

# Behavioral aspects of chickadee hybridization

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## 7.1 Introduction

Within the Paridae, hybridization is known to occur regularly in a few pairs of sibling species and sporadically between other taxa of varying degrees of evolutionary proximity (Harrap and Quinn 1995; Curry 2005). Interbreeding of black-capped chickadees and Carolina chickadees represents a unique situation in the family in that although these congeners are not each other's closest relatives (Gill *et al.* 2005), they nonetheless hybridize regularly: observations consistent with interbreeding have been reported from numerous locations along their predominantly east–west line of parapatric contact stretching from central New Jersey to south-eastern Kansas, with a dip southward in the Appalachian Mountains to western North Carolina (reviewed by Bronson *et al.* 2005; Curry 2005). Hybridization between black-capped and Carolina chickadees has been investigated most recently in Ohio, where both observational and experimental evidence have documented reduced reproductive success associated with interbreeding (Bronson *et al.* 2003a, 2005), and in Pennsylvania (Reudink *et al.* 2006).

Production of hybrids can result from either reproduction by mixed pairs or extrapair copulation involving heterospecific individuals. On a proximate level, heterospecific mating is likely to be facilitated by sexual imprinting: if individuals are exposed during development to adults or nest-mates of another species, they may develop preferences for mates of that species (Grant and Grant 1997; Irwin and Price 1999; ten Cate and Vos 1999). Additionally, exposure to heterospecifics in a zone

of contact may cause abnormal development of courtship displays such that individuals consequently produce mixed signals, or only those characteristic of another species. Even if normal mate preferences determine mating, hybridization can result if individuals produce displays that incorrectly signal their own identity.

In many songbirds, females base species recognition and mate choice in large part on songs and calls (Nowicki and Searcy 2005). Unlike morphology, vocal traits may be vulnerable to misimprinting because development of songs and calls frequently involves learning, including exposure to sounds during an early critical period. To understand mechanisms of hybridization in any songbird system, it is therefore worthwhile to examine the extent to which males within contact zones produce vocalizations that reflect their own genetic identity, and the ways in which females respond to these signals.

In this chapter, we summarize information from our studies of the hybrid zone between black-capped and Carolina chickadees in south-eastern Pennsylvania. Our focus is on patterns of vocal variation in relation to among- and within-population genetic variation. Primary questions we address include: (1) What song and call types are produced within this hybrid zone? (2) Are the vocalization types congruent with one another within individuals? (3) What insights might we derive from these patterns regarding mechanisms of hybridization in chickadees? We then review available information, and opportunities for further research, concerning patterns and mechanisms of hybridization among Parids of both North America and Eurasia.

## 7.2 Background and methods

Black-capped and Carolina chickadees are morphologically and ecologically similar. Black-capped chickadees, which inhabit much of Canada and the northern tier of the USA, have been studied extensively in Massachusetts, Ontario, and elsewhere (Smith 1993; see also this volume, Chapters 9, 12, and 14). Carolina chickadees, which are resident throughout the south-eastern USA, have been studied less overall (Mostrom *et al.* 2002) but have been the subjects of recent research, particularly on vocalizations (e.g. Chapter 13).

A prominent feature of chickadee behavior is the production of whistled song by males, mainly just prior to and during the breeding season (Hailman and Ficken 1996; Chapter 14). Development of the whistled *fee-bee* of the black-capped chickadee, despite a high degree of stereotypy across its extensive geographic range (Kroodsma *et al.* 1999), appears to involve learning (Kroodsma *et al.* 1995; Baker *et al.* 2003). Pitch characteristics appear relevant for species identification (Weisman and Ratcliffe 1989; Chapter 10). Song repertoires in Carolina chickadees are broader, with most males producing two general song types: a four-note song involving alternating high and low notes (*see-bee-see-bay*) and an song incorporating one or more high notes followed by variable numbers of lower notes (e.g. *see-see-bay-bay-bay*; Smith 1972; see also Fig. 4C in Ward and Ward 1974). Geographic variation in Carolina chickadee song is more pronounced (Ward 1966; Mostrom *et al.* 2002).

Both species also produce a wide variety of calls (Hailman and Ficken 1996). The *chick-a-dee* call, used throughout the year in pair and flock interactions and during predator mobbing, has been studied in depth (Chapter 13). Another complex vocalization, the *gargle* call, has been examined in black-capped chickadees (Chapter 11) and has been described in Carolina chickadees (Mostrom *et al.* 2002), but detailed interspecific comparisons of the call, which is used in aggressive interactions, are lacking.

Unusual vocal patterns, including bilingual singing, have been documented frequently among chickadees within or close to the presumed contact zone (e.g. Johnston 1971; Robbins *et al.* 1986). In Missouri populations shown to include hybrid individuals based on genetic analysis (Braun and Robbins 1986; Sawaya 1990), songs are intermediate

