CHAPTER FIVE

Mechanisms of Communication and Cognition in Chickadees: Explaining Nature in the Lab and Field

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1. INTRODUCTION: COMBINING THE FIELDS OF COMPARATIVE COGNITION AND BEHAVIORAL ECOLOGY

In the modern study of animal behavior, there are broadly two main schools of investigation: behavioral ecology and comparative psychology. Behavioral ecology is the study of how ecological pressures have driven the evolution of behavior in animals, starting with Niko Tinbergen's (1963) seminal "four questions." Comparative psychology (and comparative cognition, terms which we use interchangeably: see McMillan & Sturdy, 2015) is the study of the convergent and divergent psychological mechanisms by which animals learn and solve problems, informed most powerfully by the work of B.F. Skinner (1938) but also taking liberally from many areas of psychology. While each of these fields are historically influenced and populated near exclusively by biologists (behavioral ecology) or psychologists (comparative psychology), these fields are interrelated and the goal of the present paper is to demonstrate how fruitful research combining these approaches can be. We will illustrate this by exhaustively summarizing a breadth of communication research in a single animal group, the black-headed chickadee clade. Chickadees are an ideal model to examine acoustic communication, because chickadees exhibit complexity in the vocalizations they produce (for example, the types of vocalizations) and complexity in their social structure (territorial in the breeding season and group living in the nonbreeding season). In addition, chickadees learn both their calls and songs and exhibit vocal plasticity even into adulthood. Along with studying these behavioral and developmental processes in chickadees, we can also examine the underlying neural mechanisms associated with vocal learning and perception. By summarizing research conducted with black-capped chickadees, we show how the integration of behavioral ecology and comparative psychology, along with techniques from neuroscience, acoustics, and computer science, gives a fuller picture of animal behavior than any single field of study possibly could. We begin with a brief overview of the natural history of black-capped chickadees, followed by a general discussion of chickadee acoustic communication. We next discuss the vocal production and perception by chickadees, with a major focus on bioacoustic, playback, and operant conditioning studies. We also discuss the role that development plays in vocal production and perception, and we end with a discussion of studies examining the neural correlates associated with vocal communication in this species.

2. NATURAL HISTORY OF CHICKADEES

2.1 Abbreviated Natural History

Black-capped chickadees (*Poecile atricapillus*) are small songbirds found throughout much of North America (Smith, 1991). Commonly observed at backyard feeders, their diet consists of both plant and animal matter including seeds, berries, caterpillars, and occasionally small insects (Smith, 1991). In the fall, they cache food for the winter months and can remember cache locations for more than 28 days (Sherry, 1989). Their nonmigratory habits make this caching behavior useful over long periods of time.

With such a wide population range, black-capped chickadees inhabit a variety of wooded habitats, which highlight their adaptive behaviors. Seasonal changes in diet and behavior can begin at different times of year depending on local and global factors such as weather or altitude. When nesting, chickadees prefer to excavate nest cavities from rotten wood rather than nesting in existing cavities, but in areas with limited nest sites (such as in coniferous forests), birds will make use of less desirable sites (Smith, 1991). Chickadees are also nonmigratory birds, and the challenges of winter foraging and survival are thought to be correlated with behavioral flexibility (Sol, Lefebvre, & Rodriguez-Teijeiro, 2005). This flexibility and complexity of behavior also carries into chickadees' social systems, especially their communication with other individuals.

2.1.1 Diverse Repertoire of Vocalizations

Black-capped chickadees produce numerous types of vocalizations with various functions (see Ficken, Ficken, & Witkin, 1978). Similar to many songbird species, male black-capped chickadees produce songs (in chickadees, called the *fee-bee* song) to attract mates and repel rival males (Mennill & Otter, 2007); female chickadees also produce *fee-bee* songs, but the function of their song is currently unknown (for discussion, see Hahn, Krysler, & Sturdy, 2013). Males and females produce *chick-a-dee* calls under various contexts, including maintaining flock cohesion (Freeberg, 2006), and indicating the presence of a predator (Templeton, Greene, & Davis, 2005) or a food source (Carolina chickadees, Freeberg & Lucas, 2002; Mahurin & Freeberg, 2009). The most common vocalization produced by black-capped chickadees is the *tseet* call (Odum, 1942), which is an acoustically short vocalization, produced to maintain contact between individuals. Chickadees also produce *gargle* calls, usually during agonistic encounters. We will briefly discuss analyses of *tseet* calls, but *fee-bee* songs and *chick-a-dee* calls are the major focus in this review. Like many songbirds, black-capped chickadees learn their song from adult conspecifics (Shackleton & Ratcliffe, 1993), but components of their calls are also learned (e.g., *gargle* call, Ficken, Ficken, & Apel, 1985; *chick-a-dee* call, Hughes, Nowicki, & Lohr, 1998).

2.2 Distinct Aspects of Natural History

2.2.1 Nonmigratory

During the breeding season, breeding pairs defend the territory in which they nest and raise their young. These territories can be between 1.5 and 7 hectares in size depending on the quality of resources available and the rank of the pair defending it (Smith, 1991). Once their young have fledged, the breeding pair stops defending their territory and joins with other pairs in the area to form winter flocks. These flocks remain around the area of the previously defended territories. After fledging, young black-capped chickadees disperse from their nest area in apparently random trajectories (Smith, 1991). It has been suggested that this exodus decreases the likelihood of inbreeding as siblings rarely settle in the same area (Brewer, Diamond, Woodsworth, Collins, & Dunn, 2006; Weise & Meyer, 1979). These young join with other flocks forming in new areas, and while some chickadees continue to disperse after the winter, most remain in the area used by their winter flock and attempt to obtain a breeding territory the next spring (Smith, 1991). Adults often remain in the same area unless external factors such as food or territory availability, population density, or social factors force them to seek territory elsewhere.

2.2.2 Seasonal Changes in Social Behavior

Although black-capped chickadees are year-round residents, their social structure varies seasonally. In the winter, black-capped chickadees live in flocks (typically 2—12 individuals) with stable dominance hierarchies within-sex, and with males dominating females (Ratcliffe, Mennill, & Schubert, 2007; Smith, 1991). When the flocks dissolve for the spring breeding season, typically the dominant male and the most-dominant female form a mated pair (for this reason, flocks have been referred to as containing a "hierarchy of pairs": Smith, 1991). Flock ranges may overlap with the range of other flocks during the winter; however, in the spring, mated pairs will obtain and defend strict territories. Typically, birds that were dominant within winter flocks will obtain larger territories that contain better resources in the following spring (Mennill, Ramsay, Boag, & Ratcliffe, 2004).

It has been posited that the complex and dynamic social structure in this species drives, maintains, and/or requires a complex and flexible repertoire of vocalizations ("social complexity hypothesis"; for discussion, see Freeberg, 2006; Freeberg & Krams, 2015; Lucas & Freeberg, 2007). In the next section, we describe in more detail two of the most-studied chickadee vocalizations: their *fee-bee* song and namesake *chick-a-dee* call.

3. CHICKADEE ACOUSTIC COMMUNICATION

3.1 *Fee-bee* Songs and *Chick-a-dee* Calls: Description and Function of Two Well-Studied Vocalizations

Descriptions of chickadee singing behavior generally note that song production occurs at the highest rates in the spring; many of these claims were based on early descriptions of chickadee vocal production (e.g., Odum, 1942). Avey, Quince, and Sturdy (2008) set out to systematically quantify *what* vocalizations black-capped chickadees produced and *when* they produced them, considering variation across both time-of-day and season. By quantifying the production of song at discrete diurnal periods (i.e., sunrise, meridian, sunset) and at regular intervals that spanned 12 months, Avey et al. confirmed that most *fee-bee* singing occurs at dawn in the spring; however, there is also a secondary, slightly lower peak of song production at dawn during the winter. The function of *fee-bee* song production during the winter requires further examination; however, Avey, Quince, et al. (2008) postulated that chickadees may start singing during the winter as competition for mates and territories is being initiated. Additionally, this study identified that *chick-a-dee* calls were produced mostly during the middle of the day and during the fall and winter. This pattern may be related to flocking behaviors, as chickadees live in flocks during this time of year, and *chick-a-dee* calling is used to coordinate and maintain flock movements through the day (Ficken et al., 1978). *Chick-a-dee* call production also decreased during the spring, which may correspond with increased *fee-bee* song production. Finally, Avey, Quince, et al. (2008) also examined *gargle* call production and found that chickadees produced the most *gargle* calls during the middle of the day without seasonal variation.

In addition to examining vocal production by birds in the field, Avey, Rodriguez, and Sturdy (2011) conducted a complementary study examining vocal production by wild-caught black-capped chickadees that were housed in a laboratory environment. The results provided clear evidence that laboratory-housed chickadees produced a similar pattern (seasonally and diurnally) of vocalizations as their counterparts in the field.

The perception of vocal signals can also be examined in both the field and the laboratory. In a field study, Charrier and Sturdy (2005) presented playback of natural and modified *chick-a-dee* calls and measured the responses by wild black-capped chickadees. The results of this study revealed which acoustic parameters are likely important in species recognition. Specifically, chickadees vocalized less in response to modified calls presented at a lower frequency compared to unmodified calls (Charrier & Sturdy, 2005). Laboratory studies also provide evidence that frequency parameters in *chick-a-dee* calls are critical for acoustic perception. For example, by testing laboratory-house black-capped chickadees, Charrier, Lee, Bloomfield, and Sturdy (2005) found that birds rely on frequency parameters within *chick-a-dee* calls to discriminate between note types.

In general, laboratory conditions allow much stricter control over environmental variables than do observational and experimental studies in the field. Though a concern frequently expressed by ecologists is that captive subjects in laboratory conditions may not appropriately represent wild animals, this research suggests that the vocal behavior (and underlying cognition) of adult field-caught chickadees housed in captivity is at least broadly similar to those of wild birds, with the implication that captive chickadees represent an ecologically valid model system for studying vocal production and perception. Laboratory studies are quantifying the types of vocalizations that chickadees produce and when they produce them, have the added advantage of allowing for the examination of additional subtleties involved in acoustic communication. Such subtleties include variation in vocal production between individuals, sexes, age classes, or based on geographic region. Laboratory experiments are also useful for examining vocal perception, by measuring behavioral responses (e.g., playback or operant conditioning studies) or neural correlates of perception [such as immediate early gene (IEG) expression in the brain]. In addition, laboratory experiments that manipulate the developmental experience of young birds to examine how rearing experience influences both vocal production and perception allow for a degree of experimental control that would be difficult in a wild population of songbirds.

