyses (Dawson, Bloomfield, Charrier, & Sturdy, 2006) that classified introductory A, B, and C notes by species with 100% accuracy (based on a set of 9 spectral and temporal features) and classified D notes by species with 94% accuracy (based on a set of 4 spectral and temporal features), demonstrating that all chick-a-dee call-note types contain ample information for species classification.

We attempted to further understand chickadee behaviour in response to conspecific, heterospecific, and multi-species chick-a-dee calls by recording the latency to the first vocal response to each playback stimulus and the latency to approach the sound source. Although not statistically significant, we observed a trend by black-capped chickadees to more quickly vocally respond to conspecific chick-a-dee calls while maintaining their distance from the speaker. Alternatively, birds more quickly approached the speaker following the playback of both of the multi-species calls, although this result was also not statistically significant. This could suggest that birds recognized the calls as having been produced by a conspecific (due to either the conspecific introductory or the terminal portion), yet being sufficiently different from typical conspecific calls, resulting in the need to investigate further.

These results are in line with previous studies from our laboratory (Bloomfield & Sturdy, in press; Bloomfield, Farrell, & Sturdy, in press), however they provide further important information related to, but not answered in, our operant conditioning tasks. First, results suggested that allopatric black-capped chickadees, but not sympatric black-capped chickadees, respond differentially to S- (negative, or non-rewarded) black-capped chick-a-dee calls and S- mountain chick-a-dee calls (Bloomfield & Sturdy, submitted). However results of a subsequent study suggested that allopatric birds had a difficult time transferring their learning of S+ (positive, or rewarded) and S- species-specific chick-a-dee call exemplars to unfamiliar (S+ and S-) species-specific chick-a-dee call exemplars (Bloomfield, Farrell, & Sturdy, submitted). Here we provide conclusive evidence that despite not having prior experience with mountain chick-a-dee calls, free-ranging allopatric black-capped chickadees quickly (i.e., without extensive training) discriminate black-capped from mountain chick-a-dee calls.

Second, these laboratory studies examined whether chickadees are capable of discriminating black-capped from mountain chick-a-dee calls. However, laboratory-housed chickadees do not experience the dire ecological constraints that are imposed on free-ranging chickadees, and therefore any errors or lapses in their discriminations in the operant conditioning task would not have a potentially life threatening effect. Although effectively answering the question as to whether the birds can discriminate, these laboratory experiments do not answer the question as to whether these birds do in fact perform these discriminations in nature. In contrast, the current set of field playback studies asked (and answered the question) whether birds, in their natural habitat, do discriminate black-capped chick-a-dee calls from unfamiliar yet highly similar mountain chick-a-dee calls.

Finally, we previously examined the abilities of laboratory-housed chickadees to discriminate black-capped and mountain chick-a-dee calls based on certain portions or combinations of portions of each species' chick-a-dee calls (Bloomfield, Farrell, & Sturdy, in press). Similar to the current set of studies, once it was determined that birds could discriminate black-capped and mountain chick-a-dee calls, birds were intermittently presented with two-voiced conspecific and heterospecific chick-a-dee calls, multi-species calls created using different portions from the two species' chick-a-dee calls, and introductory and terminal portions (only) of chick-a-dee calls. Results indicated that compared to responding to conspecific two-voiced calls, birds responded significantly less to multi-species calls consisting of a mountain chick-a-dee terminal 'dee' portion, however responding to these multi-species calls was not significantly different from responding to multi-species calls consisting of a black-capped chick-a-dee terminal 'dee' portion. Therefore, not only can birds respond appropriately to calls consisting of a conspecific portion either in the introductory or terminal portion of the calls, the current results parallel those obtained in the laboratory and suggest that in their natural habitat, birds will respond to calls consisting of either a conspecific introductory or terminal portion.

We had initially predicted that birds would be more likely to utilize the terminal 'dee' portion of calls to discriminate between species for at least a couple of reasons. First, the introductory A-, B-, and C-type notes are very short in duration and very high in frequency (Charrier et al., 2004), rendering them more susceptible to environmental degradation (Wiley & Richards, 1982), whereas the terminal D-type notes are the lowest in frequency and the longest in duration, and therefore less susceptible to degradation. Second, while A, B, and C notes are often omitted from calls, every chick-a-dee call contains at least one D-type note. However linear discriminant analyses suggested that birds could use either the introductory or terminal chick-a-dee call notes (Dawson et al., 2006) based on their acoustical features. Results of the current set of studies agree with results of the linear discriminant analyses and indicate that birds are capable of using either the introductory or terminal portion of the chick-a-dee calls to recognize conspecific calls. Further, we suggest that the ability to utilize the introductory portion of the call to determine species membership is a prudent strategy, allowing for quick decisions regarding the appropriate action to be taken.

Future Directions

While the results of the current set of studies increase our understanding of chickadee vocal perception, several questions remain. For example, how would black-capped chickadees from a region of sympatry (where mountain chickadees occur) respond to these stimulus types? It remains possible that sympatric black-capped chickadees would respond to mountain chickadee calls, which might suggest that interspecific competition occurs among the closely related species. Although no interspecific competition occurs during breeding season (Hill & Lein, 1989), competition among closely related heterospecifics may be prevalent during the winter months when resources are scarce (e.g., Ficken et al., 1996; Minock, 1972).

In addition, what are the perceptual limits of the chickadees? For example, we do not know whether birds are capable of performing this discrimination with finer manipulations of the test stimuli. Will birds continue to respond to black-capped chick-a-dee calls that have one mountain chick-a-dee call note inserted into the call? Two mountain chick-a-dee call notes? In other words, what is the minimum number of black-capped chick-a-dee call notes (or, stated another way, the maximum number of mountain chick-a-dee call notes) that would result in birds continuing to treat these calls as conspecific? While further questions continue to be raised concerning the perceptual abilities of chickadees, the current studies corroborate previous operant conditioning results and further add to our understanding of how these songbirds perceive conspecific and highly similar heterospecific communication signals in nature.

Figure 5-1.

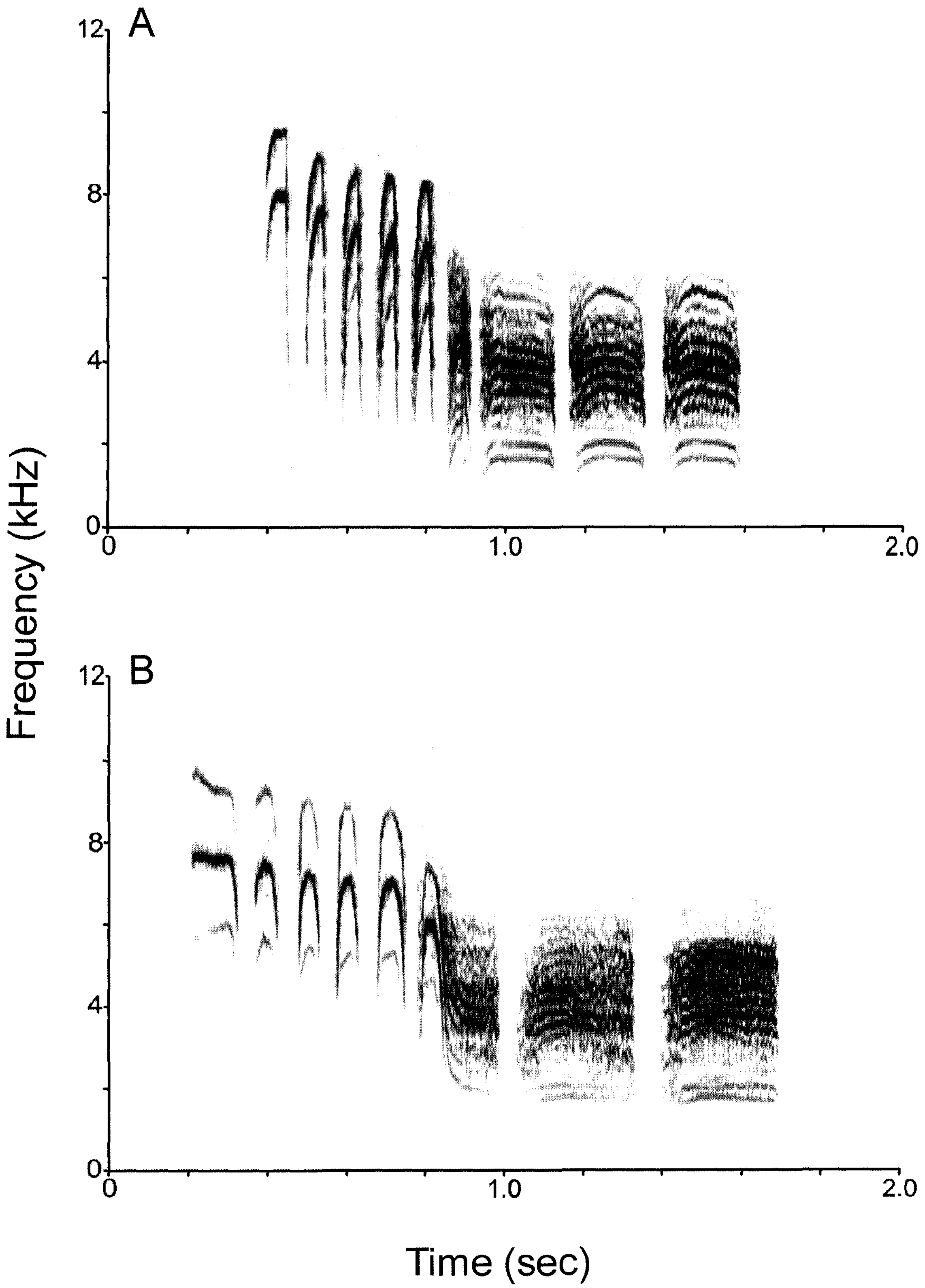


Figure 5-2.

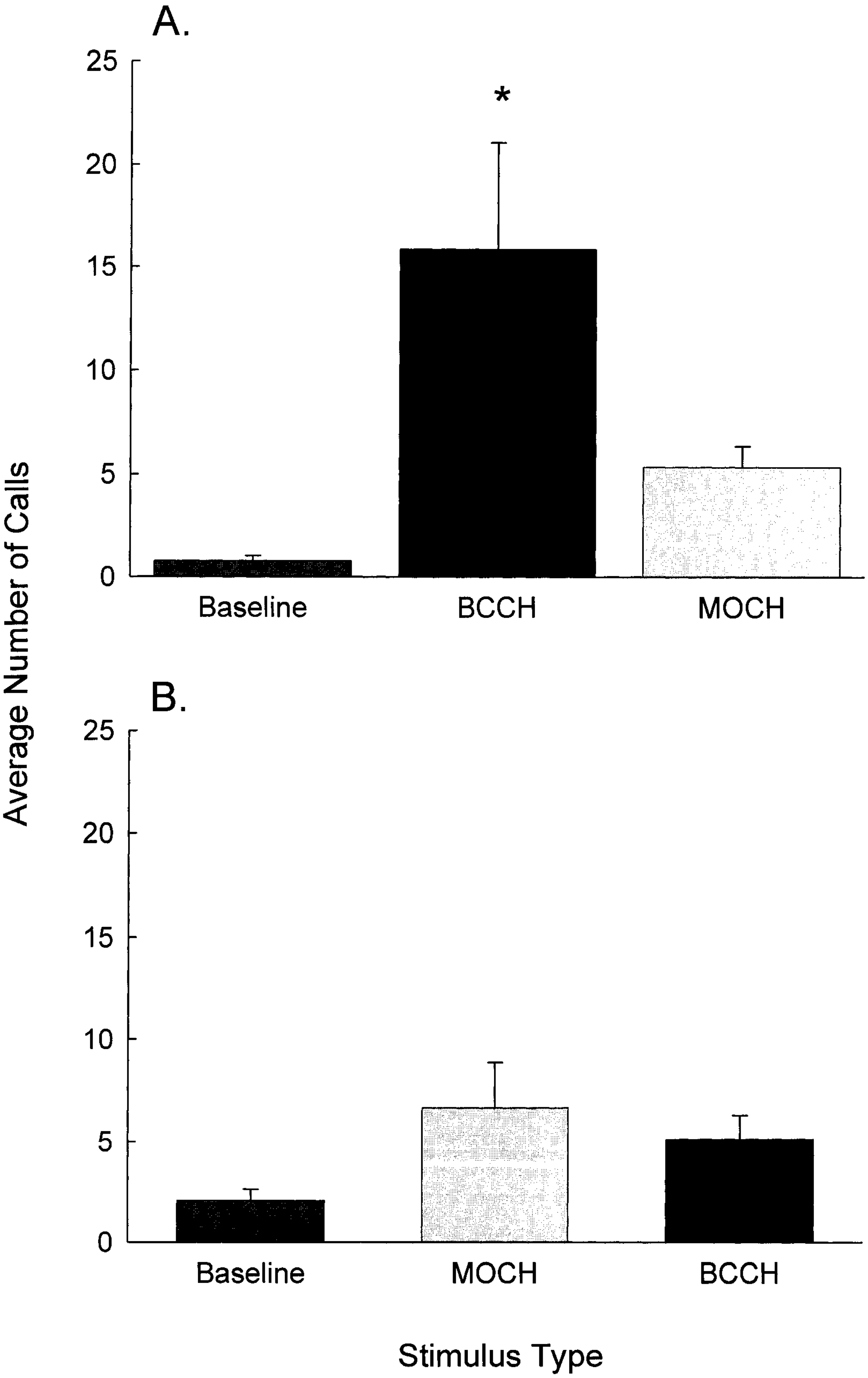

A.
25
20
15
10
5
0
*
Baseline
BCCH
MOCH
Average Number of Calls
B.
25
20
15
10
5
0
Baseline
MOCH
BCCH
Stimulus Type

Figure 5-3.