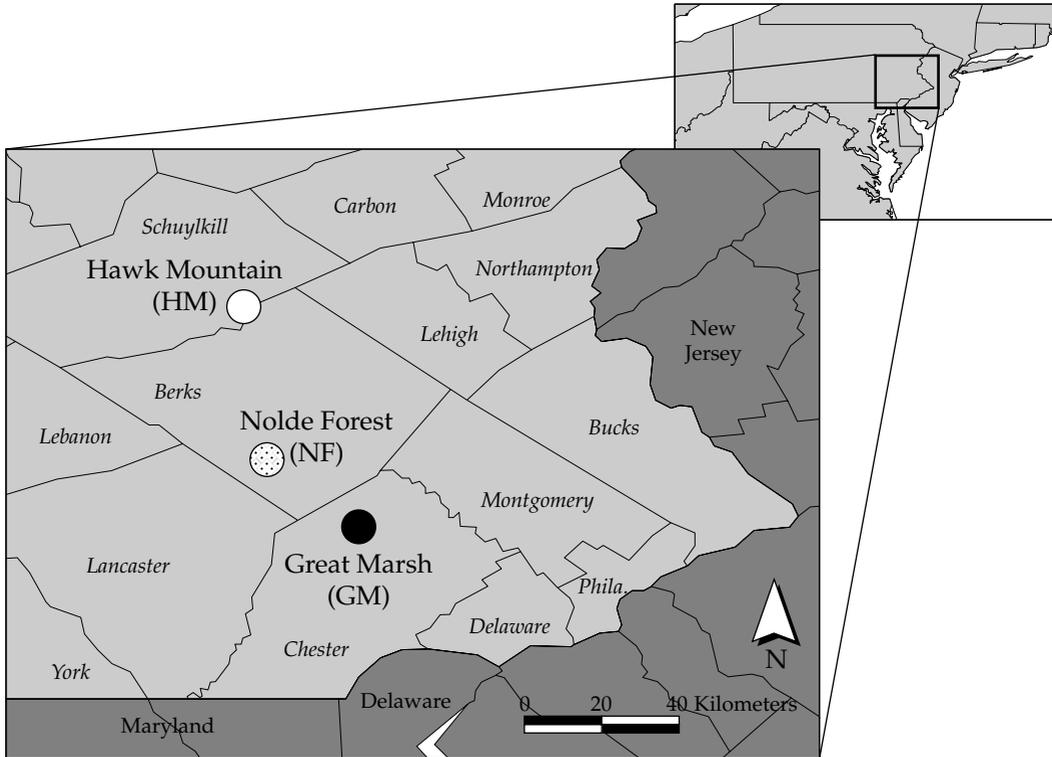
in pitch and duration of individual notes, even among songs that can be grossly categorized based on number of notes as black-capped-like or Carolina-like (Robbins *et al.* 1986). In some parts of the contact zone, an association between individual genetic identity and song parameters may exist (Sawaya 1990; Sattler 1996). No previous study has examined quantitative aspects of calls in detail for any local segment of the chickadee contact zone, nor have genotypes, songs, and calls of individuals been investigated concurrently. Here, we focus our attention on songs and on the D note of the *chick-a-dee* call, which appears to function in flock discrimination and species identity (Mammen and Nowicki 1981; Charrier and Sturdy 2005; Chapters 10 and 13).

### 7.2.1 Study sites

We have studied chickadees principally at three sites in south-eastern Pennsylvania (Fig. 7.1). The southernmost, Great Marsh (GM), covers approximately 200 ha; research here, initiated in 1998, involves resident Carolina chickadees. Nolde Forest (NF), about 24 km north-west, is a state park of 269 ha where research, initiated in 1998, focuses on a population comprising predominantly hybrid individuals (Reudink *et al.* 2006; see below). The third site (HM), about 35 km north of NF, includes ~120 ha within Hawk Mountain Sanctuary, where we began studying chickadees in 2001, as well as 10 nearby woodlots (1–23 ha, totaling ~80 ha) from which we obtained data in a companion study. As recently as 1988, all individuals studied at HM were black-capped chickadees, but beginning in 2002 we detected evidence of hybrid individuals in this population (Reudink *et al.* 2007). We also used some additional recordings from areas in Pennsylvania south and east of GM (Carolina chickadees) and from Nova Scotia, Vermont, and Massachusetts (black-capped chickadees).

### 7.2.2 Field methods

We studied mainly resident chickadees using artificial snags (based on Grubb and Bronson 1995) for nesting. We monitored up to 53 snags at GM, 152 at NF, and 212 at HM. Total samples of nests reaching at least the stage of egg-laying were 151 at GM (9–30 per season, 1998–2005); 270 at NF (6–55, in 1998–2005); and 54 at HM (1–20, in 2000–2005).



**Figure 7.1** Locations of primary study sites (names of Pennsylvania counties shown). Great Marsh (GM) is inhabited by Carolina chickadees. Nolde Forest (NF) is inhabited by hybrid chickadees. The Hawk Mountain (HM) site, inhabited mainly by black-capped chickadees, comprises property at Hawk Mountain Sanctuary and nearby woodlots. The contact zone is believed to run approximately from south-west (northern York Co.) to north-east (southern Northampton Co.).

We used mist nets to capture adults at winter feeding stations or at nests. Each received a Fish and Wildlife Service (FWS) aluminum band and two or three plastic colored bands. We banded nestlings with FWS bands at 9 to 12 days after hatching; the few that remained to breed locally later received colored bands.

### 7.2.3 Genetic methods

We collected blood samples (10–40  $\mu$ l from the brachial vein) from nestlings and adults at each nest, from which we extracted DNA using commercially available kits. Characterization of mitochondrial DNA (mtDNA) haplotypes involved polymerase chain reaction–restriction fragment length polymorphism (PCR–RFLP) analysis: amplified cytochrome *b* mtDNA was cut by the enzymes *Eco*R V (black-capped haplotype) or *Xmn* I (Carolina haplotype), based on Kvist *et al.* (1996). We investi-

gated genetic identity of individuals, as well as parentage patterns, using six microsatellite loci developed in prior studies of black-capped chickadee and blue tit; see Reudink *et al.* (2006) for details.

### 7.2.4 Hybrid index scores

Our analyses relied on the assumption that the two reference populations (HM and GM) included predominantly black-capped and Carolina chickadees respectively, and that genetic information from these populations could be used to characterize individuals at NF. This assumption has received support from analyses using the program STRUC-TURE (v. 2.1; Pritchard *et al.* 2000), which employs Bayesian methods to estimate the number of distinct populations and microsatellite allele frequencies among residents in each population (Reudink *et al.* 2007). However, this method did not allow us to characterize the genetic identities of *individuals*; to

produce a “rule” based on microsatellite genotypes that we could use to characterize individual breeders, we performed an iterative maximum-likelihood assignment test based on genotypes from the two reference populations, after omitting a few HM birds carrying Carolina mtDNA. The analysis yielded assignment probabilities, where  $p_x$  and  $p_y$  are the likelihoods of an individual belonging to population  $x$  or  $y$  respectively, and resulting hybrid index scores ( $I_H$ ) for breeders at all three sites, on a scale from 0 (Carolina) to 1 (black-capped) as follows (after Hansen *et al.* 2000):

$$I_H = 1 - \ln(p_x) / [\ln(p_x) + \ln(p_y)]$$

For additional details, see Reudink *et al.* (2006).

### 7.2.5 Song and call recordings

During the breeding seasons of 2000 and 2001, LMR recorded songs from 28 breeding males at NF (Rossano 2003). For comparison, we used songs of four individuals from predominantly or exclusively black-capped populations (HM, Nova Scotia, and Vermont) and from five birds from Carolina populations (GM and Montgomery Co., PA).

