Memory and Hippocampal Specialization in Food-Storing Birds: Challenges for Research on Comparative Cognition

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Abstract
The three-way association among food-storing behavior, spatial memory, and hippocampal enlargement in some species of birds is widely cited as an example of a new 'cognitive ecology' or 'neuroecology.' Whether this relationship is as strong as it first appears and whether it might be evidence for an adaptive specialization of memory and hippocampus in food-storers have recently been the subject of some controversy [Bolhuis and Macphail, 2001; Macphail and Bolhuis, 2001]. These critiques are based on misconceptions about the nature of adaptive specializations in cognition, misconceptions about the uniformity of results to be expected from applying the comparative method to data from a wide range of species, and a narrow view of what kinds of cognitive adaptations are theoretically interesting. New analyses of why food-storers (black-capped chickadees, Poecile atricapilla) respond preferentially to spatial over color cues when both are relevant in a memory task show that this reflects a relative superiority of spatial memory as compared to memory for color rather than exceptional spatial attention or spatial discrimination ability. New studies of chickadees from more or less harsh winter climates also support the adaptive specialization hypothesis and suggest that within-species comparisons may be especially valuable for unraveling details of the relationships among ecology, memory, and brain in food-storing species.

Introduction and Background

Food-storing by birds and other animals has long been observed in the field, and its role in dispersal of some seeds is well known [Vander Wall, 1990]. Originally, field biologists [e.g., Haftorn, 1956] suggested that by moving items from sites where they may be buried in snow into sites under tree branches and the like, storing functions to increase food availability for the storer’s social group. In this scenario, individuals that store do not remember their stores nor benefit from them any more than do their companions. However, theoretical questions that came to the fore in evolutionary biology and comparative psychology during the 1970’s inspired experimental tests of the possibility that food-storing birds remember storage sites. Functional questions in biology were stimulated by the rejection of group-selectionist in favor of individual-selectionist theorizing: how could food-storing evolve under selfish individual selection? Could there be mechanisms insuring that investing time and energy in storing increases the fitness of the individual doing the storing more than that of non-storers that only pilfer the stores of others [Andersson and Krebs, 1978; see also Ekman et al., 1996]? One way to guarantee greater benefit to the storer is for...
stорers to have idiosyncratic site preferences, and this mechanism may play a role in the wild [Brodin, 1994]. However, a more interesting possibility is that birds remember where they store individual items. Because some species may store food in hundreds or even thousands of sites for periods of days or months [see Vander Wall, 1990], remembering the locations of caches seems to demand almost incredible mnemonic powers.

Modelling predicting that food-storers should use memory [Andersson and Krebs, 1978] came at the same time that comparative psychologists were becoming interested in the idea that learning and memory were adaptively specialized in each species for the requirements of its way of life [Rozin and Kalat, 1971]. In addition, following the cognitive revolution in the study of human psychology, psychologists working with animals were beginning to study cognitive processes such as memory in nonhuman species [Wasserman, 1993]. The resulting convergence of interests among behavioral ecologists and comparative psychologists stimulated interdisciplinary collaborative research on food-storing and memory in Paridae (chickadees and tits) and Corvidae (jays, crows, and nutcrackers) that began in the early 1980's [see reviews by Kamil and Balda, 1990; Shettleworth, 1995; Sherry and Duff, 1996]. Not surprisingly, given the growth of behavioral neuroscience in general and the explosion of work on the role of the hippocampus in spatial memory in particular, behavioral work that asked whether food-storing birds really do use spatial memory to retrieve their hoards [e.g., Kamil and Balda, 1985; Sherry et al., 1981] and whether their memory was better than that of birds that do not store [Balda and Kamil, 1989; Krebs et al., 1990] soon led to comparative studies of the avian hippocampus and its role in spatial memory [Krebs et al., 1989; Sherry et al., 1989]. A similar approach was applied to other examples of possible differences in brain and spatial cognition among closely related species [Sherry et al., 1992; Reboreda et al., 1996].