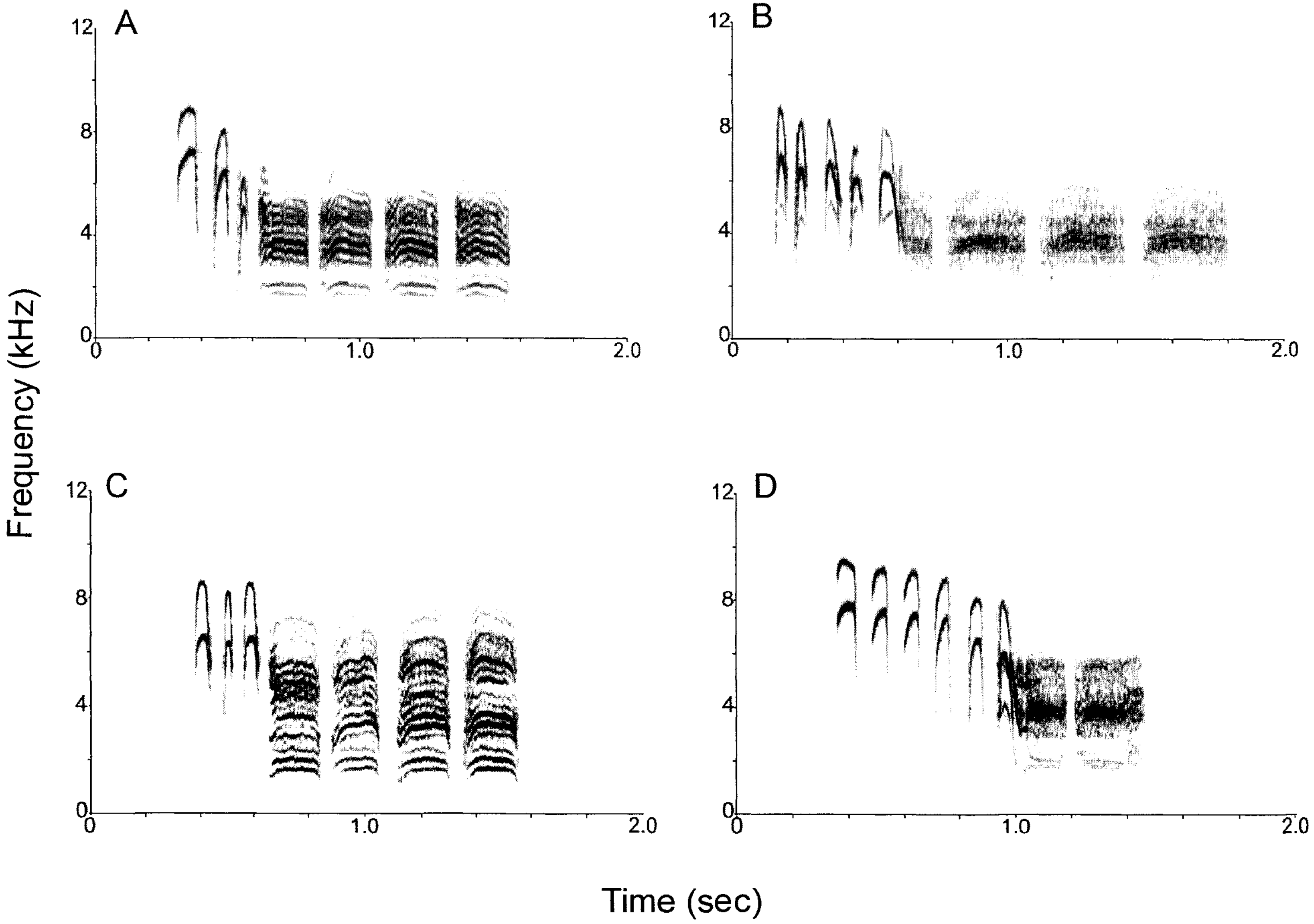


Figure 5-4.

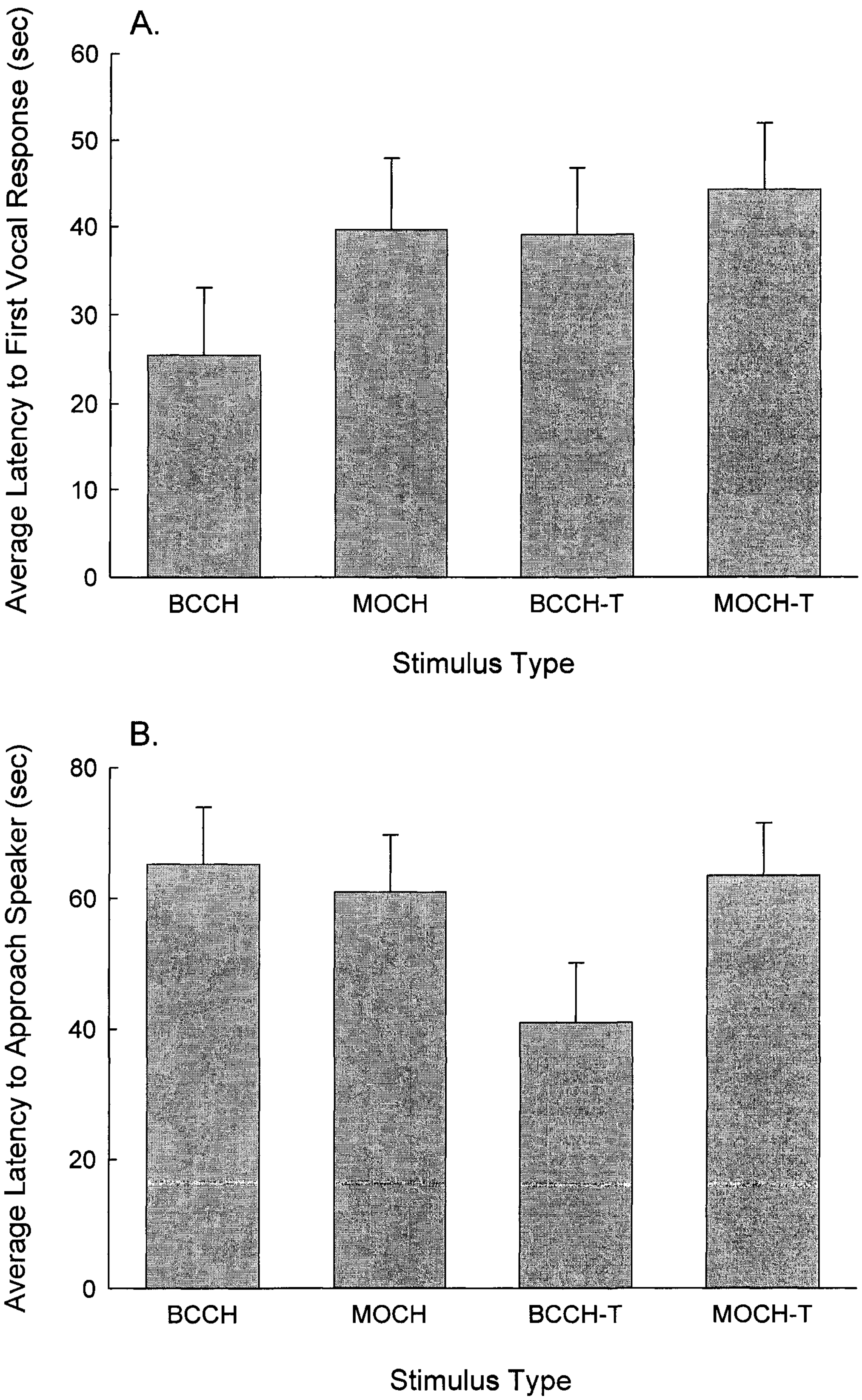
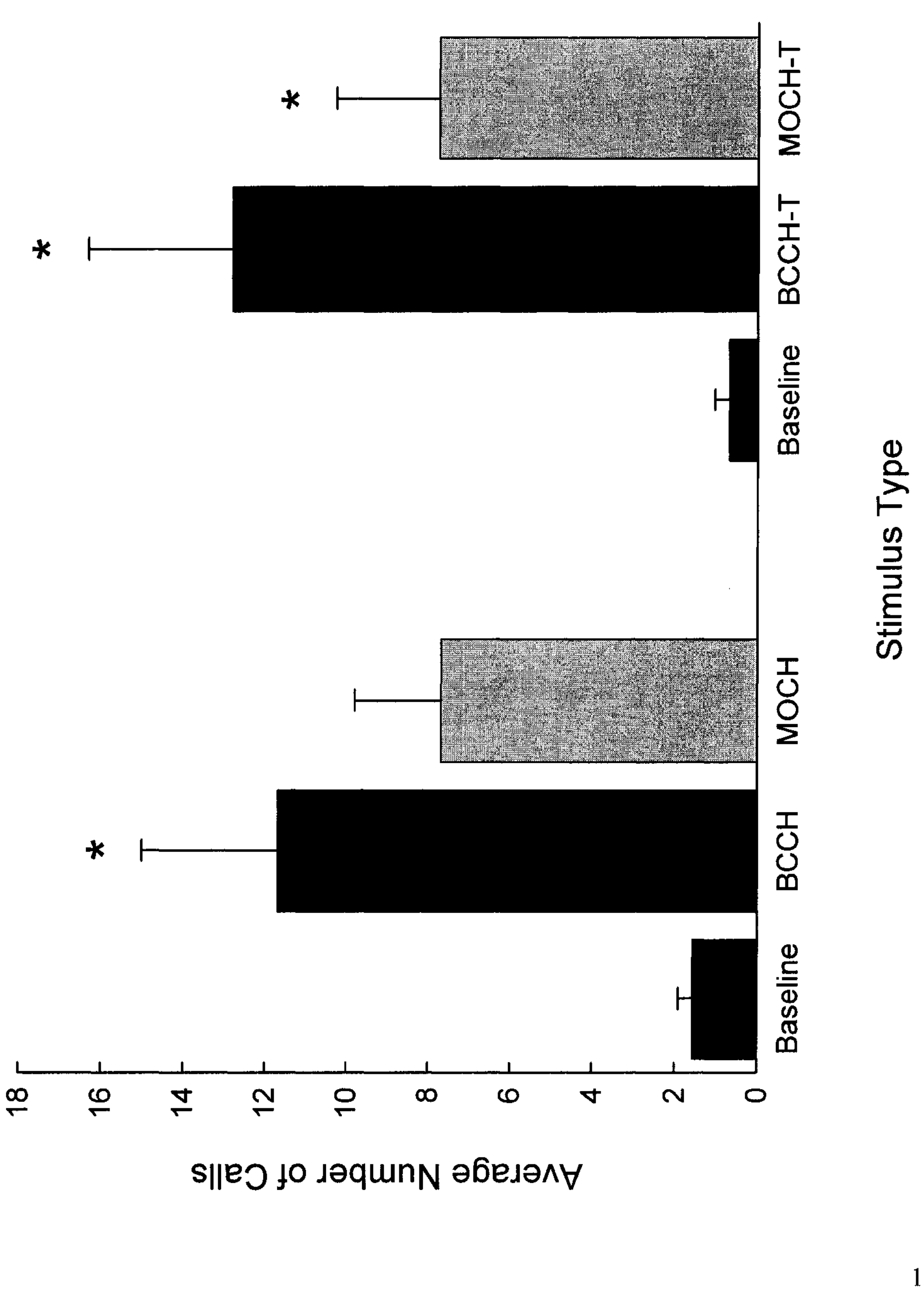

A.
Average Latency to First Vocal Response (sec)
60
50
40
30
20
10
0
BCCH
MOCH
BCCH-T
MOCH-T
Stimulus Type
B.
Average Latency to Approach Speaker (sec)
80
60
40
20
0
BCCH
MOCH
BCCH-T
MOCH-T
Stimulus Type

Figure 5-5.


