CHAPTER 10

Chickadee vocal production and perception: An integrative approach to understanding acoustic communication

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10.1 Introduction

The three key elements in the scientific study of animal communication are the sender and the receiver, and the interaction between these two elements. Senders produce a signal that is perceived by the receiver and, operationally, communication occurs when the signal leads to an observable change in the behavior of the receiver (Maynard Smith and Harper 2003). Just as production and perception are integral to communication in general, so too must both sides of the equation be considered when studying acoustic communication in any particular species or in any animal group. Here we take this integrative approach and equally consider both production and perception, in an attempt to understand acoustic communication in one of the most well-recognized and well-studied groups of North American songbirds, the chickadees.

10.2 Song production and perception

10.2.1 Song production

In the prototypic species of the genus *Poecile*, the black-capped chickadee, the species song is termed *fee-bee* (Fig. 10.1a; see Box 10.1 for notes on the "discovery" of the black-capped chickadee's song). Since song in this species has been investigated most heavily, it will be used as a model here. *Fee-bee* song is produced mainly by males and the peak of production occurs in the spring and early summer. The song of black-capped chickadees has been the subject of intensive field studies over the past decade (see Chapters 13 and 14), focusing primarily on the functional aspects of singing behavior. Our focus here will be on vocal production and structure.

Black-capped chickadees sing their two-note song at several distinct pitches (Fig. 10.1a). Initially quantified in detail by Ratcliffe and Weisman (1985) and Weisman *et al*. (1990), work over the last decade has shown that there is a frequency range over which the species' songs are produced, spanning approximately 1 kHz from lowest to highest songs, and individual males can sing at a variety of discrete pitches within this range (see Chapter 14 for further details on possible functions for pitch shifting). However, at all of these various pitches, the song remains a relatively high-frequency vocalization that approximates a pure tone. Average songs have a starting frequency of about 4000 Hz. The first note (*fee*) then falls by about 200 Hz from the start to the end. There is another frequency drop between the end of the *fee* and the start of the second note (*bee*) equal to about a 400 Hz drop. These regularities in pitch structure led Weisman and colleagues (1990) to conduct a bioacoustic analysis, of a small sample and then an

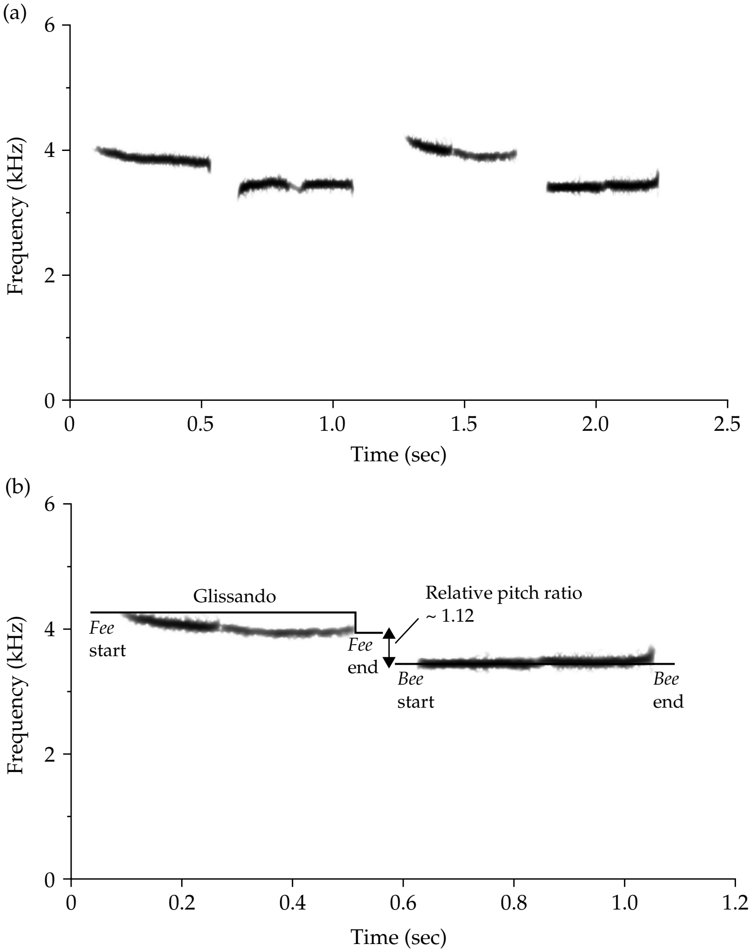

Figure 10.1 (a) Two representative *fee-bee* songs. Spectrogram settings: Hanning window, 1024 points. (b) A *fee-bee* song indicating the location of specified measurements. Time (sec) is on the x axis and frequency (kHz) is on the y axis in both spectrograms.

exhaustive sample of songs, to determine first the acoustic properties of the song and second, which if any of these properties could be used in species and individual identification.

One of the key findings from the initial bioacoustic analysis of black-capped chickadee *fee-bee* song was males produced their songs with remarkable regularity from one rendition to the next, regardless of the initial starting frequency. Another remarkable finding from these early studies of chickadee song is that it maintains a constant and equivalent relative pitch ratio between the two notes. This "relative pitch ratio" was calculated by dividing the end frequency of the *fee* note by the starting frequency of the *bee* note: this ratio was approximately 1.13 for all songs among all males. Even more remarkable was the fact that this relative pitch ratio was maintained when birds produced shifted song. That is, when birds change the overall starting frequency of the song, the frequency ratio between the two notes remained constant. In other words, male chickadees adjust the relative pitch between notes when they frequency shift, so as to maintain a constant "tune". This implies that birds were maintaining precise control over their vocal production as well as monitoring their vocal production in order to maintain this relative pitch ratio.

In the follow-up, Weisman *et al.* (1990) recorded songs from 156 males singing on their territories,

Box 10.1 What is the song of the black-capped chickadee?

