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OVERVIEW

HYBRIDIZATION IN CHICKADEES: MUCH TO LEARN FROM FAMILIAR BIRDS

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Hybridization has long fascinated ornithologists, as evidenced by both foundational and recent publications in evolutionary and avian biology (Mayr 1963; Grant and Grant 1992, 1997; Gill 1998; Randler 2002), including frequent major contributions in *The Auk*. For example, work in the United States on the classic Great Plains hybrid zones involving orioles, flickers, buntings, and other taxa continues (e.g. Rising 1983, 1996; Moore and Koenig 1986; Moore and Price 1993; Baker and Johnson 1998; Allen and Omland 2003). Recent intensive work, taking advantage of the potential for direct measures of fitness that are possible when studying entire populations of Darwin's finches on small islands, is providing critical information about ecological and evolutionary consequences of introgressive hybridization (Grant and Grant 1994, 1996, 2002; Grant et al. 2005). Still other studies have focused on the potential for introgression to put species at risk of extinction (Rhymer and Simberloff 1996); research with this emphasis includes recent work, for example, on two pairs of North American wood warblers (Gill 1997, 2004; Rohwer and Wood 1998; Pearson 2000; Shapiro et al. 2004).

An especially productive subset of hybridization work examines contact zones, geographic regions where otherwise separate populations overlap and interbreed (Moore 1977, Barton and Hewitt 1989, Harrison 1993). The parapatrically distributed Black-capped Chickadee (*Poecile atricapillus*) and Carolina Chickadee (*P. carolinensis*) have long been known to hybridize—to the chagrin of generations of birders, who often have a tough enough time telling these superficially similar species apart—but their contact zone has only recently been sufficiently well studied to yield basic understanding of important patterns and processes. Bronson et al. (2005) represents the latest installment in this expanding body of work. The new study adds to others from the same research program (Bronson et al. 2003a, b); these papers, along with additional recent and ongoing research elsewhere, have greatly increased our understanding of the causes and consequences of hybridization in these chickadees, while leaving many exciting questions yet to be answered.

Biological Context of Chickadee Hybridization

Black-capped Chickadees inhabit most of Canada and the northern half of the United States, whereas Carolina Chickadees are restricted to the southeastern United States. The species come in contact along a narrow contact zone extending from Texas to New Jersey, with the Black-capped Chickadee's range occupying the higher elevations of the Appalachian Mountains to southwestern Virginia (extending also, formerly at least, to southwestern North Carolina; Tanner 1952), producing areas of contact on both flanks of the mountain chain and in both southwestern and southeastern Pennsylvania (Mostrom et al. 2002). Hybridization has been known or suspected in the zones of contact, on the basis of field observations or analysis of specimens from Kansas (Rising 1968), Missouri (Braun and Robbins 1986, Robbins et al. 1986), Illinois (Brewer 1963), Virginia (Johnston 1971, Sattler and Braun 2000), and Pennsylvania (Ward and Ward 1974).

Analysis of mitochondrial DNA (mtDNA) has shown that Black-capped and Carolina

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chickadees are not each other's closest relative (Gill et al. 1993, 2005). The sibling species of the Black-capped Chickadee is the Mountain Chickadee (*P. gambeli*) of western North America. The Carolina Chickadee is more distantly related, but the identity of its own closest relative remains unresolved: some analyses place *P. carolinensis* closest to the *atricapillus–gambeli* clade, whereas other results suggest that its sibling species is the Mexican Chickadee (*P. sclateri*). This phylogenetic issue is important as context for studies of chickadee hybridization, because its resolution would help us understand the extent to which Black-capped and Carolina chickadees have diverged, and this in turn would have implications for understanding how and why they continue to choose each other as mates. Regardless of the placement of the taxa on phylogenetic trees, it appears clear that the latter two species are evolutionarily distinct: their mtDNA gene sequences have diverged ~4% (Mack et al. 1986, Gill et al. 2005), a level of divergence comparable to that among clearly separable species in many avian genera. That conclusion contrasts with earlier suggestions that the two species might not merit recognition as separate species, based on observed interbreeding and similarities in proteins (Braun and Robbins 1986).