Average Number of Calls
0
2
4
6
8
10
12
14
16
18
Baseline
BCCH
MOCH
Baseline
BCCH-T
MOCH-T
*
*
*
Stimulus Type

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Chapter 6: Discrimination and categorization of chick-a-dee calls by cross-fostered black-capped chickadees

A version of this paper has been submitted for publication. Bloomfield, L.L., Farrell, T.M., & Sturdy, C.B. *Behavioural Processes*.

Introduction

Songbirds use vocal signals (songs and calls) to communicate with conspecifics in a variety of different contexts such as territory advertisement, pair-bond maintenance, and flock cohesion and co-ordination. Vocal signals are often more reliable than visual signals for recognizing and communicating with conspecifics. Vocal signals are not as greatly affected by impeding obstructions such as foliage, which can negatively impact the transmission and reception of visual signals. Songbirds exist within a communication network in which they participate as active senders and active receivers of acoustic signals. Many species of songbirds have previously been shown to utilize acoustic communication as a means to recognize mates (e.g., Vignal, Mathevon, & Mottin, 2004), flockmates (e.g., Nowicki, 1989), and neighbours (e.g., Falls & Brooks, 1975). Further, birds can act as passive receivers when surrounded by the cacophony of vocalizations of other, both conspecific and heterospecific, birds. The extent to which birds' perceptual abilities are affected by their prior experience with their own and other species is the focus of the current study.

Chickadees are an excellent model system for investigating vocal production and perception. First, chickadees learn their song (Shackleton & Ratcliffe, 1993) and at least some components of some of their calls from conspecific tutors (Hughes, Nowicki, & Lohr, 1998; Mammen & Nowicki, 1981). Further, there are seven species of chickadees in North America, and in some regions one or more chickadee species can be found cohabitating in overlapping regions. For example, black-capped and mountain chickadees occupy overlapping regions in various areas of the Rocky Mountains (e.g., Hill & Lein, 1988). This allows researchers to investigate several aspects of vocal communication abilities in chickadees, including the extent to which experience with other, closely related, chickadees in the wild affects their individual and species' discriminations.

All chickadees species studied to date produce a variant of the "chick-a-dee" call, a combinatorial vocalization putatively used to maintain flock co-ordination (Smith, 1991). Unlike the calls of most songbirds, the chick-a-dee call has a learned component. For example, tape tutored chickadees will accurately produce only 2 of the 4 chick-a-dee call-note types (Hughes et al., 1998). In addition, the fine spectral features of one of the note types can be modified to converge upon a flock mean (Nowicki, 1989), acting as a flock-membership marker. Under normal conditions (i.e., in the wild), the black-capped chickadee's call consists of 4 note types, termed A, B, C and D notes (Ficken, Ficken, & Witkin, 1978). While the syntactical ordering of notes within calls remains fixed (A → D), any of the note types can be repeated or omitted from a call, resulting in a nearly infinite number of possible call variants (Hailman, Ficken, & Ficken, 1985).

Similar to the chick-a-dee call of black-capped chickadees, the chick-a-dee call of mountain chickadees also consists of A, B, C and D notes. In addition, mountain chickadees produce intermediate note types; the A/B note in the introductory 'chick-a' portion of the call and the D-hybrid note in the terminal 'dee' portion of the call (Bloomfield, Charrier, & Sturdy, 2004). Similar to the calls of black-capped chickadees, the chick-a-dee calls of mountain chickadees are produced by repetition and omission of note types while maintaining a fixed syntactical ordering of notes within calls (A → D). Although significant advances have been made in our understanding of chick-a-dee call production, we are only just beginning to understand how chickadees perceive their own and other species' chick-a-dee calls.

Despite the many similarities in morphology and phonology between the two species' chick-a-dee calls, both species perceive the calls as belonging to separate open-ended categories (Bloomfield & Sturdy, in press). Open-ended categorization is a strategy first described by Herrnstein (1990), accounting for the mechanism used by animals to discriminate and categorize stimuli. In brief, stimuli that are more perceptually similar are more likely to be classified as belonging to the same category. Further, based on these similarities, novel or unfamiliar (i.e., untrained) stimuli that are later encountered can also be accurately classified as either belonging to the category (i.e., are similar to existing category exemplars) or as not belonging to that category (i.e., are different from existing category exemplars). This is in stark contrast to the strategy of rote memorization, which refers to the ability of animals to memorize each encountered stimulus. Whereas rote memorization requires experience with each exemplar, open-ended categorization does not, and as such, is a more flexible cognitive mechanism.

While categorization and memorization abilities have been investigated using stimuli that are not found in the subjects' natural habitat (e.g., pictures of flower, cars, chair and people, Astley & Wasserman, 1992; pictures of trees, bodies of water, and women, Herrnstein, Loveland, & Cable, 1976; pictures of fish, Herrnstein & de Villiers, 1980), we suggest that further research into the categorization and memorization abilities using natural stimuli will provide greater external validity to the animals' natural history (see Sturdy, Bloomfield, Farrell, Avey, & Weisman, 2007). For example, in their natural habitat white-throated sparrows (*Zonotrichia albicollis*) discriminate the familiar songs of neighbours from the novel songs of strangers (Falls & Brooks, 1975) based on acoustic cues present in the familiar songs that are not present in the unfamiliar songs. Field sparrows (*Spizella pusilla*) can discriminate conspecific from heterospecific vocal signals based on particular frequency parameters available in conspecific songs (Nelson, 1989). Zebra finches (*Taeniopygia guttata*) and chickadees perceive their song notes and chick-a-dee call notes (respectively) as belonging to separate, open-ended categories into which novel notes can be classified (Sturdy, Phillmore, Price, & Weisman, 1999; Sturdy, Phillmore, & Weisman, 2000). Finally, and directly related to the current study, laboratory-based operant conditioning studies have provided evidence that chickadees perceive their own chick-a-dee calls and the chick-a-dee calls of other species (Carolina chickadees, *P. carolinensis*, and mountain chickadees) as belonging to separate, open-ended categories (Bloomfield, Sturdy, Phillmore, & Weisman, 2003; Bloomfield & Sturdy, in press).

One advantage to our current method of studying categorization abilities is the ability to simultaneously investigate rote memorization abilities. For example, in order to determine whether chickadees discriminate between call-categories, Bloomfield and Sturdy (in press) presented three chick-a-dee call-exemplar sets to birds. The first set of calls were designated as S+s (rewarded stimuli), a second set of calls of the same species were designated as S-s (non-rewarded stimuli), and a third set of calls of a different species were also designated as S-s. The strategies used by the birds were (1) rote memorization for responding appropriately to S+ and S- exemplars of the same species, and (2) categorization for responding appropriately to S- exemplars of the other species. By examining birds' abilities to memorize particular stimuli we can determine whether there are specialized processes involved in the perception of species-specific (i.e., conspecific) vocal signals. For example, budgerigars (*Melopsittacus undulates*), zebra finches, and canaries (*Serinus canaria*) show enhanced abilities to discriminate among calls of their own species than among calls of the other species (Dooling, Brown, Klump, & Okanoya, 1992; Okanoya & Dooling, 1991; Sinnott, 1980). However, contradictory results have suggested that in fact birds possess more generalized processes for discriminating among species' vocalizations, showing no species-specific advantage (e.g., Bloomfield et al., 2003; Bloomfield et al., in press; Park & Dooling, 1985; Phillmore, Sturdy, Turyk, & Weisman, 2002). In the current study we investigate the potential for specialized processes by providing developing birds with exposure to only one chickadee model species and examining their ability to discriminate and memorize the chick-a-dee calls of familiar and unfamiliar chickadee species.

Many previous studies have investigated the effects of abnormal rearing conditions on vocal production and perception in songbirds (the true oscines, see Baptista, 1996 for a review). For example, it was first found that chaffinches (*Fringilla coelebs*) reared without exposure to adults produced abnormal song (Thorpe, 1958), and this has been replicated in a number of other studies with many species of songbirds. In addition, birds reared without exposure to adults also have difficulty discriminating among conspecific vocalizations. For example, Phillmore and colleagues (Phillmore, Sturdy, & Weisman, 2003) found that isolate-reared black-capped chickadees discriminated among individual chick-a-dee songs more slowly than normally-reared chickadees. To summarize the general consensus of isolation rearing, both production and perception deficits not seen in normally-reared birds occur in isolation-reared birds.

However, in a majority of studies investigating the effects of abnormal rearing conditions on songbird vocal production and perception, the birds are reared in complete isolation, among isolate siblings, or with exposure to tape-tutoring. A recent review by Beecher and Burt (2004) suggests that social interaction that is not available to isolation-reared or tape-tutored birds may be a key factor in vocal learning. Eavesdropping on vocal interactions of adults, and perceiving responses to one's own vocal output may provide young birds with the necessary experience for learning to produce accurate renditions of adult vocal behaviour. Further, this type of experience may also improve upon birds' abilities to discriminate among individual vocalizations and between species' vocalizations.

To examine the effects of rearing conditions on vocal perception, we collected nestling black-capped chickadees (5-14 days post-hatch) from 4 different broods and randomly assigned them to one of two rearing conditions: among laboratory-housed black-capped chickadees or among laboratory-housed mountain chickadees. Thus the birds were provided with the opportunity to vocally interact with normal birds in the laboratory colony room, however the rearing conditions provided for these birds excluded parental interaction and physical contact with adult birds. We were interested in determining whether this intermediary rearing condition resulted in suboptimal discriminations among individual conspecific vocalizations, and whether birds reared among mountain chickadees would be more proficient at memorizing and discriminating among mountain chick-a-dee calls, suggesting a rearing-specific advantage. Ultimately, the results of this study will provide a greater understanding of the (competing effects) of genetics and environmental experience.

In the current study we examine the abilities of normally-reared and laboratory-reared chickadees to memorize and categorize conspecific and heterospecific chick-a-dee calls using a true category/pseudo category testing paradigm virtually identical to that used by Sturdy and colleagues (1999). The logic here is that if birds more quickly discriminate between species' defined categories of chick-a-dee calls (true categories) than between categories of randomly selected chick-a-dee calls of each species (pseudo categories), then we can suggest that there is greater perceptual similarity within each species' calls, facilitating species' discriminations and suggesting that each species' calls belong to separate and distinct categories. We further test for open-ended categorization abilities by presenting novel (i.e., untrained) chick-a-dee calls to birds in the true category groups and examine the extent of response generalization. Finally we investigate the potential influence of experience with each species' chick-a-dee calls by examining memorization (individual recognition) abilities of birds in the pseudo category condition.

Methods

Subjects

A total of 36 birds, at least one year of age and naïve to the experimental procedures served in the current set of experiments. Adult black-capped and mountain chickadees (N = 8 of each) were captured between January 2005 and March 2006 from several regions of Edmonton, Alberta, Canada (53° 06'N, 113° 04'W) and several regions of Kananaskis Country, Alberta, Canada (51° 02'N, 115° 03'W), respectively.

Hatchling black-capped chickadees (5-14 days post-hatch, N = 20) were collected from four different broods in several regions of Edmonton, Alberta, Canada in June 2004 and 2005. Immediately upon capture, birds were randomly assigned to one of two rearing conditions, either among normal adult black-capped chickadees in the black-capped chickadee colony room or among normal adult mountain chickadees in the mountain chickadee colony room. Birds in each rearing condition were kept together in their respective colony rooms in a round (approx. 20-cm diameter, 15-cm depth), felt-lined container. Increased mobility at about 14 days of age required the group of birds to be transferred to a cage (Jupiter Parakeet cages, 0.3m wide x 0.4m high x 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada), remaining together until 35 days of age, when each hand-reared bird was placed in a separate cage. A mixture of wheat germ, Mazuri Small Bird Maintenance Diet (Mazuri, St. Louis, MO), water, jarred baby food and spinach was hand-fed to birds until evidence of independent feeding was observed. Birds were completely weaned off the soft food mixture and onto solid food provided to all birds in housing (Mazuri Small Bird Maintenance Diet) at about 45 days of age. Water, grit mixture and cuttlebone were always freely provided.