LMR recorded calls between October 2000 and October 2001 at NF from the same 28 males whose songs were sampled either near winter feeders or within each male’s breeding season territory but away from the nest. For comparison, we used recorded *chick-a-dee* calls from eight individuals from reference populations of black-capped and Carolina chickadees.

Observations of vocalizations at the three primary sites continued in 2002–2005. In each year, we categorized the song type of each breeding male

at NF, based on repeated observations during the laying and incubation periods at active nests.

### 7.2.6 Sound analysis

We performed acoustic analyses using Canary 1.2 (Cornell Laboratory of Ornithology). We noted the total number of notes (treating the *bee* of typical black-capped chickadee song as one note) but quantified only the first two notes to permit comparisons among all songs (Table 7.1). For *chick-a-dee* calls, we focused on the middle D note in calls with an odd number of D notes, or the first D of the middle two notes in calls with an even number of D notes. We used a spectrum of a 2.0 msec section at the midpoint of the note (44.1 kHz sample rate; 1024 FFT size) to measure frequency range for sound components within 30 dB of the loudest part of the note (based on Nowicki 1989).

## 7.3 Results

### 7.3.1 Genetic composition of study populations

Analysis of mtDNA supported the assumption that the three primary sites spanned the contact zone. At GM, all breeders in all years had Carolina mtDNA ( $n = 84$  individuals, including 40 females and 44 males). At NF, the majority of breeders exhibited Carolina haplotypes: of 83 male breeders analyzed from 1998–2005, only three (3.6%, associated with four nests in 1998–2000) had black-capped mtDNA and among 67 females sampled, only two (3.0%, both breeding in 2000) had black-capped mtDNA. At HM, all chickadees breeding before 2002 (three females, three males) had black-capped haplotypes.

**Table 7.1** Song parameters in hybrid zone (NF study site) in relation to corresponding songs from sites outside of the hybrid zone; repeated-measures least-square means  $\pm$  SEM shown for each parameter

Population and song type	1st note frequency (kHz)	1st note duration (msec)	Interval between 1st and 2nd notes (msec)	2nd note frequency (kHz)	2nd note duration (msec)
Black-capped ( $n = 69$ )	$3.8 \pm 0.1$	$367.2 \pm 23.3$	$124.7 \pm 16.5^a$	$3.3 \pm 0.1$	$386.4 \pm 37.1$
NF, 2-note song ( $n = 99$ )	$3.9 \pm 0.1$	$330.6 \pm 6.4$	$101.4 \pm 4.5^a$	$3.3 \pm 0.1$	$364.6 \pm 10.8$
NF, 4-note song ( $n = 99$ )	$6.8 \pm 0.1$	$213.7 \pm 12.9^b$	$117.8 \pm 15.5^c$	$4.2 \pm 0.1$	$256.3 \pm 18.2$
Carolina ( $n = 64$ )	$6.7 \pm 0.1$	$263.1 \pm 15.4^b$	$145.2 \pm 18.6^c$	$4.3 \pm 0.1$	$253.2 \pm 21.8$

<sup>a,b,c</sup>Means sharing letter different at  $P < 0.05$ , repeated-measures ANOVA and Tukey’s HSD post-hoc contrast.

Of the HM males breeding in 2002–2005, 16 (94%) had black-capped mtDNA and 1 (6%) had Carolina mtDNA, whereas among females, 16 (72%) had black-capped mtDNA and six (27%) had Carolina mtDNA ( $\chi^2 = 3.3$ ,  $df = 1$ ,  $p = 0.068$ ).

Analysis of microsatellite genotypes from birds breeding in 1998–2003 further showed that the three sites differed with respect to the genetic identity of their resident chickadees—and that the NF population included predominantly hybrids. Hybrid index scores ranged from 0.36 to 0.46 ( $\bar{x} = 0.41 \pm 0.03$  SE,  $n = 45$ ) at GM (more Carolina-like) and from 0.53 to 0.69 ( $\bar{x} = 0.60 \pm 0.04$  SE,  $n = 24$ ) at HM (more black-capped-like; Fig. 7.2). Resident chickadees at NF had scores ranging from 0.40 to 0.58 ( $\bar{x} = 0.48 \pm 0.03$  SE,  $n = 145$ ), with 63.9% having intermediate scores falling between the upper and lower ranges of the GM and HM populations respectively (Fig. 7.2). Approximately 27.8% of NF individuals fell within the GM score range whereas 8.3% fell within the HM score range.

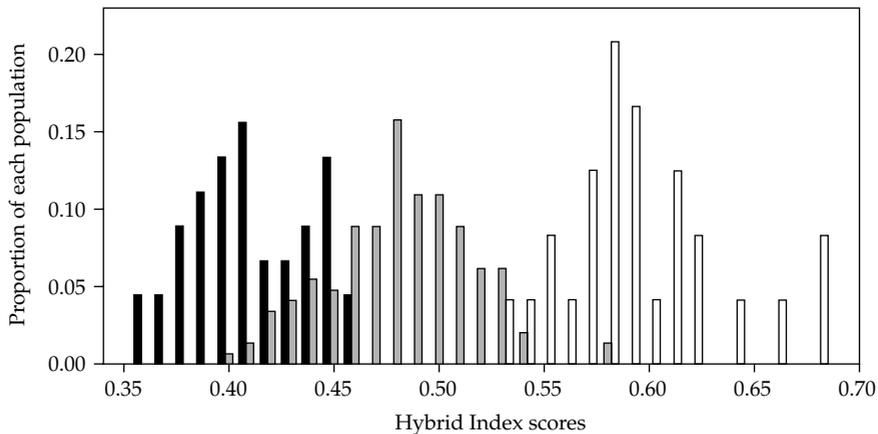
### 7.3.2 Song patterns beyond and within hybrid zone

Song patterns were consistent with the assumption that sites other than NF were outside of, or at the extreme edge of, the hybrid zone. Among songs sampled in 2000–2001 from GM and other Carolina localities, all songs analyzed matched the typical *see-bee-see-bay* Carolina chickadee song type ( $n = 51$