Hybridization between Black-capped and Carolina chickadees is not unique within the Paridae; indeed, hybridization—as at least an occasional event, but in some cases as a more regular phenomenon—has been a theme in studies of this family (Harrap and Quinn 1995). Most cases of parid hybridization have involved closely related species within clades that were considered until recently to be subgenera within the large genus *Parus*; those major groupings are now generally recognized as distinct genera (e.g. AOU 1998, based mainly on Slikas et al. 1996; see also Gill et al. 2005). Accordingly, analyses of hybridization have helped to determine species boundaries between two sibling pairs of North American titmice (*Baeolophus* spp.; Avise and Zink 1988, Dixon 1990, Cicero 1996, AOU 2002); between Coal Tit (*Periparus ater*) and Black-crested Tit (*Pe. melanolophus*) in Nepal (Löhrl 1994); and between Blue Tit (*Cyanistes caeruleus*), Azure Tit (*C. cyanus*), and Yellow-breasted Tit (*C. flavipectus*; reviewed by Harrap and Quinn 1995, Randler 2004; see also Kvist et al. 2004). Similarly, boundaries have been shown to be complex among subspecies of the Great Tit (*Parus major*) and related species, such as the Turkestan Tit (*Pa. bokharensis*; Harrap and Quinn 1995, Kvist et al. 2003).

Among the chickadees (*Poecile* spp.), Black-capped and Mountain chickadees hybridize occasionally in the mountains of western North America (Hill and Lein 1988, 1989). Occasional hybrids between Marsh Tit (*P. palustris*) and Willow Tit (*P. montana*) have been reported (reviewed by Harrap and Quinn 1995), but their frequency may be underestimated because of low detectability (Randler 2004). Hybridization between members of the brown-capped and black-capped groups within *Poecile* appears to be rare: mixed pairings and hybrid birds have been reported with regularity only between Gray-headed Chickadee (*P. cincta*) and Willow Tit in Finnish Lapland, where the former species is relatively rare and declining (Järvinen 1997). By contrast, no cases of hybridization between the broadly sympatric Boreal Chickadee (*P. hudsonica*) and Black-capped Chickadee have been documented.

Hybridization between members of different parid genera appears to be rarer still, especially given that hybrid offspring would tend to be more easily detected than those of congeneric species. Reported cases include Black-capped Chickadee × Tufted Titmouse (*B. bicolor*) hybrids (reviewed by Cockrum 1952); Coal Tit × Willow Tit mixed pairs (e.g. Hildén 1983); Blue Tit × Great Tit mixed broods or possible hybrids (Shy 1982, Godin 1984); a possible cross between Marsh Tit and Great Tit (Duquet 1995 cited in Randler 2004); apparent Great Tit × Coal Tit crosses (e.g. Fouarge 1996); and a few cases of hybrids between Willow Tit and Varied Tit (*Sittiparus varius*) in Japan (reviewed by Harrap and Quinn 1995).

Most reports of parid hybridization have involved infrequent mixing between species whose geographic ranges overlap extensively. Mixed pairing appears to occur most often at localities where one of the two species is rare (Randler 2002). Occasional mixing at an altitudinal interface by Black-capped Chickadees (lower elevation) and Mountain Chickadees (higher) represents a mosaic hybrid zone (see Gill 2004). Parid sibling species that hybridize where their parapatric distributions abut include Tufted Titmouse and Black-crested Titmouse (*B. atricristatus*) (contact zone in central

Texas), Oak (*B. inornatus*) and Juniper (*B. ridgwayi*) titmice (Modoc Plateau, northeastern California), and Blue and Azure tits (eastern Europe). Hybridization between Black-capped and Carolina chickadees represents, however, a unique combination within the Paridae: extensive hybridization between abundant birds that are not sibling species, along a contact zone that stretches across half a continent.