With the exception of the hand-reared black-capped chickadees in the mountain chickadee colony room, each species was housed separately at the University of Alberta in individual Jupiter Parakeet cages (0.3m wide x 0.4m high x 0.4m deep; Rolf C. Hagen, Inc., Montreal Canada) for a minimum of 1 month prior to the commencement of the experiments. The housing conditions allowed for auditory and visual contact between conspecific birds, but not physical contact. Birds in each colony room were maintained on a light-dark cycle typical for the season in Edmonton, Alberta (August – March). The temperature was maintained at about 20° C.

Prior to experimentation birds were given ad libitum access to lab food (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO), cuttle bone, grit, and water (vitamin-supplemented on alternate days, Hagen, Rolf C. Hagen, Inc., Montreal Canada).

Birds were also given 1 meal worm three times per week and hard-boiled egg and spinach mixture twice a week.

During the experiment, standard rations were available only when an appropriate operant response was produced. Birds were given ad libitum access to cuttle bone, grit and water (vitamin-supplemented on alternate days). Birds were also given 1 meal worm twice each day (morning and evening) to ensure good health throughout the duration of the experiments.

Apparatus

Modified budgerigar cages (0.3 m wide × 0.4 m high × 0.4 m deep) provided continuous housing for the birds during training and testing periods. To ensure the birds did not have access to spilled food, a mesh floor was attached near the bottom of the cage. Each cage was contained in a ventilated, sound-attenuated chamber illuminated by a 9-W twin-tube full-spectrum fluorescent bulb and had several perches and dispensers for water and grit. Infrared cells monitored a motor-driven feeder (Njegovan, Hilhorst, Ferguson, and Weisman, 1994) mounted beside the cage, and a perch opposite the feeder entrance monitored the bird's position. Access to the feeder was made possible by an opening (11 cm wide × 16 cm high) in the cage. A single-board computer (Palya and Walter, 2001) interfaced to a personal computer controlled a standard CD-ROM, scheduled the experiment and recorded responses to stimuli. Stimuli were played at 75-85 dB (A weighting, slow response, measured using a Radio Shack Sound Level Meter) from a CD to either a Cambridge A300 Integrated Amplifier (Cambridge Audio, London, England) or a NAD 310 Integrated Amplifier (NAD Electronics, London, England) and then to a Fostex FE108Σ full-range speaker (Fostex Corp., Japan) located beside the feeder (effective frequency response 200-16,000 Hz). The center of the speaker was at the height of the bird's head when the bird stood on the perch.

Stimuli

A total of 60 high-quality chick-a-dee calls (30 black-capped and 30 mountain), recorded using a variety of microphone and recorder types, were randomly selected from our own database of recordings, commercially available compact discs, and bioacoustics libraries (see Figure 6-1). All recorded chick-a-dee calls were unfamiliar to the experimental subjects as they originated from birds recorded in regions at least 120km from the locations of capture. Using GoldWave Version 5.12 (Goldwave, Inc., St. John's, NF), calls were bandpass filtered (1,000 – 10,000 Hz; GoldWave) to remove background noise. Using SIGNAL 4.0 sound analysis software (Engineering Design, CA) the leading and trailing 5-ms of silence were tapered to remove transients, amplitude was equalized, and each call was saved as an individual 2-s sound file. All 60 calls were then transferred to compact discs, one call per track.

Procedure

Nondifferential Training. Nondifferential training began after a bird had learned to use the perch and feeder. When a bird landed on the perch, breaking an infrared beam, the within-trial sequence began. Remaining on the perch for 1-s on average (range 900-1,100 ms) resulted in a single call being randomly selected and played once. If the bird flew or hopped to the feeder within 1-s after the stimulus was played, breaking another infrared beam, it was rewarded with 1-s access to food (i.e., reinforcement), followed by a 30-s inter-trial interval (ITI). If the bird left the perch without entering the feeder, the trial ended after 1-s. If the bird did not leave the perch, the trial ended after 1-s; a 60-s ITI followed. The 60-s ITI was used to increase the probability of the bird leaving the perch on all trials. Leaving the perch before the stimulus had finished playing (i.e., interrupted trial) resulted in the trial ending and the chamber lights turning off during a 30-s ITI. These procedures helped us to ensure that birds heard and attended to the calls and subsequently left the perch.

During nondifferential training, we presented 40 of the 60 calls to be used during discrimination training. The purpose of nondifferential training was to ensure that the birds heard and responded to all the training calls and to gather similar percentages of responses to each call as a baseline for the evaluation of training during experimental testing. Nondifferential training continued until a bird approached the feeder on a minimum of 60% of the trials (similar to the level of responding observed during discrimination by Bloomfield et al., 2003), an appropriate level considering birds are able to trigger a stimulus for every perch-landing and receive reinforcement for every feeder approach. Birds typically approached the feeder on about 80% of the trials and on average trigger about 1,000 – 2,000 total stimuli per day.

Discrimination Training. Discrimination training began after nondifferential training. During discrimination training, visits to the feeder after S+ (positive, or reinforced) calls were rewarded with access to food, but visits to the feeder after S– (negative, or nonreinforced) calls resulted in no reward and a 30-s ITI with the chamber lights off (i.e., punishment). Other contingencies and procedures initiated during nondifferential training remained in effect during discrimination training. Typically, each daylong session generated about 1,000 – 2,000 trials.

Chickadees were randomly assigned to either the true category experimental condition (N = 16: 4 normal black-capped chickadees, 4 normal mountain chickadees, 4 black-capped reared black-capped chickadees, 4 mountain reared black-capped chickadees) or the pseudo category experimental condition (N = 20: 4 normal black-capped chickadees, 4 normal mountain chickadees, 5 black-capped reared black-capped chickadees, 7 mountain reared black-capped chickadees). The true category experimental condition included two subgroups, with one group discriminating 20 S+ black-capped chick-a-dee calls from 20 S- mountain chick-a-dee calls (BCCH-S+ group) and the other group discriminating 20 S+ mountain chick-a-dee calls from 20 S- black-capped chick-a-dee calls (MOCH-S+ group). The pseudo category experimental condition also included two subgroups. Birds in the pseudo category subgroups discriminated between 20 S+ chick-a-dee calls and 20 S- chick-a-dee calls chosen at random for each subgroup. Random selection for each subgroup resulted in an equal number of black-capped and mountain chick-a-dee calls assigned as S+s and as S-s.

Probe (Test) Sessions. Probe sessions for birds in the true category conditions began after birds met the criterion for accurate discrimination (see Response Measures below). Prior to commencing probe sessions we reduced the percentage of reinforcement for the S+ calls to 85% for a minimum of 1,000 trials to decrease the discriminability of the S+ training calls from the S+ and S- test calls (all rewarded at 15%). Each probe session (n = 5) consisted of 404 stimulus presentations: 40 training calls (at 85% or 0% reinforcement for S+s and S-s respectively) presented 10 times each, and 4 of the 20 chick-a-dee test calls (2 black-capped and 2 mountain) not heard during nondifferential or discrimination training, presented one time each. Each probe session continued for a minimum of 3 404-trial blocks, resulting in 3 presentations of each test call, with one 500-trial block of the standard discrimination separating each probe session.

Response Measures

We calculated a percentage of response measure for each stimulus (whether S+ or S–) using the following formula: (R+/(N trials – N interrupted trials)) × 100, where R+ is the number of trials on which the bird flew or hopped to the feeder, N trials is the total number of trial presentations for that stimulus, and N interrupted trials is the number of trials in which the lights were extinguished for the bird leaving the perch before the stimulus was played in its entirety. As a measure of discrimination of chick-a-dee calls during training, we calculated a discrimination ratio (DR) for performance on rewarded (S+) chick-a-dee calls by dividing the mean percentage of response to all S+ calls by the mean percentage of response to all S+ calls plus the mean percentage of response to all S- calls (all of which were corrected for the number of interrupted trials). When the DR is at or near .50 birds are responding about equally to both S+ and S- calls (i.e., at chance) and when the DR is at or near 1.00 birds are perfectly discriminating S+ from S- calls. Discrimination training ended once the bird met criterion by maintaining a DR $\geq .80$ for two consecutive 500-trial blocks.

To obtain a measure of how many S+ calls were well discriminated, we adapted the (two-tailed) 95% confidence interval (CI), using the mean (*M*) and standard deviation (*SD*) of the percentage of response for the 20 S- chick-a-dee calls on the final day of discrimination training ($M \pm 1.96 \times SD$). If birds are significantly discriminating an individual S+ call from the S- calls, the percentage of response to that S+ call will be greater than the 95% CI.

Statistical Analyses

We conducted analyses of variance (ANOVAs) and Tukey's planned comparisons on the number of trials to criterion, DRs, number of S+s > 95% CI, and percentages of responses for the true category and pseudo category groups using STATISTICA (version 6, StatSoft, Inc., 2003). When percentages of responses are at or near 0% or 100% or when DRs are at or near .50 or 1.00, sample values may not be normally distributed. We therefore conducted parallel analyses using arcsine square-root transformations of the percentages of responses and DRs. Analysis of transformed data yielded virtually the same pattern of results and levels of significance as untransformed data. Therefore, only results for ANOVAs of the untransformed data are reported here.

Results

Comparisons of True Category and Pseudo Category Discriminations

Trials to Criterion. To determine whether the different groups of birds (normal black-capped chickadees, normal mountain chickadees, black-capped reared chickadees, mountain reared chickadees) assigned to the two true category discrimination groups (BCCH-S+ call group, MOCH-S+ call group) differed in their speed of acquisition, we conducted a Birds × Discrimination Group ANOVA on the number of 500-trial blocks required to reach criterion. There was a significant main effect of Birds, $F(3, 8) = 13.865$, $p = 0.002$, of Discrimination Group, $F(1, 8) = 41.108$, $p < 0.001$, and a significant Birds × Discrimination Group interaction, $F(3, 8) = 7.523$, $p = 0.01$. Tukey's post hoc analysis revealed that black-capped chickadees assigned to the mountain chick-a-dee S+ call group required significantly more trials to reach criterion compared to all other groups of birds.

To determine whether the different groups of birds assigned to the two pseudo category discrimination groups (randomization 1 or randomization 2) differed in their speed of acquisition we conducted a Birds × Discrimination Group ANOVA on the number of 500-trial blocks required to reach criterion. There were no significant main effects and no higher-order interactions among the mean number of trials required by birds in either of the two pseudo category groups, $F\text{s} < 1.212, p\text{s} > 0.341$. We therefore pooled the randomization factor in subsequent analyses.

Finally, to compare performances of birds in the true and pseudo category conditions, we conducted a Birds × Experimental Group ANOVA on the number of trials required to reach criterion. There was a significant main effect of Experimental Group, $F(1, 28) = 17.642, p < 0.001$, but no significant main effect of Birds or Birds × Experimental Group interaction, $F\text{s} < 2.7, p\text{s} > 0.064$. The true category discrimination group reached criterion after fewer trials, $M = 3{,}719$ ($SEM = 522$) compared to the pseudo category discrimination group, $M = 6{,}675$ ($SEM = 532$, see Figure 6-2). In other words, the true category and pseudo category groups required about 93 and 167 trials per call, respectively, to reach criterion discrimination performance.

DR Analysis. The discrimination ratio (DR) provides an indication of how well birds discriminated S+ from S- exemplars at each block of trials while controlling for the overall level of responding. To examine task acquisition across trials by birds in the true and pseudo category groups, we conducted a mixed model (Birds × Experimental Group × Blocks) ANOVA on the DRs. Because training to criterion required varying numbers of trials for individual birds, the first 3 blocks of 500 trials were chosen for analysis because some subjects (in the true category condition) reached discrimination criterion by the fourth block of 500 trials (i.e., their final day of performance, see below). While there was no significant main effects or higher-order interactions of Birds, Fs < 1.03, $ps > 0.418$, there were significant effects for Experimental Groups, $F(1, 28) = 28.492$, $p < 0.001$, Blocks, $F(2, 56) = 48.812$, $p < 0.001$, and for the Experimental Groups × Blocks interaction, $F(2, 56) = 15.041$, $p < 0.001$.