3.2 Unique Aspects of Chickadee Communication System

3.2.1 Vocal Structure and Complexity: Songs Versus Calls

Oscine passerines (songbirds) are known to produce two main categories of vocal signals, songs and calls, which differ primarily in function. Songs act as an acoustic ornament and are used both to attract mates and to defend territories (Catchpole & Slater, 2008). Calls are used in a variety of contexts including flock coordination and mobilization for predator defense (Marler, 2004). Since male quality is advertised through song, songs tend to be acoustically complex vocalizations in most songbirds, and often last several seconds in duration. By contrast, calls are normally less complex acoustically and shorter in duration. However, chickadees are an exception. In black-capped chickadees, the relatively simple *fee-bee* song is important for attracting a mate and defending a territory, similar to the songs of other species, while acoustically more complex *chick-a-dee* calls, like the calls of other songbirds, are produced in specific contexts related to survival (e.g., indicating a food source or potential predator; Ficken, 1981; Ficken et al., 1978). We further describe the functions of these two vocalizations.

In many songbird species, males may produce a repertoire of multiple song types (Catchpole & Slater, 2008), with song and swamp sparrows as two well-studied examples (*Melospiza melodia* and *Melospiza georgiana*; Marler & Peters, 1977, 1987, 1988). For example, song sparrows have a repertoire of 5—13 song types. Females prefer larger repertoires (Searcy, 1984) and male repertoire size is positively correlated with annual and lifetime reproductive success and male territory size (Hiebert, Stoddard, & Arcese, 1989). In contrast, male black-capped chickadees produce only one *fee-bee* song type, a long-distance signal (Dixon & Stefanski, 1970; Ficken et al., 1978; Mennill & Otter, 2007), which is conserved across most of the species range (but see Gammon & Baker, 2004; Kroodsma et al., 1999 for rare exceptions). In North American chickadees, only the black-headed species (i.e., black-capped, mountain, and Carolina) produce a whistled song, while brown-headed chickadees (i.e., boreal, chestnut-backed, and Mexican) do not produce this vocalization. Songs produced by each species are acoustically distinct. Carolina (*Poecile carolinensis*) and mountain chickadees (*Poecile gambeli*) produce multiple song types (Lohr, 2008; Lohr, Nowicki, & Weisman, 1991; Wiebe & Lein, 1999) containing two to six notes, and there is geographic variation in the songs of both Carolina chickadees (e.g., Kelemen, Zusi, & Curry, 2015) and mountain chickadees (Branch & Pravosudov, 2015). In contrast, most black-capped chickadees produce only *fee-bee* songs containing those two note types that occur in a fixed order (i.e., the first, higher-pitched "*fee*" note always precedes the second "*bee*" note). Exceptions to this two-note structure are found in relatively isolated populations (i.e., Gammon & Baker, 2004; Kroodsma et al., 1999).

During the spring, there is an onset and increase in song production at dawn (Avey, Quince, et al., 2008), with high-ranking males singing earlier, for longer duration, and at higher rates compared to low-ranking individuals (Otter, Chruszcz, & Ratcliffe, 1997). Male black-capped chickadees produce songs across a range of absolute pitches (Horn, Leonard, Ratcliffe, Shackleton, & Weisman, 1992; Weisman & Ratcliffe, 1989; Weisman, Ratcliffe, Johnsrude, & Hurly, 1990), and during a singing bout, an individual will increase or decrease the absolute frequency of the *fee-bee* song, a behavior called "pitch shifting" (Hill & Lein, 1987; Ratcliffe & Weisman, 1985) to match the frequency of another male's song, which acts as an agonistic signal (Horn et al., 1992; Mennill & Ratcliffe, 2004b). Although the overall two-note structure of the *fee-bee* song is superficially simple, information including the signaler's species (e.g., mountain chickadee songs often contain three notes; Wiebe & Lein, 1999), sex (frequency change within *fee* note; Hahn, Krysler, et al., 2013), and individual identity (multiple frequency and temporal features; Christie, Mennill, & Ratcliffe, 2004a; Wilson & Mennill, 2010) is conveyed within this song.

Compared to the short calls produced by many songbird species, the *chick-a-dee* call of black-capped chickadees is a long, acoustically complex vocalization. *Chick-a-dee* calls consist of multiple, spectrally rich note types and typically follow a semistructured order from A notes → B notes → C notes → D notes. However, note types can be repeated or omitted dynamically, so the structural complexity of *chick-a-dee* calls can vary each time a call is produced. Similar to the acoustic complexity of *chick-a-dee* calls, these calls are produced for a variety of functions, which may be one reason that the call has so many free parameters for variation (for example, the overall number and types of notes may vary, in addition to spectral or temporal features within notes).

The *chick-a-dee* call has been described in all six North American chickadee species (boreal chickadee, *Poecile hudsonicus*, Moscicki et al., 2011; Mexican chickadee, *Poecile sclateri*, Moscicki et al., 2011; chestnut-backed chickadee, *Poecile rufescens*, Hoeschele, Gammon, Moscicki, & Sturdy, 2009; Carolina chickadee, Bloomfield, Phillmore, Weisman, & Sturdy, 2005; mountain chickadee, Bloomfield, Charrier, & Sturdy, 2004; black-capped chickadee, Charrier, Bloomfield, & Sturdy, 2004), though this chapter will focus on black-capped chickadees and, to a lesser extent, their closely related sibling species: mountain chickadees(Curry, 2005; Gill, Slikas, & Sheldon, 2005).

3.2.2 Plasticity in Adulthood

Vocal plasticity is common in young songbirds as they attend to vocalizations from tutors and modify their own vocal output to produce species-typical vocalizations (Catchpole & Slater, 2008). In songbirds, it was traditionally thought that songs were learned while calls were innate (Thorpe, 1961). However, a growing body of evidence has since demonstrated that in some species, calls also have learned components (for review, see Marler, 2004; Mundinger, 1979). Additionally, in some songbird species, vocal plasticity does not end with maturity and vocalizations can change into adulthood, especially between seasons. For example, domestic canaries (*Serinus canaria*) adjust their songs during the nonbreeding season, adding and removing syllables to the songs within their repertoire, while songs remain relatively unchanged during the breeding season (Voigt & Leitner, 2008).

Black-capped chickadees also display vocal plasticity outside the breeding season. When chickadees flock during fall and winter, the *chick-a-dee* calls produced by flockmates begin to change, converging on a similar acoustic structure. Nowicki (1989), using bioacoustic analyses, found that the structure of terminal D notes varied in bandwidth and in frequency between overtones as call convergence took place. This process occurs quickly, with differences evident even 1 week after the formation of artificial flocks in captivity, and results in larger acoustic differences in *chick-a-dee* calls between flocks than within flocks (Nowicki, 1989). Individuals modify their calls to converge on a common acoustic signature that is not determined by the original call of any specific individual, suggesting that all individuals in the flock modify their *chick-a-dee* calls regardless of dominance status.

Phillmore, Macgillivray, Wilson, and Martin (2015) investigated the neural plasticity underlying behavioral plasticity in the perception, production, and acquisition of vocalizations in black-capped chickadees. They found that the volume of an area associated with vocal plasticity in the song control system of the songbird brain, HVC, changed between breeding and nonbreeding seasons. In contrast, expression of FoxP2, a transcription factor associated with song learning, was consistent across seasons but occurred in higher density in the brains of male black-capped chickadees compared to females (Phillmore et al., 2015). This could mean that males learn vocalizations more easily than females do and that the plasticity observed in *chick-a-dee* call production is associated with physiological factors (such as FoxP2 expression in the song control system). These studies by Nowicki (1989) and Phillmore et al. (2015) serve as an example of how integrating analysis types (bioacoustic and neurobiological) allow for a more complete understanding of the processes and associated mechanisms involved in observed behaviors.

4. PRODUCTION AND PERCEPTION OF CHICKADEE VOCALIZATIONS: INVESTIGATING COMMUNICATION USING COMPLEMENTARY TECHNIQUES

4.1 Bioacoustic and Discriminant Function Analyses

The field of bioacoustics examines how animals generate and receive sounds and (most pertinently to the present chapter) involves measurements of acoustic structure to distinguish between those sounds. Bioacoustic analyses are an essential first step to describe and analyze acoustic variation in vocal signals. Analyses of acoustic signals use high-fidelity (i.e., high-quality) recordings, along with computerized storage and sophisticated analysis and editing software, to generate visualizations that are intelligible to humans (e.g., sound spectrograms (Fig. 1)). From these visualizations, distinct features can be quantified (e.g., total duration, maximum frequency). This technique can be used to determine potential acoustic features that birds may use to perceive variation in vocalizations based on who is producing it those signals or the context in which the vocalization is produced. Bioacoustic analyses used along with discriminant function analyses are valuable analytical tools: bioacoustic analyses allow distinct acoustic parameters to be visualized and measured, while discriminant

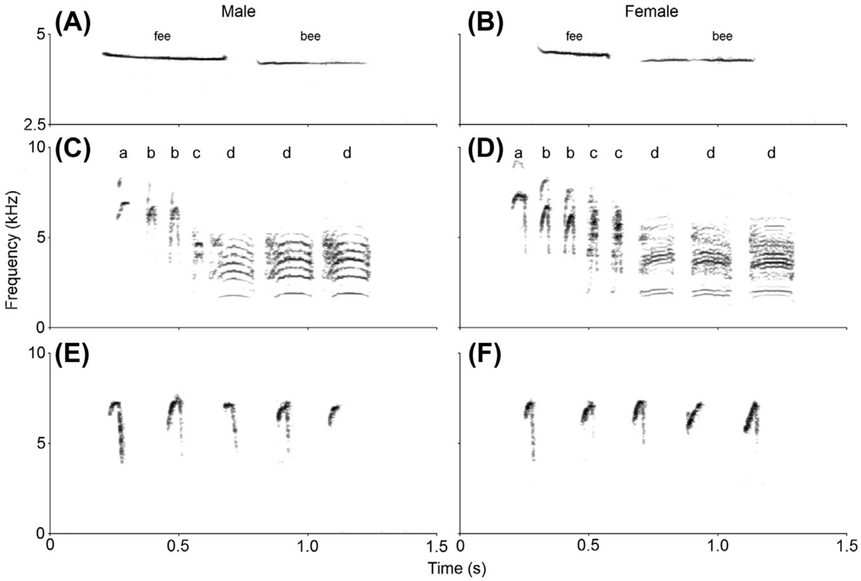

Figure 1 Sound spectrograms (transform length = 1024 points, frequency precision = 43.1 Hz) of black-capped chickadee *fee-bee* songs (A and B); *chick-a-dee* calls (C and D); and *tseet* calls (E and F) showing vocalizations produced by males (A, C, and E) and females (B, D, and F). Labels indicating note type are included aforesaid each note in *fee-bee* songs and *chick-a-dee* calls. Five *tseet* calls produced by each sex are shown.

function analyses (or similar statistical approaches) can determine patterns of differences in the measured acoustic features. Further, we discuss bioacoustical work conducted on three common chickadee vocalizations. We start with a discussion of *tseet* calls, followed by discussion of the bioacoustic analyses conducted on the two vocalizations described in detail earlier: *chick-a-dee* calls and *fee-bee* songs.