Chickadee Hybridization in Ohio

The recent work by C. Bronson and her colleagues has relied on molecular methods developed by M. Braun and students working out of the Smithsonian Institution. Those methods, which involve five species-specific molecular markers (three autosomal nuclear markers, one sex-linked nuclear marker, and one marker on the mtDNA), were first developed to analyze specimens collected from the Black-capped and Carolina chickadee contact zone in Missouri (Sawaya 1990). The same tools were then used to study chickadees collected from a transect across the Appalachian Mountains, where frequent hybridization and introgression were documented, along with minimal correlation between genotypes and morphology (Sattler and Braun 2000). A methodological advance in the work of Bronson et al. has been to extract DNA from blood samples, permitting genetic analysis of living birds. In all these studies, researchers have used the proportion of alleles at the five loci to assign a "genetic index" for each bird, with values ranging from zero for a bird having only Black-capped versions of the markers to one for a bird having only Carolina alleles.

The recent work in Ohio is the latest installment using this methodology to investigate the extended Black-capped and Carolina chickadee contact zone. It derives from Bronson's multifaceted doctoral dissertation research, completed under the direction of T. Grubb, Jr., at Ohio State University, in collaboration with Braun and Sattler. The study in this issue of *The Auk* (Bronson et al. 2005) is observational: it represents a classic approach of analyzing variation in genotypes, morphology, and reproductive success across a transect perpendicular to the line of parapatric contact between the two species. This contribution supplements related earlier work on the same system that was experimental, at two different levels.

In the first of the experimental studies, Bronson et al. (2003b) brought chickadees into captivity to investigate social relationships and mate preferences in detail. Employing a commonly used experimental design for studying mate choice, the researchers placed 20 female chickadees that were categorized as either Black-capped-like (i.e. "pure" Black-capped or nearly so, based on the genotype analysis described above) or Carolina-like individually in cages facing two adjacent cells, with each containing one male chickadee, from a pool of 20, that was also either Black-capped-like or Carolina-like. Observers then recorded the female's position in relation to the two cells, as an assumed index of relative mating preference for the corresponding males.

When females were allowed to see the males and to choose sides prior to any social interactions between the males (the males were physically and visually separated by an opaque barrier), most females of both species categories gravitated toward the side with the Black-capped-like male. However, the behavior of females changed after Bronson et al. removed the barrier and allowed the males to interact for 2 h, which was long enough for one male to exhibit dominance over the other. During this phase of the study, 7 of the 10 Carolina-like males asserted dominance over the Black-capped male with which they interacted, even though most of the Carolina-like males were smaller than their rivals, with the females watching the proceedings. When the males were again separated by the barrier and the females tested for their preference, most females of both species categories preferred the side of the dominant male, which correspondingly represented a bias in favor of Carolina-like males. Bronson et al. (2003b) concluded that behavioral dominance by Carolina Chickadees, by driving mate choice among females of both species within areas of range overlap, might account for recent northward movement of the contact zone, with Carolina Chickadees advancing at the expense of Black-capped Chickadees.

The second experimental study took place in the field (Bronson et al. 2003a). Bronson and her colleagues captured chickadees from both outside and within the contact zone and moved them in pairs to 35 woodlots within the contact zone where the researchers had previously removed resident chickadees. (Each woodlot

was large enough for just one breeding chickadee pair.) A methodological detail that has proven extremely useful in this and other studies of breeding chickadees is installing artificial nest snags constructed from plastic sewer pipe (Grubb and Bronson 1995) within each woodlot to increase the chances of having the pairs nest in locations accessible to researchers. Even so, most of the 174 pairs that Bronson et al. (2003a) released over four years disappeared, and the nesting attempts of many of the others failed for reasons independent of hybridization (e.g. predation).

