

NEUROECOLOGY

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■ **Abstract** Neuroecology is the study of adaptive variation in cognition and the brain. The origin of neuroecology dates from the 1980s, when researchers in behavioral ecology began to apply the methods of comparative evolutionary biology to cognitive processes and the underlying neural mechanisms of cognition. The comparative approach, however, is much older. It was a mainstay of ethology, it has been part of the study of neuroanatomy since the seventeenth century, and it was used by Darwin to marshal evidence for the theory of natural selection. Neuroecology examines the relations between ecological selection pressures and species or sex differences in cognition and the brain. The goal of neuroecology is to understand how natural selection acts on cognition and its neural mechanisms. This chapter describes the general approach of neuroecology, phylogenetic comparative methods used in the field, and new findings on the cognitive mechanisms and brain structures involved in mating systems, social organization, communication, and foraging. The contribution of neuroecology to psychology and the neurosciences is the information it provides on the selective pressures that have influenced the evolution of cognition and brain structure.

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INTRODUCTION

Neuroecology is the study of adaptive variation in cognition and the brain. It uses experimental and comparative methods to understand the evolution of animal cognition—specifically the effects of natural and sexual selection on cognition—and identifies correlations among ecological selection pressures, cognition, and brain structure. Although neuroecology focuses on behavior that animals exhibit in nature, it uses experimental laboratory methods to investigate cognition and comparative anatomical methods to examine the neural correlates of cognition.

Comparative neuroanatomy and the comparative study of behavior have long histories (Darwin 1872, Kruger 2004, Nieuwenhuys 1998, Striedter 2005, Tinbergen 1963). The origins of neuroecology are more recent, however, and are found in the rapid growth of behavioral ecology (Krebs & Davies 1978, 1997). Behavioral ecology examines the function and adaptive significance of animal behavior, especially animal social behavior, using mathematical models to develop theory and empirical field and laboratory research to test predictions derived from theory. Behavioral ecology was initially concerned almost exclusively with the function and evolution of behavior but later began to address causal questions about behavior, particularly questions about the role of learning, memory, and cognition in adaptive behavior. Neuroecology grew out of this interest in causal mechanisms. It examines the cognitive processes and neural structures that underlie adaptive behavior.

Neuroecological research has examined the relations between cognition and the brain in the context of mating systems, social organization, communication, and foraging. This article begins by describing an example of neuroecological research on the relation between mating system, spatial ability, and the mammalian hippocampus. This is followed by a discussion of comparative methods used in neuroecology and a review of recent research on several current topics including food storing and the avian hippocampus, sex differences in the hippocampus, the neural control of birdsong, behavioral innovation and the forebrain, and social and nonsocial influences on the evolution of the primate brain.

Mating System, Spatial Ability, and the Hippocampus: A Case Study in Neuroecology

Meadow voles (*Microtus pennsylvanicus*), like most mammals, are polygynous. Males compete for mates in a scramble competition in which a large home range

and superior spatial ability provide a competitive advantage (Spritzer et al. 2005a,b). Male home ranges are larger than are those of females, and encompass the territories of multiple females (Gaulin & FitzGerald 1986, 1989). Males perform better than females on controlled laboratory tests of spatial ability (Gaulin & FitzGerald 1989). Males with better spatial ability, assessed in the Morris water maze, have larger home ranges, visit the nests of more females, and revisit their most preferred females more often than do males with poorer spatial ability (Spritzer et al. 2005b). Males that visit the most females produce more offspring. Spritzer et al. (2005b) found, however, that although males with better spatial ability produced more offspring than did males with poorer spatial ability (4.85 ± 1.41 versus 4.00 ± 1.37 pups) this difference was not significant. They concluded that the relatively high density of female nests in the seminatural outdoor enclosures used in their studies might have reduced the advantage that males with better spatial ability would experience under more natural conditions.

Remarkably, female meadow voles that are offered a choice of mate in the laboratory prefer to mate with males with better spatial ability (Spritzer et al. 2005a). It is not clear by what mechanism female mate choice favors males with better spatial ability, but testosterone levels affect male spatial ability (Galea et al. 1999), and females are known to distinguish olfactorily among males with different testosterone levels (Ferkin et al. 1994, Leonard et al. 2001).

Pine voles (*Microtus pinetorum*) and prairie voles (*Microtus ochrogaster*), unlike most species of vole, are monogamous. Males of these species associate with females during reproduction, provide paternal care, and have home ranges equal in size to those of females (FitzGerald & Madison 1983; Gaulin & FitzGerald 1986, 1989).

While polygynous male meadow voles perform better than females on standardized tests of spatial ability, there is no sex difference in spatial ability between monogamous male and female pine voles (Gaulin & FitzGerald 1986) or prairie voles (Gaulin & FitzGerald 1989). Experiments show that activity levels and spatial experience cannot account for these species-specific sex differences (Gaulin et al. 1990, Gaulin & Wartell 1990).

Not only do male and female meadow voles differ in home range size and spatial ability, but males also have a larger hippocampus than females, a sex difference not found in monogamous prairie voles (Jacobs et al. 1990).

The relations discovered between vole mating system, home range size, spatial ability, and size of the hippocampus illustrate the major features of research in neuroecology: a focus on naturally occurring behavior and the coupling of comparative analysis of cognition with comparative analysis of the brain. The general conclusion drawn from this work is that different mating systems in *Microtus* have subjected males and females to different selective pressures. Intrasexual competition among male meadow voles for mating opportunities has resulted in sexual selection for increased home range size in males, accompanied by selection for spatial competence required to navigate a larger home range. Female meadow voles are unaffected by this selective pressure, although their preference to mate with

males with better spatial ability may result in additional intersexual, or epigamic, sexual selection for spatial ability in males. Selection for spatial ability has produced evolutionary change in one of the neural structures that serves spatial ability, the hippocampus. Among monogamous voles, males do not compete for mates by increasing their home range size and so sex-specific selective pressures on spatial ability and the hippocampus are absent. This association between mating system, cognition, and the brain has led to further questions about the causes of sex differences in spatial ability and to new findings about neuroendocrine effects on hippocampal neurogenesis and spatial ability (Omerod & Galea 2003, Omerod et al. 2004). Sex-specific correlations between home range size and brain structure have been found in prefrontal and parietal cortex of meadow voles (Kavaliers et al. 1998) and in the hippocampus of polygynous rodents in other taxa (Jacobs & Spencer 1994, Sherry et al. 1996).

THE COMPARATIVE METHOD

Neuroecology makes extensive use of the comparative method. The comparative method was a staple tool in Darwin's arguments for the efficacy of natural selection in producing evolutionary change (Darwin 1859) and has been used ever since to analyze adaptation. Ethologist Esther Cullen used the comparative method to understand differences in breeding behavior between ground-nesting gulls and cliff-nesting kittiwakes (Cullen 1957). Comparison of these two species showed that many of the differences in their behavior could be interpreted as adaptive modification of kittiwake parental care and ontogeny to nesting on narrow cliff ledges, with the attendant risk of falling into the sea. This comparison examined two closely related species that shared most of their evolutionary history and concluded that differences between them were the result of specific selective pressures acting on kittiwakes.

In psychology, research on animals is often described as "comparative" even in the absence of comparisons among different species because of the implicit comparison to humans. Some explicitly comparative research has examined the behavior of different species chosen because they represented what were thought to be higher and lower levels of complexity of a psychological process such as learning (Bitterman 1975). Comparative research of this kind foundered on the realization that the *scala naturae* was a poor model of evolutionary change (Hodos & Campbell 1969) and the realization that differences between species in a psychological process such as learning could only with great difficulty be disentangled from differences between species in perception, behavior, and responses to the conditions under which behavior was observed.