4.1.1 Tseet *Calls*

Tseet calls are the most commonly produced vocalization by black-capped chickadees (Odum, 1942) and are used as a contact call among birds. They are short, one-note vocalizations. Guillette, Bloomfield, Batty, Dawson, and Sturdy (2010) and Guillette, Bloomfield, Batty, Dawson, and Sturdy (2011) used bioacoustic analyses and discriminant function analyses to examine acoustic features in black-capped and mountain chickadee *tseet* calls. Guillette, Bloomfield, et al. (2010) found that chickadee *tseet* calls are individually distinctive and vary with species and sex of the producer. In a subsequent study, using this approach, Guillette et al. (2011) found that *tseet* calls are likely a learned vocalization similar to other chickadee vocalizations (e.g., *chick-a-dee* calls, Hughes et al., 1998; *fee-bee* songs, Shackleton & Ratcliffe, 1993).

Additional work is needed to clarify the behavioral and neurobiological mechanisms by which chickadees perceive acoustic differences in *tseet* calls. In particular, playback experiments in the field could be used to determine the extent to which chickadees differentially respond to playback of *tseet* calls. It is possible that chickadees would respond more to conspecific *tseet* calls compared to heterospecific calls. Alternatively, chickadees may generalize their response to *tseet* calls produced by multiple chickadee species, especially considering that some chickadee species form mixed flocks and even hybridize (Curry, 2005). Operant conditioning studies could be used to better understand the particular perceptual mechanisms suggested by the bioacoustic studies. For instance, a species classification experiment, in which birds were trained to respond to *tseets* of one species and withhold responding to *tseets* of another species, could allow modified signals to be presented to determine the correspondence between putative species-based acoustic differences in call structure and the perception of these differences. While these types of experiments are yet to be conducted with *tseet* calls, they have been conducted, along with bioacoustic analyses, to examine the perception of other chickadee vocalizations (e.g., *fee-bee* songs and *chick-a-dee* calls).

4.1.2 Chick-a-dee *Calls*

Similar to the analyses on *tseet* calls, bioacoustic analyses on *chick-a-dee* calls have revealed that in addition to containing distinct note types that vary based on frequency and/or duration, the calls of each species are also highly individualized (along several acoustic dimensions including frequency and temporal measures), which is a possible acoustic mechanism that would allow birds to distinguish among individual conspecific and heterospecific callers (Bloomfield et al., 2004; Charrier et al., 2004; Mammen & Nowicki, 1981). In at least two species of chickadees, *chick-a-dee* calls contain geographic variation (chestnut-backed chickadees, Hoeschele et al., 2009; Carolina chickadees, Freeberg, 2012); Geographic variation in *chick-a-dee* calls of other chickadee species, including black-capped chickadees, requires further examination. However, considering that acoustic properties within the calls of flockmates converge (Nowicki, 1989), acoustic dialects appear to exist in black-capped chickadees.

In addition to containing geographic variation, *chick-a-dee* calls produced by Carolina chickadees also contain sex differences. Specifically, the start frequency of A notes tend to be higher in female-produced *chick-a-dee* calls than in male-produced calls (Freeberg, Lucas, & Clucas, 2003). We recently conducted bioacoustic analyses on black-capped chickadee *chick-a-dee* calls in which we compared acoustic parameters in each note type between sexes (e.g., we compared acoustic features in male-produced A notes to features in female-produced A notes). Similar to the previous study with Carolina chickadees, the start frequency of A notes contained sex-based acoustic variation (Campbell, Hahn, Congdon, & Sturdy, 2016), with females producing A notes with a higher start frequency than those of males. Since *chick-a-dee* calls are produced with a variable combination of note types and not a fixed number of call components, it is possible that sex differences occur in the call's overall acoustic structure. Comprehensive examinations of sex-related differences in call structure are ongoing in our laboratory.

4.1.3 Fee-bee *Songs*

While acoustic variation is more obvious in vocalizations that have multiple variants or dialects (such as the songs of Carolina and mountain chickadees), Hahn, Guillette, et al. (2013) demonstrated that black-capped chickadee *fee-bee* songs produced at two geographically distinct locations contain site-specific acoustic variation. In particular, while all birds produced the characteristic two-note song, black-capped chickadees from British Columbia produced songs that were longer compared to the songs produced by birds in Ontario. Acoustic features in song structure have also been identified that indicate a male's dominance rank; dominant males produce songs with more consistent frequency interval ratios (Christie, Mennill, & Ratcliffe, 2004b) and more consistent amplitude ratios (Hoeschele et al., 2010), although the specific features related to dominance seem to vary with geographic region (Hahn, Guillette, et al., 2013). Specifically, dominant males in Ontario produce a more consistent frequency ratio between the *fee* and *bee* note across a song bout compared to subordinate males (Christie et al., 2004b), and dominant males in British Columbia produce a more consistent amplitude between the two notes within a single song compared to subordinate males (Hoeschele et al., 2010).

While call production has been described for both male and female chickadees, descriptions of female song are rare in this species (e.g., Hill & Lein, 1987). For temperate species in general, female song has been examined less compared to male song (Garamszegi, Pavlova, Eens, & Møller, 2007). However, in numerous temperate species, it is now recognized that both sexes produce songs (for reviews, see Langmore, 1998; Riebel, 2003) and recent evidence suggests that in the common ancestor of modern songbirds, females likely produced songs (Odom, Hall, Riebel, Omland, & Langmore, 2014). Consistent with this recent evidence suggesting that female song is more common in temperate species than initially thought, we recently described female song production in black-capped chickadees and quantified acoustic differences in male and female songs (Hahn, Krysler, et al., 2013). We began by recording both males and females singing under identical laboratory conditions. Once a large enough sample of recordings was obtained, we measured multiple acoustic features within the songs and used statistical approaches (in this case discriminant function analyses) to determine which acoustic features in *fee-bee* songs varied between the sexes. We found that both sexes produced songs with a *fee* and a *bee* note. In addition, we found frequency differences in the acoustic structure of the songs; specifically, that the *fee* note in female songs had a larger frequency decrease from the start of the note to the end of the note (called the "*fee* glissando") compared to male songs. This frequency difference is a possible acoustic cue for sex discrimination. However, further work presenting songs as auditory stimuli to chickadees is required to determine whether this acoustic feature is indeed useful to chickadees.

By quantitatively describing the acoustic structure and variance in chickadee vocalizations, bioacoustic analyses provide an important foundation for future perceptual studies. Specifically, these perceptional studies can be used to determine the extent to which the acoustic variations identified in the bioacoustic analyses are meaningful to the birds. These perceptual processes can be examined using multiple techniques including playback experiments, operant conditioning, and studies designed to examine the neural correlates of perception. We discuss studies examining the perception of chickadee vocalizations for the remainder of this review.

4.2 Behavioral Experiments

4.2.1 Playback Studies

In general, playback studies present an individual (or group of individuals) with auditory stimuli (e.g., conspecific or heterospecific vocalizations) in the field or in the laboratory, and measure the subject's response. Playback studies have been used with numerous different songbird species (e.g., white-throated sparrows, *Zonotrichia albicollis*, Brooks & Falls, 1975; song sparrows, Burt, Campbell, & Beecher, 2001; great tits, *Parus major*, Otter et al., 1999) demonstrating the utility of this experimental technique. Playback studies conducted in the field allow researchers to examine these unconditioned responses in a natural setting, including the bird's own territory. Playback studies can also be performed in a controlled laboratory setting with otherwise naturalistic stimuli. These studies have provided us with information regarding chickadee vocal perception under different seasonal social contexts (e.g., chickadees in mated pairs and chickadees living in social flocks). Laboratory playback can be used to control for outside noise, distracting stimuli, and other confounds potentially present in the field. Together, the structure of playback procedures is well-aligned with the goals of both comparative psychology and behavioral ecology, as they allow for relatively straightforward verification of how differences in vocalizations determined by bioacoustic analysis translate via perceptual processes into ecologically relevant behavior. In this section, we give examples of how playback analyses have been used to study behavioral responses in both field and captive populations of chickadees.

4.2.1.1 Playback Studies Using Free-Living Chickadee Populations

4.2.1.1.1 Male Singing During the Breeding Season Typical playback studies involve presenting a focal bird (or birds) with recordings of vocalizations (natural or experimentally modified) and observing the response by the focal animal. Playback studies can utilize one speaker, which often presents the focal bird with a fixed set of playback stimuli, or multiple speakers, which present the bird with concurrent or alternating stimuli. With both of these playback techniques (single and multispeaker) the playback continues in a fixed manner, regardless of how the bird responds. However, natural communication typically involves a fluid back-and-forth between the producer and the receiver, by which the behavior of one individual influences responses by the other. Interactive playback techniques have been useful to mimic this natural communication more realistically. With interactive playback designs, the experimenter can switch which vocalization is presented during playback based on the focal bird's response, rather than playback continuing in a rigid, predetermined manner (as with more traditional playback techniques).

Studies using interactive playback approaches have demonstrated how the resident male responds to a territorial intruder during the breeding season and how these interactions between males can influence female behavior. During singing bouts, black-capped chickadees may overlap the songs produced by other individuals (Mennill & Ratcliffe, 2004a). In addition to overlapping songs, black-capped chickadees may also frequency match the songs of singing conspecifics. By broadcasting songs that either overlapped or matched the frequency of a singing focal male, Mennill and Ratcliffe (2004b) demonstrated that these two singing characteristics can both be considered as threatening signals (for further discussion, see Naguib & Mennill, 2010; Searcy & Beecher, 2009). However, behavioral responses by focal males were different to each type of signal with males that were overlapped varying their singing behavior (e.g., song length and timing of song), while males that were frequency matched differing in nonvocal behavioral responses compared to males that were not frequency matched (e.g., more flights toward the speaker and more time farther from the speaker, but closer approach distances when approaching the speaker). These results suggest that these two singing behaviors may have different meanings. In addition, behavioral responses to playback of song overlapping vary depending on the dominance rank of the focal male. When presented with playback simulating two singing "intruder" males, high-ranking males are more likely than low-ranking males to approach the speaker playing the overlapping "intruder" (i.e., the more threatening signal; Mennill & Ratcliffe, 2004a). However, when the focal bird's songs were overlapped or frequency matched, low-ranking males more intensely engaged the playback "intruder" (e.g., more flights and closer approaches to the speaker) compared to high-ranking males (Mennill & Ratcliffe, 2004b). Mennill and Ratcliffe (2004b) suggested that high-ranking males may be reluctant to engage an intruder of unknown dominance rank, as high-ranking males are likely to be cuckolded if they lose a song contest (Mennill, Ratcliffe, & Boag, 2002). In contrast, it may be advantageous for low-ranking males to engage all intruders to defend the territory and resources they possess. Taken together, these results demonstrate that individual variation (in this case, dominance rank) can impact a subject's behavioral responses.