Bronson et al. (2003a) then examined the pattern of success among the remaining 19 nesting pairs; the sample included 7 pairs from the Black-capped region north of the hybrid zone, 5 pairs from the Carolina region south of the hybrid zone, and 7 pairs from other sites within the contact zone. The objective was to control for geographic location and possible variation in habitat quality, to see whether hybrid-zone birds exhibited problems that might be a consequence of their own genotypes or those of their offspring; Bronson et al. (2003a) labeled this possibility the "endogenous" hypothesis. The alternative, the "exogenous" hypothesis, was that some aspect of the environment in the geographic location of the hybrid zone would instead cause reduced success of all birds, regardless of their origin.

The results of this study, despite limitations of sample size resulting from the difficulty of "convincing" experimental birds to nest in the woodlots, strongly supported the hypothesis that hybridization creates its own problems, independent of effects from the environment. In agreement with the study's assumptions, compatibility of pairs originating from hybrid-zone sites was lower than that of pairs drawn from both of the "pure" species zones to the north and south, with compatibility defined as the locus-by-locus similarity of the two members of each pair. When Bronson et al. (2003a) examined the number of nestlings produced as a function of the compatibility of each breeding pair, they found a significant positive relationship: pairs comprising genetically similar adults at the species-specific loci studied were more likely to produce surviving nestlings and fledglings. The key parameter affected by hybridization was hatching success, as suggested originally for these chickadees by Brewer (1963): eggs produced by mixed pairs were much less likely to hatch than eggs produced by pairs of genetically similar chickadees.

Geographic Patterns: Genes and Breeding Success

Bronson et al. (2005) have now added further support and resolution to our understanding of the patterns and consequences of hybridization between Black-capped and Carolina chickadees. In comparison with their transplantation study, the new paper takes a broader geographic view of hybridization: Bronson and her colleagues examined reproductive success of chickadees across a 23-km north–south strip of eastern Ashland County, Ohio, centered on Highway 250 near Rowsburg. Within this region, the team studied 29 breeding pairs and their nesting attempts, from 21 different sites, using data from two breeding seasons. As in the previous experimental study, Bronson et al. (2005) obtained blood samples from resident adults and relied on artificial snags to boost the sample of nests accessible for analysis.

The results of the new research directly parallel those of the transplantation study. Examining reproductive success as a function of north–south distance, Bronson et al. (2005) detected a roughly 50% trough in performance near the center of the geographic span. Again, the main cause of reduced success was poor hatching success. An added feature of the present study is the inclusion of traditional clinal analysis of allele frequencies across the landscape studied. The results clearly reveal genetic changeover from Black-capped Chickadees in the north to Carolina Chickadees in the south, though cline shape and position were not identical for the five loci examined. Values for the genetic index of both males and females, based on alleles at these loci, correspondingly changes from near zero in the north (Black-capped Chickadees) to near one in the south (Carolina Chickadees). Taken together, those results strongly support the study's assumption that the transect sampled spanned the contact zone in this part of Ohio. Bronson et al. (2003a) showed previously that the genetic index value for each bird also correlates positively with crude estimators of external appearance, including extent of white on the greater secondary coverts and outer tail margins and straightness of the bib, that distinguish the two species.

A general question raised by Bronson and her coauthors concerns the suitability of their particular indices of genetic identity and compatibility for exploring the structure and dynamics of a hybrid zone (see also Edmands 2002). The methods used in the Ohio studies have the advantage of diagnostically separable alleles evaluated additively; the compatibility of each pair is therefore based on the explicit likelihood of the pair to produce offspring with a mix of heterospecific alleles. As the authors note, the approach yields conservative analyses, because pairs comprising genetically similar hybrid adults receive relatively high compatibility scores. It is not yet clear whether the markers used in these studies are neutral, and thus whether they are direct and independent targets of selection as introgression takes place. Alternative approaches involving use of neutral markers, such as microsatellites, are providing insights in studies of hybridizing Darwin's finches (Grant et al. 2005) and chickadees (Reudink et al. 2005).