Tukey's post-hoc analysis revealed significant differences in the DRs across each of the first 3 blocks of training for birds in the true category experimental group but not for birds in the pseudo category experimental group. In other words, the discrimination abilities of birds in true category group increased significantly from one trial-block to the next, whereas the discrimination abilities of birds in the pseudo category group required significantly more trials for accuracy to improve (see Figure 6-3). Further, while the DRs for the first two blocks of trials did not differ between the two experimental groups, birds in the true category group had significantly higher DRs than birds in the pseudo category group by the third block of training. On the final 500-trial block (i.e., the final day of training, FD, see Figure 6-3), the difference in DRs between the true and the pseudo category experimental groups was not significantly different, $F(1, 28) = 0.743$, $p = 0.396$. There were also no significant differences among the groups of Birds, $F(3, 28) = 2.281$, $p = 0.101$.

Number of S+s > 95% Confidence Interval (CI). Birds can obtain a high DR due to exclusive responding to only some S+ calls while responding less to other S+ calls and all the S- calls. Determining the number of S+s to which birds responded > 95% CI can provide an indication of how many of the S+ calls were successfully discriminated from the S- calls. We conducted Tukey's planned comparisons ($p < 0.05$) at each 500 trial block to determine whether the groups of birds assigned to the true category conditions (BCCH-S+ group and MOCH-S+ group) differed in the number of exemplars responded to greater than the 95% CI. We limited our analysis to the first 3 blocks of trials as some birds reached criterion by the fourth (i.e., final day) block. Across the first 3 blocks of trials (i.e., 1,500 trials) there were no significant differences among birds in the number of S+ calls to which birds responded. On the final day of training there were no significant differences in the number of successfully discriminated calls (> 95% CI) among birds in the true-category BCCH-S+ and MOCH-S+ conditions ($M = 19.25$ of 20 ± 0.37 and $M = 19.13$ of 20 ± 0.61, respectively).

Birds in the pseudo category discrimination group were required to perform two simultaneous within-category discriminations. That is, birds were trained to discriminate among S+ and S- black-capped chick-a-dee calls and among S+ and S- mountain chick-a-dee calls. Determining the number of S+ black-capped chick-a-dee calls to which birds responded > 95% CI can provide an indication of how many of the S+ black-capped chick-a-dee calls were successfully discriminated from the S- black-capped chick-a-dee calls. Similarly, determining the number of S+ mountain chick-a-dee calls to which birds responded > 95% CI can provide an indication of how many of the S+ mountain chick-a-dee calls were successfully discriminated from the S- mountain chick-a-dee calls.

We examined our *a priori* prediction that birds would more likely discriminate among conspecific S+ and S- calls than among heterospecific S+ and S- calls using Tukey's planned comparisons ($p < 0.05$). Across the first 6 blocks of trials (after which some birds reached criterion), there were no significant differences in the number of S+ calls successfully discriminated by each of the groups of birds. On the final day of training, the number of significantly discriminated S+ black-capped chick-a-dee calls (> 95% CI) was $M = 8.95$ of 10 ($SEM = 0.29$) and the number of significantly discriminated S+ mountain chick-a-dee calls (> 95% CI) was $M = 8.75$ of 10 ($SEM = 0.38$). There were no significant differences among groups of birds in the number of black-capped and mountain chick-a-dee exemplars responded to > 95% CI, $F\text{s} < 2.372$, $p\text{s} > 0.109$.

On the final day of training, birds in the true category condition significantly discriminated $M = 19.19$ of 20 ($SEM = 0.34$) S+ calls and birds in the pseudo category condition successfully discriminated $M = 17.85$ of 20 ($SEM = 0.69$) S+ calls. In a Birds × Experimental Group ANOVA, there was no significant difference between the mean number of calls > 95% CI for the true category and pseudo category groups, $F(1, 28) = 2.120$, $p = 0.156$; and there was no significant main effect or interaction with Birds, $F\text{s} < 0.187$, ps > 0.984.

Percentages of Responses. Finally, we were interested in whether birds in the pseudo category condition learned the two discriminations (black-capped chick-a-dee S+ and S- discrimination and mountain chick-a-dee S+ and S- discrimination) at different rates. While the DR analysis utilizes the overall ratio of responding to all S+s and to all S-s, examining the obtained percentages of responses to each S+ and S- exemplar set within blocks of trials and across blocks of trials provides us with a more sensitive measure with which to test our *a priori* prediction: that birds would show an advantage for memorizing conspecific calls over heterospecific calls.

The results of Tukey's planned comparisons ($p < 0.05$) across the first 6 blocks of trials revealed that, in general, hand-reared birds more quickly learned to discriminate among S+ and S- exemplars compared to normal birds. Both groups of hand-reared birds successfully discriminated among mountain chick-a-dee S+ and S- calls by 2,000 trials, but by 3,000 trials birds were no longer discriminating among these exemplar sets. At this point, however, hand-reared birds were successfully discriminating among the black-capped chick-a-dee S+ and S- calls. Alternatively, normal birds were not reliably discriminating among S+ and S- exemplars of either species' calls by 3,000 trials. By the final day of discrimination all birds responded significantly more to S+ exemplar sets than to S- exemplar sets, and there were no significant differences among groups of birds in their levels of responding to S+ exemplars or to S- exemplars; all birds were successfully discriminating (see Figure 6-4).

Transfer of Training to Test Calls

Once birds in both the black-capped chick-a-dee S+ true category group and the mountain chick-a-dee S+ true category group had reached criterion, we intermittently presented them with black-capped and mountain chick-a-dee calls not used in the training sets. In a mixed model (Birds × S+ Group × Stimulus Set) ANOVA on the percentages of responses to training and test calls, we found a significant main effect of Stimulus Set, $F(3, 21) = 4.807, p = 0.011$, and a significant S+ Group × Stimulus Set interaction, $F(3, 21) = 122.67, p < 0.001$, but no main effect of Birds or any higher-order interactions, Fs < 1.04, ps > 0.441. Tukey's post-hoc analysis revealed that birds in the BCCH-S+ group responded least to the S- mountain chick-a-dee training and test calls, more to the S+ black-capped chick-a-dee test calls, and most to the S+ black-capped chick-a-dee training calls. Similarly, birds in the MOCH-S+ group responded least to the S- black-capped chick-a-dee training and test calls, more to the S+ mountain chick-a-dee test calls, and most to the S+ mountain chick-a-dee training calls (see Figure 6-5). In other words, the birds transferred their discrimination of S+ and S- training calls to the test calls, but responded less to test S+ calls than to training S+ calls.

Discussion

In the current study we asked whether birds would sort chick-a-dee calls into two separate, species-defined categories, and whether their performance would exceed that of birds sorting randomly selected calls of each species. Further, we were interested in the possible effect that experience might have on discriminating black-capped from mountain chick-a-dee calls (true category discrimination) and discriminating among the calls of each species (pseudo category discrimination). By testing black-capped chickadees collected as hatchlings and reared among either black-capped chickadees or among mountain chickadees, we were able to control for the effect that experience (with black-capped and mountain chick-a-dee calls) might have on species' discriminations.

True Category Discrimination Task

During the acquisition phase, all birds learned the true category discrimination in about half the number of trials than was required by birds learning the pseudo category discrimination. This was especially evident in the early stages of training, where birds on the true category task were discriminating at DR = 0.76 after only about 50 trials per call whereas birds on the pseudo category task were discriminating at DR = 0.58. That the true category discrimination was easier to learn that the pseudo category discrimination suggests that birds perceived the calls of the two exemplar sets (black-capped chick-a-dee calls and mountain chick-a-dee calls) as different, and possibly as belonging to two separate categories based on these perceptual distinctions.

An additional and perhaps more important test for categorization is the ability to classify novel, or unfamiliar exemplars into previously defined categories (Herrnstein, 1990). Following training, we presented birds with calls with which birds had no previous experience, and birds were able to sort these calls into the same species' categories as the training calls. That is, birds in the BCCH-S+ group responded to novel black-capped chick-a-dee calls and birds in the MOCH-S+ group responded to novel mountain chick-a-dee calls. While responding to the novel chick-a-dee calls was lower compared to responding to training calls, this provided additional information regarding the categorization abilities of chickadees. Birds did not show perfect transfer to novel calls, not because they did not perceive them as belonging to their species' defined categories, but rather because they were able to detect that these calls were not the same calls presented during training. Discrimination within a category is yet another important feature to open-ended categorization (Herrnstein, 1990), and suggests that the chickadees in the current study were not only able to discriminate between black-capped and mountain chick-a-dee calls, but the birds were also able to discriminate among individual black-capped chick-a-dee calls and among individual mountain chick-a-dee calls.

Pseudo Category Discrimination Task

Further evidence for discrimination within a category is provided by birds in the pseudo category condition, as all birds were able to discriminate among the 20 calls of each species. In order to successfully perform this discrimination, birds were required to memorize each individual black-capped and mountain chick-a-dee call and their associated contingency (either S+ or S-). Based on previous evidence (e.g., Dooling et al., 1992), we predicted that birds would be better able to memorize conspecific (or in the case of black-capped chickadees reared among mountain chickadees, rearing conspecific) chick-a-dee calls, however we did not find any conclusive evidence for this advantage.

Birds appeared to have employed different strategies during discrimination training: respond at high levels to all stimuli and learn over trials which exemplars to withhold responding to, or respond at low levels to all stimuli and learn over trials which exemplars to increase responding to. Eleven birds used the former strategy while 9 birds, including 7 hand-reared birds, used the latter strategy. In addition, both groups of hand-reared chickadees appeared to have utilized a "learn one species' calls at a time" strategy, focusing their learning on one (species') discrimination first and focusing on the other (species') discrimination afterward. For example, both groups of hand-reared birds learned the mountain chick-a-dee call discrimination after 2,000 trials, but after 3,000 trials this discrimination was no longer significant, whereas birds had successfully learned the black-capped chick-a-dee call discrimination at this point.

We did detect a small but significant difference in the memorization abilities of normal and hand-reared birds in the pseudo-category discrimination task. Both groups of hand-reared birds required fewer trials than normal black-capped and mountain chickadees to discriminate among S+ and S- black-capped chick-a-dee calls and among S+ and S- mountain chick-a-dee calls. The difference in the rates of learning between normal- and hand-reared birds is not in the same direction as we had predicted or as observed in previous studies with isolate-reared birds. Sturdy and colleagues (Sturdy, Phillmore, Sartor, & Weisman, 2001) found greater perceptual deficits in isolate-reared zebra finches compared to normally-reared zebra finches, and Phillmore and colleagues (2003) found impairments on individual discrimination tasks in isolate-reared black-capped chickadees. One difference that may account for the opposing results between the aforementioned studies and the current study is the rearing environment provided to the hand-reared birds. Specifically, birds in the current study were reared among normal adult (non-related) birds in the laboratory, whereas birds in the previous studies were reared in the absence of normal birds. Therefore exposure to singing and calling adults in any environment may provide young birds with sufficient experience for performing individual discriminations.