Most recent comparative research on behavior and the brain, including research in neuroecology, compares species selected with greater attention to phylogeny, the evolutionary genealogy of species. These comparisons can involve a small number of closely related species that differ in some important aspect of their

ecology or behavior such that differences discovered can be attributed to specific evolutionary selection pressures acting within an evolutionary history that is largely shared. Cullen's (1957) study of kittiwakes is an example of this approach, as is the research on voles described above. Other comparative research examines species that share a common feature of their ecology or behavior but are not closely related phylogenetically. In analyses of this kind, similarities between species, given their differing evolutionary histories, are attributed to the shared feature of ecology or behavior. Unrelated species of food-storing birds, for example, share some properties of memory and brain organization and are an example of this kind of comparative analysis (see Food-Storing Birds and the Avian Hippocampus, below). Phylogenetic comparative methods provide general statistical procedures for comparing species of any degree of relatedness and have become the standard in neuroecology.

Phylogenetic Comparative Methods

Phylogenetic comparative methods test for associations among traits using phylogeny—the evolutionary relations among species—to control for features shared by descent from a common ancestor. These methods, developed largely within biology in the 1980s, are statistically much more sophisticated than were earlier comparative techniques. This sophistication developed because statistical tests on data obtained on different species require a way of dealing with the nonindependence of these data caused by the evolutionary relations among the species examined.

The goal of comparative analysis is to determine whether there is a consistent association between characters of interest, such as size of the song repertoire and size of the song control nuclei of the avian brain, or between a character such as song and a feature of the environment. A character is any recognizable trait, attribute, feature, or property of an organism that can be used as the basis of comparison (Lincoln et al. 2001, Ridley 1996). Characters can be discontinuous, like the presence or absence of antlers, or continuous, like the size of a brain structure. Physical traits, behavior, social system, geographic distribution, population size, or any other attribute can be treated as a character in comparative analyses. If statistical tests show that an association among characters occurs more often than expected by chance, then it also shows that the characters tend to evolve together. If a character is consistently found in association with some feature of the environment, it is therefore likely that the character is an adaptation to that feature of the environment. The statistical advances in phylogenetic comparative methods deal with the fact that characters can also be associated with each other, or with a feature of the environment, not because of evolutionary adaptation but because of shared ancestry.

Closely related animals are similar to each other, a phenomenon called phylogenetic inertia. This observation is so obvious that we rarely ask why closely related animals are similar. Phylogenetic inertia, however, has at least three causes (Harvey & Purvis 1991). The first is that the time elapsed since two species

diverged may not have allowed for much change in the characters of interest. The second is that closely related animals tend to occur in the same ecological niche—fast-flowing streams or muskeg bogs, for example—and this environment exerts the same selective pressures on both species. The third cause of phylogenetic inertia is that responses to selection are affected by phenotype. The range of adaptive responses that closely related animals can make to changing selection pressures is very similar. For these reasons, many characters are similar in closely related animals. How can adaptive responses among characters, or between characters and features of the environment, be distinguished from characters that are shared as a consequence of phylogenetic inertia?

Independent Contrasts

Species are not drawn randomly from a common distribution in the way the null hypothesis of most statistical tests assumes samples of data are drawn from a common population. Species are instead points at the terminals of a hierarchically branching evolutionary tree (Figure 1), and this introduces the problem of statistical nonindependence (Felsenstein 1985, Harvey & Mace 1982). Similar nonindependence due to history, known as Galton's problem, occurs in comparative analyses of culture and language (Mace & Holden 2005). A number of solutions have been proposed, but the most widely accepted in current practice are variations on Felsenstein's method of independent contrasts (Felsenstein 1985). The method of independent contrasts requires that the true phylogeny of the species compared is known. The method of independent contrasts consists of taking contrasts, or difference measures, on pairs of points in the phylogenetic tree (Figure 2). Statistical tests can then be performed to determine whether the magnitude of contrasts in one variable is related to the magnitude of contrasts in another. Contrasts, unlike data for the species themselves, are independent because a contrast between Species A and Species B does not influence the contrast between Species C and Species D. Furthermore, these contrasts are independent of contrasts taken at higher branching points in the tree, such as the contrast between the mean value for Species A and B and the mean for Species C and D. The logic is similar to that of orthogonal comparisons in conventional statistical analysis. In a phylogenetic comparative analysis, a data set of n species will yield $n - 1$ independent contrasts.

The method of independent contrasts requires an accurate phylogeny for the group of animals under study, and Felsenstein saw this as the principal limitation of his method (Felsenstein 1985), but as more phylogenies become available through the use of molecular techniques, the method of independent contrasts has become the preferred statistical procedure in comparative analyses of behavior and the brain (MacDougall-Shackleton & Ball 1999, Madden 2001, Nicolakakis & Lefebvre 2000, Reader & Laland 2002). As Harvey & Purvis (1991) point out, obtaining a satisfactory phylogeny is not always straightforward, and any phylogeny has built into it implicit or explicit assumptions about how evolution works. Different assumptions can lead to different phylogenetic trees, and these different trees can

Poecile

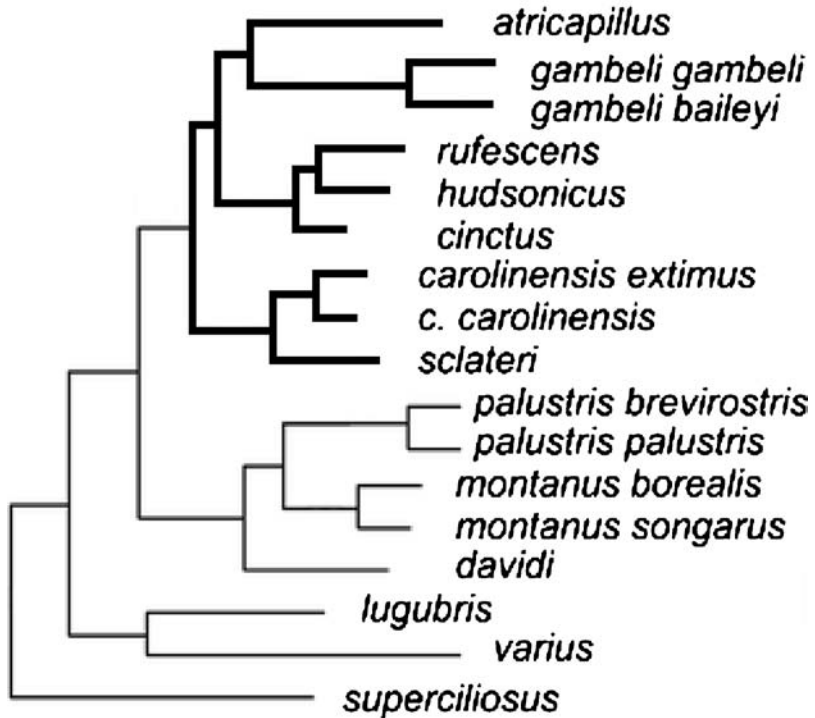


Figure 1 Phylogeny of the genus *Poecile*, part of a larger phylogeny proposed by Gill et al. (2005) for the family Paridae, the chickadees and tits. Associations among characters in this genus will be strongly influenced by the many North American members of the group (heavy lines). These species are closely related and are likely to share characters as a consequence of common descent, making data obtained on them nonindependent. Redrawn with permission from Gill et al. (2005).

sometimes lead to different conclusions about adaptive relations among characters or the relation of characters to a feature of the environment (Iwaniuk 2004). A solution to the problem of imperfectly resolved phylogenies that Harvey & Purvis (1991) describe is sensitivity analysis, essentially performing the comparative analysis using each plausible phylogenetic tree and then determining to what extent the conclusions depend on phylogeny.