Chickadee song, or more specifically what is considered chickadee song, has been a matter of debate (Ficken 1981). Although chickadees produced several vocalizations, the particular vocalization that functioned as "song" *per se*, was contested. Two main contenders were identified: the *fee-bee* and the acoustically complex *gargle* call (Chapter 11). In fact, early reports termed what is now considered to be chickadee song (*fee-bee*) their call (Dwight 1897). This is in large part due to the fact that chickadees do not conform to commonly held truism for songbird vocal production, this being that songs are thought to be a complex vocalization, produced mainly by males, are produced mainly during the breeding season, and are acquired through imitative learning. Calls, by contrast, are thought to be less complex, produced by both sexes throughout the year in contexts outside mate attraction and territory defense, and are largely innate (Catchpole and Slater 1995). These facts made the identification of the chickadee song somewhat contentious. An additional factor, that likely enhanced the confusion around the issue, was not all chickadee species produce a whistled, tonal vocalization. In the end, the whistled song was accepted as the species-typical vocalization that served the typical functions of song—mate attraction and territorial defense.

and measured a greater number of acoustic features than simply the constant frequency of the *fee* and *bee*, along with temporal measures. Several important findings regarding song production arose from Weisman *et al*.'s more extensive study. Absolute pitch was found to be relatively consistent within birds but variable among birds. Thus, as a species marker, absolute pitch would provide a coarse assessment of species identity, but it could be used for individual recognition. It was when attention was turned to relative pitch cues, however, that things got particularly interesting.

Relative pitch production can be further subdivided into at least two other categories, relative pitch contour and relative pitch ratio, both of which were examined by Weisman *et al*. (1990). Relative pitch contour refers to the ordinal pitch relationships between adjacent notes, or features of notes. In black-capped chickadee song, these relationships were constant in almost every song sampled, with the starting pitch of the *fee* greater than the end of the *fee*, and the end of the *fee* greater than the pitch of the *bee* note. A constant pitch ratio, on the other hand, requires there to not only be the ordinal relationships described for pitch contour, but it requires the additional feature of maintaining the same pitch ratio between acoustic features, both between the *fee* start and *fee* end, and between the end of the *fee* and the start of the *bee* note. Importantly, and strikingly, these relationships could be perfectly accounted for with a linear regression, so that, for instance, as the pitch of *fee* start increased, so did the pitch of *fee* end. A similar pattern also emerged for the ratio of *fee* end to *bee*, and these relative pitch findings were consistent regardless of the starting pitch of the song. Moreover, variation in the relative pitch cues observed within birds was tiny compared to those among birds and even smaller than the within-bird variation seen for absolute pitch cues. Put another way, birds could potentially use relative pitch cues, present in either normal or shifted songs, for species and individual identification.

As intriguing as these findings were, they were only one side of the coin, that of song production. Whether the birds used any or all of the features for species or individual recognition was unclear. Perceptual experiments were required to systematically determine the role of each of these features identified in the production analyses. We will therefore turn to song perception momentarily.

10.2.2 Song perception

Once potentially relevant, or at least invariant, song features were identified, the next critical step was to determine whether and how any or all of these features were related to song perception in black-capped chickadees. This required perceptual experiments in which natural and manipulated versions of the songs, or, in some cases, synthetic representations of the songs, were presented to birds and their responses compared. To this end, two main classes of experiments were conducted, playback experiments and laboratory-based operant conditioning experiments, with each approach having its own advantages and limitations.

10.2.2.1 *Playback experiments of song perception*

Laboratory playback procedures were carried out by Ratcliffe and Weisman (Ratcliffe and Weisman 1986, 1988; Weisman and Ratcliffe 1989) as first steps towards determining which, if any, features identified in the initial bioacoustic analyses were used for species recognition in chickadees. Initially, Ratcliffe and Weisman (1986, 1988) focused on whether chickadees attend to the pitch contour and number of notes present in their songs. This was accomplished in a similar manner in each experiment; individual male chickadees were isolated from other birds for a period of time, followed by presentations of various versions of altered song (e.g. only the *fee*, *bee-fee*, *bee-bee*, *fee-bee-bee*, etc.). These experiments returned several interesting results. Ratcliffe and Weisman (1986) found that birds discriminated between *fee* and *bee* notes and also responded less to songs that were either artificially lengthened or shortened. Ratcliffe and Weisman (1988) extended these results by showing that birds responded more slowly to songs that contained an extra note at the beginning, such as *fee-fee-bee*, but not when an extra note was added to the end, such as *fee-bee-bee*. These latter results implied that birds were in fact sensitive not only to the duration of their songs, but also to the temporal locations of the two different notes in their songs. Taken together, it became clear that chickadees perceived rather strict rules in their seemingly simple songs, with pitch contour playing an important role.

While these experiments dealt with issues of note type and number discrimination, along with pitch contour perception, they did not deal specifically with the role of absolute or relative pitch cues in black-capped chickadee song. Two separate laboratory playback experiments were devised; one each to test birds' reactions to songs altered either in absolute or relative pitch. To alter the absolute pitch, normal "base" songs were linearly shifted in pitch so that they ranged from below to above the absolute range of what is typical for black-capped song production. In order to test for only absolute pitch perception, the relative pitch ratio between the end of the *fee* and start of the *bee* note was maintained. To alter the relative pitch, base songs were manipulated to produce several renditions that started with the original *fee* start frequency, but that contained various pitch ratios between the *fee* end and *bee* start. Thus, in the second set of songs, the absolute starting pitch remained consistent while the relative pitch ratio between the *fee* and *bee* notes varied.

When chickadees were presented with songs outside of the species-typical range of absolute pitch, either higher or lower, birds in general responded less to these than to normal songs. In particular, birds were less likely to respond with "social" vocalizations when song was played outside the typical absolute frequency range.

Relative pitch-altered songs also lead to a differential response when presented to male chickadees, but not in the same manner as those altered in absolute pitch. When the relative pitch cues were altered outside the species-typical range, birds again responded less to altered songs than to normal songs, but whereas birds responded with less social vocalizations when presented with absolute pitch-altered songs, birds responded less aggressively when presented with relative pitch-altered songs. Therefore, not only were black-capped chickadees processing both absolute and relative pitch information in their songs, but they were doing so in a way that led to different classes of behavioral responses depending on the type and magnitude of frequency deviations.