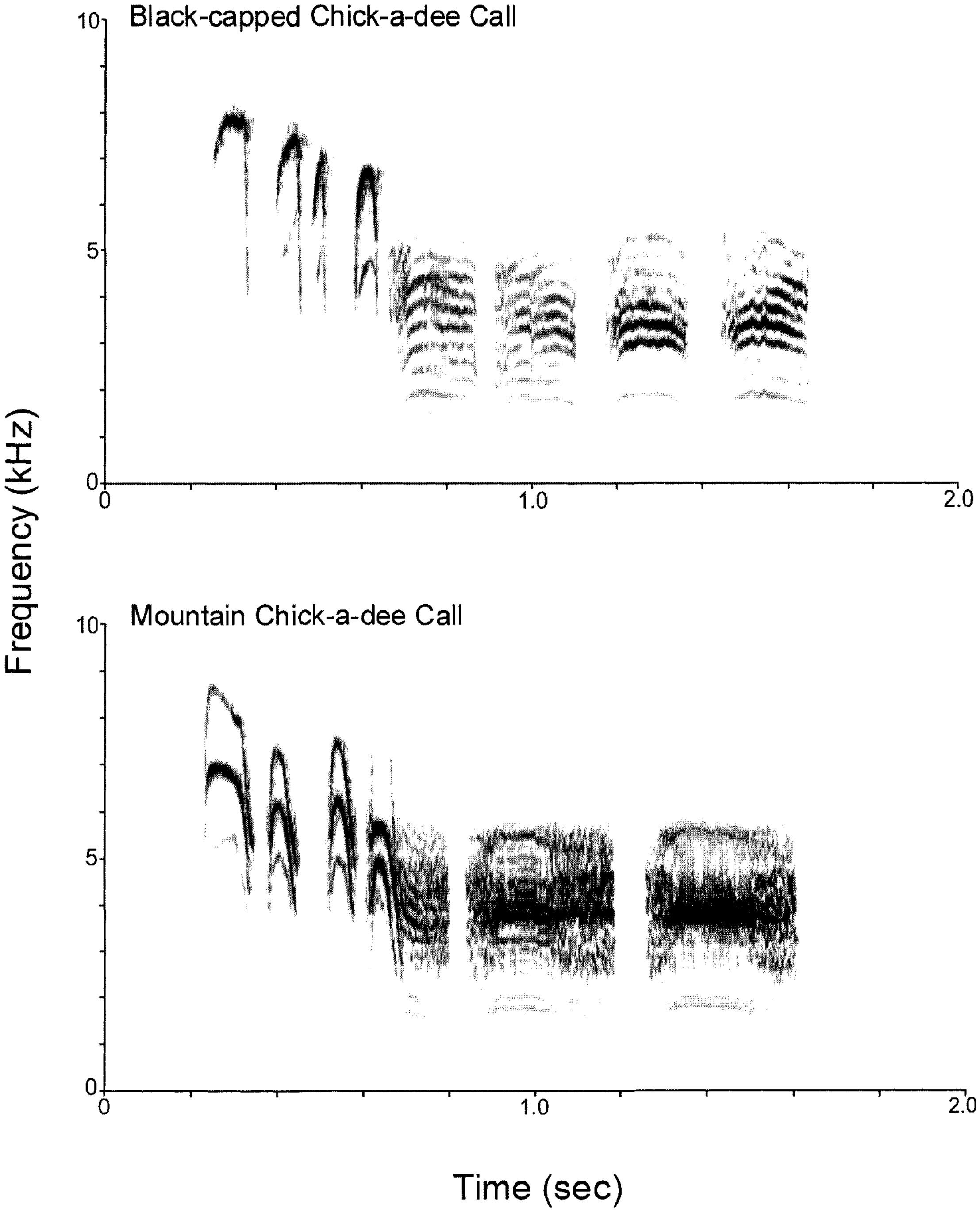
While one might suggest that the hand-reared birds were responding to only a few of the S+ chick-a-dee calls and withholding responding to the rest of the calls, both S+ and S-, thereby memorizing fewer calls, this was not the case. Normal black-capped and mountain chickadees correctly discriminated an average of 17.5 and 18 of 20 S+ exemplars (respectively) and black-capped and mountain reared chickadees discriminated an average of 18.4 and 17.5 of 20 S+ exemplars (respectively) by the final day of training. Therefore, this does not explain why hand-reared birds in the current pseudo-category discrimination task learned at a faster rate than normal-reared birds. In nature, normal birds typically socialize with about 2-10 conspecifics on a daily basis; their natal family prior to fledging and their mate and flock mates after fledging (e.g., McCallum, Grundel, & Dahlsten, 1999; Smith, 1993). Black-capped chickadees discriminate flock mates from non-flock mates (Nowicki 1983), presumably using the acoustic structure of the D notes of chick-a-dee calls (Mammen & Nowicki, 1981), and chickadees can possibly discriminate among individual flock mates (see Charrier, Bloomfield, & Sturdy, 2004). In contrast, birds reared in our laboratory were exposed to 20-40 different laboratory-housed individuals on a daily basis, and the housing conditions allowed for vocal (but not physical) interactions among birds. Thus, the increased number of individuals in a birds' communication network may enhance performance on such individual recognition tasks, and may explain why hand-reared birds were able to memorize 40 individual chick-a-dee calls and their associated contingencies over fewer trials than normal-reared birds.

Conclusions and Future Research

In the current study we expected to find perceptual deficits in hand-reared birds performing the species' discrimination task (true category) and the individual discrimination task (pseudo category), however this was not the case. Further, we expected to find that hand-reared birds would have less well defined species' categories, and would therefore struggle with the transfer test provided to birds in the true category discrimination group. However, all birds accurately transferred their learning to novel chick-a-dee call exemplars. Finally, we expected to find a species- or rearing-specific advantage to memorizing chick-a-dee calls, but did not observe this for either the normal birds or the hand-reared birds. Therefore although songbirds require exposure to singing and calling adults early in life in order to later accurately produce their songs and calls, experience with their own or other species' vocalizations, at least with chickadees and their chick-a-dee calls, does not appear to be necessary for individual recognition or for perceiving the calls as belonging to separate open-ended, species-defined categories. These results are in line with previous studies from our laboratory indicating that allopatric black-capped chickadees (i.e., birds with no previous experience with mountain chickadees or their calls) are equally as capable of discriminating between species' calls as are sympatric black-capped chickadees (Bloomfield & Sturdy, in press; Bloomfield, Farrell, & Sturdy, in press).

Birds in the current study were exposed to either conspecific or heterospecific chickadees and their songs and calls; however we do not know how birds reared in total isolation would perform on this task. While the ability to perceive objects (visual, acoustic) as belonging to a category relies mainly on the inherent perceptual similarities of the objects, experience with even just one of the two species' calls may have contributed to their perception of the calls. In other words, birds that have experience with at least one species' call have the opportunity to recognize and memorize the salient features, and can subsequently discriminate among stimuli with and without these features. Alternatively, birds that have no experience with any songbird vocalizations may show a profound deficit in this discrimination. Therefore, we suggest that in order to conclusively determine the ontogenetic effects on memorization and categorization strategies, birds with no previous experience with any other species be tested in a manner similar to those tested here. Ultimately, the current results further our understanding of the effects of early experience on higher cognitive mechanisms, and provide an intermediary step to previously conducted research on the ontogeny of vocal perception.

Figure 6-1.



Black-capped Chick-a-dee Call

Mountain Chick-a-dee Call

Figure 6-2.

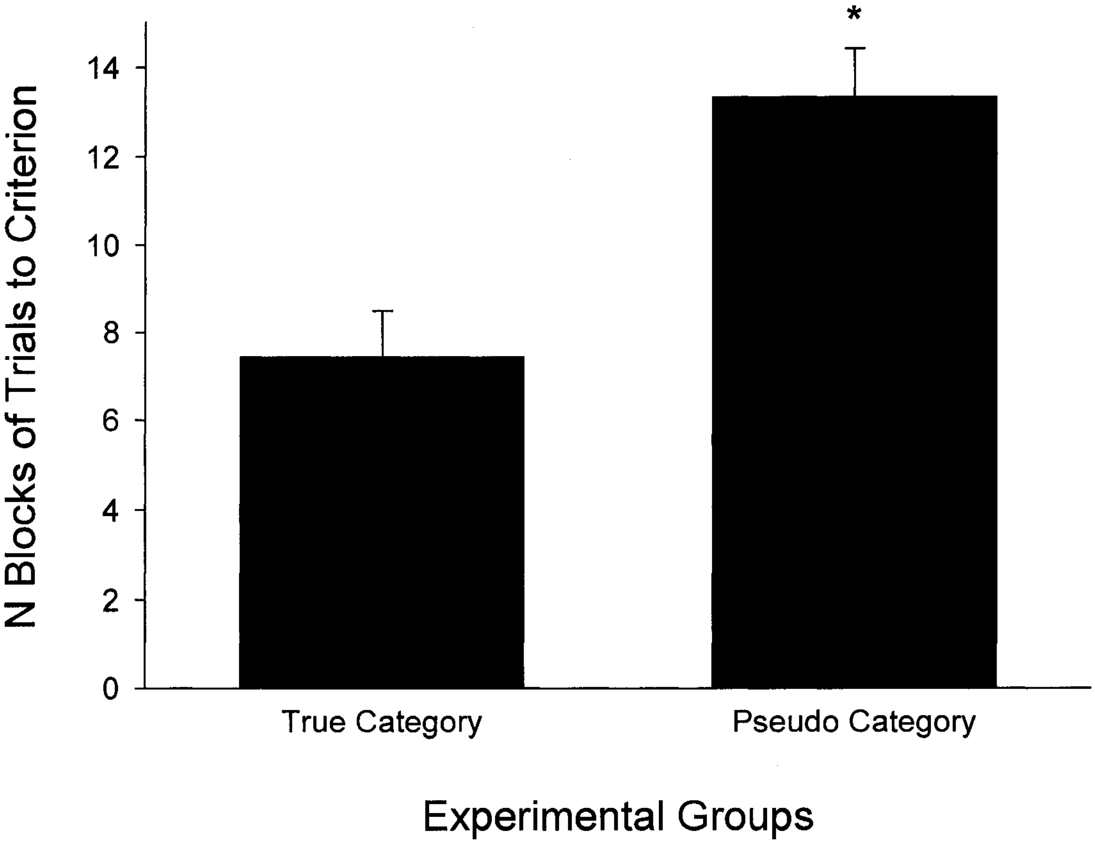
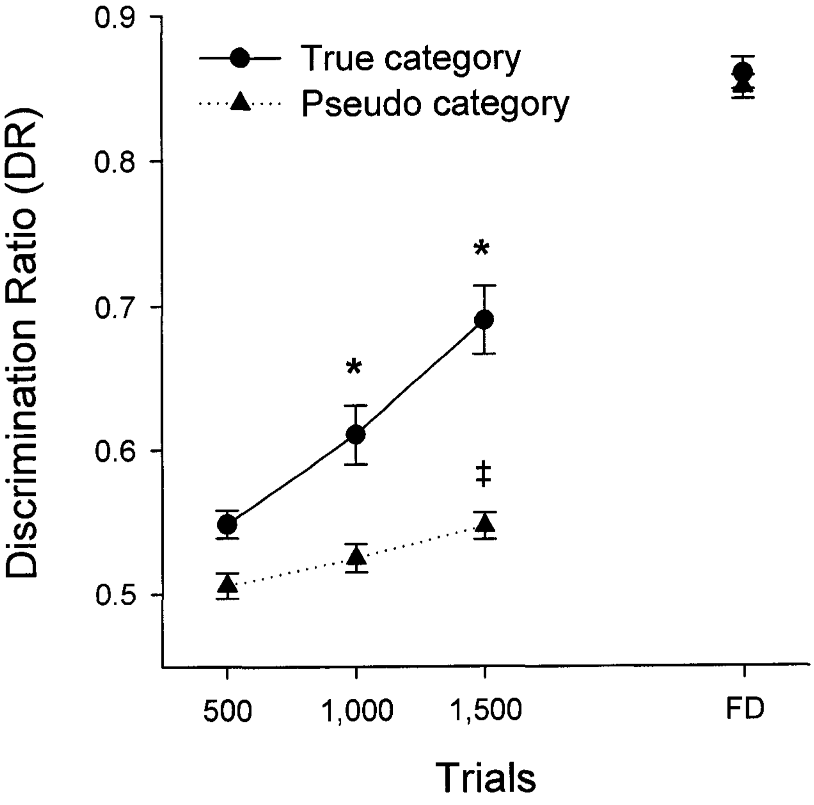

N Blocks of Trials to Criterion
0
2
4
6
8
10
12
14
*
True Category
Pseudo Category
Experimental Groups

Figure 6-3.



True category
Pseudo category
Discrimination Ratio (DR)
0.9
0.8
0.7
0.6
0.5
*
*
‡
500
1,000
1,500
FD
Trials

Figure 6-4.