Phylogenetic Signal

Two further aspects of phylogenetic comparative methods have generated a good deal of discussion. The first is that natural selection may sometimes have a stabilizing effect, in which case the result of intense selection is no discernable change

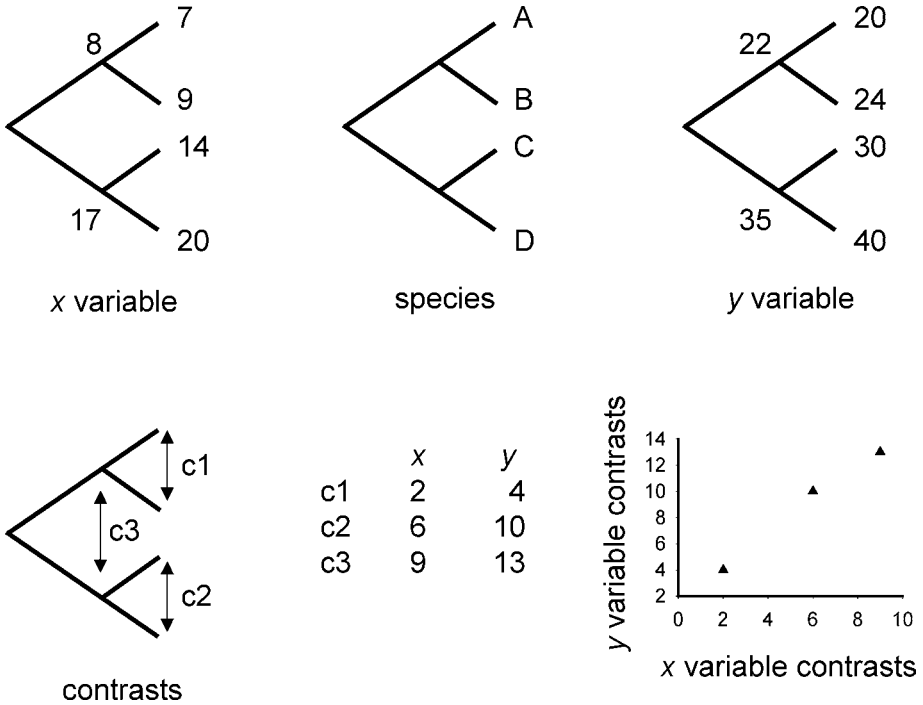


Figure 2 The method of independent contrasts. Two variables, x and y , are measured on four species, A, B, C and D. The phylogenetic tree for these species, and the values of variables x and y for each species, are shown in the upper row of the figure. Values shown at branching nodes are mean values for species at the terminal branches of the node. Contrasts, or differences, can be calculated for each variable between species A and B, C and D, and the branching nodes, as shown. The calculated contrasts are independent of each other, unlike values for the species themselves. Contrasts can then plotted against each other, as shown in the bottom right of the figure. This plot shows that the contrasts are correlated, that is, the magnitude of a change in character x between species is associated with the magnitude of a change in character y . Redrawn with permission from Purvis & Rambaut (1995).

in a character (Martins 2000). This effect of selection will not be detected by the method of independent contrasts because the method is designed to detect change in a character, not the effects of stabilizing selection. The second is that for characters that change rapidly between speciation events, the phylogenetic comparative method may be inappropriate and introduce problems of nonindependence where none existed (Rheindt et al. 2004). Characters such as birdsong, for example, may change rapidly within a species. When this is the case, the character may show little trace of its phylogenetic history. Rheindt et al. (2004) looked at the relation between the acoustic structure of birdsong and the habitat in which the song is broadcast. Previous studies have shown that the properties of song are correlated

with the physical properties of the habitat in which the song is sung (Brown & Handford 2000, Morton 1975). This is because different habitats cause different kinds of degradation in sound, making the song difficult to recognize or detect at a distance. The hard surfaces of forest trees introduce echo while the movement of air in open grassland causes “dropouts,” or inaudible segments within a song. The structure of birdsong may be adapted to the acoustic environment, much as Haydn and Mozart adapted their music for performance in a sound-absorbing room, a resonant concert hall, or out-of-doors (Forsyth 1985).

However, Rheindt et al. (2004) found that the physical properties of a bird's song are not correlated with its phylogenetic history. The rates of evolution of birdsong, they concluded, are much more rapid than speciation events, with the result that the properties of song they measured—highest frequency, lowest frequency, and dominant frequency—retain no trace of their phylogenetic origin. Correcting for phylogenetic inertia when none is present can influence the outcome of comparative analyses. Rheindt et al. (2004) therefore recommend testing for “phylogenetic signal”—statistical indication that phylogeny does introduce nonindependence—before using methods like independent contrasts that remove the effects of phylogeny. There is not yet enough information to tell whether brain structure and cognition exhibit the kind of rapid evolutionary change described by Rheindt et al. (2004), but their recommendation seems a sensible one and is not difficult to apply in neuroecological analyses.

Control Variables

The constituent parts of large animals are also large, and this applies to the brain as it does to other structures. Allometric relations between brain and body size and among parts of the brain have been extensively described (Harvey & Krebs 1990). The metrics used to estimate the size of the brain and its component parts can make a great deal of difference to the conclusions drawn from comparative analyses. De Winter & Oxnard (2001) and Finlay & Darlington (1995) came to radically different conclusions about major patterns in the evolution of the mammalian brain largely as a result of using different methods to control for total brain size. Finlay & Darlington (1995) concluded that for major brain regions, relative size was essentially the same across mammals, whereas de Winter & Oxnard (2001) found that the relative size of major brain areas varied independently in primates, insectivores, and bats in ways that reflected the perceptual and motor specializations of these animals.

The methods used to control for allometric effects are sometimes justified by empirical observations, sometimes justified only by convention. Corrections for body weight, brain weight, brain volume, or size of a brain structure such as the fore-brain or the brainstem are commonly used. In general, measurements on the brain make better control variables than do body weight measurements because body weight can vary within individuals depending on nutrition, season, reproductive condition, and migratory state. In large-scale studies, data on brain size and body

size often come from different sources, and differences in body size can occur between individuals of the same species due to sex, age, and the population from which the sample was drawn.

Byrne & Corp (2004) make the further point that using body size as an allometric control for size of a brain region assumes a particular model of brain function, namely that large bodies require more brain to control them. According to this model, if two animals both have brains that are 10% larger than expected for their body weight, then they both have the same additional capacity beyond that required for control functions. This clearly is not the case, however, for a mouse and an elephant that are both found to have brains 10% larger than expected. The greater-than-expected brain size of the elephant provides more information processing capacity, in terms of neurons and synaptic connections, than that of the mouse. For this reason, Byrne and Corp argue, the proportion of total brain size taken up by a particular neural structure is a more realistic measure of resources devoted to that structure and the functions it performs.

There is a variety of ways of using control variables, including taking ratios of the size of the structure of interest to the control variable, calculating residuals from a regression between the structure of interest and the control variable, and including control variables in multiple regression or general linear models. Ratios are widely used, but multivariate methods like regression or the general linear model have the advantage that they make the most use of the relations among measured variables in the data set (Darlington & Smulders 2001).

With the logic of the comparative method in mind, we move on to areas of current research in neuroecology.