Female behavioral responses are also influenced by male singing encounters, and singing contests between males can impact a female's perception of her mate. Females mated to high-ranking males whose songs were overlapped and frequency matched laid more eggs sired by other males, suggesting these females were more likely to seek extra-pair copulations compared to females mated to high-ranking males whose songs were not overlapped or frequency matched (Mennill et al., 2002). Individual variation can also influence female behavioral responses, as the behavior of females mated to low-ranking males did not change with playback type; regardless of whether her mate's songs were overlapped and frequency matched, females mated to low-ranking males had a similar proportion of eggs sired by other males. Clearly, song perception in black-capped chickadees is a vitally important behavior for both males and females.

These results from Mennill et al. (2002) demonstrate that vocal communication often does not occur within a simple dyadic context between a single vocal producer and perceiver. Instead, communication occurs over a larger network with multiple individuals "eavesdropping" on communication signals. To examine the responses by multiple individuals to singing interactions in a neighboring territory, researchers can use an acoustic location system. An acoustic location system allows researchers to simultaneously record multiple focal individuals, while also monitoring the location and movements of these individuals (Mennill, Burt, Fristrup, & Vehrencamp, 2006). Because black-capped chickadees defend and live in territories during the spring, they are a good model to examine the extent to which individuals eavesdrop on interactions occurring in neighboring territories. Fitzsimmons, Foote, Ratcliffe, and Mennill (2008) simulated dyadic countersinging outside of established male black-capped chickadee territories and used an acoustic location system with a 16-microphone array to examine how males in surrounding territories would respond to countersinging interactions of two unknown males. They found that there was an increase in song output by all chickadees within the recording area following playback of singing interactions containing overlapping and frequency matched singing (compared to singing interactions containing neither overlapped nor matched singing). In addition, males with territories adjacent to the playback speaker had higher song output compared to males with more distant territories. These results demonstrate that male chickadees eavesdrop and respond to song interactions that occur between other individuals in neighboring territories. Using a similar 16-microphone acoustic location system, Foote, Fitzsimmons, Mennill, and Ratcliffe (2011) found that black-capped chickadee dawn chorus singing is influenced by the vocal behavior of social competitors. Specifically, playback of an unknown male's song was broadcast from within a focal male's territory before the focal bird began his own dawn singing.

When this playback was broadcast, focal males began singing earlier compared to nonplayback days. Additionally, males in neighboring territories also began singing earlier on playback days, suggesting that the dawn singing of one individual influences the singing behavior of neighboring males. Taken together the results of these studies using acoustic location systems to simultaneously record multiple black-capped chickadees provide evidence that communication should be considered as a complex network involving numerous individuals, beyond the signaler and a single receiver.

4.2.1.1.2 *Chick-a-dee* Calling and Mobbing Behavior Playback studies have also proved fruitful in observing the involvement of *chick-a-dee* calls in mobbing behavior in response to a potential predator. In this context, calls are produced to organize conspecifics and heterospecifics to harass and drive off a nearby predator. As mentioned previously, black-capped chickadee *chick-a-dee* calls are composed of four note types: A, B, C, and D. Templeton et al. (2005) found that the number of D notes produced within mobbing-associated *chick-a-dee* calls are related to a predator's threat level, with chickadees producing more D notes per call when exposed to small, high-threat aerial predators than to large, low-threat predators (i.e., the number of D notes per call negatively correlates with predator wingspan and body length). A smaller aerial predator is thought to be of higher threat to a chickadee than a larger one, as a small predator can easily maneuver through trees when hunting (Howland, 1974). Note variation in *chick-a-dee* calls of Carolina chickadees in response to predators of varying threat has also been reported: Carolina chickadees produce calls with more D notes and few A, B, and C notes in the presence of high-threat predators, and they produce few D notes and more A, B, and C notes in the presence of low-threat predators (Soard & Ritchison, 2009).

Using predator models (i.e., stuffed toy cats), Book and Freeberg (2015) found that tufted titmice (*Baeolophus bicolor*), a species in the same family (Paridae) as chickadees, use head and body orientation of a potential predator to determine predation risk. Titmice avoided feeders more when cat models faced a food source than when facing away. In addition to altered foraging behavior, vocal production was differentially affected depending on whether cats were known to frequent the area. Titmice produced more introductory notes if the cat models faced the food in areas with cats compared to areas without, suggesting that birds attend to and alter their behavior based on the specific orientation of predators, and this response was dependent on whether birds were likely to have prior experience with house cats. In a similar experiment, Kyle and Freeberg (2016) found that head and body orientation of the hawk and owl models affected foraging and vocalizations produced by tufted titmice and Carolina chickadees. Chickadees and titmice avoided feeders, and chickadees produced more *chick-a-dee* calls when the model avian predator faced toward rather than away from the food source, suggesting that chickadees and titmice potentially used this information to assess different levels of predator threat. In response to both feline (Book & Freeberg, 2015) and avian (Kyle & Freeberg, 2016) predator models, subjects produced *chick-a-dee* calls with a similar number of D notes, regardless of whether the predator was oriented toward or away from the food source, suggesting that while D note production may indicate the degree of threat related to the species of predator present (Templeton et al., 2005), the number of D notes within a call does not relate to more subtle differences in perceived threat, such as predator orientation.

While studies have demonstrated that *chick-a-dee* call structure (i.e., number of D notes; Templeton et al., 2005) can encode threat level, other acoustic parameters, including the rate of calling may also indicate perceived threat. To examine the influence of call frequency, Wilson and Mennill (2011) conducted a field playback study that manipulated both the signaling rate (i.e., duty cycle) and the note composition of calls that were presented. Playback stimuli included *chick-a-dee* calls with 2 D notes played with a low duty cycle, *chick-a-dee* calls with 2 D notes played with a high duty cycle, *chick-a-dee* calls with 10 D notes played with a high duty cycle, and a silent control. Receivers, including conspecifics and heterospecifics, approached more quickly and closer to the speaker during playback with a high duty cycle; however, the manipulated call structure (i.e., 2 D notes vs. 10 D notes) did not influence chickadee responses. This finding suggests that chickadees may express the urgency of a situation with varying call rate.

4.2.1.2 Playback Studies Using Captive Chickadees

Field studies allow researchers to examine behavior in a naturalistic setting; however, in general playback studies in the laboratory give researchers more experimental control, while still providing insight into how animals respond to different types of vocalizations. Following the identification that *chick-a-dee* calls used in a mobbing context contain acoustic variation that correlates with predator threat level (i.e., contain more D notes in response to a high-threat predator), Templeton et al. (2005) conducted a playback experiment using calls produced in response to raptors and owls representing varying levels of threat. They found that chickadees approached a playback speaker more often when the playback stimulus was a call indicating a high-threat rather than low-threat predator. Congdon, Hahn, McMillan, Avey, and Sturdy (2016) conducted a laboratory playback experiment investigating black-capped chickadee behavioral responses to predator (high and low threat) and chickadee (high and low threat) vocalizations. Subjects produced more *chick-a-dee* calls to high-threat predator vocalizations compared to low-threat predator vocalizations, suggesting that chickadees may respond to high-threat predator vocalizations by producing more *chick-a-dee* calls, potentially as an attempt to initiate mobbing with conspecifics. Congdon et al. found that vocal behavior also increased to high-threat *chick-a-dee* call playback conditions, suggesting the urgency to respond was similar across high-threat contexts, regardless of whether the vocal signal was produced by a heterospecific (predator call) or conspecific (*chick-a-dee* mobbing call). Chickadees' general movement activity (i.e., perch hopping) increased more to predator calls compared to conspecific *chick-a-dee calls*; this result may suggest that chickadees mobilize more in response to hearing predator vocalizations compared to hearing vocalizations by a conspecific.

Hoeschele et al. (2010) conducted bioacoustic analyses and a follow-up playback experiment using black-capped chickadee *fee-bee* songs produced by males of different relative dominance status. They found acoustic differences between dominant and subordinate black-capped chickadee songs: dominant males produced more consistent amplitude between the two notes within a single song compared to subordinate males. They also found greater activity by females following playback of dominant songs compared to subordinate songs, and more vocalizations than baseline to dominant male vocalizations only. These results suggest that female chickadees likely attended to amplitude differences in male song and could differentiate status, which is important for mate selection given the numerous reproductive advantages for dominant birds (e.g., acquire a larger territory, are more attractive to females, and fledge more young; see Ratcliffe et al., 2007: Table 9.1 for a comprehensive list).

These playback studies demonstrate how birds respond to different types of vocal signals, suggesting perceptual differences for these vocalizations. While playback studies can provide evidence that birds perceive differences in different types of acoustic signals, they often do not describe the perceptual mechanism(s) that birds use to differentiate among signals (i.e., by isolating specific acoustic features that birds use to discriminate between different classes of vocalizations). To answer this type of question, we use operant conditioning tasks.

4.2.2 Operant Conditioning Studies

Operant conditioning is the experimental technique, originated by B.F. Skinner (1938), wherein subjects are trained to perform particular responses (in the presence of particular stimuli) based on the consequences of those responses. While playback experiments ask whether and how animals naturally respond to stimuli (e.g., a *chick-a-dee* mobbing call vs. a great horned owl call) based on innate preferences or prior learning in the wild, operant experiments can answer whether animals are capable of differentiating between stimuli. For example, if a playback experiment determines that a chickadee responds similarly in the presence of a male or female *tseet* call, that result can only provide information that chickadees tend to behave similarly across those contexts: it cannot determine if chickadees were incapable of perceiving the difference between the two classes of stimuli. In contrast, operant experiments that provide food for responses to male calls, but not female calls, might determine that subjects acted differently in response to the two stimulus classes, which would require that chickadees could perceive those differences. Further, the rate at which the discrimination task is learned, and subjects' ability to incorporate new test stimuli into rewarded classes, has proven to be the gold standard by which categorization and concept learning is studied in animals (Herrnstein & Loveland, 1964; Lea, 1984; Wasserman, Kiedinger, & Bhatt, 1988).

In general, operant studies in the domain of auditory discrimination often begin with a pretraining phase, in which subjects are presented with and rewarded for responding to all experimental stimuli. This phase is critical, especially for species, such as chickadees, that are highly neophobic. Once subjects are responding at a high and uniform rate, discrimination training can begin by training the subjects to respond to certain stimuli by providing food for doing so (i.e., reinforced stimuli: S+) while simultaneously withholding responses to stimuli that are not linked with food reward (i.e., nonreinforced stimuli: S−). Subjects continue this discrimination training until they meet a predetermined criterion (i.e., a level of "expert" discrimination). Once this discrimination criterion is met, subjects complete a pretest phase, in which S+ stimuli are reinforced with a reduced probability (for example, reinforced 85% of the time). The pretest phase prepares subjects for later phases in which some stimuli (i.e., test stimuli) are presented without reinforcement. Once a subject meets criterion on pretest, the researcher can present subjects with new "probe" stimuli (also called test stimuli) and examine how they respond. Often, responding to these new stimuli results in no feedback (e.g., there is no food reinforcement). If a subject responds to these new stimuli, it indicates that the subjects consider these stimuli to be similar to those that were reinforced during discrimination training. In contrast, if the subjects do not respond to the new stimuli, it is an indication that they consider the new stimuli to be different from the stimuli for which responses were previously reinforced (see Fig. 2 for a schematic of the typical operant discrimination procedure). When compared against control subjects that are trained to memorize individual S+ and S− stimuli that are not sorted into categories, subjects that respond preferentially to novel test stimuli that are perceptually and/or conceptually similar to the S+ category provide evidence that perceptual differences exist between the stimuli. In turn, positive results in these studies provide evidence that there must be informational differences present in the stimulus classes (e.g., a perceptible frequency difference in a call between males and females), and in concert with bioacoustic analyses it is possible to isolate components of the signal used by the animal for this determination.