Parentage as a Complication in Hybridization Studies

A potential complication in research on avian hybridization arises from discrepancies between social and genetic mating systems. If researchers aim to test for a reduction in reproductive success or subsequent success of offspring as a consequence of hybridization, it is important to determine whether the offspring in nests tended by mixed pairs are indeed hybrids. Putatively hybrid offspring may not in fact be hybrids, if females socially paired with heterospecific males engage in successful extrapair copulations with conspecific males; precisely this pattern has been observed in hybridizing Collared (*Ficedula albicollis*) and Pied (*F. hypoleuca*) flycatchers in Scandinavia (Veen et al. 2001). Furthermore, broods assumed not to contain hybrids because of the identity of the social parents could include hybrid offspring resulting from extrapair copulations between females and heterospecific partners.

Bronson et al. (2003a, 2005) considered these possibilities in both of their field studies, but concluded that their analyses were unaffected because they found no extrapair paternity. This result is striking, because extrapair offspring (EPO) have been detected frequently in previous work on Black-capped Chickadees, as in several other species of parids: in a series of field studies in Ontario, L. Ratcliffe and her students have found that 29–50% of nests contain EPO, including 9–21% of all offspring (Otter et al. 1994, 1998; Ramsay et al. 2000; Mennill et al. 2004; Doucet et al. 2005). My students and I have found similar rates of extrapair paternity in Carolina Chickadees in southeastern Pennsylvania (R. Curry and A. Ruscica unpubl. data). Most recently, we have found even higher rates within the Black-capped and Carolina contact zone in Berks County, Pennsylvania, where at least 26% of nestlings in at least 56% of nests were EPO (Reudink et al. 2005).

There are at least three potential explanations for the absence of extrapair paternity in Ohio, although it occurs elsewhere. First, as discussed by Bronson et al. (2005), it seems unlikely that the Ohio result derives from an error associated with use of multilocus DNA fingerprinting for paternity analysis. That approach, while no longer used widely, has nevertheless produced informative results in a host of studies on many species, including chickadees (Otter et al. 1994, 1998). Although the higher rates detected in recent studies in Ontario and Pennsylvania are based on analysis of microsatellite markers, differences in methodology alone should not account for the disparity. Second, there could be substantive geographic variation in mating strategies such that chickadees in Ohio, both within and outside the contact zone, do not engage in extrapair copulations. Geographic variation in mating system within a species has been documented in some other taxa, so the differences in frequencies of EPO reported among the geographically separated chickadee studies are not completely extraordinary. A possible difference between the studies in Ohio and those in both Ontario and Pennsylvania concerns the landscape context of the work: whereas the work by Bronson et al. (2003a, 2005) involved birds breeding mainly in small, isolated woodlots, chickadees in the other studies were breeding within large areas of contiguous forest. It is conceivable that the Ohio birds had few opportunities for engaging in extrapair copulations because of the spatial arrangement of sites where they were studied. Third, the field methods used by Bronson and her colleagues for both studies examining reproductive success could have biased the paternity results: as

Bronson et al. (2005) suggest, the Ohio researchers, by catching birds at feeders, may have disproportionately sampled dominant pairs. Given that females of high-ranking chickadee pairs are known to engage less frequently in extrapair copulations than lower-ranking pairs (Mennill et al. 2004), the way in which Bronson et al. (2003a, 2005) conducted their fieldwork may have effectively eliminated extrapair copulations from their sample.

An additional potential source of extrapair parentage that merits consideration in hybridization studies is brood parasitism by conspecifics (Yom-Tov 2001) and—in a contact zone—by females laying hybrid eggs. (Quasiparasitism, in which the sire of a parasitic egg is the social male at the nest [Birkhead et al. 1990], is also a possibility, though not documented in parids.) Several cases of parasitism involving different species of parids have been reported, as revealed by a mixed set of eggs and brood care by pairs of both species (reviewed by Shy 1982). Intraspecific parasitism, as revealed by molecular parentage analysis, occurs rarely in Black-capped Chickadees (Mennill et al. 2004), in Carolina Chickadees (R. Curry and A. Ruscica unpubl. data), and within the hybridizing population in Pennsylvania (M. Reudink and R. Curry unpubl. data). Parasitism within a hybrid zone complicates analyses of reproductive success, because the odds are small that a parasitic egg's genotype would match those of other eggs in the nest (e.g. a hybrid egg added to a clutch of similarly hybrid eggs). Bronson and colleagues did not detect parasitism in their studies, so this phenomenon does not present any difficulties for their analyses. Nevertheless, researchers should be on the lookout for brood parasitism in such studies, especially among cavity nesters, both as a potential analytical complication and because heterospecific egg-dumping, followed by imprinting in the offspring that causes subsequent mixed pairing, represents a possible mechanism for the onset of hybridization (Hildén 1983, ten Cate and Vos 1999).