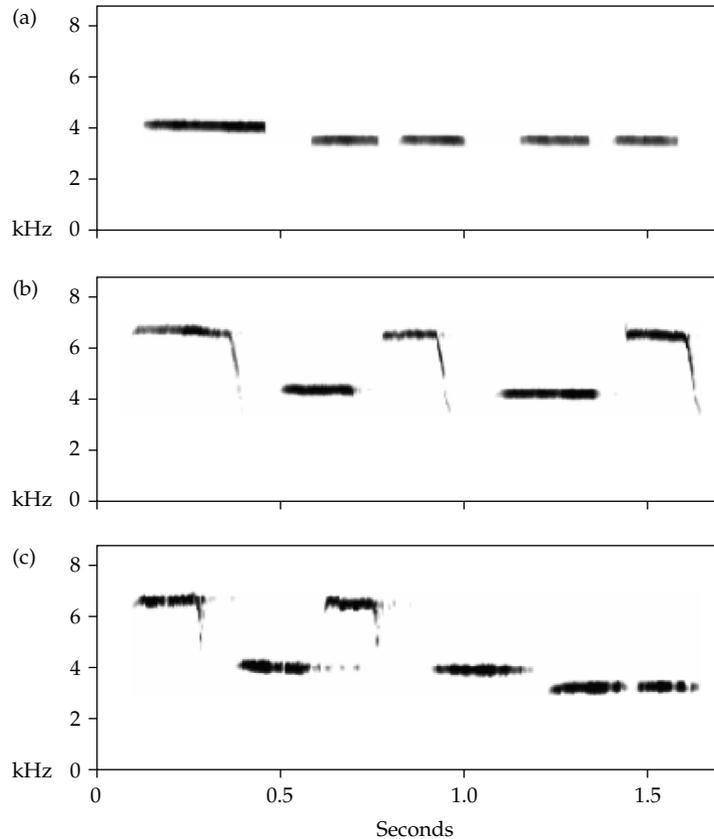
songs), except we recorded one bird in southern Montgomery Co., Pennsylvania, that gave only three-note songs (*see-bay-see*;  $n = 13$ ) representing the Song Variant category of Smith (1972). All songs in 2000–2001 ( $n = 69$ ) from areas occupied predominantly or exclusively by black-capped chickadees, including HM, represented the characteristic black-capped *fee-bee*. Despite genetic evidence of introgression at HM, this pattern had not changed as of 2005: we have yet to hear any HM male include Carolina song, or even variant black-capped song (see below), in his repertoire.

At the NF hybrid zone site, 80% of the songs ( $n = 813$ ) produced by the 28 resident males in 2000–2001 matched the typical black-capped *fee-bee*. Other songs observed, in declining order of occurrence, included: four-note typical Carolina song (*see-bee-see-bay*; 9%); variant black-capped type (e.g. *fee-bee-bee*; 5%); variant Carolina type (e.g. *see-bay-see-bay-see*; 3%); and mixed song, combining typical elements of both songs (2%) (Fig. 7.3 and Rossano 2003).

Although songs at NF sounded superficially like the typical songs of one of the parental species, values of several variables differed between the songs from NF relative to the corresponding parental areas (Table 7.1). In particular, two-note songs at NF differed from typical black-capped *fee-bee* songs in having a shorter pause between the notes. Four-note songs at NF differed from those of typical Carolina chickadees in having shorter first



**Figure 7.2** Hybrid index scores ( $I_H$ ), based on microsatellite genotypes, of resident chickadees from three primary study sites in south-eastern Pennsylvania. Values range from low for Carolina chickadees to high for black-capped chickadees. Vertical axis shows relative proportions among individuals from each site; gray bars, GM ( $n = 45$ ); white bars, NF ( $n = 145$ ); black bars, HM ( $n = 24$ ).



**Figure 7.3** Variant and mixed songs from the hybrid zone study site at Nolde Forest. (a) Example with quantitative characteristics of typical black-capped *fee-bee-ee* but with repetition of *bee-ee* note. (b) Example with quantitative characteristics of typical Carolina chickadee *see-bee see-bay* but with extra terminal *see* note. (c) Example of mixed song, with quantitative characteristics of typical Carolina chickadee *see-bee-see bay* followed by *bee-ee* note of typical black-capped chickadee song.

notes and a shorter interval between the first and second notes.

Of the 28 different NF males recorded in 2000–2001, 19 (68%) produced only typical black-capped *fee-bee* songs and one gave normal black-capped song and a black-capped variant. Six (21%) of the males were bilingual, producing both two-note black-capped song and four-note Carolina song types. Two other bilingual birds (7%) produced typical songs of both species as well as mixed songs that included notes characteristic of both species (Fig. 7.3).

Based on the number of notes sung (pending detailed acoustic analysis), we detected a trend toward increasing representation of bilingual

singing over time. When our observations began at NF in 1997–1998, we detected no males that produced Carolina-type songs. Birds including aberrant or Carolina song types in their repertoires appeared in 1999. Of the males examined in 2000–2001, 71% gave only black-capped songs while 29% were bilingual (see above). Among males breeding at NF in 2005 ( $n = 45$ ), the proportion of males singing only two-note black-capped song had declined to 47% ( $\chi^2 = 4.40$ ,  $df = 1$ ,  $p = 0.036$ ), while 53% of males gave both song types ( $n = 23$  males) or only songs involving a mix of note types from both species ( $n = 1$ ).

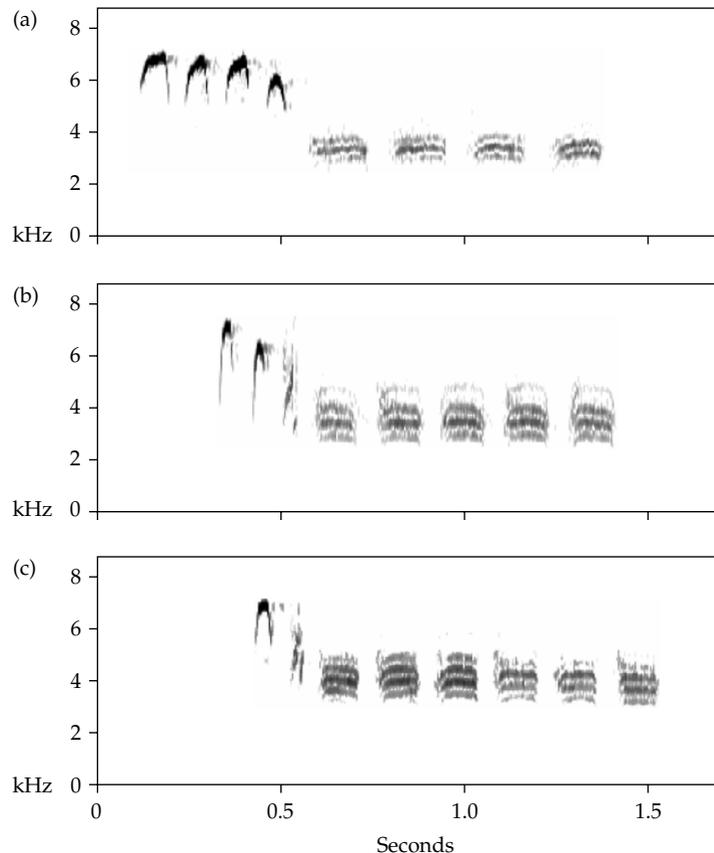
Song patterns at NF contrast with vocal behavior in nearby Carolina chickadee populations in two