4.2.2.1 Categorization and Mechanisms of Call and Call Note Perception

As stated earlier, chickadees produce numerous vocalizations that are used in multiple contexts, including the acoustically complex *chick-a-dee* call and the relatively simple *fee-bee* song. Prior analyses provided a fundamental understanding of the acoustics of *chick-a-dee* calls produced by various chickadee species (black-capped chickadees, Charrier et al., 2004; mountain chickadees, Bloomfield et al., 2004; Carolina chickadees, Bloomfield et al., 2005; chestnut-backed chickadees, Hoeschele et al., 2009; Mexican chickadees, Moscicki, Hoeschele, & Sturdy, 2010; boreal

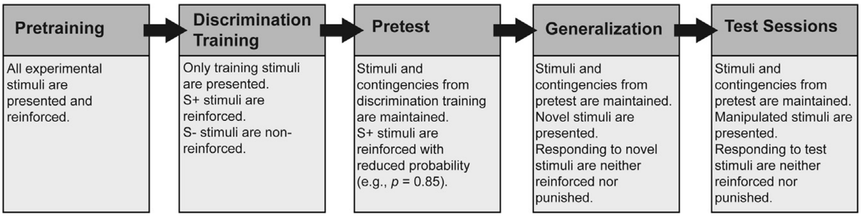

Figure 2 Flowchart depicting a typical procedure for an operant discrimination task, the order of the experimental procedure. The name and a brief description of each phase are given (see text for details).

chickadees, Moscicki et al., 2011). The extent to which chickadees could discriminate between different species' calls, and which acoustic features they used to differentiate the calls, was not known. To investigate species-based discrimination abilities and the perceptual mechanisms underlying them, we focused on two closely related species: black-capped and mountain chickadees. Black-capped chickadees live throughout much of the northern United States and southern Canada, including regions in the Rocky Mountain foothills, while mountain chickadees live in mountainous habitat in the western United States and Canada (e.g., at higher elevations in the Rocky Mountains). These differences in habitat and species' ranges provided us with an ideal system to examine perception of vocalizations produced by phylogenetically similar species, and in particular individuals with and without experience of both species' calls, as these species occur in both sympatry and parapatry.

Our first objective was to determine the extent to which black-capped and mountain chickadees could discriminate between the calls produced by these two species. To examine this, we used a true category/pseudo category discrimination task. Using a go/no-go paradigm, one group of subjects discriminates a "true" category (e.g., black-capped chickadee calls are S+; mountain chickadee calls are S−), while another group of subjects discriminates a "pseudo" category (e.g., half of the black-capped and mountain chickadee calls are S+; the other half of the black-capped and mountain chickadee calls are S−). If *chick-a-dee* calls belong to perceptual species-based categories, subjects should learn the "true" category discrimination faster (i.e., in fewer trials) compared to the "pseudo" category discrimination; this result is precisely what our study revealed (Bloomfield, Farrell, & Sturdy, 2008b). In addition, regardless of whether subjects had prior experience with both species of chickadees or not, chickadees discriminated between the species' calls in a similar manner (Bloomfield & Sturdy, 2008). With evidence that calls belonged to species-based categories, our next objective was to determine the specific acoustic information chickadees were using for this discrimination.

Bloomfield, Farrell, and Sturdy (2008a) used a go/no-go operant discrimination task to determine if black-capped and mountain chickadees relied on the introductory (A, B, C) or terminal (D or Dhybrid) notes within *chick-a-dee* calls to discriminate between the two species. Dhybrid notes are commonly produced by mountain chickadees but can also be produced by black-capped chickadees (see Campbell et al., 2016); these notes contain a frequency modulated portion (similar to an A or B note), which continues into a harmonic-like portion (similar to a D note; see Bloomfield et al., 2004 for full acoustic description). For the discrimination task, birds were trained to respond by flying to a feeder following the presentation of one species' complete *chick-a-dee* call and withholding responding following exposure to the other species' call. Following acquisition training, chickadees were presented with *chick-a-dee* calls that were experimentally manipulated. These modified calls contained introductory notes produced by one species (black-capped or mountain) and terminal notes produced by the other species. Control call stimuli were also presented that contained introductory and terminal notes from one species (black-capped or mountain), but produced by different individuals. Results revealed that chickadees of both species rely more on the terminal (D or Dhybrid) notes when discriminating between the species. Further studies confirmed that D notes within *chick-a-dee* calls are likely an important component in species discrimination.

Previous bioacoustic analyses of black-capped (Charrier et al., 2004) and mountain (Bloomfield et al., 2004) chickadee calls suggested that sufficient acoustic variation exists between the call notes produced by the two species; however, it was unknown which note types would be discriminated most easily by chickadees. Guillette, Farrell, Hoeschele, and Sturdy (2010) conducted an operant discrimination task in which individual notes types (i.e., A, B, C, and D) were presented singly as stimuli during the task, and for a given subject responding to A, B, C, and D notes from one species was reinforced, while responding to A, B, C, and D notes from the other species was not. In addition, while previous evidence (i.e., Bloomfield et al., 2008a) suggested that chickadees rely on the terminal notes within the call, this previous study did not examine the acoustic discrimination of A, B, and C notes individually (these notes were always manipulated together as the "introductory" portion) and the manipulated calls always contained the D notes at the end of the call following a string of introductory notes. Guillette, Farrell, et al. (2010) found that black-capped and mountain chickadees learned to discriminate between D notes in the fewest number of trials, providing corroborative evidence that D notes are a particularly salient component of the call for species identification.

4.2.2.2 Categorization and Mechanisms of Song Perception

4.2.2.2.1 Geographic Variation One of our first aims was to examine chickadees' perceptual abilities at discriminating songs based on geographic variation. Historically, black-capped chickadee songs were considered relatively invariant across the species range (Kroodsma et al., 1999), but recent results (Hahn, Guillette, et al., 2013) revealed potential geographically specific acoustic cues in male *fee-bee* songs.

To determine if there were meaningful acoustic differences in songs based on geography that chickadees could perceive, we conducted a go/no-go operant conditioning task (Hahn et al., 2016). As in our studies with *chick-a-dee* calls, birds were divided into true and pseudo category groups. With this experimental paradigm, we could examine if chickadees use open-ended categorization when discriminating among vocalizations. Open-ended categorization is a strategy that would allow individuals to categorize stimuli using a general category rule that is based on perceptual similarity, rather than memorizing each stimulus and its associated category. In general, open-ended categorization is a more flexible cognitive mechanism compared to rote memorization, because an individual can learn to discriminate using general rules (e.g., respond to male songs but do not respond to female songs), and the subject can then categorize new stimulus exemplars based on those already-learned discrimination rules. This difference associated with using an open-ended categorization strategy versus rote memorization allows researchers to examine whether subjects are indeed using open-ended categorization by also examining how subjects respond to novel or manipulated auditory stimuli.

In a series of two experiments, Hahn et al. (2016) found evidence that birds used open-ended categorization to discriminate among songs, suggesting that songs contain perceptually salient acoustic features that vary geographically. In the first experiment, chickadees in the true category group discriminated between songs significantly faster (i.e., in fewer trials) compared with chickadees in the pseudo category group. In addition, chickadees in the true category group transferred this discrimination to new songs, while birds in the pseudo category did not. These results with *fee-bee* songs are similar to those with *chick-a-dee* calls (Bloomfield et al., 2008b), suggesting that chickadee vocalizations belong to open-ended categories.

In a second experiment, we tested different subjects on the same geography-based discrimination; however, we used different song exemplars as our stimuli and we also presented birds with manipulated songs to identify mechanisms of the discrimination (Hahn et al., 2016). Unlike the results of experiment 1, chickadees in the true category group did not learn the discrimination in fewer trials compared to chickadees in the pseudo category group. However, in experiment 2, chickadees in the true category group generalized to novel song exemplars (i.e., birds reinforced for responding to British Columbia songs responded more to novel British Columbia songs compared with novel Ontario songs). This positive generalization is evidence that chickadees again were using open-ended categorization.

To determine why chickadees in the true category group learned the discrimination in fewer trials compared to chickadees in the pseudo category group in experiment 1, but not in experiment 2, we examined the stimulus exemplars used in each experiment. Results revealed that in experiment 1, there was a significant difference in the total duration of the rewarded and unrewarded songs for the true group, but not the pseudo group. This difference involved the same acoustic feature (total duration) that was found to differ significantly between the songs from these two geographic regions in our initial bioacoustic analysis (Hahn, Guillette, et al., 2013). For the songs used as stimuli in experiment 2, there was no statistical difference between rewarded and unrewarded songs for any of the acoustic features that we measured, a result that corresponded with our behavioral results, in which birds in the two groups learned the discrimination in a similar number of trials. However, consist with our previous bioacoustic analysis and the analysis of the stimuli from experiment 1, the total duration of the song stimuli used in experiment 2 trended toward a significant difference ($P = .094$), which may explain how chickadees still demonstrated positive generalization following discrimination training. We further presented chickadees with songs in which we manipulated the total duration of the songs, and results provide additional support that chickadees used the duration of the song when discriminating. However, it is likely that chickadees also used other acoustic features, but further acoustic analyses are required to determine which acoustic features chickadees may have used.

Our perceptual results with black-capped chickadees reinforce the idea that the acoustic variation in male songs produced by chickadee species (i.e., black-capped and mountain chickadees) can be used by birds to discriminate regional differences. For example, black-capped chickadees originating from different habitat types (i.e., high- and low-quality habitats; Grava, Grava, & Otter, 2012) or habitats that vary in levels of anthropogenic noise (Proppe et al., 2012) produce songs that differ measurably in acoustic features. Measurable acoustic differences have also been reported in songs produced by mountain chickadees originating in high- versus low-elevation habitats (Branch & Pravosudov, 2015), suggesting that regional song discrimination abilities could be widespread.

4.2.2.2.2 Variation Based on Singer's Sex In a separate series of experiments, we tested perceptual abilities associated with female black-capped chickadee song production. Black-capped chickadee songs produced by males and females may belong to open-ended categories that black-capped chickadees perceive. To answer this question, we again used a true category/pseudo category operant discrimination task. We had previous evidence to suggest that sufficient acoustic differences exist in the songs produced by male and female black-capped chickadees for the songs to be separated purely based on signaler sex (Hahn, Krysler, et al., 2013). However, chickadees in our first experiment in the pseudo category group learned the task in a similar number of trials as chickadees in the true category group, suggesting that there was no acquisition benefit to using open-ended categorization compared with strictly memorizing each individual stimulus and its associated reward contingency.

