

Parid reproductive behavior

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North American Parids are excellent organisms for research on the evolution of avian reproductive behavior, and how these are influenced by intra- and interspecific interactions. As cavity-nesting birds, they exhibit high reproductive success and populations of most Parid species exist in high numbers throughout their range. As social birds, their reproductive behavior is shaped by group dynamics, including flock hierarchy and territorial behavior. Being non-migratory, their behavior can be studied throughout the year, and their breeding activities can be easily related to their non-breeding activities. This section of the book covers a diversity of topics within the general field of Parid reproductive behavior, using ongoing research on several species of North American chickadees. The various chapters discuss: phylogenetic structure within populations, hybridization between closely related species, nesting ecology, and the influence of social dominance on reproductive biology.

Chapter 6 examines the phylogenetic structure of chestnut-backed chickadee populations in western North America and compares the resulting patterns to those found in other North American and Eurasian Parids. Chestnut-backed chickadees are associated with cedar-hemlock ecosystems, and their movement into an area is dependent on the availability of suitable habitat. Much of the chestnut-backed chickadee's current range was glaciated during the Pleistocene and was recolonized following the retreat of the Cordilleran ice sheet. Four genetically distinct groups are recognized: Queen Charlotte Islands; southeastern British Columbia; mainland Alaska; and a large coastal group. Several

scenarios may explain the current distribution patterns found in chestnut-backed chickadees: multiple colonizations from a single refugium, colonization from multiple refugia, or a single colonization from a single refugium and possible introgression. Northern populations possess a large number of alleles that are absent in other populations, indicative of prolonged isolation. Whether this isolation is the result of historical isolation in different glacial refugia or different founding populations is not known. The second pattern that emerged from studying the phylogenetic structure of chestnut-backed chickadees is that disjunct and peripheral populations are genetically isolated from the central core population. A similar pattern is found in other Eurasian and North American Parid species. Dispersal across large expanses of unsuitable habitat and between the periphery and core portions of the species range appear to be limited, resulting in population substructuring.

Future phylogenetic research may determine the origin of the private alleles in the northern populations of chestnut-backed chickadees. Is the large number of unique alleles the result of hybridization with another species, such as the boreal chickadee? Hybridization between two brown-capped chickadee species has not been reported; however, hybridization between several other Parid species is common (Curry 2005; Chapter 7). Do other populations of chestnut-backed chickadees in the interior Pacific North-west show the same pattern of differentiation as the south-eastern British Columbia population? Similarly, are we able to determine the source population of the recent

expansion into central California? On a larger scale, further studies need to be conducted examining population structure in other chickadee species, expanding on the previous work by Gill *et al.* (1993, 2005). Are the patterns of peripheral isolation and isolation of disjunct or island populations found in chestnut-backed chickadees—as well as preliminary studies of other North American chickadees—present when more extensive sampling is conducted? By addressing these questions, we can further increase our understanding of movements and speciation in Parids.

Chapter 7 continues on this theme by examining the behavioral aspects of hybridization along the extended contact zone between black-capped chickadees and Carolina chickadees in south-eastern Pennsylvania. Intensive field research in this contact zone since 1998 has focused on three large study sites, with a specific focus on variation in vocalizations among color-banded individuals, while concurrently investigating genetic variation among and within the populations. The most striking finding concerns discrepancies between the songs, calls, and genotypes of chickadees at a geographically intermediate site. Within this population, which mainly comprises hybrid individuals, up to half of all males are “bilingual,” singing the typical songs of both black-capped and Carolina chickadees. The rest of the males sing only black-capped songs, although the proportion of the population falling into this category has gradually declined over time. This pattern of song variation probably represents cultural persistence of learned behavior. Virtually all males in the population have Carolina mitochondrial DNA, and no overall difference in nuclear genotype, assessed using microsatellite DNA, is apparent between the two types of males based on songs. On the other hand, characteristics of the *dee* note of the *chick-a-dee* call of the same birds are intermediate between those of black-capped and Carolina chickadees; call characteristics show no apparent correlation with either song category or genetic background.

Numerous unresolved questions about behavioral mechanisms associated with Parid hybridization remain, both in the black-capped/Carolina chickadee contact zone and for other members of the family more broadly. Most investigators have