ways. First, we have yet to detect any NF males that give *only* Carolina songs; vocally, the population included black-capped males and bilingual or mixed-song males, but no males with a “pure” Carolina repertoire. Second, those males that are bilingual produce only the four-note *see-bee-see-bay* Carolina song type; we have not heard any male at NF give any version of Song Variant (e.g. *see-see-bay bay-bay*) that Carolina chickadees in south-eastern Pennsylvania routinely include in their repertoire (Smith 1972; R. Curry, unpublished data), whereas all breeding males at GM have done so in every year (1998–2005).

### 7.3.3 Chick-a-dee calls beyond and within hybrid zone

Analysis of *dee* notes of black-capped and Carolina chickadees (Fig. 7.4) revealed clear differentiation

between the parental species in all parameters measured (Table 7.2; repeated measures ANOVA and Tukey’s HSD post-hoc contrasts,  $P < 0.05$ ) except minimum frequency. Discriminant function analysis (DFA) indicated that the variables most informative for distinguishing between the two sets of calls were duration, peak amplitude frequency, and maximum frequency of the *dee* note. DFA categorized 46 (92%) of 50 calls recorded at black-capped sites as black-capped (i.e. having a probability of being black-capped  $\geq 0.8$ ). The four calls categorized as Carolina were produced by a single male at HM; this bird had black-capped mtDNA but could have been a hybrid. Of the calls recorded from Carolina chickadee localities ( $n = 81$ ), 80 (99%) were categorized as Carolina. The one other call was intermediate (probability of being Carolina = 0.74), produced by a bird that also gave 14 other calls classified as Carolina.



**Figure 7.4** Chick-a-dee calls from hybrid zone study site (NF) categorized by discriminant function analysis as: (a) black-capped; (b) Carolina-like ( $0.5 < \text{probability of being Carolina} < 0.8$ ); and (c) Carolina.

**Table 7.2** Quantitative characteristics of “D” notes of “chick-a-dee” calls at localities beyond and within the chickadee contact zone

Population	“dee” duration (msec)	Peak amplitude frequency (kHz)	Maximum frequency (kHz)	Interval between “dee” notes (msec)
Black-capped <sup>a</sup> (n = 50 calls)	152 ± 21	3.9 ± 0.5	5.0 ± 0.8	62 ± 16
Nolde Forest (n = 453)	114 ± 13	4.2 ± 0.3	5.8 ± 0.6	49 ± 12
Carolina <sup>b</sup> (n = 81)	105 ± 12	4.1 ± 0.4	5.8 ± 0.6	48 ± 15

<sup>a</sup>Includes samples from Hawk Mountain supplemented with recordings from Nova Scotia, Vermont, Massachusetts, and New York.

<sup>b</sup>Includes samples from Great Marsh supplemented with recordings from Montgomery and Delaware Cos., Pennsylvania; Maryland; and North Carolina.

We used the same DFA formula to categorize calls (n = 453), based on *dee* notes, from the 28 males at NF whose song were also recorded (see above). Most calls (87%) at NF were Carolina (probability >0.8); 8% were Carolina-like (0.5 < probability <0.8); 3% were black-capped-like (0.5 < probability <0.8); and 2% were black-capped.

All males at NF gave individual calls that varied in their quantitative characteristics and thus fell into different categories. Of the 28 males, 17 (61%) produced exclusively calls categorized as Carolina or Carolina-like. Three other males gave calls that were mostly Carolina/Carolina-like (≥70% of individual’s calls) with the remaining calls being black-capped-like. The six other birds (21%) gave calls spanning all types of calls, including at least a few calls categorized as black-capped.

### 7.3.4 Lack of congruence between songs and calls

Using the quantitative categorization of *chick-a-dee* calls from DFA, there was no association between an individual’s song and call categories among 27 males at NF. Of the 20 males that produced only black-capped chickadee song, 14 (70%) gave Carolina-type calls and six (30%) gave variable calls; among the eight males that sang both song types or mixed songs, seven (88%) gave Carolina-type calls and one (12%) gave variable calls ( $\chi^2 = 4.40$ ,  $df = 1$ ,  $P = 0.31$ ).

Similarly, we detected no significant differences in *dee* note components between NF males that fell into the two categories of singer. Therefore, there was an overall pattern at NF of males producing relatively normal black-capped songs—with or

without also singing Carolina-type songs in the case of bilingual males—but with all males giving at least some *chick-a-dee* calls that were Carolina-like, and with some doing so exclusively.

### 7.3.5 Relationships between behavior and genetics

Vocal patterns in the contact zone at NF were not correlated with genetic variation among individuals. Among 23 males whose songs we categorized and whose microsatellite genotypes we evaluated (all of which had Carolina mtDNA), those giving only black-capped songs had average hybrid index scores ( $\bar{x} = 0.47 \pm 0.036$  SD,  $n = 16$ ) that were similar to those of all other bilingual and mixed-song males ( $n = 7$ ;  $\bar{x} = 0.48 \pm 0.037$  SD;  $t = -0.50$ ,  $df = 20$ ,  $P = 0.63$ ). Birds categorized as giving Carolina-like calls also had hybrid index scores that were no different ( $\bar{x} = 0.48 \pm 0.031$  SD,  $n = 17$ ) from scores for males categorized as producing intermediate calls ( $\bar{x} = 0.46 \pm 0.031$  SD,  $n = 7$ ;  $t = 1.72$ ,  $df = 22$ ,  $P = 0.10$ ).