FOOD-STORING BIRDS AND THE AVIAN HIPPOCAMPUS

Birds in three passerine families store food: the Paridae, chickadees and tits; the Corvidae, jays and crows; and the Sittidae, nuthatches. Birds in all three groups store food in widely scattered distributions within their home range. For chickadees and tits, this is an area of several hectares, whereas for birds like Clark's nutcracker, cache sites may be distributed over many square kilometers. The birds place either a single food item or a small number of items in each cache. Having scattered their stored food over a wide area, probably to protect it from other animals that pilfer caches, food-storing birds face the problem of retrieving this food. Early research showed that food-storing birds retrieve their caches by remembering where they placed them (Cowie et al. 1981, Sherry et al. 1981, Shettleworth & Krebs 1982, Tomback 1980, Vander Wall 1982), and a large body of experimental results has since confirmed this basic finding and added a great deal of new information on how memory for cache sites works (Balda et al. 1997, Shettleworth 2003, Smulders & DeVoogd 2000a). Birds remember the locations of caches with respect to landmarks near cache sites, remember the geometric relations among cache sites

and landmarks, and use sun compass information to orient to cache sites (Balda & Wiltschko 1991, Duff et al. 1998, Wiltschko & Balda 1989). Memory for cache sites can be very long lasting (Balda & Kamil 1992, Hitchcock & Sherry 1990), and retrieval behavior indicates the birds remember what kind of food was stored at a particular site (Clayton & Dickinson 1998, Sherry 1984). Clayton & Dickinson (1998) found that birds integrate the spatial location of a food cache with the kind of food placed in the cache and the time this was done. Although subsequent work has questioned Clayton and Dickinson's claim that memory for cache sites resembles human episodic memory (Hampton et al. 2005, Hampton & Schwartz 2004, Roberts 2002), it seems likely that food-storing birds retain in some form information of different kinds about cache sites, including the risk of cache loss (Hampton & Sherry 1994) and whether or not the bird has retrieved the stored food itself (Sherry 1984).

Lesions of the hippocampus disrupt the ability of food-storing birds to retrieve their caches (Krushinskaya 1966, Sherry & Vaccarino 1989) and produce a selective deficit in memory for spatial locations (Broadbent & Colombo 2000; Hampton & Shettleworth 1996a,b; Shiflett et al. 2003). Lesions of the hippocampus have similar selective effects on components of orientation in homing pigeons (Bingman et al. 1995).

Comparisons between food-storing and non-food-storing birds have shown some interesting relations between behavior and the relative size of the hippocampus. Comparisons at the taxonomic level of families and subfamilies showed that food-storing birds have, on average, a larger hippocampus than do non-food-storing birds (Krebs et al. 1989, Sherry et al. 1989). Within families of food-storing birds, there is also evidence that species that store more have a larger hippocampus than do species that store less (Hampton et al. 1995, Healy & Krebs 1992). This relation between the intensity of food storing and hippocampal size was recently questioned in a reanalysis of existing data by Brodin & Lundborg (2003), who found no consistent relation between behavior and hippocampal size in either Parids or Corvids. In subsequent work, however, Brodin and his colleagues found that their initial analysis was confounded, remarkably, by differences in hippocampal size between North American and European birds. This continental difference in hippocampal size, with Eurasian species having larger hippocampuses than those of North American species, occurs among non-food-storing birds as well as food-storing birds (Garamszegi & Lucas 2005). Reanalysis confirmed that food-storing birds have consistently larger hippocampuses than do non-food-storing species when continental differences are taken into account (Lucas et al. 2004). In a similar large-scale study using phylogenetic contrasts, Garamszegi & Eens (2004) found a positive relation between food-hoarding behavior and relative size of the hippocampus.

Seasonal Change in the Hippocampus

Food storing is seasonal in birds. Chickadees and tits begin storing food in fall and continue through the winter and early spring (Haftorn 1956, Ludescher 1980,

Nakamura & Wako 1988, Odum 1942). Food storing in these birds is a short-term strategy. Much of the food they store is retrieved within a few days at most (Cowie et al. 1981, Stevens & Krebs 1986). Storing probably serves to reduce within-day variability in food availability and to guarantee a supply of food at night-fall, before beginning the overnight fast (Lucas & Walter 1991, McNamara et al. 1990). In some food-storing tits, however, stored food is recovered months after it was first cached (Brodin & Ekman 1994). In corvids such as Clark's nutcracker, there is also pronounced seasonality in food storing. These birds harvest and store pine seeds when they are produced in abundance in fall, move to lower elevations during the winter, and return in spring to breed and collect their caches (Tomback 1980).

Smulders et al. (1995, 2000) found the relative size of the hippocampus changed seasonally in black-capped chickadees, reaching a maximum in October at about the time food storing begins. Subsequent attempts to uncover the factors controlling seasonal change in hippocampal size, however, have not been successful (Krebs et al. 1995, MacDougall-Shackleton et al. 2003). A number of experiments have shown that whereas changes in day length, from a summer to a fall photoperiod or from a winter to a spring photoperiod, have the expected effect on food-storing behavior, they have no effect on the relative size of the hippocampus (Krebs et al. 1995, MacDougall-Shackleton et al. 2003). It is possible that these studies, conducted in captivity, could not duplicate the high level of food storing with attendant demands on the hippocampus that chickadees experience in the wild and for this reason showed no effect of photoperiod on hippocampal size. Research with brood parasitic cowbirds, in which sex differences in hippocampal size are associated with the mode of brood parasitic behavior, has reported seasonal change in hippocampal size (Clayton et al. 1997), as have studies of rodents that are sexually dimorphic in hippocampal size (Yaskin 1984), so it is possible that seasonal change in the size of the hippocampus occurs in food-storing birds in the wild but is not easily observed in captivity.

Hippocampal Neurogenesis

Whether or not the avian hippocampus undergoes seasonal change in overall size, it is clear that it does undergo seasonal change in its neuron population. Barnea & Nottebohm (1994, 1996) gave black-capped chickadees the cell birth-maker tritiated thymidine, which is incorporated into the nuclei of dividing cells at the DNA synthesis phase of cell division. Birds were released into the wild and recaptured six weeks later. There was a peak in the incorporation of new neurons—called neuronal recruitment by Barnea and Nottebohm—into the hippocampus in October. The production of new hippocampal neurons does not vary seasonally (Hoshoolley & Sherry 2004), indicating that the observed pattern in neuronal recruitment is due to seasonal change in survival and incorporation of new neurons into the hippocampus.

Woodpeckers, Storm-petrels, and Bowerbirds

Food storing is known to occur in other birds, including shrikes, New Zealand robins, hawks, owls, and woodpeckers. There is very little information about memory for cache sites or the relative size of the hippocampus in these birds, with the exception of a study by Volman et al. (1997) of woodpeckers. Two species in the genus *Melanerpes* store food in quite different ways. The red-bellied woodpecker *Melanerpes carolinus* creates scattered caches of food, rather like food-storing chickadees and jays. The red-headed woodpecker *Melanerpes erythrocephalus* stores food concentrated in a "larder" that it defends against other animals. Scatterhoarding red-bellied woodpeckers must move through their home range to retrieve their caches and it is likely, though not proven, that they make demands on memory that the larder-hoarding red-headed woodpecker, with its concentrated supply of stored food, does not. The hippocampus is larger, relative to the size of the rest of the brain in red-bellied woodpeckers, than in red-headed woodpeckers (Volman et al. 1997). Volman and her colleagues also looked at two other species, the hairy woodpecker *Picoides villosus* and the downy woodpecker *Picoides pubescens*. The relative size of the hippocampus in these birds was comparable to that of the scatter-hoarding red-bellied woodpecker, even though neither *Picoides* species is thought to store food extensively. This result is not what one would predict from an association between food hoarding and hippocampal size. The lack of correlation between food hoarding and hippocampal size in *Picoides* woodpeckers may show that there is, in general, no consistent relation between food storing and hippocampal size (Bolhuis & Macphail 2001), but the pattern observed in passerine food-storers and *Melanerpes* woodpeckers suggests otherwise. It may be that other selective pressures, for example for spatial ability appropriate to the large home ranges of hairy and downy woodpeckers, have acted to increase hippocampal size in these birds (Volman et al. 1997). It is also possible that *Picoides* woodpeckers store food more than is generally realized (Burchsted 1987, Volman et al. 1997). In any case, data for two species of *Melanerpes* woodpeckers conform to the pattern observed in passerine food storers, whereas data for two species of *Picoides* woodpeckers do not.