Based on the results of previous bioacoustic analyses and playback studies on pitch ratio perception (discussed above), Shackleton *et al.* (1992) investigated a more subtle pitch change in the chickadee song, the small but reliable pitch change of about 200 Hz over their approximately 400 ms duration of the *fee* note, the glissando (Fig. 10.1). Testing whether the glissando was either perceptible or meaningful to the birds in species recognition poses a slight methodological challenge. This must be done by creating or finding a *fee* note with little or no pitch change over the course of the note. This problem was overcome through the use of synthetic songs of three varieties. Normal "songs" had a typical pitch change from the start to the end of the *fee* (i.e. a glissando) and from the end of the *fee* to the start of the *bee*. The alternative "songs" were of two types: one started and ended on the same pitch as normal *fee* notes started, with no pitch change across the note (i.e. no glissando) while the other type started on the pitch of the end of normal *fee* notes, also with no pitch change across the note. The result was not only a comparison of the effect of pitch changes in the *fee* note, but was also a test of the consequence of the manipulations. The pitch ratio between the two notes was also tested, with the first alternative "song" having a larger than normal ratio and the second having a normal ratio.

Altering the pitch ratio of the *fee* note had a significant effect on the birds' behavior. Birds were significantly less likely to approach the speaker or to emit vocalizations upon hearing either of the two altered versions of song. Therefore, even subtle deviations in the relative pitch structure of chickadee song had serious implications for behavioral responses. The question that then arose from this work was what role in particular did this small but reliable pitch drop in the *fee* note play in species recognition? One possibility was that this was used as a cue for distance estimation, as the higher frequencies at the start of the *fee* note would be expected to degrade more rapidly over distance than the lower pitched remainder of the note. Thus, the pitch change would conceivably become muted at longer distances, an idea that was tested directly by Fotheringham and Ratcliffe (1995).

Fotheringham and Ratcliffe (1995) conducted a two-part field study that included both a transmission/recording component and a playback component. Black-capped chickadee songs were broadcast in both open and forested environments and then re-recorded at a number of distances. Various acoustic measures were then taken to estimate the effect that propagation over distance had on song features. Specifically, they were investigating whether the initial portion of the *fee* note would be differentially degraded compared with the rest of the *fee* note. If this were the case, the behavioral responses observed by Shackleton *et al*. could be accounted for by distance estimation. If not, the conclusion was likely that birds used the pitch ratio in the *fee* note as a species marker. Bioacoustic analyses, combined with playback results indicating that chickadees did not respond differentially to degraded and non-degraded songs when equalized for playback amplitude, were unequivocal; the glissando in the *fee* note appears to serve, as does the pitch ratio between the *fee* end and *bee* start, as a species marker in black-capped chickadee songs.

In addition to the pitch change in the *fee* note and the pitch ratio between *fee* and *bee* notes being species markers, more recent research has indicated a number of other key findings with respect to other aspects of signaling. First, not only are the fine acoustic features in song relatively unaffected by distance (Christie *et al*. 2004a), as was seen for the glissando, but there are individually identifiable features within the song that remain even after degradation over distance. Moreover, the ability of a particular male to produce a reliable pitch ratio is related to male quality, and can be used by females to choose a high quality mate (Christie *et al*. 2004b).

10.2.2.2 Operant conditioning experiments of song perception

While field studies are essential to understanding the puzzle that is chickadee communication, they can not ask or answer all research questions. Furthermore, it is not always feasible or even possible to test some hypotheses through the use of field experimentation. For example examining details of the fundamental perceptual grouping mechanisms underlying song perception and species-recognition, or the comparative perception of signals by birds raised under different developmental conditions, are best conducted via laboratory-based, operant conditioning techniques.

Results of playback studies indicated that chickadees were attentive to both absolute and relative pitch cues in their songs, but the types of responses to these cues varied. To assess song perception on a more detailed and controlled level, Weary and Weisman (1991) conducted an operant discrimination experiment to determine the role of relative pitch cues in the discrimination and generalization of chickadee song.

In the first of two experiments, stimulus songs were constructed from a sample of natural songs. Positive, or food-rewarded songs, were those that had a near-normal pitch ratio of 1.12. Negative, or non-food-rewarded songs, were those with a larger or smaller than normal pitch ratio. Once training was complete and male chickadees showed significant learning and steady-state discrimination performance, they were tested with novel songs. These songs were composed in the same manner as training songs, with some having normal and others having abnormal intervals. Surprisingly, birds did not transfer their training neatly to those novel songs with normal pitch ratios. Instead, there appeared to be a strong absolute pitch component to the discrimination, with birds allocating more responses to test songs that had similar starting pitches to rewarded training songs. The fact that birds attended to absolute pitch in their songs was not entirely surprising, as previous studies had shown that it did indeed have a role in song perception. What was surprising was that birds attended to this cue even when they were explicitly trained to attend to relative pitch. A follow-up experiment was carried out that, instead of using natural songs as discriminative stimuli, used wholly synthetic songs. The results of this study were more in line with expectations—birds did in fact attend to relative pitch cues, but there was still a strong influence of absolute pitch in their results.

Because of the influence of absolute pitch cues in the perception of relative pitch cues seen in Weary and Weisman's work with natural or synthetic songs, Njegovan and Weisman (1997) adopted a different approach to further understanding the mechanisms of song perception. For their design, Njegovan and Weisman used as their stimuli-of-choice pure sine wave pairs that approximated the acoustic parameters of normal songs. In common with Weary and Weisman, Njegovan and Weisman trained birds to discriminate between rewarded tone pairs with a frequency ratio equal to that seen in the wild (a ratio of 1.12) and non-rewarded tone pairs with one of two ratios not seen in nature (ratios of 1.00 and 1.24). Njegovan and Weisman went further still—if birds were actually using the pitch ratio as a mechanism of determining whether a song is produced by a black-capped chickadee or not, then it stands to reason that this task should be accomplished quickly. One way that this could be done is if birds treated pitch relations between notes as perceptual categories. To determine whether this was indeed the case, Njegovan and Weisman used a "pseudo" category discrimination where rewarded stimuli were selected at random and had no common pitch relationships (i.e. the rewarded stimuli were not united by a common 1.12 frequency ratio). In this way they could determine whether birds were treating pitch ratios as perceptual categories. If they were, the true category discrimination would be performed much more rapidly. If not, there would be no difference between the two discriminations.