We were interested in whether chickadees would rely on acoustic features within one of the song's two notes when discriminating between male and female songs. Hahn, Hoang, et al. (2015) presented subjects with four types of manipulated songs: songs with a male-produced *fee* note and male-produced *bee* note, songs with female-produced notes, songs with a male-produced *fee* note and a female-produced *bee* note, and songs with a female-produced *fee* note and a male-produced *bee* note. For each stimulus, the two notes used to produce the "song" were taken from recordings of two different individuals (all probe stimuli were created by splicing together songs from different birds). Results from these manipulated song tests indicated that chickadees were using open-ended categorization (rather than just rote memorization) to discriminate songs, as chickadees whose responses to male songs were reinforced continued to respond significantly more to manipulated songs containing two male notes compared with manipulated songs containing two female notes. Similarly, chickadees whose responses to female songs were reinforced continued to respond significantly more to manipulated songs containing two female notes compared with manipulated songs containing two male notes. The results from these manipulated song tests also revealed sex differences in what acoustic features chickadees used when discriminating: male subjects seemed to rely more on acoustic features within the first (*fee*) note, while females seemed to rely on acoustic features within the second (*bee*) note (see Hahn, Hoang, et al., 2015: Figure 4; experiment 1). It is possible that these sex differences are related to function of this vocalization in the wild. Males may need to respond quickly to another male's song, as they are the principal defender of the territory. In contrast, important information relating to a male's quality (i.e., dominance rank) is contained within a song's internote interval (dominant males produce a more consistent frequency ratio between *fee* and *bee* notes across a song bout; Christie et al., 2004b) and amplitude between the two notes (dominant males produce songs with a more consistent amplitude; Hahn, Guillette, et al., 2013; Hoeschele et al., 2010), so females may be under increased selection pressure to listen to a mate's entire song before responding.

We conducted a second experiment with a separate group of subjects in which we increased the number of song stimuli used during discrimination training, requiring birds in the pseudo category discrimination group to memorize more song exemplars, which should be more difficult compared to using open-ended categorization (i.e., true category discrimination). The results from discrimination training in experiment 2 were strikingly similar to the results from experiment 1, even though the number of discrimination stimuli was nearly doubled (16 vs. 30 rewarded and unrewarded stimuli): chickadees in the pseudo category group acquired the discrimination as quickly as chickadees in the true category group. One possible reason for a lack of difference between the two groups is that the discrimination stimuli did not contain sufficient acoustic differences between male and female songs, so that all birds had to rely on rote memorization. However, we analyzed the training stimuli and found that the stimulus songs contained sufficient acoustic differences for sex-based discrimination. The results provide evidence that the *fee* glissando was a likely acoustic mechanism used for the discrimination (Hahn, Hoang, et al., 2015), a result which directly corresponds with our previous bioacoustic analyses (Hahn, Krysler, et al., 2013). Another possible reason that we did not find a difference between the two groups in the number of trials needed to acquire the task is that regardless of whether chickadees could use open-ended categorization or had to use rote memorization, chickadees could efficiently use either strategy to learn the task because the songs are naturally salient (i.e., chickadees could easily memorize or categorize songs). We did, however, find evidence that birds in the true category group used open-ended categorization in test trials following discrimination training. When presented with novel songs, subjects in the true category groups continued to respond based on the contingencies from discrimination training: chickadees whose responses to male songs were reinforced responded significantly more to novel male songs compared to novel female songs; and chickadees whose responses to female songs were reinforced responded significantly more to novel female songs compared to novel male songs (these results were similar to a trend observed during similar test trials in experiment 1; however, in the first experiment the results were not significant). In addition, subjects in the pseudo category group responded equally to novel male and female songs. The results of these test trials from experiment 2 provide compelling evidence that chickadees in the true category group were using open-ended categorization when discriminating between male and female songs.

Taken together, operant conditioning studies in chickadees have determined that these birds can discriminate between vocalizations based on signaler species, sex, and geographic origin. Signals that sound highly similar to humans contain acoustic information that is both measurably distinct and perceptible to chickadees. The degree of expertise shown by the chickadees on these tasks suggests that these discrimination abilities are ecologically relevant, as might be expected. That categories can be classified based on the *fee-bee* song also reveals that this superficially simple song contains important sex-specific information that humans find difficult to perceive but that can carry important and meaningful differences to chickadees. Further, chickadees are both able to group classes of stimuli based on particular category membership (e.g., species, sex, geographic origin) and respond flexibly to new stimuli based on their similarity to these categorical differences. Chickadees display sophisticated cognitive capabilities for categorization, rather than simply memorizing individual stimuli or responding (or withholding responses) solely on the basis of innate preferences.

4.3 Development

Black-capped chickadees offer a unique opportunity to examine the effects of early developmental experience, not only because both songs and calls are learned in this species but also because in the wild black-capped chickadees live in sympatry with other chickadee species (e.g., mountain chickadees) that produce similar, but acoustically distinct vocalizations. This allows researchers to compare the vocal production and perception of birds that were reared with conspecific adults, closely related heterospecific adults, or in the absence of adults.

4.3.1 General Vocal Development in Songbirds

While most species' vocalizations develop without external input, some animal groups (including but not limited to humans, bats, cetaceans, hummingbirds, parrots, and songbirds) learn their vocalizations. The basic model of vocal learning in songbirds involves a critical period in which a juvenile must hear adult vocalizations from a conspecific tutor to later produce normal, species-typical vocalizations as an adult. However, individual species differ in the role of the tutor and the duration of learning required to produce species-typical vocalizations (reviewed by Beecher & Brenowitz, 2005). Marler (1970) found that white-crowned sparrows (*Zonotrichia leucophrys*) have a critical period between the age of 20 and 50 days in which they attend to their own species' vocalizations but ignore those of other species. In this instance, birds learned from taped songs of conspecific adults. Some species, however, do not learn from tapes and require live tutors or, as is the case with white-crowned sparrows, they learn more accurately and for longer periods from live models than from tapes (Baptista & Petrinovich, 1984). In zebra finches, males use tutors to learn song production and quality, while females use tutors to learn song preference (Zann, 1996).

After the critical period, most species experience a period of sensorimotor integration where sensory information memorized from tutors during the critical period is used to rehearse and refine their own vocal repertoires (Woolley, 2012). This period begins with subsong, a behavior that has been analogized to human babbling, then progresses to more adult-typical vocalizations that remain relatively plastic until sexual maturity, at which song is "crystallized." If a juvenile is exposed to a tutor during the critical period, but the tutor is removed before the young bird begins singing, the bird still tends to develop species-typical vocalizations, though these will not develop normally if they are unable to hear and correct their own vocalizations (i.e., if they are deafened) during sensorimotor integration (reviewed by Woolley, 2012).

4.3.2 Call and Song Learning: Unique Aspects of Chickadee Vocal Development

Most research on vocal learning in songbirds has focused on song learning; however, since black-capped chickadees produce numerous acoustically complex calls, in addition to songs, research in this species has examined call and songs learning. Multiple studies have provided evidence that black-capped chickadees learn their song and components of various calls, including their *gargle*, *tseet*, and *chick-a-dee* calls. Baker, Baker, and Gammon (2003) examined the vocal development of *fee-bee* songs, *gargle* calls, and *chick-a-dee* calls in black-capped chickadees in the field from the nestling and fledgling period through juvenile dispersal (at approximately 40 day posthatch). They compared the vocalizations of these young chickadees with the vocalizations produced by the social parents. Results suggested that all components of *chick-a-dee* calls develop from a single, simple vocalization that birds start producing as day old nestlings, with adult-like D notes emerging first, followed by A, B, and C notes. Juveniles began producing *fee-bee* songs at approximately 20 days posthatch (following fledging) and these were found to be remarkably similar to adult songs. Juveniles *fee-bee* songs had similar duration and relationships among note frequencies as adult songs, but juveniles often produced songs with more than the characteristic two notes. At 30 days posthatch, chickadees produce a vocalization termed "subsong" (Ficken et al., 1978; Clemmons & Howitz, 1990) that later develops into *gargle* calls. Juvenile *gargle* calls are acoustically distinct from those of adults within the natal population, suggesting plasticity in the production of *gargle* calls until at least the postdispersal period (Baker et al., 2003). While field studies have provided important insights into the vocal development of black-capped chickadees in their natural environment, laboratory experiments have also proved useful in examining the role of vocal learning during development, and how various developmental experiences affect perceptual abilities.

4.3.3 Effects of Altered Development on Vocal Production

4.3.3.1 Fee-Bee Songs

In the field, juvenile black-capped chickadees begin producing songs after fledging (Baker et al., 2003). In the laboratory, black-capped chickadees will produce normal songs as adults if they are exposed to adult conspecific vocalizations (Shackleton & Ratcliffe, 1993). However, if black-capped chickadees are not exposed to conspecific adult vocalizations during development, they will produce abnormal songs as adults. When tutored with songs of Carolina chickadees, young black-capped chickadees learn components (frequency and temporal features) of the heterospecific tutor songs, suggesting that social factors like song exposure can overcome genetic factors related to song production (Kroodsma, Albano, Houlihan, & Wells, 1995). Male black-capped chickadees that are tutored with audio recordings (starting at approximately 30 days posthatch) with songs that contain only the first (*fee*) note will produce two-note *fee-bee* songs as adults, but these songs do not contain the species-typical frequency interval (Shackleton & Ratcliffe, 1993). This finding suggests that while some aspects of song production do not require a live tutor, some species-typical acoustic parameters may be refined with live tutoring during development.

The production of vocalizations can also be impacted by environmental factors such as habitat. Grava et al. (2013) investigated the role of natal habitat quality in the development of the vocal control system in the brains of juvenile male black-capped chickadees. Birds that settled in higher quality habitats (habitats with more resources) had higher levels of feather corticosterone (a measure of conditional state prior to dispersal) and heavier syringes than those that settled in lower quality habitats. Since males from higher quality habitats are known to produce more consistent song (Grava et al., 2012), these differences in vocal neuroanatomy and musculature may be related to the quality of song produced. These results suggest that environment during development (which may include resources such as food availability) impact this developing vocal musculature and the brain circuits that subserve vocal learning and production.

4.3.3.2 *Gargle* Calls

Vocal learning also plays a role in the production of *gargle* calls. Ficken and Popp (1995) found that the *gargle* repertoires of males within a population share several *gargle* types and that those types will continue to occur in that population across generations but *gargle* types differ across populations, implying that young birds learn at least some of their *gargle* calls from adults. Evidence from the field (Baker et al., 2003) suggests that *gargle* calls are learned; *gargle* calls produced by juvenile black-capped chickadees converge on the local *gargle* repertoire when they arrive in an area. Through this vocal convergence, chickadees that share territory boundaries (i.e., territory neighbors) also produce similar *gargle* types within the local dialect, which limits territorial interactions that commonly occur among unfamiliar individuals (Ficken & Weise, 1984; Baker, Howard, & Sweet, 2000).