Leach's storm-petrels nest in dense colonies in burrows in the ground. They forage at night and return to their burrows in darkness. Abbot et al. (1999) compared the size of the hippocampus in two populations of storm-petrels with different nest site preferences: forest, where reproductive success was higher but burrows appeared difficult for the birds to relocate, and open meadows, where reproductive success was lower but burrows appeared easier to find. The relative size of the hippocampus was greater in forest-nesting storm-petrels than in meadow-nesting birds (Abbott et al. 1999). This difference in hippocampal size between forest-nesting and meadow-nesting birds could come about in a number of ways. Birds that differ in hippocampal size may prefer different nesting habitats, experience with a nesting habitat may affect hippocampal size, or the storm-petrels nesting in the two habitats may be different subpopulations exposed to different selection

pressures on hippocampal size. Whatever the reasons for the observed difference in hippocampal size, the results show a relation between hippocampal size and the difficulty of relocating the home burrow.

Male bowerbirds build complex bowers, sometimes decorated with colorful objects that are attractive to females. Madden (2001) determined endocranial volume from X rays of museum specimens for nine species of bowerbirds, one related non-bower-building species, and four unrelated but ecologically similar Australo-Papuan species. Because a number of these species are endangered, brain tissue was not collected and instead endocranial volume was treated as a measure of total brain size. Bowerbirds had significantly larger brains than did either related or non-related nonbower builders. Within bowerbirds, bower complexity was positively correlated with brain size for both major groups of bowerbirds, the avenue-building and the maypole-building species. The method of independent contrasts showed a strong overall relationship between brain size and bower complexity (Madden 2001). Bower building is known to improve with experience and probably makes demands on learning, memory, and other cognitive capacities, including memory for the sources of colorful objects. As Madden points out, it would be informative to determine which brain regions contribute to the overall differences in brain size that were found, but data of this kind are unlikely to become available. As it stands, the results of this research indicate that sexual selection, in the form of female preference for bower complexity, has affected both bower building behavior and total brain size.

SEX DIFFERENCES IN THE HIPPOCAMPUS

Research on vole mating systems, described above, showed that the relative size of the hippocampus differed between the sexes in the presence of sex-specific selection for spatial ability. Males of a polygynous species had a larger hippocampus than did females, whereas no sex difference occurred in monogamous species. Most mammals are polygynous, and a larger hippocampus is found in males in many species (Galea et al. 1999, Jacobs & Spencer 1994, Sherry et al. 1996).

Sex differences in a cognitive or neuroanatomical character are particularly strong evidence for the action of natural or sexual selection because alleles favored by selection in one sex are passed on to both sexes, unlike genes favored by selection in one species but not another. For sex differences in the effects of autosomal genes to occur, not only must there be selection for particular alleles but there must also be selection for modifiers that restrict the effects of these alleles to only one sex (Lande 1980).

It is possible that greater hippocampal size in males has little to do with sex differences in cognition or behavior but is instead a consequence of sexual differentiation. Greater male hippocampal size may be a pleiotropic effect of genes selected for other functions, a side effect of maleness rather than a character associated with spatial ability, home range size, and polygyny. Evidence against this

interpretation comes from research on hippocampal size in brood parasitic birds in which selection on female spatial ability has produced a larger hippocampus in females than in males.

Brood Parasites

Brown-headed cowbird (*Molothrus ater*) females lay their eggs in the nests of other species, where the cowbird eggs are incubated and the young cowbirds are raised by their host parents. Female cowbirds lay at or before dawn and therefore search little if at all for host nests at this time (Rothstein et al. 1984). They spend the rest of the morning in host nest habitat, where field studies describe them walking on the forest floor while scanning the canopy, watching the nest-building activity of other birds, and flying into understory vegetation and flushing incubating birds from their nests (Clotfelter 1998, Norman & Robertson 1975, Scott 1991). It is likely that they are searching for potential nests in which to lay eggs on subsequent days. There is evidence that females are selective about the stage of completion of host nests and avoid laying eggs in nests that are unfinished, contain no other eggs, or have a complete host clutch (Nolan 1978). This latter preference may prevent placing a cowbird egg among host eggs that are about to hatch. Males do not assist females in their search for host nests (Rothstein et al. 1987). About midday, females join males and feed in grain fields and livestock yards, often at a considerable distance from forest habitats where host nests are found.

The hippocampus of female cowbirds is larger, relative to the size of the rest of the brain, than the hippocampus of males (Sherry et al. 1993). No sex difference is found in closely related nonparasitic members of the Icterid blackbird family to which cowbirds belong (Sherry et al. 1993).

Cowbirds are a diverse group, most species of which are found in South and Central America. The screaming cowbird (*Molothrus rufoaxillaris*) is a specialist brood parasite, laying eggs in the nests of only one host species. Male and female screaming cowbirds search together for nests of their host. The host is a cowbird, the nonparasitic bay-winged cowbird (*M. badius*). Bay-winged cowbirds usurp the nests of other birds but incubate their own eggs and care for their own young themselves. A third species, the shiny cowbird (*M. bonariensis*), is a generalist parasite. Like the North American brown-headed cowbird, it parasitizes hundreds of host species, and females search for host nests unassisted by males.

Female shiny cowbirds have a larger hippocampus, relative to the size of the rest of the brain, than that of males (Reboreda et al. 1996). No sex difference in the size of the hippocampus occurs in either the specialist screaming cowbird (in which both males and females search for host nests) or the nonparasitic bay-winged cowbird (Reboreda et al. 1996). As with food-storing birds and small mammals, there is some evidence for seasonal change in the size of the hippocampus in female shiny cowbirds (Clayton et al. 1997). Sex differences in nest-searching behavior in the wild, coupled with sex differences in the size of the hippocampus, would predict a sex difference in favor of females in spatial ability, but the only

experimental data on sex differences in cognition in cowbirds show an unexpected pattern of female superiority when visual cues indicate the presence of food but not when spatial cues indicate the presence of food (Astié et al. 1998). It is possible that searching for food in the task used by Astié et al. (1998) does not tap the cognitive abilities used by female shiny cowbirds to find host nests, but it is also possible that sex differences in cognition in cowbirds, if they exist, are not what one might predict from results with food-storing birds and polygynous voles.