Njegovan and Weisman also tested black-capped chickadees that had been hand-reared in the absence of song stimuli on this discrimination. Since at least the 1950s and the pioneering work of Thorpe and Marler (e.g. Thorpe 1958; Marler, 1970), it had been clear that young songbirds needed to hear an adult conspecific if they were to develop normal song. This has been shown in a variety of species, including black-capped chickadees (Shackleton and Ratcliffe 1993). One of the main failures in hand-reared black-capped chickadee song is the lack of normal relative pitch cues seen reliably in the songs of normal, wild-caught birds. The logic, therefore, for including hand-reared birds in the frequency ratio discrimination was simple: birds that had not learned to produce or been exposed to normal relative pitch cues in song may be at a perceptual disadvantage when asked to perform a discrimination that is based on this feature.

The results of Njegovan and Weisman were clear cut. Normal birds learned the true category discrimination, that is the discrimination where all normal tone pairs were rewarded, much more quickly than the pseudo-category discrimination, where rewarded tone pairs were selected at random. The implication is that birds can use perceptual grouping mechanisms to quickly ascertain whether a particular tone pair matches a particular relative frequency ratio and then act accordingly. A further implication, of course, is that they could use just such a mechanism in the wild to quickly and efficiently determine whether a song is produced by a black-capped chickadee or not.

The second main finding of Njegovan and Weisman was also very clear. Birds that were hand-reared in the laboratory, without exposure to normal song, did not perform nearly as well as wild-caught birds on the true category discrimination. In fact, even when given significantly more training than normal birds, hand-reared chickadees could not even approximate performance by normal birds. This finding raised the possibility, which has been confirmed in other species with other acoustic discrimination tasks, that songbirds need exposure to adults during development not only to learn to produce species-typical song, but also to perceive song accurately.

10.3 Call production and perception

10.3.1 Call production

Of all chickadee vocalizations, probably their most well known is the species *chick-a-dee* call (Fig. 10.2). This call, especially in black-capped chickadees, has been exceedingly well studied in a formal sense

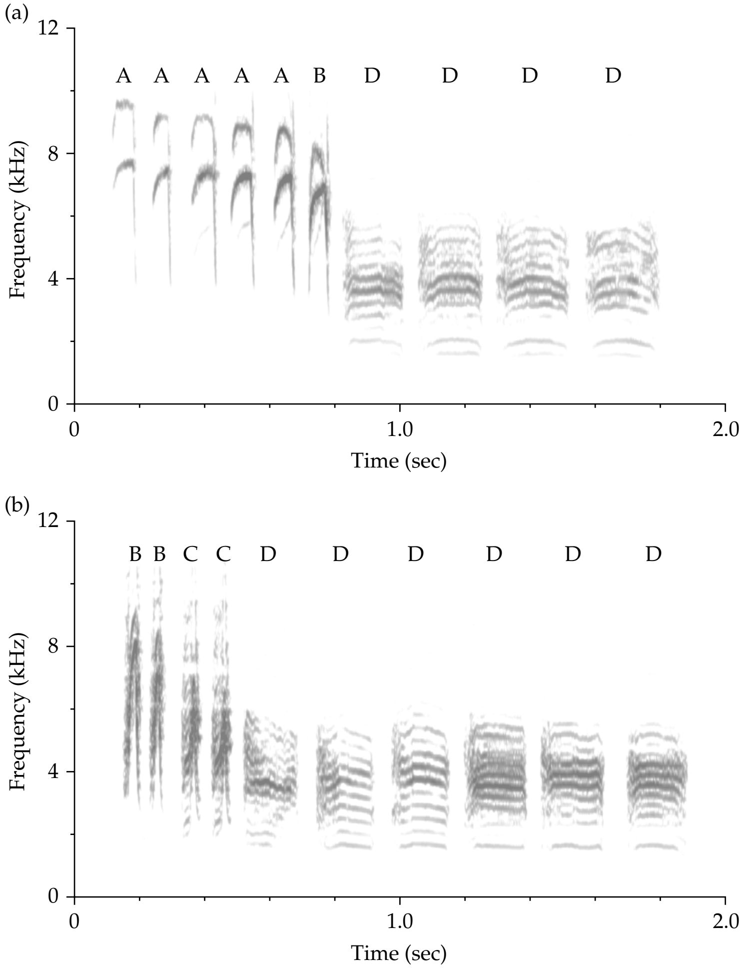

Figure 10.2 Two representative *chick-a-dee* calls with note types **AAAAABDDDD** (a) and **BBCCDDDDDD** (b). Spectrogram settings: Hanning window, 512 points. Time (sec) is on the x axis and frequency (kHz) is on the y axis in both spectrograms.

since about the early to mid 1970s. A description of the call and its usage by Ficken *et al*. (1978) still stands as a benchmark study. As they and others have noted (e.g. Odum 1942; Saunders 1951), the call is produced all year by both sexes and is composed of four note types; A, B, C, and D. It is used as a social signal to co-ordinate flock movements and to indicate mild alarm. Recently it has been further demonstrated that the note type composition, specifically the number of D notes, of this call varies depending on the degree of perceived threat (Templeton *et al*. 2005).

During the winter months, chickadees form flocks of between four and 12 birds that defend a group foraging territory. One question that arose from early observational work was by what mechanism did birds recognize the calls of their flock-mates? Classic work by Mammen and Nowicki (1981) investigated this issue by conducting an acoustic analysis of the *chick-a-dee* call from free-ranging flocks, and comparing these measures among flocks. The results of this initial analysis demonstrated that one of the mechanisms whereby birds were able to recognize flock-mates was through flock-specific convergence of their *chick-a-dee* calls, specifically via a convergence of D note acoustics. Mammen and Nowicki then captured these wild flocks and formed *ad hoc* artificial flocks in aviaries. After 1 month, call convergence was observed on the same acoustic features posited to control flock recognition from the field analyses.