Questions for Current and Future Work

The research of Bronson and her team, including the present study, represents a major contribution to the literature on both avian hybridization and parid biology. Still, there is much we do not fully understand about chickadee hybridization. Key questions for further work concern historical aspects of the relationship, mechanisms of hybridization, structure of the contact zone, and reasons for ongoing changes in the location of the contact zone.

The historical biogeography of neither Black-capped nor Carolina chickadees is sufficiently well understood to evaluate fully the context of their hybridization. For example, no study has thoroughly addressed the question of when the two species first came into parapatric contact. Pleistocene glacial advances certainly must have affected the distributions of both species: the Black-capped Chickadee must have been pushed southward almost completely beyond its current range limit to refugia in the south (and perhaps east, on coastal nunataks). The Carolina Chickadee was likely pushed southward; a discontinuity in its mtDNA further suggests that this species was at some point separated into eastern and western populations (Gill et al. 1999). Whatever the timing, a striking aspect of the biology of Black-capped and Carolina chickadees is that their present range interface represents secondary contact between species that have been evolutionarily distinct for several million years, and are not each other's closest relatives. This context distinguishes this hybrid system from most of the others in the Paridae, but when and where did secondary contact begin? Has their lack of morphological differentiation coincidentally promoted hybridization because their ecology and social organization have remained so similar? Would reproductive isolating mechanisms have been more likely to evolve if these had been sister species—and are such mechanisms more pronounced, resulting in less frequent hybridization, between parid sibling pairs such as Black-capped and Mountain chickadees? Another notable detail is that Black-capped and Carolina hybridization occurs along a very long range border, and on both sides of the incomplete east–west divide within *P. carolinensis* noted by Gill et al. (1999). This suggests that the traits within Carolina Chickadees that promote hybridization with Black-capped Chickadees—whatever these may be—are relatively ancient.

These evolutionary issues prompt researchers to address questions about proximate mechanisms, such as sexual imprinting (Grant and Grant 1997, Irwin and Price 1999, ten Cate and Vos 1999), that facilitate mixed pairing

or extrapair copulations involving birds of different species. The aviary experiments of Bronson et al. (2003b) showed that the chickadee system is no exception in terms of prompting such proximate questions. However, the importance of dominance in comparison with several other potentially important factors, as they affect both social pairing and extrapair mate choices, remains to be determined. Pair formation in chickadees is believed to take place in fall or winter while the birds live in stable flocks, and dominance clearly is one of the factors that determines the pattern of pairing in Black-capped Chickadees (Smith 1991, 1993). However, there may be more to pairing in chickadees than just social rank: recent work has suggested that plumage brightness may have an even stronger influence on mating behavior than dominance alone (Mennill et al. 2003, Doucet et al. 2005).

Whether and how these factors contribute to chickadee hybridization is not known, because no work on dominance or its correlates, such as plumage brightness, has been completed for free-living birds in any part of the contact zone. Indeed, it is not even clear whether dominance within winter flocks plays the same role in pairing in Carolina Chickadees, because the social organization of that species has been little studied (Mostrom et al. 2002). The task of evaluating the role of dominance in the hybrid zone is all the more daunting because of the extent of hybridization, combined with the phenotypic similarity of the two parental species. In southeastern Pennsylvania, at least, populations in the heart of the contact zone comprise mainly hybrid individuals, with few if any "pure" birds (Reudink 2004, R. Curry unpubl. data).