THE SONG CONTROL NUCLEI

Research on birdsong and the neural circuitry controlling the production of birdsong is probably the prototype for neuroecological research. Male songbirds learn the songs that they sing, and this phenomenon has become a model system for the study of learning and the neural basis of behavior. Research on birdsong has had a profound influence on our understanding of communication, learning, neural plasticity, neurogenesis, and sex differences in brain and behavior. Zeigler & Marler (2004) provide an extensive survey of recent research. Given the wealth of research findings in this area, I narrow the focus to phylogenetic comparative analyses of birdsong. Surprisingly, there are relatively few phylogenetic comparative studies of the neural control of song. Recent reviews, in fact, have urged greater use of phylogenetic comparative methods to dispel current misconceptions about birdsong due to reliance on a few model species in the laboratory (Beecher & Brenowitz 2005, Brenowitz & Beecher 2005).

Two circuits in the avian brain control the learning and production of song. Area HVC—HVC being the preferred name of the area, rather than an acronym (Reiner et al. 2004)—is part of both the anterior circuit that is primarily involved in song learning and the posterior circuit that is primarily a motor control circuit responsible for song production. Area HVC undergoes dramatic seasonal variation in size in many passerines. One hypothesis is that this increase in size is related to the learning of new songs (Nottebohm 1981), but HVC varies seasonally not only in species that learn new songs each season but also in species that sing the same song from year to year (Tramontin & Brenowitz 2000). Because variation in HVC size is not always associated with learning new songs, it has been proposed that its increase in size, and the recruitment of new neurons into HVC, provides more precise motor control of song, which becomes highly stereotyped during the spring breeding season, when song production is at its highest level (Tramontin & Brenowitz 2000).

In most species of passerine birds, males have much more varied songs and a much higher level of song output than do females. Indeed, in most temperate-zone species, females do not sing at all. The principal functions of song are territory defense and mate attraction, and it is therefore not surprising that males sing more than do females. Dramatic differences between males and females in the size of the song control nuclei HVC and RA (robust nucleus of the arcopallium), another

nucleus in the posterior song control circuit, have been described in many species, and these sex differences in the brain are often associated with sex differences in song complexity or song production. MacDougall-Shackleton & Ball (1999) performed a phylogenetic comparative analysis of 20 species of songbirds and found a clear association between sex differences in song and sex differences in the relative size of HVC. Earlier claims of no association between sex differences in song and sex differences in the brain (Gahr 1998) were not supported.

In a comparative phylogenetic study of 45 species of songbirds, DeVoogd et al. (1993) found a clear association between song repertoire size and size of area HVC, but not area X, a nucleus in the anterior song circuit. The number of syllables per song was not associated with the size of either structure. Despite the lack of any association between area X and the song variables measured, the size of area HVC and area X were positively associated. Because area X is part of the anterior song circuit, it is usually assigned a greater role in song acquisition than in song production. It appears that evolution of a larger song repertoire exerts a greater selective pressure on the size of HVC, part of the motor control circuit for song output, than on the size of area X, part of the song-acquisition circuit. As might be expected, this study found no association between relative size of the hippocampus and song repertoire size (DeVoogd et al. 1993).

Further phylogenetic comparative analyses examined the relation between song complexity and the size of song control nuclei within a more restricted group, the European warblers in the family *Sylviidae* (Székely et al. 1996). The advantages of restricting analysis to a smaller group is that measures of song complexity, in this case song repertoire size, are more likely to be comparable than in comparisons within large taxonomic groups, where songs may vary in complexity along many dimensions. In addition, it was possible to standardize histological and volumetric methods for this smaller group of species. The results showed a clear positive relation between contrasts in repertoire size and contrasts in HVC volume among the eight species examined. No relations between repertoire size and size of the song nuclei RA, area X, or LMAN (lateral magnocellular nucleus of the anterior nidopallium) were found (Székely et al. 1996). European warblers were not included in the large-scale phylogenetic study of DeVoogd et al. (1993), described above, so the present study, in addition to providing greater precision in measures of repertoire size and song nucleus volume, also provides an independent test of the relation between song complexity and the brain. As shown in research on the hippocampus, augmentation of specific behavioral and cognitive functions is associated with evolutionary change in specific structures in the brain.

INNOVATION AND THE AVIAN FOREBRAIN

In neuroecological studies of cognition, there are limits to the number of species for which it is possible to obtain behavioral data. In their study of song repertoire size, Székely et al. (1996) felt that restricting analysis to a small number of species

allowed greater precision in the measurement of behavior. There are also purely practical limitations to collecting data on a large number of species. The number of species of food-storing birds far exceeds the number of species for which there are controlled laboratory studies of memory and spatial ability. In addition, it is necessary that data be collected under the same conditions, using the same control procedures and protocols if results are to be truly comparable, and it is not always possible to ensure that different species are actually being observed under comparable conditions. One hour of food deprivation may be effective in motivating one species to respond for food, but ineffective for another. Because the animals are different, and that is the purpose of comparative studies, differences in their reactions to laboratory manipulations are to be expected. As the number of species increases, obtaining comparable data on cognitive ability quickly becomes a formidable task.

Lefebvre and his colleagues have found an ingenious way around this problem by using archival sources of data on the behavior of a very large number of bird species (Lefebvre et al. 1998, 1997; Nicolakakis & Lefebvre 2000; Nicolakakis et al. 2003; Sol & Lefebvre 2000; Sol et al. 2002; Timmermans et al. 2000). Scientific journals of ornithology often contain, in addition to research papers, a section of short notes. The contents of these notes range from brief reports of empirical research to more informal observations on distribution, breeding, migration, and other behavior. A traditional feature of these notes is observations on unusual behavior noted by professional or amateur ornithologists. Lefebvre and his colleagues systematically searched the short notes sections of ornithological journals published in North America, Britain and Europe, Australia, New Zealand, and Asia for reports of unusual feeding behavior, which they termed "feeding innovation." Behavior had to meet at least one of two criteria to be included in the innovation data set. The food or foraging technique had to be highly unusual for the species, or the author or editors had to state explicitly that this was the first known published report of the behavior. Innovations included such behavior as American robins capturing and eating salmon smolts (Bayer 1980) and house sparrows searching car radiator grilles for insects (Simmons 1984).

The frequency of these reports, tabulated by taxonomic order, could then be compared to expected frequencies of innovation, calculated using the total number of innovations observed for all species and the proportion of species in each taxonomic order. From the observed and expected values, Lefebvre and colleagues calculated a relative index of innovation (Lefebvre et al. 1997). The correlation between mean forebrain size, obtained from Portmann (1947), and the index of innovation could then be calculated.

Several notable results emerge from this analysis. There is considerable variation in innovation rate among avian orders. The highest rates of innovative feeding behavior are shown by one group of Passeriformes, the Corvids (crows and jays), and by the Ciconiiformes (storks, herons, and ibises) and the Falconiformes (eagles, hawks, and falcons). The lowest rates of innovation occur among the Anseriformes (ducks and geese), the Galliformes (pheasants and quail), and the Columbiformes

(pigeons and doves). There is a strong correlation between innovation rates calculated separately for different geographic areas, for example between Great Britain and North America. The major result of these studies, however, is a strong correlation between innovation rate and relative forebrain size in birds (Lefebvre et al. 1997, 1998; Nicolakakis & Lefebvre 2000; Nicolakakis et al. 2003; Sol & Lefebvre 2000; Sol et al. 2002; Timmermans et al. 2000).

The use of such an archival source of information on feeding innovation has both advantages and disadvantages. In its favor, it is not affected by motivational variables, reactions of animals to captivity, laboratory artifacts, or the use of particular experimental paradigms to assess animal cognition. This latter advantage may be particularly crucial for avoiding assumptions about the nature of animal cognition that are implicit in any experimental paradigm. The innovation index is, at least potentially, vulnerable to a number of biases, however, and Lefebvre and his colleagues have performed extensive statistical tests for the presence of such biases (Nicolakakis & Lefebvre 2000). The purpose of these statistical refinements was to test whether the relation between forebrain size and innovative feeding behavior was due to the behavior of the birds or the behavior of human observers of birds.