While vocal patterns at NF were not associated with genetic variation, aspects of the mating system varied in relation to male genotypes (Reudink *et al.* 2006). Females at NF that engaged in extrapair mating were socially paired with males having higher hybrid index scores (i.e. more black-capped-like) than the social mates of females that did not produce any extrapair offspring. Furthermore, extrapair sires had hybrid index scores that were lower (more Carolina-like) than those of corresponding social males. Because there was no relationship between hybrid index scores and vocalizations among NF males, it is unlikely

that this pattern of extrapair mating was influenced by male vocal behavior, but we have not tested these relationships directly.

## 7.4 Discussion

### 7.4.1 Hybridization in south-eastern Pennsylvania

Our results indicate that extensive hybridization occurs within the region sampled. The genetic data reveal an overall difference between the GM and HM populations, and intermediacy of chickadees at NF; the results also provide evidence that the contact zone is shifting northward (see also Reudink *et al.* 2007). At NF, black-capped genes appear to be decreasing in the population, while at HM, birds with Carolina-like genotypes are increasing. Because all individuals at GM already had Carolina genotypes at the start of our study, changes were not apparent there during our study, but the absence as of 1998 of black-capped songs, reported in the vicinity of GM in the 1960s (Ward and Ward 1974), suggests that the southern edge of the hybrid zone has shifted north as well. The persistence at NF of some black-capped chickadee genetic influence contemporaneous with appearance of birds at HM carrying Carolina genes indicates that the hybrid contact in south-eastern Pennsylvania is at least 50 km wide.

The patterns in Pennsylvania are broadly consistent with evidence from other portions of the chickadee contact zone with respect to hybrid zone structure and northward movement. Genetic data suggest a somewhat narrower zone (<30 km wide) in Missouri and in the mountains of the Virginias (with some evidence of introgression over longer distances in these regions) and in north-central Ohio (Sawaya 1990; Sattler and Braun 2000; Bronson *et al.* 2005). The hybrid zone in Ohio is believed to have moved ~100 km northward over approximately 70 years (Bronson *et al.* 2005).

Our finding that a large percentage of resident chickadees within the contact zone may be hybrids also is consistent with other studies. In Missouri and in the Virginias, the proportion of hybrids among samples of 100 or fewer specimens was 44 to 58% (Sawaya 1990; Sattler and Braun 2000). Determining

whether genetic and behavioral variability at NF is similar to that in other areas will require further molecular work in Pennsylvania and additional field study at the local level elsewhere.

### 7.4.2 Song patterns in the Pennsylvania contact zone

A striking finding in our study was the retention of black-capped chickadee songs at NF, where essentially all resident adults are now hybrids (and where some may be genetically “pure” Carolina chickadees). Even those males with the ability to sing at least one Carolina song type continue to produce black-capped songs as well.

That existence of “bilingual” chickadees may indicate interbreeding has been long assumed, with some even suggesting that bilingual males in zones of overlap might gain a functional advantage by being able to deter rivals of both parental species (Robbins *et al.* 1986). However, retention of black-capped song long after hybridization has occurred at a given site has not been appreciated previously. This finding has implications for the accuracy of distributional surveys, such as the breeding bird atlas program, where judgments about residency are often based primarily on songs heard. The tendency for hybrid males to produce relatively normal black-capped song underscores the likely existence of developmental mechanisms that result in song stereotypy across most of the black-capped chickadee’s range, but the nature of those mechanisms remains unknown (Kroodsma *et al.* 1999).

A distinct but related aspect of vocal patterns in the hybrid zone concerns production of aberrant song types. Song variants are particularly rare in most black-capped chickadee populations; exceptions may be restricted to isolated populations at the geographic range limits (see Chapter 14). Defining aberrant song in Carolina chickadees is more challenging, because of greater inherent variability among and within populations in this species. Regardless, the tendency for chickadees in contact zone populations to produce songs not characteristic of parental populations has been noted frequently.

Aberrant songs fall into two main categories: (1) songs with the number of notes and pattern typical of parental forms, but with different quantitative

characteristics; and (2) songs that combine notes of the typical songs of both parental species. We observed both of these song categories at NF, although many males—including some bilingual males—never produced markedly aberrant songs. However, our finding that some seemingly “normal” songs had some intermediate quantitative characteristics matches results from Missouri (Robbins *et al.* 1986) more so than those from the Virginias, where the pattern was bimodal (Sattler 1996). Our study adds detail to understanding of song patterns the hybrid zone by showing that males producing relatively normal black-capped songs—with or without Carolina song as well—can have Carolina mtDNA, along with microsatellite genotypes consistent with hybrid status.

The vocal and genetic patterns we detected suggest that many chickadees in the contact zone, but perhaps not all, are capable of learning heterospecific songs. This finding is consistent with previous findings that individuals of these species can, when reared together, learn notes of the other (Kroodsma *et al.* 1995). However, the specific mechanisms that cause some chickadees to become bilingual while others continue to sing only black-capped song remain to be determined.

### 7.4.3 Chick-a-dee calls across the hybrid zone

That the D notes of the black-capped chickadee’s *chick-a-dee* call are longer in duration and lower in pitch than those of the corresponding Carolina chickadee call has been known for a long time (see Chapter 13). It is therefore surprising that this vocalization has not previously received particular attention in relation to the hybrid zone between the species, apart from an unpublished thesis (Crock 1975). As Crock observed using a broad geographic approach, we found that parameters of D notes from the hybrid zone were quantitatively intermediate on average. Our observation that individual chickadees in the hybrid zone produce highly variable D notes is novel.

Two aspects of our results suggest that genetic and environmental influences on development of calls operate differently than those affecting song learning. First, a disparity exists at NF between the average D notes characteristics (mainly Carolina-like) at the population level and the persistence of black-capped

song. Second, we observed “mismatches” at the level of individual males that produced quantitatively variable or intermediate calls, independent of the song types that the same birds sang.

Several explanations for conflicting patterns are possible. One is that songs are learned whereas call development is subject to stronger genetic influence, such that birds with hybrid genotypes produce acoustically intermediate call notes. Alternatively, development of both vocalizations may involve learning (Chapters 10, 11, and 13), but with different influences such as the age at which learning occurs or the social context. Because song is primarily produced by males, chickadees could be learning the song of their father or those of neighbor males. In contrast, calls are produced by both sexes and develop early in life; accordingly, chickadees could learn their calls not only from their father but from their mother, as might happen when she is brooding.