These initial observational and experimental studies of call convergence were completed by a final study from Nowicki (1989), who examined in detail both the nature and speed with which these acoustic changes occurred in wholly artificial flocks. This final study allowed for analysis of the precise acoustic features—namely the first and second frequency components in D notes, and, to a lesser degree, the total frequency bandwidth of D notes—that control flock identity. Moreover, Nowicki showed that no one bird controlled the convergence and that the pattern of convergence observed was not determined by dominance relationships (i.e. the flock did not converge on the acoustic structure of the dominant bird). Rather, birds modify the acoustic properties of their D notes to converge on a common mean and did so within about 1 week. Taken together, these results gave insight into the mechanisms of call production and a possible acoustic basis of flock recognition.

Several studies of *chick-a-dee* call production conducted by Jack Hailman and colleagues (e.g. 1985, 1986, 1987) have lead to an amazing understanding of other aspects of this ubiquitous call, that is the call variety, call syntax, and call note-type composition. One early finding was that the note types of which the call is composed seem to form a graded continuum, from A→ B→ C→ D, with As gradually becoming Bs and so on. Hailman and others also demonstrated that the call follows strict syntactical rules, with A notes always preceding B notes, always preceding C notes, always preceding D notes. This set of syntactical rules, combined with the fact that the variety of call types produced is seemingly endless, makes the chickadee call system one of the most complicated non-human animal signaling systems ever described. In fact, Hailman and others also proposed that the call's meaning could vary with the note-type composition and the context in which it is used.

Other more recent bioacoustic and playback studies, many of which are discussed in Chapter 13, tested these assumptions derived from research on black-capped chickadees directly in Carolina chickadees and have shown that Carolina chickadees do respond differentially depending on note-type composition of calls. These findings, combined with those of Nowicki and Mammen discussed above, along with the more recent findings of Templeton *et al*. (2005), clearly point to the fact that this is a sophisticated call system that we are still trying to fully understand. That said, in order for any of the research on call note composition etc. to be reliable, one must be able to confidently assign the notes produced in this call into types or classes. This problem of defining natural categories has been around for as long as acoustic signals have been studied scientifically, and has been the topic of much debate (see Marler, 1982 and Hauser, 1996 for extensive discussions of this problem). It is to this area, with specific reference to the *chick-a-dee* call that we now turn.

One of the first steps in analyzing any vocalization is reducing the chaos that naturally occurs in biological signals into workable units. This reductionism requires sorting large numbers of events into a few manageable types. For the black-capped chickadee call this was relatively straight forward. Ficken *et al*. (1978) labeled four obvious notes types, based on their distinct acoustic structures, A through D.

Nowicki and Nelson (1990) revisited the note-type classification in the chickadee call by contrasting several classification methods in an attempt to determine the reliability, and to some degree the validity, of this classification scheme. Multidimensional scaling, k-means cluster analysis and visual classification techniques lead to reliable and converging classifications. Recent work from our laboratory (Dawson *et al*. 2006) has found similar results using both artificial neural networks and linear discriminant analyses. An open question that numerous researchers, including Hailman and Nowicki and Nelson, have pointed out is that such human-based classifications need to be verified by the animals that produce the vocalizations being classified. Just such studies are described in the following section on call perception.

Charrier *et al*. (2004) set out to conduct a similar analysis of the *chick-a-dee* call of the black-capped chickadee with three main goals. The first goal was to provide a detailed acoustical account of the call and its note types. The second goal was to determine which features, in which note types, had potential individual markers. The third goal was to determine the acoustic features that were responsible for distinguishing among the various note types.

When Charrier *et al*. (2004) analyzed the call notes for individualized features, several of the acoustic features had the potential to identify individual birds. That is, the between-bird variability on several features was larger than the within-bird variability, making it theoretically possible for birds to identify individuals on the basis of these acoustic features. Of the four note types, C notes had the greatest potential for individual identity; support for the special status of C notes was observed by Freeberg and Lucas (2002) who demonstrated clearly that Carolina chickadees responded differentially to calls with or without C notes.

Interestingly, when the features that could be used for note-type identification were examined, some clear winners emerged. Specifically, starting frequency and the ascending frequency modulation of notes was found to be the most distinctive among all note types, and therefore likely to play an important role in note-type discrimination and classification. Just how much of a role would be determined in an operant discrimination task, as described in the following section.

10.3.2 Call perception

As well as a significant body of work on call production, there is a growing understanding of call perception, both from playback studies and operant conditioning experiments. Playback experiments have been aimed at a variety of issues, including identification of species and flock through the chickadee call. Operant conditioning experiments have been aimed at related topics of inquiry including species classification and discrimination of different species' *chick-a-dee* calls, note-type categorization, and the mechanisms of note-type discrimination. We will deal with research from field playback designs first, followed by research from operant conditioning designs.

10.3.2.1 Playback studies of call perception

Acoustic analyses of field and laboratory recordings (Mammen and Nowicki 1981; Nowicki 1989, discussed above) discovered acoustic features that could potentially identify flocks on the basis of their *chick-a-dee* calls. In an experimental test of flock identification, Nowicki (1983) examined whether birds discriminate their own flocks' calls from those of others, and also whether they respond aggressively to non-flock-mates' calls. To investigate these questions, Nowicki broadcast resident and foreign flocks' calls to resident chickadee flocks while they were foraging. The results were unambiguous; when chickadees heard playbacks of their own flocks' *chick-a-dee* calls, they continued to forage and did not engage in any calling behavior above baseline levels. Alternatively, playbacks of foreign calls led to significant decreases in foraging behavior and significant increases in chickadee calling. This study provides the functional basis for call convergence and clearly demonstrates that chickadees are not only attending to the macroacoustical characteristics in their calls, but also the microacoustical characteristics.