The most obvious bias is that some orders of birds may be more *speciose*, that is, richer in species, than are others. Studies of innovation control for this by comparing the frequency of innovation records for each order to the frequency expected given the number of species of birds in that order. Another potential bias is that some species may be more abundant than others, or more readily seen by the casual observer. If either is the case, then these species would contribute more records of innovative feeding behavior not because they show greater behavioral innovation but simply because they are more often encountered by human observers. Nicolakakis & Lefebvre (2000) tested for such biases by examining an additional category of behavior, reports of unusual nesting behavior, chosen because nesting in birds is generally viewed as less flexible and less open to change by the effects of experience. If biases and confounding variables are responsible for the relation between unusual feeding behavior and forebrain size, then a relation should also be observed between unusual nesting behavior and forebrain size. If, however, behavioral flexibility and innovation is related to forebrain size, then the relation should be observed for feeding alone. They found a significant relation between forebrain size and feeding innovation but not between forebrain size and nesting innovation.

In addition, Nicolakakis & Lefebvre (2000) calculated interrater reliabilities in the scoring of short notes and controlled for mode of juvenile development, population size, reporting bias, and research effort devoted to each species by adding each of these variables to their analysis of the relation between innovation rate and forebrain size. Finally, the method of independent contrasts was used to include phylogeny in the analysis and was compared to a nonphylogenetic analysis that used multiple regression.

As in earlier studies, the number of species per taxonomic group had a major effect on reports of innovation, but this could be controlled for by calculating

expected innovation rates. Population size, reporting bias, and research effort accounted for no significant variation in reported innovation rate for either feeding or nesting, and interrater reliabilities were high. Analysis of the data using independent contrasts produced the same result as multiple regression, a significant effect of forebrain size on feeding innovation but not on nesting innovation.

An analysis of Australasian records yields essentially the same relation between innovation rate and forebrain size found in Europe and North America (Lefebvre et al. 1998) along with some additional information that could be extracted from the Australasian records. One of the journals from which observations of innovative feeding methods were taken changed editorial policy in the middle of the period surveyed, yielding two 28-year periods: 1940–1968, when short notes were contributed primarily by amateur ornithologists, and 1969–1997, when they were contributed primarily by professionals with institutional affiliations. Reported innovation frequencies were highly correlated for the two periods.

Components of the Forebrain

The avian forebrain is made up of many regions serving different sensory systems and integrative functions. Comparative analysis of the kind described above has shown that some forebrain areas are more strongly correlated with innovation rate than are others (Timmermans et al. 2000). Avian brain forebrain nomenclature was recently revised by Reiner et al. (2004), and the following discussion uses the revised terminology with the original designation by Timmermans et al. (2000) in parentheses. The forebrain area most strongly correlated with innovation rate is the mesopallium (hyperstriatum ventrale). Other brain regions, such as the nidopallium (neostriatum), lateral striatum and globus pallidus (striatopallidal complex), and Wulst (Wulst) are positively correlated with innovation frequency but make only nonsignificant contributions when entered in a multiple regression model that includes the mesopallium. The size of many of these areas is correlated. Mesopallium and nidopallium are highly correlated in size, and the size of the mesopallium + nidopallium is highly correlated with total forebrain size. Nevertheless, the results of Timmermans et al. (2000) show that the primary contribution to the relations found between forebrain size and innovation rate is made by the mesopallium, a complex area of the avian brain serving many cognitive functions also served by the mammalian neocortex.

THE PRIMATE BRAIN

Comparative research on the primate brain has a long history, motivated in large part by attempts to trace the evolutionary history of humans and identify the selective pressures that produced the human brain and the unique repertoire of human cognitive capacities. Recent neuroecological research on the evolution of the primate brain has focused on hypothesized selective factors that may have influenced

evolution of the primate brain, including social learning, innovative feeding and foraging, tool use, and social manipulation. A recurring theme in recent research has been the relative importance of social versus nonsocial influences on evolution of the primate brain. Neocortex size has been found to correlate with group size, and much current discussion of primate cognition focuses on the evolutionary importance of social manipulation and deception (Byrne & Whiten 1988, Whiten & Byrne 1997). Two studies illustrate recent neuroecological research on the primate brain.

Reader & Laland (2002) used the approach of Lefebvre and his colleagues, described above, to examine the relation between social learning, innovation, and tool use. They collected reports of these three behaviors from journals of primatology, relying on the original authors' descriptions of social learning, tool use, and behavior to adjudicate whether or not the behavior was novel (Reader & Laland 2001). Most of the records of innovation pertained to foraging. They then correlated frequency of social learning, tool use, and innovation with size of the neocortex plus striatum, a set of structures they called the "executive brain." Brainstem size was used as a control variable, and phylogeny was controlled using independent contrasts. Control for research effort devoted to different species consisted of determining the frequency of articles devoted to each species in the journals examined and taking residual values from a plot of the frequency of observed behavior against research effort. This procedure essentially determines whether there is a higher or lower frequency of reports of the behavior of interest given the amount of research effort devoted to that species. Interrater reliability tests were also conducted along with statistical controls for field versus laboratory studies, possible effects of experimental manipulation, food provisioning, and human influences on the primates observed in the corpus of studies examined. They found strong positive associations between two of their three measures of executive brain size and the frequencies of innovation, social learning, and tool use. The same pattern emerged with and without phylogenetic correction. Significant associations were found for both uncorrected measures of neocortex plus striatum and for the ratio of this measure to brainstem size.

Interestingly, Reader & Laland's (2001, 2002) results also show strong correlations between their behavioral measures, that is, between innovation and social learning, innovation and tool use, and social learning and tool use. There are a number of possible interpretations for this pattern of results. It may be that all three are manifestations of a single underlying cognitive capacity. It is also possible that each results from a different underlying cognitive capacity but all three evolved together. The possibility that can be rejected by these data is that there have been tradeoffs, as is sometimes proposed, between social learning and the more asocial innovative acquisition of skills and novel behavior.

Byrne & Corp (2004) performed a similar analysis using frequencies of deception in primate social groups obtained from a survey of researchers conducting long-term field studies of primates. They found significant associations between the frequency of reports of deception (corrected for research effort) and neocortex

size. Interestingly, these associations were independent of group size. The authors take these results as support for the idea that social manipulation and tactical deception have played a role in the evolution of large primate brains.

THE NEUROECOLOGICAL APPROACH

A Critique of Neuroecology

The term neuroecology came into general use, ironically, following its use in a critique that took researchers in the field to task on many fronts (Bolhuis & Macphail 2001, Macphail & Bolhuis 2001). Neuroecologists, according to Bolhuis and Macphail, confused the causes and functions of animal behavior, drew unwarranted conclusions from data, and invoked a notion of modularity that differs from Fodor's (1983). A number of their arguments reiterate earlier assertions that memory is a central system with no domain specificity, rather than multiple systems with functional specialization, and that there is no evidence for differences in cognition among species of animals or for associations between brain structure size and cognition (Macphail 1982). Many of the specific points of the critique, especially those regarding interpretation of data, have been rebutted in a series of replies and commentaries (Dwyer & Clayton 2002, Flombaum et al. 2002, Hampton et al. 2002, Healy et al. 2005, MacDougall-Shackleton & Ball 2002, Shettleworth 1998). The consensus that has emerged from the ensuing discussion is that Bolhuis and Macphail misunderstood a number of fundamental ideas in neuroecology and found fault with their own versions of these ideas [though this is not the view of Bolhuis (2005)]. They asserted, for example, that neuroecological research on song learning predicts that male songbirds should be better than females at auditory learning (Bolhuis & Macphail 2001). Bolhuis & Macphail (2001) then describe research showing that this is not so. As MacDougall-Shackleton & Ball (2002) point out, however, there is no reason to expect that male songbirds are better than females in general at auditory learning. Both males and females learn the songs of their local population and learn to recognize and discriminate among songs. The correct prediction is that males are better than females at learning to sing, and the preponderance of empirical evidence shows this. In the exceptional cases in which females do learn to sing, they, too, have song control nuclei of the kind usually found only in males (MacDougall-Shackleton & Ball 1999), which supports the neuroecological prediction of an association between song learning and the song control nuclei (MacDougall-Shackleton & Ball 2002).