In many songbirds, male advertising song serves as a major influence on choices of social mates and as a barrier to hybridization (see Remsen 2005). Hybridization can result if normal processes of song-learning break down. However, the whistled song of chickadees can probably be ruled out as a primary reason for formation of mixed chickadee pairs, because chickadees generally produce these vocalizations only in spring, just before egg-laying and long after pairs have formed within winter flocks (Smith 1991). Still, this does not necessarily mean that vocalizations are irrelevant to hybridization in chickadees: singing behavior has been shown to influence extrapair mating decisions in Black-capped Chickadees (Mennill et al. 2002, Mennill and Ratcliffe 2004). If female chickadees in contact-zone populations are similarly influenced, hybrid offspring could result from extrapair liaisons influenced by song contests among males.

How this all may work in the chickadee hybrid zone is especially intriguing, because at least some males are capable of producing the typical whistled song of both species ("bilingual" males), whereas other males give only the song of one of the two species, but not necessarily one matching their own genotype (Rossano 2003; R. Curry and M. Reudink unpubl. data); these observations are consistent with an aviary study that suggests that both species are capable of learning several vocal variations (Kroodsma et al. 1995). The vocal diversity of chickadees in the hybrid zone is particularly striking given the extraordinary stereotypy of the simple whistled song of the Black-capped Chickadee across almost its entire broad geographic range (Kroodsma et al. 1999). Social learning of song, and misimprinting because of early experiences, in a mixed chickadee population could cause females to mate with heterospecific males in a variety of complex ways that have yet to be studied in detail.

A third set of questions regarding chickadee hybridization concerns the evolutionary dynamics of contact-zone populations. The work by Bronson et al. (2003b, 2005) showing reduced reproductive success of mixed pairs represents a beginning: their data support the idea that chickadee hybridization involves a tension zone, where parental species mix but are penalized evolutionarily because their offspring are both few and of low fitness in comparison with offspring of pure pairs. The long-term dynamics of the system will depend, however, not just on patterns of hatching and fledging success, but also on the subsequent viability, fertility, dispersal, and breeding behavior of hybrid offspring over successive generations. Tackling these aspects of the system directly will not be easy, because so much detailed information would be required. Tracking the relative success of individual hybrids is feasible on an island such as Daphne Major in the Galapagos (Grant and Grant 2002), but dispersal distances of chickadees seem to be great enough (Weise and Meyer 1979) to make it impractical to accumulate large amounts of unbiased data.

An alternative way to address questions about contact-zone dynamics is indirectly, through examination of expected correlated patterns. An example of this type of analysis concerns Haldane's rule, which predicts in birds that problems of fecundity or viability deriving from hybridization will affect females, the heterogametic sex, most severely; this could result in a sex ratio skewed toward males. Bronson et al.'s (2005) data include some support for such a skew, because all the birds sampled with intermediate genetic index scores (i.e. hybrid individuals) were males. However, in our work in Pennsylvania, my students and I have observed many hybrid individuals of both sexes (Reudink et al. 2005). We have also investigated Haldane's rule more directly by examining sex ratio of nestlings in a contact-zone population, especially within broods where some eggs failed to hatch, but we did not find strong support for a bias toward males (Cornell 2001; R. Curry et al. unpubl. data). If there is no sex-ratio skew among nestlings, data regarding survival of hybrid males and females would be needed to explain the pattern noted by Bronson et al. (2005).