While the studies of Nowicki and Mammen described above clearly showed how chickadees react to a foreign flock's calls, an unresolved question remained: what is a *chick-a-dee* call? Put another way, what particular acoustic features are chickadees attending to that allow them to identify the call as species specific? As obvious as this question seemingly is, it had not been tackled until recently (Charrier and Sturdy 2005). In contrast to the *fee-bee* song that was more easily paramatized and the putative relevant features identified and tested, the *chick-a-dee* call is highly complex with multiple parameters that may function in or aid species recognition. Based on a detailed bioacoustic analysis already described (Charrier *et al*. 2004), Charrier and Sturdy set out to test the limits of species recognition via *chick-a-dee* calls using a field playback design.

To accomplish this, several stimuli were constructed, including broadband noise signals, pitch shifted calls, and calls in which the tempo had been increased or decreased. Several signals were responded to significantly less compared to normal chickadee calls, including the negative control gray-crowned rosy-finch (*Leucosticte tephrocotis*) calls, synthetic stimuli, and manipulated natural calls, white noise calls, calls that were delivered at a slower tempo than normal, calls that were time reversed, as well as those in which the typical syntax was reversed. Moreover, in common with research conducted on song, birds also responded less vigorously to *chick-a-dee* calls that were shifted up and down in frequency. Interestingly, the responsiveness to frequency-shifted calls was not symmetrical, with those shifted up by either 500 Hz or 1000 Hz or shifted down by 500 Hz not treated differently than normal calls, whereas or those shifted down by 1000 Hz were treated as different from normal calls. Another unexpected finding was that calls in which the amplitude modulation was removed elicited less response than normal calls, suggesting that in contrast to many other species tested, amplitude modulation may play a role in species recognition in black-capped chickadees. Taken together, the acoustic properties that appear to control species recognition in chickadee calls appear in many ways to parallel those documented for species recognition via song, with some important caveats that will be the subject of future research.

10.3.2.2 Operant conditioning studies of call perception

While research on call perception in the field has dealt mainly with large-scale issues of flock and species recognition, research in the laboratory has the ability and control to study finer-scale issues of the mechanisms of call perception (but see Clucas *et al*. 2004 and Chapter 13 for a recent change in this trend). In particular, one of the outstanding issues in the area of chickadee call perception is the classification of call notes into types. Typically, the classification is done by humans and is based either on visual sorting of sound spectrograms or analyses of note features taken from sound spectrogram measurements. However, whether the birds that produce these calls perceive the same note types as humans and statistical techniques needs to be verified by testing the birds that produce the vocalizations that are classified.

To begin to answer this question, Sturdy *et al*. (2000) trained black-capped chickadees to discriminate among their call-note categories in an operant discrimination task. The goals of this task were twofold. The first goal was to determine whether the birds perceived the note-type categories of bioacousticians as such. The second related goal was to determine the mechanism behind call-note perception. Earlier work (Sturdy *et al*. 1999a), also using operant conditioning techniques, found that zebra finches' (*Taeniopygia guttata*) perception of their song notes agreed with human-based classification methods of these notes (Sturdy *et al*. 1999b). It also showed, through the use of transfer tests, that zebra finches perceived their song notes as natural, open-ended categories. This suggested that songbirds use this fundamental perceptual mechanism of treating similar but discriminable auditory objects as classes, to perceive the building blocks of their vocalizations.

Black-capped chickadees agree with human classification and use open-ended categorization to perceive their call-note types. Birds learned to discriminate among the four call-note types, and along the way, provided clues to support the open-ended categorization hypothesis. First, birds were slower to learn the within-category discrimination than the between-category discrimination. This provides clear evidence that note types within a class (defined by humans) were more similar than those among classes. Second, birds showed strong transfer of inhibition (i.e. generalization) from unrewarded, between-category note types used in discrimination training to novel notes from these same note categories during reversal training; this in spite of the fact that these note types were now rewarded (i.e. the contingencies were reversed relative to during discrimination training). Finally, when birds were exposed to previously unrewarded notes following a period of retraining with rewarded notes from those same classes, they based their responding on the contingencies most recently in effect. This last evidence provided the strongest test of transfer of training and, taken together, these results suggested that birds did agree with human sorters and used open-ended categorization as a perceptual mechanism to perceive their note types.

Interestingly, an analysis of errors lent support for an earlier observation of Hailman (Hailman *et al*. 1985); he suggested that chickadee call-note types formed a continuum from A → D notes, with each note type "grading" into the next. By inspecting how birds responded to non-rewarded notes, Sturdy *et al*. (2000) were able to show that in fact birds were more likely to confuse adjacent note types (e.g. A with B) than they were non-adjacent note types (e.g. A with C). But how was this accomplished? What features were birds using to discriminate among their call-note types?

Bioacoustic analyses by Charrier *et al*. (2004) identified some acoustic features, namely that start frequency and the initial ascending portion of notes, that are more variable between note types than within note types and are therefore likely to contribute to note-type discrimination and classification. To determine the extent to which these features were in play, Charrier *et al*. (2005) trained birds to discriminate adjacent note types (e.g. **A+/B-**, **A-/B+**; see Fig. 10.2 for example note types) and then tested them with novel, altered notes. Test stimuli consisted of notes that were linearly shifted either up or down in pitch by 0.5 SD steps, or "cut" notes, with only the first or the second half presented. The results of the test sessions were striking. Birds altered their response based on the pitch of the note; when A notes were reduced in pitch and therefore made more B-note like, birds responded to them as if they were B notes, and *vice versa* for B notes shifted up in pitch to be made more A-note like. The same was true for B versus C notes. Furthermore, birds could generally maintain their discrimination using only the ascending portion of the note whereas the descending portion of the notes was not sufficient to maintain discrimination performance. Whether, and to what extent, other acoustic features in call notes control discrimination and categorization remains to be determined. The results from Charrier *et al*. (2005), however, showed a role for frequency and initial frequency modulation in note perception and provide another example of how a solid understanding of a signal can drive research into the perception of the same.