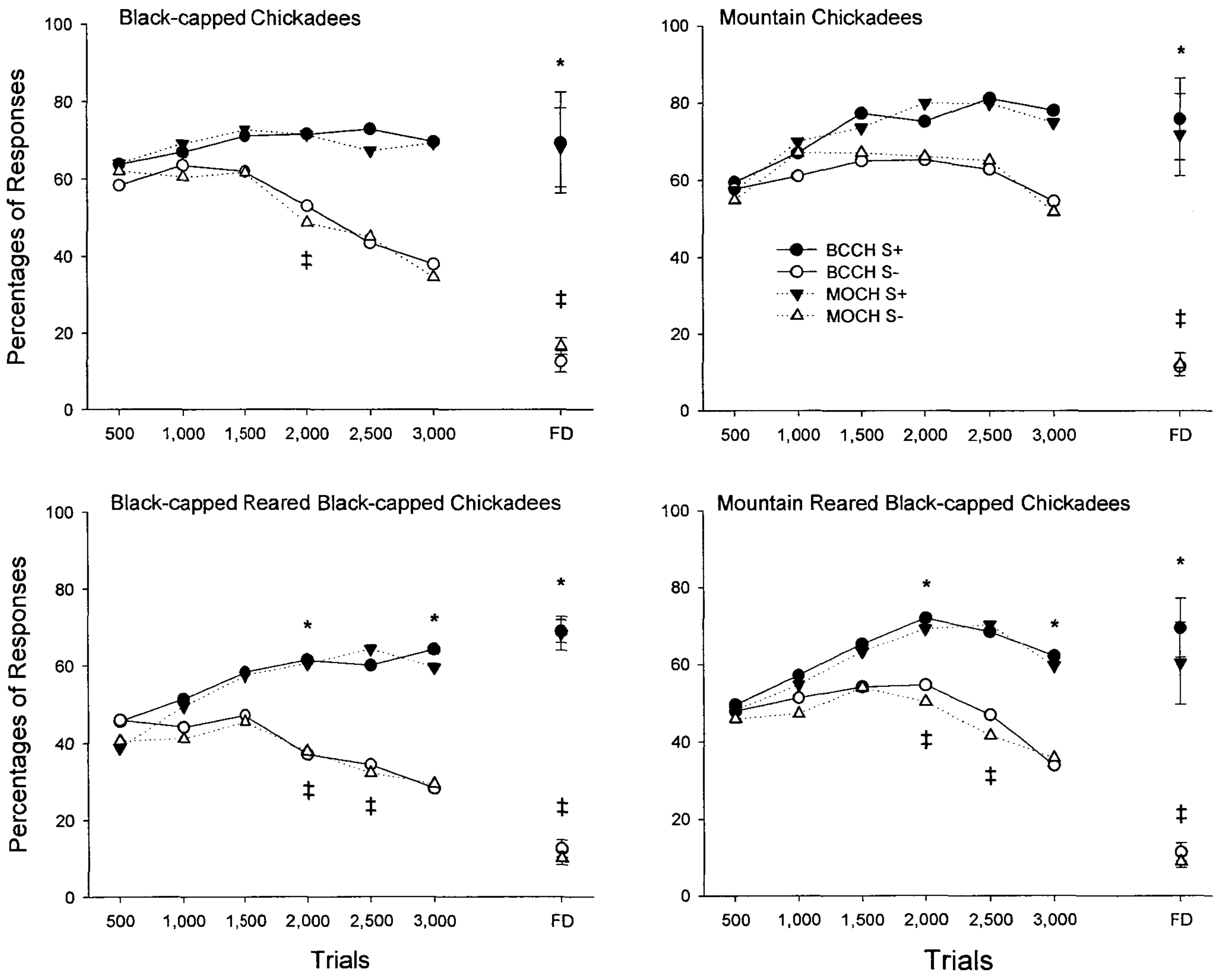
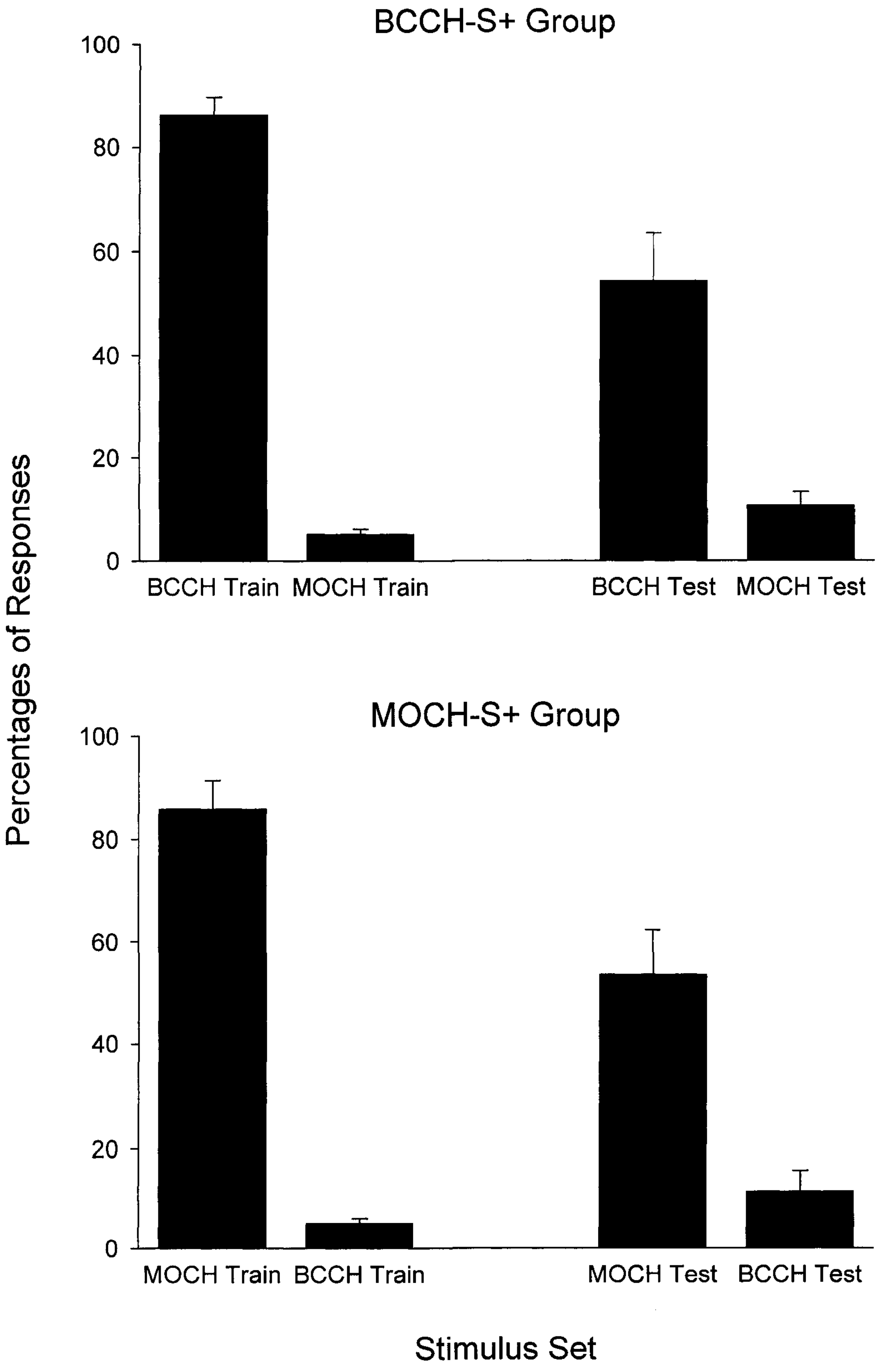

Black-capped Chickadees
Mountain Chickadees
Black-capped Reared Black-capped Chickadees
Mountain Reared Black-capped Chickadees
Percentages of Responses
0
20
40
60
80
100
500
1,000
1,500
2,000
2,500
3,000
FD
Trials
*
‡
BCCH S+
BCCH S-
MOCH S+
MOCH S-

Figure 6-5.


BCCH-S+ Group
Percentages of Responses
100
80
60
40
20
0
BCCH Train
MOCH Train
BCCH Test
MOCH Test
MOCH-S+ Group
100
80
60
40
20
0
MOCH Train
BCCH Train
MOCH Test
BCCH Test
Stimulus Set

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Bloomfield, L. L., Farrell, T. M., & Sturdy, C. B. All "chick-a-dee" calls are not created equally. Part II: Mechanisms for discriminations by sympatric and allopatric chickadees. *In press.*

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Chapter 7: General Discussion

This thesis examined production and perception of chick-a-dee calls by two closely related songbird species, black-capped and mountain chickadees, from several perspectives. An initial bioacoustic analysis provided a basis for understanding the units of production in the chick-a-dee call of the mountain chickadee and for comparison of this species' call with calls of the black-capped chickadee. Subsequent operant and field playback studies suggested that birds perceived the two species' calls as belonging to separate open-ended categories, and the mechanism for discriminating and categorizing the calls by species may be a reliance on the second half of both species' calls. Further, black-capped chickadees that had no previous experience with mountain chickadees and their calls performed similarly to experienced chickadees on these tasks. Finally, these studies investigated the potential for a species-specific advantage in memorizing individual chick-a-dee calls, and how early exposure and learning may have contributed to this advantage. Results suggested that individual recognition of chick-a-dee calls (i.e., memorization) may be a general phenomenon that all chickadees are capable of performing with familiar and unfamiliar conspecific and heterospecific calls. Taken together, the culmination of this research builds upon previous studies investigating the perceptual abilities in chickadees, and further implicates a general process involved in species' and individual recognition and discrimination tasks.

Bioacoustic Analysis of Mountain Chickadee Chick-a-dee Calls

Based on the results of the bioacoustic analysis conducted on the chick-a-dee call and call notes of mountain chickadees (Chapter 2), a better understanding of the similarities and differences between the calls of these two chickadee species has been gained. A previously published account of the mountain chick-a-dee call (Gaddis, 1985) failed to use similar nomenclature assigned to the black-capped chick-a-dee call notes (Ficken, Ficken, & Witkin, 1978), and did not provide quantitative details relating to variability across note types and across individuals. I followed the advice of Kroodsma and Byers (1991) by first describing the chick-a-dee call and call notes prior to conducting empirical studies to investigate the perception of these calls by chickadees.

Mountain chickadee calls consist of the "standard" A, B, C, and D notes observed in the calls of black-capped chickadees (Ficken et al., 1978), with significant overlap in the temporal and spectral features of the two species' call notes (see Charrier, Bloomfield, & Sturdy, 2004). The extent of the similarities suggested that chickadees may have difficulties in discriminating between the two species' calls. However, mountain chickadee calls contain an intermediate note type in the introductory 'chick-a' portion of the call (the A/B note) and an additional note type in the terminal 'dee' portion of the call (the D-hybrid note), neither of which is reliably observed in the calls of black-capped chickadees. While previous research has lumped intermediate notes into one of the standard note-type categories (e.g., Carolina chick-a-dee calls, *Poecile carolinensis*, Freeberg, Lucas, & Clucas, 2003), I chose to treat these notes as belonging to separate categories for several reasons.

First, the intermediate A/B note was produced by every bird sampled in the study (N=20), whereas this was not observed for the other note types (with the exception of D-hybrid notes, see below). Second, these note types comprised about 20% of our entire sample of call notes. Finally, this note type occurred in more than half of our sample of calls. Based on these facts, I treated this note type as a separate entity rather than an erroneous or intermediate A or B note produced in a transitional manner.

Concerning the D-hybrid note, this too was considered as separate from the standard D notes observed in the mountain chick-a-dee call for several reasons. First, this note type was produced by every bird sampled in the study (N=20), and occurred in nearly every single call in our sample. Second, the morphology of the note necessitated a different method for measuring spectral features than did the standard D note. Finally, compared to the D note, the rules of production for D-hybrid notes differed. Specifically, while calls often terminated with one or more D notes, calls never contained more than one D-hybrid note. Indeed, to conclusively state that the A/B and D-hybrid notes are in fact different types, the chickadees themselves need to provide this evidence, perhaps in an operant conditioning experiment (e.g., Sturdy, Phillmore, & Weisman, 2000). Nonetheless, with complete descriptions of the chick-a-dee call and call notes of mountain chickadees, and with comparisons with the chick-a-dee call and call notes of black-capped chickadees, I began investigations into how the birds perceived these calls.

Open-ended Categorization of Chick-a-dee Calls

There is no doubt that humans classify all sorts of stimuli into the same category based on the similarities of the stimuli, or into different categories based on the differences between the stimuli (e.g., perceptual concepts, see Zentall, Galizio, & Critchfield, 2002). Once thought to be a higher cognitive ability limited to humans, it is now becoming increasingly evident that non-human animals also utilize an open-ended categorization strategy when confronted with environmental stimuli (see Herrnstein, 1990; Huber 2001; Urcuioli, 2001 for reviews). Open-ended categorization is an advantageous strategy that does not necessitate previous experience with the stimuli for determining the appropriate response, ultimately reducing memory load and speeding decision making. In Chapter 3, I address the potential for open-ended categorization of black-capped and mountain chickadee chick-a-dee calls, and investigate the role that experience may play.

Chickadees may (1) treat each species' chick-a-dee calls as belonging to one overarching chick-a-dee call category, or (2) treat the calls as belonging to two separate, species-defined categories, each of which is possible for several reasons. First, sympatric (i.e., experienced) birds may treat conspecific and heterospecific chick-a-dee calls as similar, provided that birds benefit from attending to the calls of heterospecific mountain chickadees. For example, increased vigilance against the presence or approach of a predator can be accomplished by responding appropriately (i.e., fleeing) to the alarm and mobbing calls of heterospecifics, as has been previously observed in birds (e.g., Templeton & Greene, 2007). In addition, birds in sympatric regions may experience interspecific competition for resources (e.g., territory), and learn to respond aggressively to the vocalizations of heterospecifics to maintain their territory (e.g., Sedlacek, Cikanova, & Fuchs, 2006). In this context, sympatric black-capped chickadees may treat both conspecific and heterospecific chickadee calls as belonging to one, vocalization-type category rather than as two, species-specific categories. Allopatric (i.e., inexperienced) birds may also treat both species' chick-a-dee calls as belonging to one category given that in their natural habitat they are only ever confronted with the chick-a-dee calls of one species (conspecifics). Therefore the only experience that these birds have had is discriminating the chick-a-dee calls of conspecific familiar birds (e.g., flockmates) from the calls of conspecific unfamiliar birds (e.g., non-flockmates, see Nowicki, 1983). Thus, upon hearing an unfamiliar (yet similar) heterospecific call, inexperienced birds may simply perceive it as an unfamiliar conspecific call.