Contact-zone dynamics lead, finally, to questions concerning movement of the Black-capped and Carolina hybrid zone. That the chickadee contact zone has been shifting rapidly northward in recent decades is clear. As summarized by Bronson et al. (2005), hybrids in Ohio now occur north to northern Ashland County, well beyond the limit described in previous regional surveys. Similarly, all birds collected in the early 1980s in Eckville, Pennsylvania, adjacent to Hawk Mountain Sanctuary, had Black-capped mtDNA, leading Mack et al. (1986) to estimate that the collection site was 24 km north of the contact zone at that time. Analysis of mtDNA from birds collected at the same site in 1988 supported the same conclusion (Mullen 2001). However, analysis of haplotypes of birds sampled at Hawk Mountain in 2000–2004 has shown that as many as 25% of the resident birds now carry Carolina mtDNA (Reudink 2004; R. Curry and M. Reudink unpubl. data). Additional evidence from Pennsylvania involves observations of song structure. As of the late 1960s, birds singing songs of both species or variant versions of the parental songs were known from Lancaster County and Chester County (Ward and Ward 1974). Today, however, all birds at the same localities give Carolina songs only; whereas most males in the population at Nolde Forest near Reading, where all males produced exclusively Black-capped songs as recently as 1997, now are "bilingual" and have Carolina mtDNA (Rossano 2003, R. Curry unpubl. data).

The apparent preference for socially dominant Carolina males among both Black-capped and Carolina females measured in Bronson et al.'s (2003b) aviary experiments suggest a possible proximate explanation for shifts in the contact zone. Such biases could translate into an asymmetry in mating success in the field, through an advantage either in pairing or in extrapair copulations. Data from our Nolde Forest population in Pennsylvania are consistent with this hypothesis: females socially paired with Black-capped-like males were disproportionately likely, irrespective of their own genotype, to have extrapair offspring in their nests, and the sires of those nestlings were genetically more Carolina-like than the corresponding social fathers (Reudink et al. 2005). A difficulty of the hypothesis, however, is its assumption that populations exist where both Carolina and Black-capped females have the option of mating with males of both species. Whether such populations exist is questionable: data from sites such as Hawk Mountain seem to indicate that the hybridization process begins when Carolina-like females move into "pure" Black-capped populations (Reudink 2004, M. Reudink and R. Curry unpubl. data), a pattern that is consistent with the general trend toward female-biased natal dispersal among passerines. If northward movement of the chickadee contact zone thus depends initially on matings between Carolina females and Black-capped males, dominance relationships between males of the two species might not be critical, at least not until after considerable mixing and further immigration have occurred.

Even if a mechanism involving dominance operates at a proximate level, explicit ultimate explanations for the observed northward shift are lacking. It is tempting to invoke mechanisms involving climate change (global warming), for several reasons. First, the overall distribution of the two species correlates well with climate patterns: not only does the overall east–west line of contact match up well with thermal isoclines across the continent, but the southward dip of the range interface into the Appalachians, with Black-capped Chickadees occupying higher elevations, is also consistent with the idea that

Black-capped and Carolina chickadees have different climate tolerances. If temperature increases are occurring in the latitudes where the species abut, Carolina Chickadees may be gaining a fitness advantage that is facilitating their northward advance at the expense of Black-capped Chickadees—but we do not yet know if critical physiological differences between the species exist. Alternatively, climate change could be causing a northward shift in some ecological factor, such as the distribution of a key food resource, but this possibility remains entirely speculative because whether the species differ in dietary requirements is unknown. One aspect of the system seems clear: the range interface does not match up in any obvious way with a discontinuity in habitat type. Northward movement of the contact zone is occurring in regions where there is no abrupt boundary in terms of major vegetation assemblages, and at a rate that is too fast to be explained by changes in the geographic distributions of particular plant species. Determining whether and how the chickadee contact zone is dependent on ecological factors, and on changes in those factors over time, represents a major area of further work on this system.

The research of Bronson et al. has established a solid foundation on which future studies addressing a wide variety of questions about chickadee biology in particular, and avian hybridization in general, can be based. As additional research approaches are pursued and integrated in the future at all levels of explanation, the opportunity exists to make the interbreeding of Black-capped and Carolina chickadees a textbook example of avian hybridization. That such a rich and important set of questions can be addressed through studies of abundant backyard birds underscores a fundamental fact of ornithology: there is always much to be learned about even our most familiar avian neighbors.

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