While laboratory studies are ideal for studying fine-grained problems of vocal perception, more holistic questions can also be dealt with quite effectively. In a series of two operant conditioning experiments, Bloomfield *et al*. (2003) and L. L. Bloomfield and C. B. Sturdy (unpublished data), extended the initial findings of Sturdy *et al*. (2000) for open-ended classification of call-note types to species classification of *chick-a-dee* calls. Specifically, Bloomfield and colleagues trained chickadees (black-capped only, 2003; black-capped and mountain chickadees, unpublished data) to discriminate and classify both their own and other species' *chick-a-dee* calls to determine: first, to what degree birds could perform the task with their own and other species calls; and second, whether birds treated these higher-level species categories in an open-ended way as they did for lower-level note-type categories. Results of these studies paralleled those of Sturdy *et al*. (2000), with clear evidence through transfer and propagation tests that chickadees classified species based on their *chick-a-dee* call. Taken together, the results of both the low-level note-type classification and the high-level species classification tasks point to a general perceptual mechanism driving discrimination and classification, much in the same way as relative pitch perception drove song perception as described earlier in this chapter.

10.4 Summary and future directions

Our understanding of vocal communication in the North American chickadees has continued to grow over the last 35 plus years, with more research being added each year. This has greatly increased our knowledge not only of how chickadees use acoustic communication, but has also provided more general insights into communication in songbirds and in other animal group as well. One of the reasons, we believe, for the success that this field has seen is due in large part to the reliance on complimentary and integrative studies of vocal production and perception using a variety of techniques in the field and in the laboratory. Much has been learned about chickadee production and perception, and, importantly, the growth of this knowledge has occurred in tandem. That is, production research has been followed with research aimed at understanding the perception of features elucidated in the studies on production.

This general approach has also been profitable in the understanding of one of the chickadee's European relatives, the great tit. Weary and McGregor and colleagues (Falls *et al*. 1982; McGregor and Avery 1986; Weary *et al*. 1990; Weary and Krebs 1992; Weary 1989, 1990, 1991), in a series of studies of song production and perception, have produced similar insights as those described above for the vocalizations of the black-capped chickadee. For example, in common with the results of Charrier *et al*. (2005) for note-type perception in black-capped chickadees, Weary (1990), also using an operant conditioning task, found that great tits relied mainly on note frequency, and far less on other acoustic parameters, when classifying their note types. Also in common with findings for the individualization of black-capped chickadee *fee-bee* song and *chick-a-dee* calls (Christie *et al*. 2004a; Weisman *et al*. 1990; Charrier *et al*. 2004), great tits produce individualized songs, accomplished in part via the production of individual-specific song types (Weary *et al*. 1990). In addition, great tit songs contain cues to individual recognition, and great tits can use the individual voice characteristics contained in their songs to recognize individuals (Weary and Krebs 1992). This suggests that great tits can form an open-ended category for each individual male into which novel songs can be assigned, highly similar to that observed by Phillmore *et al*. (2002) for black-capped chickadees. Although the studies just described provide wonderful complementary evidence to those conducted on North American chickadees, there are many tit species that remain to be explored and tested if we are to come to a more extensive comparative understanding of Parid communication in general. This is not only true of tits, but it is also relevant in North America, where the majority of studies have focused on chickadee species and largely ignored titmice, leaving a further void in our understanding. Further research into vocal production and perception for chickadees, tits and titmice is sure to add even more to our understanding of Parid communication and perception.

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The authors dedicate this chapter to Ron Weisman: mentor, collaborator, and friend.

References

Bloomfield, L. L., Sturdy, C. B., Phillmore, L. S., and Weisman, R. G. (2003). Open-ended categorization of *chick-a-dee* calls by black-capped chickadees (*Poecile atricapilla*). *Journal of Comparative Psychology*, **117**, 290–301.

Catchpole, C. K. and Slater, P. J. B. (1995). *Bird Song: Biological Themes and Variations*. Cambridge University Press, Cambridge, UK.

Charrier, I. and Sturdy, C. B. (2005). Call-based species-recognition in Black-capped chickadees. *Behavioral Processes*, **70**, 271–281.

Charrier, I., Bloomfield, L. L., and Sturdy, C. B. (2004). Note types and coding in parid vocalizations. I: The *chick-a-dee* call of the black-capped chickadee (*Poecile atricapillus*). *Canadian Journal of Zoology*, **82**, 769–779.

Charrier, I., Lee, T.-Y., Bloomfield, L. L., and Sturdy, C. B. (2005). Acoustic mechanisms of note-type perception in Black-capped chickadees. *Journal of Comparative Psychology*, **119**, 371–380.

Christie, P. J., Mennill, D. J., and Ratcliffe, L. M. (2004a). Chickadee song structure is individually distinctive over long broadcast distances. *Behavior*, **141**, 101–124.

Christie, P. J., Mennill, D. J., and Ratcliffe, L. M. (2004b). Pitch shifts and song structure indicate male quality in the dawn chorus of black-capped chickadees. *Behavioral Ecology and Sociobiology*, **55**, 341–348.

Clucas, B. A., Freeberg, T. M., and Lucas, J. R. (2004). Chick-a-dee call syntax, social context, and season affect vocal responses of Carolina chickadees (*Poecile carolinensis*). *Behavioral Ecology and Sociobiology*, **57**, 187–196.

Dawson, M. R. W., Charrier, I., and Sturdy, C. B. (2006). Using an artificial neural network to classify note types in the '*chick-a-dee*' call of the black-capped chickadee (*Poecile atricapillus*). *Journal of the Acoustical Society of America*, **119**, 3161–3172.

Dwight, J. (1897). The whistled call of *Parus atricapillus* common to both sexes. *Auk*, **14**, 99.

Falls, J. B., Krebs, J. R., and McGregor, P. K. (1982). Song matching in the great tit (*Parus major*): the effect of similarity and familiarity. *Animal Behaviour*, **30**, 997–1009.

Ficken, M. S. (1981). What is the song of the black-capped chickadee? *Condor*, **83**, 384–386.

Ficken, M. S., Ficken, R. W., and Witkin, S. R. (1978). Vocal repertoire of the black-capped chickadee. *Auk*, **95**, 34–48.

Fotheringham, J. R. and Ratcliffe, L. (1995). Song degradation and estimation of acoustic distance in black-capped chickadees (*Parus atricapillus*). *Canadian Journal of Zoology*, **73**, 858–868.