4.3.3.3 *Tseet* Calls

Guillette et al. (2011) investigated the development of *tseet* calls produced by black-capped chickadees raised with either adult conspecifics, adult heterospecific mountain chickadees, or in the absence of adults. They found frequency differences in the calls produced by birds reared with conspecifics and birds reared with heterospecifics. In contrast, chickadees reared in the absence of adults produced calls that differed in numerous ways from either of the other two laboratory-reared groups along multiple acoustic parameters (frequency and duration measures). Additionally, black-capped chickadees raised with adults (either conspecifics or heterospecifics) produced individually distinct *tseet* calls, while the calls produced by birds reared without adults were less individualized. Specifically, discriminant function analyses correctly classified *tseet* calls by the individual producer in only 58% of all cases for chickadees reared without adult conspecifics, compared to 73% of all cases for chickadees reared in the presence of adult conspecifics. In addition, acoustic features in *tseet* calls (including the descending duration, end frequency, and loudest frequency) produced by chickadees reared without adult conspecifics contained more intraindividual variability compared to interindividual variable, suggesting these acoustic features would not be useful for individual identification (Guillette et al., 2011). These results provide evidence that the production of *tseet* calls involves learning during development and that while exposure to conspecific adults is required for learning species-typical *tseets*, exposure to adults of a closely related heterospecific species (mountain chickadees) can alter the vocal development of *tseet* calls produced by black-capped chickadees. Not having exposure to adults during development can hinder the development of species-typical and individualized contact calls.

4.3.3.4 *Chick-a-dee* Calls

Black-capped chickadee *chick-a-dee* calls contain components that are learned and those that are innate. Hughes et al. (1998) reared black-capped chickadee nestlings in the laboratory in either total isolation, isolated from adults, exposed to adults from time of capture (i.e., heard conspecific vocalizations for all of development), or exposed to adults at 38-day posthatch, but not earlier in development. Chickadees reared with adults throughout development produced species-typical *chick-a-dee* calls, but birds that were exposed to conspecific calls more than a month into development produced notes with measures that fell between species-typical notes and those of the isolate birds. These results indicate a vocal learning impairment when tutors are not available until later in development, suggesting a sensitive period. Only birds that had exposure to tutors at any point during development produced normal B and C notes; however, birds in all conditions produced species-typical A notes, suggesting that learning is required for the development of B and C notes, but not A notes. Hughes et al. (1998) did not examine the vocal development of *chick-a-dee* call D notes; however, field observations have shown that D notes develop first and are thought to derive from another call in their vocal repertoire, the "begging see" (Baker et al., 2003). Black-capped chickadees reared in the absence of adult conspecifics produce notes that resemble D notes, but do not contain species-typical acoustic features (Hahn, Guillette, et al., 2015). In adulthood, the production of D notes continues to exhibit vocal plasticity, as the D notes of winter flocks converge each year, involving a coordinated learning process whereby the calls produced by flockmates converge and contain D notes that share acoustic parameters (Mammen & Nowicki, 1981; Nowicki, 1983, 1989).

4.3.4 Effects of Altered Development on Perception

Exposure to vocalizations of adult conspecifics is crucial to produce normal *fee-bee* songs, *tseet* calls, *gargle* calls, and *chick-a-dee* calls in black-capped chickadees. If experience can impact the production of these vocalizations, it is possible that developmental experience can also affect the perception of these and even other auditory stimuli. Njegoven and Weisman (1997), for example, showed that black-capped chickadees raised in isolation have an impaired ability to discriminate relative frequency relationships compared to field-raised chickadees and must instead rely on memorizing absolute frequencies. This study suggests that auditory experience may be necessary for the development of auditory perception.

Phillmore, Sturdy, and Weisman (2003) conducted an operant discrimination experiment in which they tested the ability of both wild-caught and hand-reared isolate black-capped chickadees to categorize heterospecific zebra finch distance calls and conspecific *fee-bee* songs based on distance to and identity of the caller. Despite being able to discriminate distance cues, hand-reared isolates were unable to identify individual callers. *Fee-bee* songs are involved in establishing and defending territories, where males attend to the songs of their neighbors to identify who they are and where they are singing. Birds who cannot identify individuals may be unable to differentiate between their normal neighbors and new, unknown chickadees encroaching on their territory. In another operant experiment, Bloomfield et al. (2008b) found that black-capped chickadees reared in the presence of adult mountain chickadees performed as well as those reared with adult conspecifics when discriminating between *chick-a-dee* calls of both species. Taken together, these studies suggest that not all auditory discriminations are impeded by exposure to adult conspecific vocalizations.

Avey, Hoeschele, Moscicki, Bloomfield, & Sturdy (2011) conducted a playback experiment investigating the neural response (by measuring IEG expression) to hearing predator calls of varying threat levels and hearing the mobbing-related *chick-a-dee* calls of black-capped chickadees exposed to mounts of the same predators. They found that wild-caught black-capped chickadees had similar neural activation (i.e., similar amounts of IEG expression) in response to both the predator calls and corresponding (i.e., of the same threat level) *chick-a-dee* calls, suggesting that despite the acoustic differences, they are perceived to have similar meaning. However, laboratory-reared black-capped chickadees had significantly greater IEG expression following playback of *chick-a-dee* calls compared to the predator calls. In addition, presentation of predator calls lead to similar levels of IEG expression as calls produced by a nonpredator species (red-breasted nuthatch), suggesting that the threat associated with predator calls may be learned.

This collection of research illustrates the complex interplay of biological and environmental factors on both the production and perception of vocalizations (Table 1). Multiple black-capped chickadee vocalizations, or components of vocalizations, are acquired through vocal learning. Exposure to the vocalizations of adult conspecifics, the vocalizations of heterospecifics, and even experience with certain habitat types can influence what young chickadees learn and how they perceive the world around them. Experimental results from the laboratory must be viewed in conjunction with observations from the field to capture the effects of numerous interconnected factors and to interpret the results correctly in relation to their biological implications.

4.4 Neurobiology

4.4.1 Vocal Control System and Perceptual Areas

Vocalizations produced by black-capped chickadees (similar to other songbird species) are controlled by a set of interconnected brain areas (see Fig. 3A), known as the song system (Ball & MacDougall-Shackleton, 2001). HVC (abbreviation used as proper name), a nucleus in the telencephalon, projects vocal information to the robust nucleus of the arcopallium (RA), which then sends projections to the 12th cranial nerve (XIIts) and nucleus intercollocularis (ICo). Vocal information is then sent from the XIIts to muscle fibers of the syrinx in the throat, where the vocalization is produced (Nottebohm, Stokes, & Leonard, 1976). Songbirds also have a secondary vocal pathway, thought to be involved in behavior modification, song learning, and song maintenance (Brenowitz, 1991). In this second pathway, information also originates in HVC and is then sent to Area X also in the telencephalon. Area X projects to the dorsolateral nucleus of the anterior thalamus (DLM) that in turn projects to the lateral section of the nucleus magnocellularis of the anterior neostriatum (LMAN). The LMAN sends information to the RA where it will then continue through

Table 1 Research articles that examined the effects of developmental rearing condition on vocal production and/or perception in black-capped chickadees

Article	Vocal production or perception	Rearing condition	Technique	Stimuli
Avey, Hoeschele, et al. (2011)	Perception	Reared with conspecific or heterospecific (mountain chickadee) adults	Immediate early gene expression (ZENK)	Conspecific *chick-a-dee* mobbing calls Predator calls
Baker et al. (2003)	Production	Field	Field study	n/a
Bloomfield et al. (2008b)	Perception	Reared with conspecific adults Reared with heterospecific (mountain chickadee) adults	Operant conditioning	Black-capped chickadee *chick-a-dee* calls Mountain chickadee *chick-a-dee* calls
Ficken and Popp (1995)	Production	Field	Field study	n/a
Grava et al. (2013)	Production	Field	Field study	n/a
Guillette et al. (2011)	Production	Reared with conspecific adults Reared with heterospecific (mountain chickadee) adults Reared without adults	Bioacoustic/statistical analyses	n/a
Hahn, Guillette, et al. (2015)	Production; Perception	Reared with conspecific adults Reared with heterospecific (mountain chickadee) adults Reared without adults	Bioacoustic/statistical analyses Immediate early gene expression (ZENK)	Conspecific *chick-a-dee* call D notes
Hughes et al. (1998)	Production	Reared in total isolation Reared without adults Reared with adults starting at hatching Reared with adults starting at approximately 38 days posthatch	Bioacoustic/statistical analyses	n/a

Kroodsma et al. (1995)	Production	Reared without adults and tape-tutored with black-capped chickadee *fee-bee* song Reared without adults and tape-tutored with Carolina chickadee *fee-bee* song	Bioacoustic/statistical analyses	n/a
Njegoven and Weisman (1997)	Perception	Field reared Reared without adults in isolation	Operant conditioning	Pairs of sine wave tones with constant frequency ratio or random frequency ratio
Phillmore, Sturdy, et al. (2003)	Perception	Reared without adults in isolation Field reared (i.e., wild caught)	Operant conditioning	Male black-capped chickadee *fee-bee* songs Female zebra finch distance calls
Shackleton and Ratcliffe (1993)	Production	Reared without adults and tape-tutored with complete *fee-bee* song at either high frequency (3.30 kHz) or low frequency (2.84 kHz) Reared without adults and tape-tutored with *fee* only songs	Bioacoustic/statistical analyses	n/a

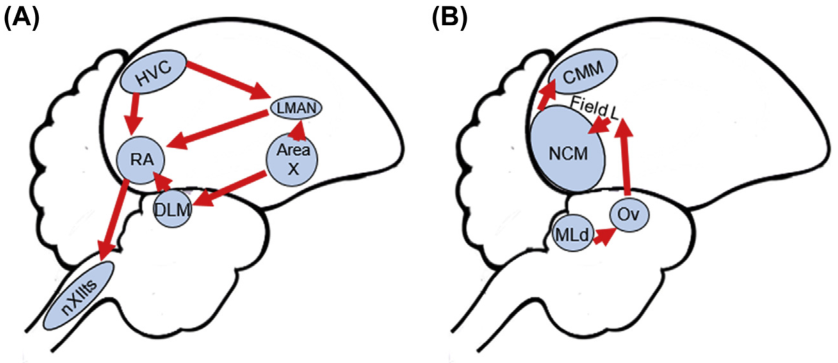

Figure 3 Diagram depicting the vocal (A) and auditory (B) pathway in sagittal cross sections of the songbird brain (see text for details). *CMM*, caudomedial mesopallium; *DLM*, dorsolateral nucleus of the anterior thalamus; *LMAN*, nucleus magnocellularis of the anterior neostriatum; *MLd*, dorsal lateral mesencephalic nucleus; *NCM*, caudomedial nidopallium; *nXllts*, nucleus of the 12th cranial nerve; *Ov*, nucleus ovoidalis; *RA*, robust nucleus of the arcopallium.

the primary pathway until it reaches the syrinx (Ball & MacDougall-Shackleton, 2001).

