SYNOPSIS I

Proximate mechanisms in behavior and evolution

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Chickadees and tits have long been known as highly tractable subjects for research in behavior and ecology. Studies of Eurasian tits and North American chickadees have made substantial contributions to our understanding of breeding phenology (Chapter 4; Chapter 5), food-storing (Chapter 2; Chapter 3), social behavior (Chapter 9), communication (Section III), foraging, and other topics. More recently, research on the Paridae has begun to address questions about the proximate neural and neuroendocrine causes of behavior. There are many reasons for the intense focus on these small, familiar birds. Most Parids are relatively tame, year-round residents that live in small home ranges and are easily attracted to feeders. Some, such as great and blue tits, readily breed in artificial nest boxes (though the most intensely studied North American Parid, the black-capped chickadee tends not to). These traits make it possible, at least in principle, to obtain complete observations on development, social organization, communication, and reproduction in individually-marked birds over their entire lifetime. In both North America and Eurasia there are enough species to permit comparative analyses, and some species, such as the black-capped chickadee, have distributions large enough to permit comparisons between populations living in very different environmental conditions (Chapters 3 and 5).

Most chickadees and tits thrive in captivity. Early in the 1700s Baron von Pernau kept marsh tits in his room to observe their food-storing behavior (Stresemann 1947). The ease of holding birds in captivity has made possible a great deal of research on behavior, cognition, and neurobiology in species for which there is extensive information on behavior in the wild (Chapters 2, 3, and 4). The integration of field and laboratory work has, for example, led to advances in research on control of the annual cycle. Although temperature, food supply, and other factors exert important effects on the timing of reproduction, photoperiod is the stimulus that initiates the sequence of events leading to gonadal recrudescence, mating, egg laying, and parental care. These behavioral and physiological changes are not, strictly, controlled by day-length but instead, as Phillmore and MacDougall-Shackleton describe, by an annual cycle in sensitivity to day-length. Successive stages of photorefractoriness and photosensitivity prepare birds to respond to increasing day-length in spring and initiate breeding. These responses include change in size of the song control nuclei HVC and RA, and the recruitment of new neurons into these structures. Some recent research also shows an annual pattern in the recruitment of new neurons into the hippocampus and change in the overall size of this structure, but data from different studies have not been consistent. There are different opinions about the function of such patterns (Chapter 3) and seasonal change in the hippocampus continues to be a topic of active investigation.

Remarkably, for both the song control nuclei and the hippocampus, laboratory and field studies present rather different pictures. Change in the size of song control nuclei can be produced in the laboratory by manipulating photoperiod but is not found in samples of birds taken from the wild at different times of year. In contrast, change in the size of the hippocampus has been found in samples of birds collected in the field but does not occur when photoperiod is manipulated in the laboratory. There are a number of possible explanations for these seemingly contradictory outcomes, discussed by Phillmore and MacDougall-Shackleton in Chapter 4. These results illustrate, however, one of the significant challenges for research on chickadees and tits, and other passerines, as well. In many field studies, samples are collected from wild populations at different times in order to understand changes occurring over time within individuals. The conclusion that change in a temporal series of samples represents change within a typical individual is, however, an inference. When annual change is observed in samples collected in the wild, as is the case for hippocampal size, the observed change may occur not because of annual change within individuals but because of demographic changes in the population from which the samples are drawn (Chapter 3). In the laboratory, control over diet, housing, temperature, and the timing of experimental manipulations may make it possible to detect annual change within individuals, for example in the song control nuclei, that is masked in samples collected from the wild because individuals undergo annual change out of phase with each other or exhibit other individual differences (Chapter 4).

The many influences on behavior and physiology in the wild may lead to a more complex determination of events such as the timing of laying than might be suspected from laboratory studies. As Ramsay and Otter (Chapter 5) describe, there is considerable variation among females in the timing of laying, which probably reflects variation in the ability to obtain the resources for egg production, heritable and perhaps adaptive variation in response to environmental cues, and exposure to varying environmental conditions. Although a great deal is known about factors that influence the timing of laying in females, there has been much less work, as Ramsay and Otter describe (Chapter 5), on fertility in males, who are exposed to the same environmental cues as females but face the problem not of timing hatch to the peak in insect food for the young but timing sperm production to the peak in female fertility.