Taken together, this work has provided some evidence for a three-way association among food-storing behavior or other extraordinary demands on spatial memory, performance on laboratory tests of spatial memory, and hippocampal enlargement in some species of birds and mammals, and it is widely cited as an example of a new 'cognitive ecology' [e.g., Healy and Braithwaite, 2000]. However, in the case of food-storing birds, whether this association is as strong as it may appear and what it might mean have recently been the subject of some controversy [Bolhuis and Macphail, 2001; Macphail and Bolhuis, 2001; Hampton et al., 2002; MacDougall-Shackleton and Ball, 2002; Dwyer and Clayton, 2002]. A very simple and straightforward hypothesis – that food-storing species have greater capacity and/or longer-lasting spatial memory than species that do not store – has guided much of the research comparing food-storing and non-storing species. The results do not unanimously support this simple hypothesis [Shettleworth, 1995; Macphail and Bolhuis, 2001; Balda and Kamil, 2002]. For example, food-storing black-capped chickadees (Poecile atricapilla) perform better than non-storing dark-eyed juncos (Junco hyemalis) on some spatial memory tasks [e.g., Shettleworth and Westwood, 2002], but not on spatial delayed alternation [Hampton and Shettleworth, 1996b]. Bolhuis and MacPhail [2001] have recently suggested that such inconsistencies arise because the adaptationist approach to brain and cognition (which they dub 'neuroecology') is fundamentally flawed and should be discarded. Taken to an extreme, this recommendation amounts to divorcing the study of brain and cognition from the rest of biology [Biegler, personal communication]. As critics of Bolhuis and MacPhail's view [e.g., Hampton et al., 2002; MacDougall-Shackleton and Ball, 2002] have pointed out, the study of food-storing and memory is a good example of how science progresses by refining initial simple hypotheses and crude experimental methods in the light of data. Some recent directions in such progress and possible future directions are discussed later in this article. First, however, I discuss some misconceptions and oversimplifications that are evident in the recent critiques [Bolhuis and Macphail, 2001; Macphail and Bolhuis, 2001] of research on avian food-storing, memory, and brain.

**Misconceptions and Oversimplifications: The Nature of Adaptive Specializations**

From the time of Darwin, the comparative study of learning and other cognitive processes in nonhuman species has been focused on documenting commonalities among species rather than species-specific adaptations [see Macphail and Bolhuis, 2001; Papini, 2002]. Learning theory was devoted to species-general processes such as simple associative learning that were studied more or less in isolation from any consideration of how learning might play a role in the natural lives of animals. Perhaps as a result, when the term *adaptive specialization* first appeared in discussions of learning [Rozin and Kalat, 1971], it was in the context of claims that some examples of apparently functionally appropriate learning – primarily conditioned taste aversion in rats – were qualitatively dif-
ferent from previously-studied kinds of learning. Further analysis made clear that, although it has some quantitative specializations, in fact, conditioned taste aversion has similar properties to other forms of classical conditioning [Domjan, 1980]. Nevertheless, the suggestion that adaptive specialization refers only to wholly different kinds of learning or memory systems remains [e.g., Sherry and Schacter, 1987]. It is nowhere more evident than in MacPhail and Bolhuis's [2001] title, 'Adaptive specializations versus general process' (italics in original). The implication of this phrase is at variance with the basic facts of evolutionary biology. Evolution produces both generality across species, through common descent or convergence, and species-specific adaptations in those general characters [for an excellent discussion of how these ideas apply to learning see Papini, 2002]. Just as beaks (a structural 'module') are both general across bird species and specialized for particular feeding niches, so might we expect both generality and specificity in specific parts of memory and brain. As is so well known in sensory systems, species-general processes can be seen as evolved adaptations to general features of the world, but at the same time they are adaptively tweaked for particular niches. Adaptation and modularity are well accepted principles of biological organization [Raff, 1996; Barton and Harvey, 2000], but there has been surprising resistance to applying these ideas in comparative cognitive psychology [see Bitterman, 2000; Plotkin, 1997; Shettleworth, 2000]. And the argument for quantitative adaptations of spatial memory in food-storing birds is very compelling, as a few facts make clear.