### 7.4.4 Potentially confounding variables in analysis of vocal patterns

Our understanding of the vocal behavior of hybridizing chickadees is limited in some respects, because in our observational study we cannot control for several potentially confounding variables. With respect to songs, an important factor is our ability to thoroughly characterize the full repertoire of a large sample of breeding male chickadees at each site. In general, male chickadees display their full repertoire most reliably during dawn chorus song bouts that they deliver close to active nests, during the phase of the breeding season when females have begun laying eggs or are within a few days of beginning to do so (see Chapter 14). However, male chickadees at NF do not seem to participate consistently in the dawn chorus, even during the critical period of the breeding season; characterizing song repertoires therefore has had to depend additionally on observations throughout the day, when each male sings intermittently throughout its territory. While we continue to investigate this impression, we can be confident about characterizing males as bilingual once we observe production of both black-capped and Carolina song; we can, however, be less certain that males that we classify as producing only

black-capped song are not in fact bilingual. Similarly, our ability to determine precisely which males produce aberrant or mixed songs is likely dependent on the sample size of songs of each bird. The number of songs recorded at high sound quality also influences our ability to characterize fully the relatively subtle variation in quantitative song parameters, above and beyond the major categories based on note number, duration, and pitch. However, because we can easily identify nearly all notes as either black-capped-like or Carolina-like, we believe that our conclusions about general patterns of vocal variation—including especially the persistence of black-capped song types, and the absence to date of the Song Variant version of the Carolina song, in the hybrid zone—are robust.

Assessing vocal variation with respect to other chickadee calls is even more challenging because of the inherent complexity of chickadee vocal repertoires. Even when focusing only on the *chick-a-dee* call, many sources of variation come into play. Our population-level averages for the D notes, especially given relatively small sample sizes, could incorporate biases caused by inadvertently sampling different proportions of males and females, birds of different flocks, calls produced in different contexts, or notes taken from calls that vary in overall syntax—all factors that may influence note structure (see Chapter 13). The same considerations apply to our characterization of calls at the level of individual birds, along with an even greater challenge regarding adequate sampling. Nevertheless, we are confident of the overall conclusion that mismatches exist at NF between black-capped/bilingual singing and Carolina-like calls. Recent observations offer further support: in 2005–06, many large chickadees with black-capped plumage wintered at NF as part of a major regional irruption. We easily distinguished these individuals, based on calls, from the local (hybrid) residents; mtDNA data have invariably confirmed that the irruption birds had black-capped chickadee haplotypes.

#### 7.4.5 Completing the behavioral picture of chickadee hybridization

The finding that black-capped chickadee song persists in a hybridizing population, coupled with

documented patterns of extrapair paternity (Reudink *et al.* 2006), suggests that chickadees in the hybrid zone probably do not base mating decisions on song categories. Pairing in chickadees generally occurs within winter flocks, long before males sing actively at the start of the nesting season (see Chapter 9). It is therefore unlikely that a female's choice of a social mate would be based on the male's song repertoire.

However, extrapair mating decisions could be influenced by the singing behavior of males in the hybrid zone, as in allopatric populations of black-capped chickadees (Chapter 14). We are currently investigating whether differences exist in the tendency to engage in extrapair mating between females socially paired with bilingual males versus males that sing only black-capped song. Regardless of whether such a pattern exists, it is unlikely to be correlated with the previously observed tendency (Reudink *et al.* 2006) for females paired with black-capped-like males to engage in extrapair mating, and to do so with Carolina-like extrapair mates, because there does not appear to be an association between genetic identity and song types in the NF population. Still, it will be interesting to assess whether females could use song as a honest signal of male quality within the hybrid zone, as might be true if the vocal performance of hybrid males were impaired by developmental stress (Nowicki and Searcy 2005).

## 7.5 Hybridization throughout the Paridae

### 7.5.1 Other examples in North America

While the extended contact zone between black-capped and Carolina chickadees has been studied most intensively, three other examples of interbreeding among North American Parids—all involving sibling species pairs—also have been examined in some detail. Mountain and black-capped chickadees hybridize at least occasionally in western North America, where their geographic ranges overlap broadly (McCallum 1998). However, these species remain ecologically separated by differences in habitat use (Hill and Lein 1989 Chapter 8); the circumstances leading to

hybridization remain to be worked out. Tufted and black-crested titmice hybridize in a narrow zone in Texas and were formerly considered conspecific, but the combination of geographic stability of the contact zone, genetic distinctiveness, and vocal differences have supported their treatment as separate species (Banks *et al.* 2002). Similarly, oak and juniper titmice in the western United States were formerly considered conspecific (plain titmouse) until recent work revealed a low incidence of hybridization in a small area of secondary contact in north-eastern California (Cicero 1996, 2004). Whether songs and calls, which differ between these titmice (Cicero 2000), serve as barriers to hybridization is a subject of current study.

Opportunities exist for research on potential hybridization (or the avoidance of interbreeding) in several other pairs of New World Parids that are at least partly sympatric. No studies have explored in detail breeding relationships between any species pairs within the clade of brown-capped chickadees (see Gill *et al.* 2005). Hybridization in the past between chestnut-backed and boreal chickadees represents one possible explanation for phylogeographic patterns (Chapter 6), but barriers to interbreeding between these sibling species have not been investigated. The lack of a whistled song in the brown-capped species suggests that song recognition cannot serve as a primary isolating mechanism. Boreal chickadees also are not known to hybridize with Siberian tits where these species co-occur in Alaska (Ficken *et al.* 1996), but knowledge of the latter species in North America is limited (Hailman and Haftorn 1995). Similarly, no study has investigated reasons why black-capped chickadees apparently never interbreed with boreal chickadees, though the species have broadly overlapping geographic ranges and habitat preferences that are shared at least in part. A parallel situation exists between mountain and chestnut-backed chickadees; again, no hybridization has been observed (McCallum 1998) but further study is merited. Sympatric overlap occurs between juniper and bridled titmice in Arizona, at the southern extreme of the former's range, but no hybridization has been reported (Nocedal and Ficken 1998).