Auditory information is sent (via the auditory nerve) to the cochlear nucleus in the hindbrain, which then projects to the dorsal lateral mesencephalic nucleus (MLd) in the midbrain (Fig. 3B). Auditory information is then projected to the thalamus and nucleus ovoidalis (Ov; Mello, Velho, & Pinaud, 2004). Projections from the Ov are sent to the telencephalon where they terminate in Field L. Field L in turn projects to the dorsal and ventral portions of the caudomedial nidopallium (NCM), a secondary auditory area, which is also interconnected to the caudomedial mesopallium (CMM). While mainly used in song production, HVC and RA also have a role in processing auditory input after it has been processed earlier in the auditory perceptual pathway (Matragrano et al., 2012; Mello & Clayton, 1994). These auditory forebrain regions are critical for processing auditory information including conspecific vocalizations.

Studies measuring IEG expression have been useful for examining neural responses to auditory stimuli. There is robust expression of the IEG ZENK (*zif*-268, *egr*-1, NGFI-A, *krox*-24) in the secondary auditory areas NCM and CMM following presentation of biologically important vocal signals (e.g., Mello & Clayton, 1994; Sockman, Gentner, & Ball, 2002). In the next section, we discuss studies that quantify IEG expression in chickadees to examine the neural correlates of auditory perception.

4.4.2 Using Immediate Early Genes to Examine Neural Correlates of Perception

Early work examining IEG expression in songbirds revealed differential levels of expression in response to conspecific compared to heterospecific songs (Mello, Vicario, & Clayton, 1992). However, in addition to differing in their biological relevance to the subjects (conspecific songs are presumed to be of greater salience compared to heterospecific songs), the vocalizations used by Mello et al. (1992) as stimuli were also produced by species that were phylogenetically not close relatives (i.e., zebra finches and canaries) and the vocalizations varied greatly in acoustic structure. Chickadees are an ideal group to examine auditory perceptual correlates of phylogenetic relatedness, because multiple chickadee species (which are close relatives phylogenetically) produce vocalizations with similar acoustic structure. Avey et al. (2014) used D notes from *chick-a-dee* calls produced by three Parid species (black-capped, chestnut-backed chickadee, and tufted titmouse) and *distance* calls produced by male and female zebra finches to examine IEG expression in black-capped chickadees. Similar amounts of IEG expression were induced regardless of which species' calls were presented, rather than according to phylogenetic similarity. IEG expression is thus not always higher in response to conspecific vocalizations compared to heterospecific vocal signals. Instead, acoustic structure (broadband calls with many harmonics or overtones in this case) can also influence IEG response. Because all of the acoustic stimuli used in Avey et al. (2014) were acoustically similar to a biologically important component of conspecific calls, we therefore cannot rule out the influence of biological relevance on the IEG response. Additionally, since the subjects used by Avey et al. (2014) were adult black-capped chickadees reared in the wild, experience with conspecific adult *chick-a-dee* calls also likely influenced the IEG response.

To examine the influence that experience with adult chickadees has on IEG response to conspecific vocalizations, Hahn, Guillette, et al. (2015) conducted an experiment using black-capped chickadees that were reared under various social environments. Nestling black-capped chickadees (10—14 days posthatch) were hand-reared in the laboratory and housed under one of three conditions: (1) in the presence of conspecific black-capped chickadee adults, (2) in the presence of heterospecific mountain chickadee adults, or (3) in the presence of other hand-reared birds but no adults. As adults, all hand-reared birds and a group of field-reared adults (i.e., birds with auditory exposure during development that would be typical in the wild) were presented with conspecific D notes and IEG expression was quantified. The results revealed similar levels of IEG expression in field-reared black-capped chickadees and black-capped chickadees lab-reared in the presence of conspecifics, suggesting that laboratory rearing did not significantly affect the auditory processing of the subjects. However, chickadees lab-reared in the absence of adults had significantly less IEG expression compared to chickadees lab-reared with conspecifics, while chickadees lab-reared with heterospecific mountain chickadees had intermediate levels of IEG expression. Quantification of the IEG expression therefore suggests that acoustic characteristics alone do not drive IEG expression, instead, experience with adults (either conspecifics or closely related heterospecifics) and/or adult vocalizations during development can also influence auditory responses later in adulthood. Hahn, Guillette, et al. (2015) also conducted a bioacoustic analysis of the vocalizations produced by lab-reared chickadees to examine how acoustically similar D notes produced (and heard) by the subjects were to species-typical D notes (i.e., the notes presented as stimuli during the experiments). This bioacoustic analysis revealed that only birds reared with conspecifics were producing species-typical D notes. These results suggest that acoustics and/or experience influence IEG expression; however, another factor that has been shown to affect auditory responses is the biological relevance associated with auditory stimuli. For example, presentation of male songs that are preferred by females induces higher levels of IEG expression (canaries, Leitner, Voight, Metzdorf, & Catchpole, 2005; European starlings, Gentner, Hulse, Duffy, & Ball, 2001), suggesting that vocalizations associated with greater salience to the perceiver correlate with this type of neural response. The salience associated with a vocalization is likely to vary depending on the individual responding to the signal. In accord with this idea, Phillmore, Bloomfield, and Weisman (2003) demonstrated that presentation of black-capped chickadee *fee-bee* songs induced more IEG expression presentation of *chick-a-dee* calls, and male subjects had greater levels of IEG expression compared with females. These results suggest that both the *type* of vocalization and the sex of the bird hearing the vocalization can influence this type of neural response. In a similar study, Avey, Kanyo, Irwin, and Sturdy (2008) examined the effect of sex of the vocal producer by presenting male and female black-capped chickadees with *chick-a-dee* calls or *fee-bee* songs produced by males or females. Similar to the results of Phillmore, Bloomfield, et al. (2003), Avey, Kanyo, et al. (2008) found greater levels of IEG expression in male subjects compared to females. Additionally, in CMM, Avey, Kanyo, et al. (2008) found that in both male and female subjects, male-produced *chick-a-dee* calls elicited the greatest IEG response, while for male subjects, female song induced the least expression, and for female subjects, female calls induced the least expression. Taken together, the results of Phillmore, Bloomfield, et al. (2003) and Avey, Kanyo, et al. (2008) reveal that sex of the producer and receiver, as well as the type of vocalization, influences the auditory neural response of hearing conspecific vocal signals.

Other factors could also influence the biological salience associated with vocal signals, including social context (e.g., breeding vs. nonbreeding season; see Phillmore, Veysey, & Roach, 2011) or information conveyed by the signal (e.g., food-associated vs. predator-associated call). Predator calls offer a unique opportunity to examine responses to heterospecific vocalizations that can vary in their salience to the receiver (e.g., high- vs. low-threat predator calls, as discussed in previous sections). Additionally, because black-capped chickadees produce mobbing-related calls that vary depending on the degree of threat of a potential predator (Templeton et al., 2005), black-capped chickadees are a species in which responses to heterospecific (i.e., predator) calls and corresponding conspecific (i.e., mobbing-related *chick-a-dee*) calls can be compared. Avey, Hoeschele, et al. (2011) conducted an experiment to examine the neural correlates (by quantifying IEG expression) associated with the perception of functionally similar (high or low threat), but acoustically distinct vocalizations (predator or *chick-a-dee* calls). Black-capped and mountain chickadees were presented with either vocalizations indicating a high-threat context (i.e., calls produced by a northern saw-whet owl, or calls produced by a black-capped chickadee in response to seeing a northern saw-whet owl) or a low-threat context (i.e., calls produced by a great horned owl, or calls produced by a black-capped chickadee in response to seeing a great horned owl). Following presentation of the vocalizations, Avey, Hoeschele, et al. (2011) quantified the expression of the IEG ZENK in the auditory regions CMM and NCM. The results demonstrated that while there were different levels of IEG expression depending on the degree of threat (high or low) encoded within the vocal signal, the authors found similar levels of IEG expression following both types of high-threat signals (i.e., northern saw-whet owl calls and high-threat *chick-a-dee* calls) and similar levels of IEG expression following both types of low-threat signals (i.e, great horned owl calls and low-threat *chick-a-dee* calls). Therefore, it appears that auditory regions are not simply responding based on whether a predator or a chickadee produced the vocalizations or on the acoustic structure of the vocalization. Rather results suggest that the auditory neural response is sensitive to the degree of threat encoded within the signals, which is also likely associated with different levels of salience.

5. SUMMARY OF CONCLUSIONS AND FUTURE DIRECTIONS

Through the course of this chapter, we have summarized a breadth of research on the mechanisms of behavior in a single animal group, the black-headed chickadee clade, with specific focus on black-capped chickadees. We have emphasized that chickadees are an ideal model system to examine questions that have broad implications for understanding vocal communication, and more generally, animal behavior, at various levels of investigation. Specifically, we have demonstrated that chickadees sing in winter as well as spring and that females sing as well as males. We have shown how bioacoustic analyses can discern features in *tseet, chick-a-dee*, and *fee-bee* vocalizations that differ among species, geographic origin, sex, or individual identity of the caller; and further, we have summarized behavioral analyses showing that chickadees can discriminate between vocal categories based on these features (showing that these vocalizations can carry an impressive amount of information between individuals). *Chick-a-dee* calls, for example, can indicate predator threat, and analysis of chickadee brain and behavior illustrates that they can perceive these differences as similar to the actual presence of a predator, yet may act according to both predator threat and presence. These feats are all built on a complicated vocal system that is learned during development and processed in a complex vocal control and auditory neural network.

These studies have encompassed both behavioral ecology and comparative cognition using techniques from operant conditioning, developmental biology, behavioral neuroscience, and bioacoustics. This research has been successful in furthering the aims of our subdomains: in better understanding behavioral ecology of this species, specifically as it pertains to how chickadees' vocalizations and vocal perception function in their environment; as well as understanding the species' use of perceptual and conceptual categorization, especially in comparison to visual categorization experiments in other animals.

Perhaps most importantly, we assert that the sum of the conclusions reported here could not have been found without leveraging and integrating the knowledge and techniques of all the fields used. Understanding behavior in all its capacities and functions requires laboratory research as well as field studies; neuroscience along with direct observation; and an understanding of both the ecological bases that drive typical behavior in species and the psychology of learning in individuals. It is no longer sufficient in animal behavior to adhere to only one subfield of knowledge and study, nor is ignorance of the techniques and findings of related domains a tenable position. Instead, cooperation and collaboration is the best way forward in understanding the highly complex systems that drive animal behavior.

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