As a buffer against environmental variation in food availability, many chickadees and tits, though not all, have available to them the tactic of food storing. A food-storing chickadee can create many thousands of food caches over the fall and winter and these caches make an important contribution to over-winter survival. Caches are widely scattered over the bird's home range and chickadees and tits have been shown to retrieve stored food by remembering where they put it. Remembering large numbers of scattered spatial locations for up to several weeks is a striking cognitive achievement and a great deal of recent research, described by Sherry and Hoshooley (Chapter 2), has investigated exactly how chickadees and tits manage this feat. Controlled studies tend to show that chickadees and tits are sometimes not much better than other birds at laboratory spatial memory tasks. What chickadees and tits do possess is a predisposition to solve problems spatially, rather than by using non-spatial cues such as color or form. Food-storing birds, including Parids, also have a hippocampus that is dramatically larger relative to the size of the rest of the brain than the hippocampus of non-storing birds such as thrushes, sparrows, and wood warblers. The hippocampus is a forebrain structure found in both birds and mammals and is known to play a role in a variety of cognitive functions, including spatial memory (Chapter 2). The enlarged hippocampus of food-storing birds may thus provide new information on the evolution of the brain and the neural basis of spatial cognition.

Despite a great deal having been learned about the behavior and brain of food-storing Parids, much basic information remains tantalizingly out of view. As Pravosudov (Chapter 3) points out, there is little solid evidence on the exact annual pattern of food storing in chickadees. There is conflicting evidence about how long chickadees leave their caches in place before retrieving them, and, as noted above, about seasonal changes in the brain of food-storing chickadees. There is current debate over whether differences in the size of the hippocampus that occur between food-storing and non-storing families of birds (Krebs *et al*. 1989; Sherry *et al*. 1989) occur within families like the Paridae that contain both storing and non-storing species (Brodin and Lundborg 2003; Garamszegi and Eens 2004; Lucas *et al*. 2004; Garamszegi and Lucas 2005). There is also controversy over whether recently reported differences between North American and European Parids in the relative size of the brain and hippocampus (Lucas *et al*. 2004; Garamszegi and Lucas 2005) are simply the result of procedural differences between laboratories (Pravosudov and de Kort 2006) or the consequence of differences in life history traits (Garamszegi and Lucas 2005). Research on food storing would benefit enormously from an omniscient glimpse of just one annual cycle of the caching activity of the members of a single, winter flock of chickadees and the fate of the food they stored. Better make that ten annual cycles, to deal with year-to-year variation in seed and insect abundance, flock demographics, weather, habitat change, and other factors that influence food storing behavior. Short of such omniscience, however, a clearer partial picture of food caching in the wild would still be invaluable.

As with the discovery of large capacity long-lasting spatial memory in food-storers, research on the Parids continues to uncover new and unexpected properties of proximate mechanisms of behavior. Research described by Pravosudov (Chapter 3) on the influence on memory of corticosterone—an adrenal steroid that plays an important role in energy metabolism, stress and immune function—is a good example. Unlike previous results, which tend to show a positive effect on memory of acute corticosterone elevation and a negative effect of chronic elevation, mountain chickadees show a positive effect on spatial memory of prolonged, moderate corticosterone elevation.

The future of research on proximate mechanisms of behavior will surely lie in controlled laboratory studies of the neural and neuroendocrine causes of behavior. Along with the control and repeatability of laboratory research, however, comes the risk of losing touch with the natural history of behavior that both inspires new questions about proximate mechanisms (Sherry 2005) and grounds studies of causation with reliable information about how chickadees behave in the wild. Field studies remain the indispensable source of new questions about the Paridae and the raison d'être for bringing to bear the powerful techniques of laboratory research.

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