Other combinations of sympatric Parids in North America involve titmouse/chickadee pairs, such as

bridled titmouse with Mexican chickadee; oak or juniper titmice with black-capped chickadees; or tufted titmouse with Carolina or black-capped chickadees. Hybridization appears to be exceedingly rare in these cases, despite large areas of geographic overlap; the only known example involved a black-capped chickadee  $\times$  tufted titmouse cross (Cockrum 1952). The rarity of such matings is unsurprising given that titmice typically are at least 50% larger than sympatric chickadees, except in the case of bridled titmouse and Mexican chickadee, which differ little in size but greatly in appearance.

### 7.5.2 Hybridization among Eurasian Parids

Observations of mixed breeding pairs, or of phenotypically intermediate individuals, have provided evidence for hybridization among numerous European and Asian Parids. Rare hybridization, implied by anecdotal reports of mixed pairs or intermediate specimens, has involved willow  $\times$  marsh tit; willow  $\times$  coal tit; willow  $\times$  crested tit; coal  $\times$  crested tit; blue  $\times$  great tit; marsh  $\times$  great tit; great  $\times$  coal tit; and willow  $\times$  varied tit (reviewed by Harrap and Quinn 1995; Curry 2005; McCarthy 2006). Interbreeding occurs more frequently between Siberian and willow tits in Finnish Lapland where the former species is rare and the latter is more common (Järvinen 1997), an example illustrating a general principle that large differences in relative abundance facilitate hybridization in passerines (Randler 2002). Blue, azure, and yellow-bellied tits exhibit a complex pattern: hybridization between the former two species has occurred following irruptive movements or range expansion of azure tit into the blue tit's range, whereas azure and yellow-bellied tits, which some consider conspecific, appear to maintain a more stable contact zone; the case is complicated by evidence suggesting that azure tits are evolutionarily nested within the blue tit clade (Salzburger *et al.* 2002). In a different case involving sibling species, a stable contact zone appears to exist between coal tits and black-crested tits in Nepal (Löhrl 1994; but see Harrap and Quinn 1995:302). Until recently, the great tit was considered a ring species exhibiting terminal contact in Siberia, in addition to hybridization with the

Turkestan tit in Central Asia. However, comprehensive analysis of genetic, morphological, and vocal patterns support separation into three species—great tit (including the Turkestan tit), Japanese tit, and cinereus tit—with five different contact zones (Päckert *et al.* 2005).

Analysis of hybridization has progressed to analysis of potential isolating mechanisms in studies of several Eurasian Parids, with a major focus on songs (reviewed by Martens 1996). In southwestern Germany, blue tits do not respond territorially to normal songs of azure tits, but they sometimes react to artificially constructed combinations of azure tit notes; natural similarity in song appears sufficient to permit heterospecific pairing, but no introgression, where both species occur at low density (Martens and Schottler 1991). Breakdown of species recognition based on song also has been suggested to account for hybridization between great and Japanese tits in Siberia (Päckert *et al.* 2005). Intraspecific vocal variation within willow tits is particularly complex (Martens 1996). Two song types, “alpine” and “lowland,” have been identified based on note structure; in Central Europe, populations whose males sing only one version are parapatrically separated. However, throughout much of the northern and eastern range of the species, males of the “Siberian” song category are bilingual with respect to the two song types, as they are in some local European populations where interbreeding occurs between song types. Full understanding of this system awaits research focused on the responses of both males (as rivals) and females (as mates) to individual males as a function of their song type(s). In contrast, there is less differentiation in song than in morphology in coal and black-crested tits (Martens 1996).

Mechanisms that facilitate heterospecific pairing can be explored by cross-fostering, an approach that has been pursued recently using blue and great tits. Cross-fostered blue and great tit males both react territorially to heterospecific intruders (Hansen and Slagsvold 2003). Blue tits reared by great tits have normal pairing success but occasionally pair with great tits; in contrast, great tits raised by blue tits suffer low pairing success, and the few that pair do so with blue tits (Slagsvold *et al.* 2002).

Cross fostering tends to reduce dominance status (Hansen and Slagsvold 2004), which could indirectly affect the tendency to be chosen as a mate; females that pair with cross-fostered males do not, however, engage in elevated rates of extrapair paternity (Johannessen *et al.* 2005).

Though blue and great tits seldom hybridize in nature, the cross-fostering work is relevant to the study of Parid hybridization in two ways. First, the experiments explore one possible mechanism for the initial stage of interbreeding, that is interspecific egg-dumping or brood takeover, followed by sexual misimprinting and heterospecific mate choice (Slagsvold and Hansen 2001). Second, results demonstrate that exposure to both adults and nestmates of another species during an individual's development can have diverse and long-lasting effects on its subsequent behavior and success. The work suggests that far-reaching imprinting effects—on vocalizations, dominance, mate preferences, and more—should be expected as well during naturally occurring hybridization.

## 7.6 Future directions

The largest gap in understanding of the behavioral ecology of hybridization in chickadees concerns dominance interactions and their relationships with both social pairing and extrapair mating. To date, no thorough field study of dominance relationships has been completed within any part of the contact zone. Bronson *et al.* (2003b) found a tendency for Carolina-like males in aviaries to dominate black-capped males, and for females of both species to associate with the dominant Carolina males. However, proximate mechanisms involved in neither establishment of dominance nor mate choice by females were examined as part of the study. Furthermore, because the work was carried out using captive birds, its relevance for understanding patterns and mechanisms in the field is not yet known (Curry 2005).

The preceding discussion underscores a paucity of available information about relationships between vocal patterns, dominance relationships, and mating systems in Parid hybrid zones. Because chickadees give calls at all times of the year, those vocalizations potentially play a greater

role in establishing or maintaining dominance relationships than do the songs that chickadees give only in the spring, after pairs have already become established. However, several other factors besides vocal behavior could be important determinants of dominance, and thus of any mating patterns dependent on dominance; these include, but are not limited to, age and plumage brightness (Chapter 9).

An important question is whether song invariably trumps other cues as the predominant ethological isolating mechanism in the Paridae, as has been accepted by European investigators (Martens 1996). That two distantly related North American chickadees with different songs can continue to hybridize challenges this view—unless the ability to learn the other's song, perhaps because both retain ancestral song characteristics, facilitates interbreeding through sexual misimprinting. The importance of vocalizations relative to other influences, including calls and social dominance, on mating decisions in hybridizing Parids can only be assessed through further research that addresses these relationships directly, as we are attempting to do in our ongoing studies of chickadees.

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