assumed or concluded that vocalizations play key roles in species recognition within the Parids. However, it seems clear that song development, and possibly song recognition, in most (if not all) Parids involves strong learning components (see also Section III). Accordingly, the vocal behavior of an individual male may inaccurately reflect its genotype, but whether hybridization results from female mate choice contingent on song features remains incompletely tested. A second, and possibly independent, aspect of Parid behavior that could exert a strong influence on pairing patterns is social dominance. Extensive results from black-capped chickadees have revealed that dominance rank strongly influences both pairing success and mating fidelity (Ramsay *et al.* 2000; Mennill *et al.* 2004; Chapter 9). Research on captive birds from the hybrid zone has further suggested that mate choice may depend mainly on relative dominance, more so than vocal or physical phenotype (Bronson *et al.* 2003). Nevertheless, work on black-capped chickadees has also shown that both singing behavior (e.g. Otter *et al.* 1997; Mennill *et al.* 2002) and plumage coloration (Doucet *et al.* 2005) relate to patterns of extrapair paternity and reproductive success. Studies using both observational and experimental approaches to thoroughly evaluate the relative strengths of social dominance, song, and plumage features within Parid hybrid zones are needed to produce clearer resolution of the behavioral mechanisms underlying hybridization in the family. Further research on vocal development, through experimental studies of captive birds subjected to various acoustic and social stimuli, represents an additional area with great promise for advancing our understanding of the role of vocal behavior in Parid hybridization.

Interspecific interactions can also influence reproductive ecology in manners other than hybridization, and these are not limited to include only other Parids. Chapter 8 examines the nesting biology of black-capped and mountain chickadees and their ecological relationships within cavity-nesting vertebrate communities. Parids live in communities structured by hierarchical guilds termed nest webs whereby some species depend on others to produce cavities for breeding or roosting, and interspecific and intraspecific interactions are

centered around nest site availability (Martin and Eadie 1999). Despite similar size, ecology, and coexistence on the same sites, mountain and black-capped chickadees exhibit strong segregation in nesting habitats in the mixed forests of central British Columbia. From 1995 to 2004, mountain chickadee numbers showed a strong increase, with similar increases in their small bodied competitors (red-breasted nuthatches) and potential predators (red squirrels), and also a strong reduction in the health of conifer trees, especially lodgepole pine. Overall nesting densities of mountain chickadees were positively correlated with the proportion of lodgepole pine trees that had been attacked by bark beetles, nesting densities of red-breasted nuthatch and downy woodpeckers, and negatively correlated with density of red-naped sapsuckers, red-breasted nuthatches, and tree density. Nest density of mountain chickadees was significantly greater in years of high beetle and western spruce budworm abundance. Population growth rates demonstrated strong negative density-dependent responses to chickadee density the previous year, but were enhanced by an abundance of forest insects and density of trees, and reduced by high abundance of red squirrels. Thus mountain chickadees show strong functional and numerical responses to pulses in resource availability despite strong increases in their competitors and predators.

While mountain chickadees showed the strongest ability to adapt to local differences in habitat conditions, black-capped chickadees declined in density in 2003 and 2004. Since black-capped chickadees are behaviorally dominant to mountain chickadees and able to excavate their own cavities, it is puzzling why they were not able to capitalize on the resource pulse in the enhanced habitat conditions. It is interesting that black-capped chickadees, reasonably strong excavators, could not respond to the increase in forest insects to the same extent as mountain chickadees; perhaps an ecologically-equivalent situation to subordinate blue tits depressing reproductive success of the dominant great blue tits in sympatric populations. Martin and Norris assumed that the functional and numerical responses observed were driven by local pulses in resource availability or mild winter conditions. However, it is possible that some of the

temporal changes observed in chickadee abundance were driven by larger-scale environmental or ecological influences, as the dramatic changes in annual fecundity of mountain chickadees they observed in 2005 were similar to those observed in the Sierra Nevada. Future research exploring regional- or continental-scale patterns of Parid breeding biology will help elucidate these critical influences on demography.

Within-species, reproductive potential may be influenced by social interactions, especially by the dominance hierarchies established in wintering chickadee flocks. The naturally- and sexually-selected fitness consequences of social dominance, the mechanics of dominance interactions, and the relationship between dominance and lifetime reproductive success in black-capped chickadees are explored in Chapter 9. Data from over 10 years of research on the dominance relationships and breeding behavior of black-capped chickadees at Queen's University Biological Station in eastern Ontario show that social dominance rank plays an important role in structuring several aspects of an individual's life history, from winter flock behavior to territorial behavior and reproductive activities. Dominant and subordinate birds show distinct phenotypic characteristics (e.g. enhanced plumage contrast, higher song output for high-ranking males) and life history characteristics (e.g. higher nesting success, larger clutch sizes for high-ranking males). Longitudinal and cross-sectional analyses of survival and reproduction show that social rank is a better predictor than age of individual survival from one winter to the next. In common with other avian life history studies, lifespan was the best predictor of average lifetime reproductive success. However, male rank history also influenced lifetime realized reproductive success: individuals that attained higher rank earlier had more offspring.

Dominance relationships mediate social interactions in many Parids, and future studies should explore how widespread are these patterns among the Paridae. Future research exploring the early ontogeny of social rank, as well as attributes associated with high and low rank such as plumage color and singing behavior, is needed. The process of flock formation in the autumn requires more careful behavioral study, as this period of the

annual cycle of black-capped chickadees has been neglected in the eastern Ontario studies.

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