Near Anchorage, Alaska in December, daylight lasts less than six hours. This is the only time during which diurnal birds can forage. Moreover, the average temperature is more than 5°C below freezing, and there is nearly a meter of snow on the ground [Pravosudov and Clayton, 2002]. Black-capped chickadees in this climate are the behavioral ecologist's proverbial 'small bird in winter' struggling to survive each long cold night. The conclusion seems inescapable that the conditions they face select intensely for successful foraging, and in this species that includes retrieving stored food. Indeed, there is experimental support for the idea that storing and retrieving food contribute to fitness [e.g., Nilsson et al., 1993]. Further, some species possess a whole suite of morphological and behavioral adaptations related to reliance on storing. The best example is the Clark's nutcracker (Nucifraga columbiana), a pine seed specialist of the American Southwest [Vander Wall and Balda, 1981]. Compared to other corvids such as scrub jays (Aphelocoma coerules-

cens) that live in similar areas, the Clark's nutcracker has an especially long sharp bill, used for prying seeds out of unripe pine cones before other birds can get them. It also possesses a sublingual pouch, a structure used for carrying large numbers of pine seeds to suitable storing areas, and it is a strong flier, sometimes traveling several kilometers with loads of seeds to store. Moreover, it breeds exceptionally early, feeding its young on stored seeds [Vander Wall and Balda, 1981]. A bill, flying ability, seasonality in breeding – these characters are shared among birds but adaptively specialized in each species for its particular niche. Similarly, one might expect to find adaptive specializations of cognition and brain because retrieving food stored in many scattered locations after days to months seems to create an extra demand on spatial memory over and above the demands faced by species that do not store. Given that the avian hippocampus is involved in memory for storage sites [Sherry and Vaccarino, 1989], the relatively large hippocampus of food-storing species [Krebs et al., 1989; Sherry et al., 1989] would appear to be part of such an adaptive specialization.

Misconceptions and Oversimplifications: The Comparative Approach

Nevertheless, comparisons of spatial memory and hippocampus in food-storing and non-storing birds do not unanimously support the simple adaptationist hypothesis [Shettleworth and Hampton, 1998; Bolhuis and Macphail, 2001; Macphail and Bolhuis, 2001; Balda and Kamil, 2002]. For instance, there are exceptions to a simple linear relation between relative hippocampal volume and amount of storing thought to occur in the wild [e.g., Basil et al., 1996]. What accounts for these inconsistencies? One possibility is that the hypothesis is too naïvely simple. Or perhaps, as discussed further below, it is framed in the wrong way. However, not even broadly correct functional hypotheses are necessarily consistent with every relevant datum. Applications of the comparative method to functional hypotheses about brain structures, social group size, or other characters typically involve regressions across many taxa that are significant despite a certain amount of scatter [Harvey and Pagel, 1991]. The scatter can reflect any number of factors. For example, if the data are based on different sample sizes and different methodologies, not all of them may be equally good estimates of population values. In any case, most characters are subject to multiple selection pressures. For example, social group size is influenced by factors related to preda-


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tion and to food availability, so a significant effect of, say, food distribution, does not mean other factors are not involved that cause particular taxa to deviate from an overall trend. In the case of food-storing and memory, a possible example is that species which hoard both perishable and nonperishable items may need to remember what and when they stored in addition to remembering where the stores are, and this may be reflected in a further increase in hippocampal volume over and above that supporting exceptional spatial memory [see Dwyer and Clayton, 2002].

Even MacPhail and Bolhuis's [2001] and Bolhuis and MacPhail's [2001] grant that, on the whole, the trend in comparisons of hippocampus or memory in food-storers is predicted by the simple adaptive specialization hypothesis, even if the ordering of species is not always exactly as would be predicted from their dependence on stored food in the wild. Nevertheless, there are a number of reasons why the results could be somewhat variable. One factor that is often overlooked, the phylogeny of food-storing, suggests that similar results need not be obtained when corvids and parids are tested in similar ways in the laboratory. The phylogetic distance between corvids, parids, and some other food-storing species indicates that food-storing evolved more than once [see Papini, 2002]. The patterns of relatedness among storing and non-storing species are also different in parids and corvids. Because there may be a number of ways to increase the efficiency with which stored items are retrieved, comparative studies of memory within parids and corvids — not to mention birds in other families that have not been tested so extensively — need not give parallel results. Efficient retrieval could evolve by means of changes in how the locations of items are encoded (for instance, storers might have very good spatial discrimination ability), retained (i.e., memory), or strategies for locating storage sites in the first place could change without any change in memory encoding, retention, or retrieval [see Andersson and Krebs, 1978; Brodin, 1994]. Furthermore, different behavioral tests of spatial memory in the laboratory may tap somewhat different capacities [for discussion see Chapter 6 in Shettleworth, 1998; Shettleworth and Hampton, 1998]. Finally, unlike the original applications of the comparative method to all available data on avian hippocampus which showed that hippocampal volume relative to telencephalon was greater in food-storing than in non-storing families [Krebs et al., 1989; Sherry et al., 1989], most comparisons of brain or behavioral measures within parids or corvids are based on small numbers of individuals from a very small sample of species.