Alternatively, black-capped chickadees (both sympatric and allopatric) may treat each species' calls as belonging to separate, species-specific categories. In their natural habitat sympatric birds must form flocks, find a mate, and defend their breeding territory. Sympatric black-capped chickadees and mountain chickadees rarely flock together (pers. obs.), do not interbreed (although rare instances have been reported, Howe, 1985; Martin & Martin, 1996), and mountain chickadees do not pose a threat to resources during the breeding season (Hill & Lein, 1988). This suggests that sympatric black-capped chickadees would be more likely to treat heterospecific chickadees and their calls as different from conspecific calls. Similar results have been found with the song of chickadees (Hill & Lein, 1989) and with other co-habitating species (e.g., chaffinches, *Fringilla coelebs* and *F. teydea*, Lynch & Baker, 1991). Similarly, given their extensive experience with conspecific calls and their lack of experience with heterospecific calls, allopatric chickadees may be more likely to notice that heterospecific calls differ from the familiar conspecific calls, and as such, treat them as different from their own calls. Indeed, previous studies have suggested that experience with heterospecifics and their vocalizations differentially affects responding among sympatric and allopatric populations (e.g., Baker, 1991), and therefore the possibility remains that sympatric birds would respond in one manner and allopatric birds would respond in the other manner. In the current study I investigated the potential for species-specific category perception (or the alternative, vocalization-type category perception) in sympatric and allopatric chickadees.

The results of this study suggested that both sympatric and allopatric black-capped chickadees, and indeed mountain chickadees, treated the two species' calls as belonging to separate species-defined categories. Specifically, chickadees quickly learned to respond to rewarded within-category calls, but required more trials to learn to withhold responding to nonrewarded within-category calls compared to nonrewarded between-category calls. Further, these categories were open-ended in that unfamiliar (i.e., untrained) calls were accurately sorted (based on the distribution of responses) into their species-specific categories. Interestingly, allopatric chickadees were more accurate in their responding to between-category calls. That is, these birds more quickly learned to withhold responding to nonrewarded between-category calls compared to nonrewarded within-category calls.

One interpretation of this result is that inexperienced birds were in fact better able to detect the differences between the two species' calls, and the perception of these deviations from their own calls culminated in better defined species' categories. In contrast, and compared to inexperienced birds, experienced birds appeared to have more difficulty discriminating between the calls of the two species, suggesting that perhaps in nature, sympatric chickadees attend to the calls of their heterospecifics. This may be a prudent strategy, as these two co-habitating species rely on similar nutritional resources and are threatened by similar predators. Therefore treating all chick-a-dee calls as belonging to one category would allow these birds to take advantage of the foraging and predator-detecting efforts of mountain chickadees. Nonetheless, further testing, perhaps with inexperienced mountain chickadees, would be necessary to make this conclusion.

Mechanisms for Species' Discriminations of Chick-a-dee Calls: Laboratory Birds

In spite of the potential difference between sympatric and allopatric black-capped chickadees in categorizing chick-a-dee calls, both black-capped and mountain chickadees successfully discriminated conspecific from heterospecific calls. The purpose of the following experiment (Chapter 4) was to identify the feature(s) that birds used for performing this discrimination. Based on the bioacoustic analysis (Chapter 2), I defined chick-a-dee calls as consisting of two portions: the introductory 'chick-a' portion and the terminal 'dee' portion. I chose to separate the calls in this manner to determine, as a first step, whether the mountain chickadee A/B note (in the introductory portion) or the D-hybrid note (in the terminal portion) were main contributors to species' discriminations. Birds were first trained on a species' discrimination task, followed by intermittent presentation of these call-portions either in isolation or in hybrid combination (i.e., introductory portion produced by one species combined with the terminal portion produced by the other species, and vice versa), and responding was compared.

In general, all birds appeared to have used the terminal 'dee' portion for discriminations. Compared to control calls (i.e., calls consisting of 'chick-a' and 'dee' portions produced by two different individuals of the same species), birds responded about equally to the terminal 'dee' portions but not to the hybrid calls with the appropriate terminal 'dee' portion. This suggested that birds did attend to the introductory 'chick-a' portion, otherwise similar responding to these hybrid test calls would also have been observed. However, this result remains unclear, as birds typically responded very little to introductory portions presented in isolation. This result is in contrast to the result of a similar study with song sparrows (*Melospiza melodia*, Horning, Beecher, Stoddard,

& Campbell, 1993), which found that birds typically attended to the beginning elements of their song. Black-capped chickadees have finely-tuned perceptual abilities, and are capable of discriminating conspecific introductory ‘chick-a’ call notes based on only the first half of each note (i.e., only about 20-40 ms of information, Charrier, Lee, Bloomfield, & Sturdy, 2005). At first glance, attending only to the second half of the call does not seem like a practical strategy, suggesting that chickadees must wait up to one second from the start of the signal to identify the species of the caller. Further analyses, for example presenting each species’ introductory note types in isolation, are needed to conclusively determine whether chickadees can discriminate each species’ introductory ‘chick-a’ call notes.

Mechanisms for Species’ Discriminations of Chick-a-dee Calls: Wild Birds

As a next step to understanding the mechanisms for discriminations, the same control and hybrid calls were played back to wild chickadees during the winter (Chapter 5), when resources are scarce and presumably competition among birds is greater. While the operant study suggested that birds *would* use the terminal ‘dee’ portion of the calls to discriminate, while virtually ignoring the introductory ‘chick-a’ portion, I sought to determine whether free-ranging birds *do* use the terminal ‘dee’ portion more often than the introductory ‘chick-a’ portion. In their natural habitat, black-capped chickadees responded to (normal) conspecific chick-a-dee calls but not to heterospecific (mountain chickadee) chick-a-dee calls (Study 1). When hybrid calls were presented, the results were mixed.

As predicted, chickadees increased their responding above baseline levels to control (two-voice) calls and hybrid calls consisting of a black-capped chickadee terminal ‘dee’ portion. Less expected, however, was that birds also responded to hybrid calls consisting of a mountain chickadee terminal ‘dee’ portion (Study 2). Based on the fact that birds did not respond to heterospecific calls in Study 1 but did respond to hybrid calls consisting of conspecific introductory portions in Study 2, it may be presumed that birds attended to the introductory portions of the chick-a-dee calls. These results parallel those of a previous study (Horning et al. 1993), which found a preference for one portion of song sparrow song in the operant chamber (similar to the results presented in Chapter 4), but found that wild birds attended to both the front and back portions in nature.

Chickadees often repeat note types within their chick-a-dee calls, which may provide listeners with the redundancy necessary to ensure that the pertinent information (such as the species of the caller) is perceived. That D-type notes are the most frequently repeated notes in both species’ chick-a-dee calls (Chapter 2 and Charrier et al., 2004) suggested that this portion of the call would be most useful for songbirds needing to receive that pertinent information. Indeed this appeared to be the case in the operant study (Chapter 4), however in the field playback study (Chapter 5) birds appeared to be less conservative in their responding. Perhaps more informative was the latency to approach measure in this study. Although not statistically significant, birds tended to more quickly approach and investigate the caller (i.e., speaker) following playback of hybrid calls consisting of a black-capped chickadee terminal portion. This behaviour may provide an indication that birds attended to both portions of the calls, and when confusion arose, birds sought out further information (e.g., visual cues, see Matyjasiak, 2005). Future studies, possibly employing a modification in the number of note repetitions in the introductory and terminal portions, may solve this discrepancy between laboratory and field results and determine whether note repetition is the determining factor for responding by birds.

Effects of Restricted Rearing Environments on Memorization and Categorization

Finally, to gain a further understanding of chick-a-dee call perception and the influence of experience, I hand reared hatchling black-capped chickadees in the laboratory among either adult black-capped chickadees or adult mountain chickadees, and subsequently examined their memorization and species' discrimination abilities (Chapter 6). By restricting birds' exposure to one of the two species, I intended to further contribute to the literature the effect of experience during the vocal learning process. Songbirds must have exposure to vocalizing adults in order to learn to produce accurate renditions of their vocalizations (see Chapter 1). Further, previous evidence suggests that birds are better able to discriminate among the vocalizations of conspecific individuals than heterospecific individuals (e.g., Dooling, Brown, Klump, & Okanoya, 1992). However, results of a previous study (Chapter 3) did not provide evidence of a species-specific advantage in normally-reared chickadees discriminating among conspecific and heterospecific chick-a-dee calls.

Here I attempt to determine whether the species-specific advantage observed in other species is also observed in chickadees, and whether this ability is under the influence of genetics or environment (e.g., nature vs. nurture). Should genetics be a determining factor, then I would expect black-capped chickadees, reared among mountain chickadees, to be better at discriminating among black-capped chickadee calls, despite the fact that these birds have had little to no experience with this species and their calls. Alternatively, if environment is a determining factor, then I would expect black-capped chickadees, reared among mountain chickadees, to be better at discriminating among mountain chickadee calls.

In the main, neither group of hand-reared birds provided evidence of a specialized process for discriminating among genetic-conspecific chick-a-dee calls (in the case of birds reared among black-capped chickadees) or among rearing-conspecific chick-a-dee calls (in the case of birds reared among mountain chickadees). Similar to adult black-capped and mountain chickadees, hand-reared birds learned to discriminate between each species' calls at about equal rates and learned to discriminate among black-capped chick-a-dee calls and among mountain chick-a-dee calls at about equal rates. This supports previous evidence suggesting that a species-specific advantage does not exist in chickadees (e.g., Phillmore, Sturdy, Turyk, & Weisman, 2002). Furthermore, perceptual deficits previously observed in hand-reared chickadees were not evident in the current study. Specifically, chickadees reared in isolation from adults had greater difficulties compared to wild chickadees in a tone and an individual discrimination task (Njegovan & Weisman, 1997; Phillmore, Sturdy, & Weisman, 2003). It remains possible that birds in the current study did not show similar deficits in discrimination abilities because of the differences in rearing conditions (i.e., reared in total isolation compared to being reared in a colony room).

This study further suggested that a lack of experience with one of the two species' chick-a-dee calls did not interfere with open-ended categorization abilities. Hand-reared birds were intermittently presented with novel chick-a-dee calls following discrimination training, and similar to previous studies with adult birds (e.g., Chapter 3), all birds correctly responded (or withheld responding) to these calls. Thus the ability of chickadees to discriminate, categorize, recognize/memorize conspecific and heterospecific chick-a-dee calls appear to be a general phenomenon in chickadees, and previous experience with both species and their calls does not appear to be a requirement for performing these tasks.

Indeed it is difficult to imagine the evolutionary advantage of discriminating among the calls of heterospecifics. Individual recognition is a skill that conspecifics can potentially use to choose a mate and recognize flock mates (and perhaps offspring and parents). However, the current set of studies were not designed to imply that birds *do* discriminate among individual heterospecifics, but rather that they *can*. Further testing would be required to understand this behaviour in the birds' natural habitat.

Conclusions

The five studies contained in this thesis were designed to gain further insight into the cognitive abilities in songbirds, including the processes of attention, discrimination, memorization, and categorization. Further, rather than investigating specialized processes in one species, I used a comparative approach in an attempt to illuminate more generalized processes that may be inherent to all songbird species. By directly comparing two different, albeit closely related, chickadee species, we are indeed several steps closer to determining not only the morphology and phonology of chick-a-dee calls, but also how these calls are perceived by the birds themselves. Although further studies are necessary, the data presented here suggest that chickadees do not possess specialized adaptations for dealing with their own species' calls, and restricting their ontogenetic experience to only one species' chick-a-dee calls does not affect their memorization and categorization of conspecific and heterospecific chick-a-dee calls. Finally, we can conclude that open-ended categorization, a ubiquitous strategy used by humans, is also used by chickadees in particular and possibly all songbirds in general when confronted with conspecific and heterospecific vocalizations, providing yet another cognitive link between humans and songbirds.

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