Freeberg, T. M. and Lucas, J. R. (2002). Receivers respond differently to *chick-a-dee* calls varying in note composition in Carolina chickadees (*Poecile carolinensis*). *Animal Behaviour*, **63**, 837–845.

Hailman, J. P. and Ficken, M. S. (1986). Combinatorial animal communication with computable syntax: *chick-a-dee* calling qualifies as 'language' by structural linguists. *Animal Behaviour*, **34**, 1899–1901.

Hailman, J. P., Ficken, M. S., and Ficken, R. W. (1985). The '*chick-a-dee*' calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English. *Semiotica*, **56**, 191–224.

Hailman, J. P., Ficken, M. S., and Ficken, R. W. (1987). Constraints on the structure of combinatorial '*chick-a-dee*' calls. *Ethology*, **75**, 62–80.

Hauser, M. D. (1996). *The Evolution of Communication*. MIT Press, MA.

Mammen, D. L. and Nowicki, S. (1981). Individual differences and within-flock convergence in chickadee calls. *Behavioral Ecology and Sociobiology*, **9**, 179–186.

Marler, P. R. (1970). A comparative approach to vocal learning: song development in white-crowned sparrows. *Journal of Comparative Physiological Psychology Monographs*, **71**, 1–25.

Marler, P. R. (1982). Avian and primate communication: The problem of natural categories. *Neuroscience and Biobehavioral Reviews*, **6**, 87–94.

Maynard-Smith, J. and Harper, D. (2003). *Animal Signals*. Oxford University Press, NY.

McGregor, P. K. and Avery, M. I. (1986). The unsung songs of great tits (*Parus major*): Learning neighbours' songs for discrimination. *Behavioral Ecology and Sociobiology*, **18**, 311–316.

Njegovan, M. and Weisman, R. G. (1997). Pitch discrimination in field- and isolation-reared black-capped chickadees (*Parus atricapillus*). *Journal of Comparative Psychology*, **111**, 294–301.

Nowicki, S. (1983). Flock-specific recognition of chickadee calls. *Behavioural Ecology and Sociobiology*, **12**, 317–320.

Nowicki, S. (1989). Vocal plasticity in captive black-capped chickadees: the acoustic basis and rate of call convergence. *Animal Behaviour*, **37**, 64–73.

Nowicki, S. and Nelson, D. A. (1990). Defining natural categories in acoustic signals: comparison of three methods applied to '*chick-a-dee*' call notes. *Ethology*, **86**, 89–101.

Odum, E. P. (1942). Annual cycle of the black-capped chickadee-3. *Auk*, **59**, 499–531.

Phillmore, L. S., Sturdy, C. B., Turyk, M. R., and Weisman, R. G. (2002). Discrimination of individual vocalizations by black-capped chickadees (*Poecile atricapilla*). *Animal Learning and Behaviour*, **30**, 43–52.

Ratcliffe, L. and Weisman, R. G. (1985). Frequency shift in the *fee-bee* song of the black-capped chickadee. *Condor*, **87**, 555–556.

Ratcliffe, L. and Weisman, R.G. (1986). Song sequence discrimination in the black-capped chickadee (*Parus atricapillus*). *Journal of Comparative Psychology*, **100**, 361–367.

Ratcliffe, L. and Weisman, R. G. (1988). Representation of conspecific song by chickadees: comparisons among embedded '*fee-bees*'. *Behavioural Processes*, **17**, 199–203.

Saunders, A. A. (1951). *A Guide to Bird Songs*. Country Life Press, NY.

Shackleton, S. A. and Ratcliffe, L. (1993). Development of song in hand-reared black-capped chickadees. *Wilson Bulletin*, **105**, 637–644.

Shackleton, S. A., Ratcliffe, L., and Weary, D. M. (1992). Relative frequency parameters and song recognition in black-capped chickadees. *Condor*, **94**, 782–785.

Sturdy, C. B, Phillmore, L. S., Price, J. L., and Weisman, R. G. (1999a). Song-note discrimination in zebra finches (*Taeniopygia guttata*): Categories and pseudocategories. *Journal of Comparative Psychology*, **113**, 204–212.

Sturdy, C. B., Phillmore, L. S., and Weisman, R. G. (1999b). Note types, harmonic structure, and note order in the songs of zebra finches (*Taeniopygia guttata*). *Journal of Comparative Psychology*, **113**, 194–203.

Sturdy, C. B., Phillmore, L. S., and Weisman, R. G. (2000). Call-note discriminations in black-capped chickadees (*Poecile atricapillus*). *Journal of Comparative Psychology*, **114**, 357–364.

Templeton, C. N., Green, E., and Davis, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. *Science*, **308**, 1934–1937.

Thorpe, W. H. (1958). The learning of song patterns by birds, with special reference to the song of the Chaffinch *Fringilla coelebs*. *Ibis*, **100**, 535–570.

Weary, D. M. (1989). Categorical perception of bird song: how do great tits (*Parus major*) perceive temporal variation in their song? *Journal of Comparative Psychology*, **103**, 320–325.

Weary, D. M. (1990). Categorization of song notes in great tits: which acoustic features are used and why? *Animal Behaviour*, **39**, 450–457.

Weary, D. M. (1991). How great tits use song-note and whole-song features to categorize their songs. *Auk*, **108**, 187–190.

Weary, D. M. and Krebs, J. R. (1992). Great tits classify songs by individual voice characteristics. *Animal Behaviour* **43**, 283–287.

Weary, D. M. and Weisman, R. G. (1991). Operant discrimination of frequency and frequency ratio in the black-capped chickadee (*Parus atricapillus*). *Journal of Comparative Psychology*, **108**, 253–259.

Weary, D. M., Norris, K. J., and Falls, J. B. (1990). Song features birds use to identify individuals. *Auk*, **107**, 623–625.

Weisman, R., Ratcliffe, L., Johnsrude, I., and Hurly, T. A. (1990). Absolute and relative pitch production in the song of the black-capped chickadee. *Condor*, **92**, 118–124.

Weisman, R. G. and Ratcliffe, L. (1989). Absolute and relative pitch processing in black-capped chickadees, *Parus atricapillus*. *Animal Behaviour*, **38**, 685–692.