Misconceptions and Oversimplifications: What Cognitive Adaptations Are Interesting?

MacPhail and Bolhuis's [2001] and Bolhuis and MacPhail's [2001] critique of the research on food-storing betrays an obsession with differences in learning and memory to the exclusion of other mechanisms that may contribute to differential performance of food-storing and non-storing species. For the traditional comparative psychology of learning they espouse, species differences in cognitive processes other than learning — for example perception or attention — are not only theoretically uninteresting but troublesome confounds that must be ruled out by painstaking experimentation. However, if one wants to discover what possible cognitive differences contribute to differences in natural behavior, it may be helpful to take a broader view that encompasses all aspects of information processing and use, from perception and attention through to motivational factors and decision making [see Shettleworth, 1998]. To take another example involving the comparative analysis of brain and developmental processes, researchers wanting to know why many birds sing only their species-specific song needed to consider a whole range of mechanisms from species-specific perceptual selectivity or motor capacities through to selective learning. It would not have made sense to confine investigations to a single kind of mechanism. Of course this does not mean that theoretical distinctions among different kinds of cognitive mechanisms are unimportant. Among other reasons, in the case of food-storing birds, the results of behavioral tests designed to distinguish among possible kinds of cognitive mechanisms are key to understanding the possible function of hippocampal differences. Such data may or may not point to species differences in memory per se, but any non-memory differences cannot simply be dismissed as having nothing to do with adaptive specialization.

Alternative Approaches to Species Comparison: 1. Relative Differences

The numerous variables contributing to performance in a laboratory test of learning — type of stimuli used, size and kind of reward, age and past history of the animals, and so on — are summarized by MacPhail [e.g., 1987] as contextual variables. Bitterman [1975] originally suggested that the way to control for these variables is by systematic variation of the suspect factors. In the case of testing for superior spatial memory in food-storing as compared
to non-storing species, systematic variation could mean, for example, seeing whether food-storers do better than non-storers over a range of reward sizes. However, in principle this approach can lead to an infinite regress: it is never possible to prove the null hypothesis that no contextual variable has produced an observed species difference in performance [Kamil, 1988]. Kamil’s [1988] suggested solution to this problem is to vary the tasks. For example, species differences in spatial memory durability and capacity may be tested both in operant tasks and in more naturalistic tasks in which the animals move around in larger spaces [Shettleworth, 1995]. Of course the absolute level of performance varies drastically across these tasks in a way attributable to ‘general process’ factors. For example, in typical operant tasks, many trials are given in quick succession and the remembered items are very close together. Such tasks are high in interference, and memory is accordingly rather poor in absolute terms, lasting seconds rather than minutes. In naturalistic tasks where birds fly around in a large room, the places to be remembered may be several feet apart and the trials are more separated in time. Memory is accordingly much better than in operant tasks. Nevertheless, food-storing species tend to outperform close relatives that do not store or that store less food in both operant and avairy tasks. Hippocampal lesions also degrade performance in both types of tasks [Sherry and Vaccarino, 1989; Hampton and Shettleworth, 1996a; but see Hampton and Shettleworth 1996b].

The approach to testing for cognitive generalization that has guided most of the comparisons among food-storing and non-storing species differs in a fundamental way from the approach used for comparing their hippocampi in that it looks for absolute differences. In contrast, the comparative analysis of brain structures looks at the volume of the structure of interest relative to overall body size or the volume of some control brain structure assumed not to be affected by the same selection pressure [Harvey and Krebs, 1990]. Hippocampus-to-telencephalon ratios have generally been used in comparing food-storers to non-storers. The analogous approach to comparative studies of cognition would consist of regressing performance of each species on a spatial task against its performance on a similar but non-spatial control task [Lefebvre, 1996; Lefebvre and Giraldeau, 1996]. Just as regressing volume of one brain region against body weight or volume of another brain region controls for differences due to overall body or brain size, Lefebvre [1996] suggests that this relative approach to comparing species on cognitive tasks controls for generalized differences in performance due to factors like adaptability to the lab or motivation to perform in the tasks. At the same time, however, it is not asking the original question, ‘Do food storing birds perform exceptionally well on tests of spatial memory?’ Rather, it asks, ‘Do food storing birds perform better on spatial tasks relative to non-spatial tasks than other birds?’ This new hypothesis is not related in such a straightforward way to the natural history and presumed adaptive value of spatial memory in these animals as is the simple hypothesis of absolute superiority in spatial memory. However, existing data from experiments in which storing and non-storing species have been compared on both spatial and non-spatial memory in the same setting do lend themselves very well to this kind of analysis [see also Shettleworth and Hampton, 1998]. These data and some new tests of what they might mean are discussed next.