Bolhuis and Macphail may also have had expectations for a simpler and more consistent pattern of results in neuroecology than do most researchers in this field. Complicating factors, data that do not fit expectations, and predictions that are disconfirmed are well known to neuroecological researchers and are the norm in any area of the life sciences. To return to the example presented at the very beginning of this chapter, polygynous male meadow voles have larger home ranges than do females, better spatial ability, and a larger hippocampus. These males compete

for mates by expanding their home ranges, and males with better spatial ability have an advantage in this competition. Males with larger ranges and better spatial ability should therefore mate with more females and have more offspring. They do mate with more females, but they do not have more offspring (Spritzer et al. 2005b). Males that mate more frequently should produce more offspring, almost of logical necessity, but results of Spritzer et al.'s (2005b) study show that they do not. Researchers must therefore choose between discarding all that has gone before—correlations among behavior, home range size, spatial ability, the hippocampus, and mating frequency—as being in error, or instead conclude that there is still something about the relation between spatial ability and reproductive success that is not understood. Perhaps, as Spritzer et al. (2005b) suppose, the close spacing of female nests in the seminatural enclosures that made it possible to collect data on competition by male meadow voles for mating opportunities eliminated any advantage that males with better spatial ability would normally possess. Perhaps it did not. In any case, unanswered questions are surely the origin of all scientific inquiry (MacDougall-Shackleton & Ball 2002).

A number of points raised by Bolhuis and Macphail are clearly correct, however, and had been addressed earlier within the field of neuroecology. One of these points is that there is a limit to the kinds of questions that can be answered by examining the relative size of parts of the brain. The same criticism could be made, and has been made, of electrophysiological recording, lesion studies, brain imaging, and immediate early gene expression. The point is nevertheless correct. Any one method can only provide certain kinds of information, and answering the most general questions about cognition and the brain requires converging evidence of many kinds. For this reason, neuroecology is increasingly turning to methods that provide different information than can be obtained by examining structure size or changes in structure size. Current research on the hippocampus of food-storing birds, for example, examines patterns of neurogenesis (Barnea & Nottebohm 1994, 1996; Hoshooley & Sherry 2004; Smulders et al. 2000), immediate early gene expression (Smulders & DeVoogd 2000b), NMDA (N-methyl-d-aspartate) receptor activity (Shiflett et al. 2004), and glucocorticoid (Pravosudov 2003) and social influences (Pravosudov & Omanska 2005) on hippocampal anatomy and function.

Future Directions

The central idea of neuroecology is that there are relations between brain structure and cognition that can be predicted from selection pressures that animals are exposed to in the wild. There are at least two ways this could come about. Natural selection, acting on behavioral outcomes, may select from among the naturally occurring variation in neural traits those that more effectively serve the function in question, for example, remembering the spatial location of scattered food caches or producing a large song repertoire. One of the many outcomes of such selection is differences between species in the relative size of different brain areas and correlations between brain structure and specific cognitive abilities. An alternative

account of relations between brain structure and cognitive functions is that the brain is not modified by selection for these functions but instead by other selective or nonselective processes in evolution, and the outcome is structural features of the brain that permit certain cognitive functions. The human brain permits reading, for example, but natural selection for reading ability, if there is any, is probably too recent to have had much effect on brain structure. As Lefebvre et al. (1997) note, the correlational approach used in comparative studies cannot distinguish between these two alternatives, which need not be mutually exclusive. If, however, the correlations that have been described between behavior, cognition, and the brain are not the result of selection for specific cognitive functions and neural mechanisms, the challenge is to identify and describe the nonselective or nonspecific processes that have produced these correlations. Finlay & Darlington (1995) proposed changes in the timing of neural development and changes in overall brain size to account for the broad patterns they observed in the size in mammalian brain structures. Their analysis also found few differences among major taxonomic groups, whereas alternative analyses detected significant adaptive modification of components of the mammalian brain (de Winter & Oxnard 2001). Although the nonspecific processes proposed by Finlay & Darlington (1995) may indeed play a role in evolutionary change in the brain, they do not account for the correlations between behavior, cognition, and the brain identified in neuroecological research.

Neuroecology seems at times preoccupied with the size of brain structures, whether the hippocampus, song control nuclei, or other structures. In part, this is mere convenience. Structural size differences are conspicuous, technically easy to measure, and available for many species, whereas more fine-scale measures such as dendritic arborization, patterns of immediate early gene expression, distributions of receptor types, or rates of neurogenesis—that probably do reveal more about how the brain works—are obtained more slowly and are available on far fewer species. In fact, given the many ways brain function could be modified, it is surprising that gross size differences crop up so often in comparisons between species or between the sexes. As noted above, neuroecology is increasingly moving toward more fine-scale analyses of brain structure and function. Several questions remain, however. Central among them is the question of why differences in behavior are so often associated with differences in brain structure size. What does an increase in size provide, in functional terms? Jerison (1973) articulated the “law of proper mass,” which states that the relative proportion of the brain devoted to a structure reflects the relative importance in the life of the animal of the function or functions performed by that structure, but this is really a statement of the question.

One way of viewing the problem is in terms of costs of maintaining a brain structure of any size. A large hippocampus may provide increased processing capacity for many hippocampus-dependent cognitive operations, but at a cost. Neural tissue is energetically costly to operate (Laughlin 2001). Systems that act to maintain a neural structure and regulate its activity, such as the neuroendocrine system, may also be costly (MacDougall-Shackleton & Ball 1999). These costs of maintaining an increased structure size limit the resources that can be used in other ways, may

force tradeoffs, and result in differences between species, differences between the sexes, and seasonal differences within individuals in brain structure size.

CONCLUSIONS

Neuroecology developed from an increased appreciation of the importance of cognitive processes and their neural correlates within the field of behavioral ecology. It uses phylogenetic comparative methods to identify cognitive processes and neural structures that are associated with specific selective pressures that animals are exposed to in nature. Neuroecological research on species and sex differences in cognition is usually conducted in controlled laboratory settings, and neuroanatomical methods are used to identify species or sex differences in brain regions that play a role in specific cognitive processes. The size of candidate brain structures is often the neuroanatomical correlate examined, but more fine-scale measures of neural structure and activity are increasingly used in neuroecology. This approach has identified a variety of associations between apparent selective pressures that animals are exposed to in the wild and cognitive processes and neural structures. Species and sex differences in the hippocampus of birds and mammals, in the song control nuclei of birds, in the avian forebrain, and in regions of the primate brain have been found that are associated with selective pressures imposed by foraging, mating system, communication, and social organization. The phylogenetic comparative methods used in many of these studies have identified a number of these selective pressures and indicate that natural selection and sexual selection have modified cognitive processes and brain structures across a broad range of animals.

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