**Why Do Food-Storers Choose Space over Color whereas Non-Storers Don’t?**

Most studies of memory in food-storing and non-storing birds have compared them on the capacity and/or persistence of spatial memory. However, quite early in the laboratory studies of food storing it was shown that the memory used, at least by Clark’s nutcrackers, is specifically spatial [Vander Wall, 1982; see also Sherry and Duff, 1996], and this finding led to interest in whether food-storing birds might selectively use spatial cues when redundant non-spatial cues were also available and relevant for memory [Brodbeck, 1994]. The functional argument for strong reliance on spatial cues is that in nature local features of a storage site may change over time as leaves fall, snow cover comes and goes, but spatial location does not change. And indeed, an enhanced tendency to use spatial as opposed to non-spatial cues in a short term working memory task turns out to be perhaps the most robust difference between storing and non-storing species described so far [see below and Macphail and Bolhuis, 2001].

David Brodbeck [1994] first reported this finding, using black-capped chickadees and dark-eyed juncos, an unrelated non-storing passerine that also winters in Southern Ontario, where the work was done. Both species were trained in a one-trial associative memory task designed to be as similar as possible to food-storing without actually requiring the birds to store food. In the first part of each trial, the bird flew into a large aviary which had four differently decorated feeders (small blocks of wood)
hanging in various locations on one wall. Each feeder had a hole big enough to hold half a peanut, and one had a peanut. The holes were visible to the birds in this phase, so a bird familiar with the task would fly immediately to the peanut and begin to eat it. After 30 s, the lights were turned out, and the bird returned to its home cage for the retention interval, in this case just a few minutes. During the retention interval the holes in all the feeders were covered with a small piece of Velcro. When the bird returned for the second phase of the trial, it could pull off the Velcro and finish the nut. New feeders in new locations were used for each trial, mimicking the situation faced by a scatter-hoarding bird in nature.

Both chickadees and juncos learned this task readily, soon relocating the baited feeder on the first look on most trials. Once they were performing well, unrewarded test trials were administered in which local features of that trial’s correct feeder were dissociated from its location by swapping the correct feeder with another feeder in the array. Thus a bird had to choose between the formerly baited location and the actual feeder that had been baited in the first part of the trial. Chickadees showed a strong preference for location in these tests, whereas juncos chose about 50:50 between location and color/pattern. Because they never found a peanut in the tests, the birds made second, third, and fourth choices. Chickadees tended to choose color/pattern second, showing that they remembered local features in addition to location, as did juncos, whose second choice tended to be of the feature they had not chosen first. The same pattern of species differences appeared when chickadees and juncos were tested in an operant analogue to the aviary task, with colored rectangles on a computer touchscreen as the stimuli to be remembered [Brodbeck and Shettleworth, 1995]. Chickadees also preferred spatial over local cues in an analogous food storing task [Brodbeck, 1994]. Clayton and Krebs [1994] found the same effect in a comparison of a storing and a non-storing parid (marsh tit and blue tit, Parus palustris and P. caeruleus) and a storing and a non-storing corvid (European jay and jackdaw, Garrulus glandarius and Corvus monedula). In fact, a preference for spatial over local cues to food location may be more generally characteristic of species that need to rely heavily on spatial memory in the wild [Platt et al., 1996; Healy and Hurly, 1998; but see Strasser and Bingman, 1996].

The robust species difference in use of spatial over color (and sometimes pattern) cues by food-storing as compared to non-storing birds is viewed by MacPhead and Bolhuis [2001] as a trivial effect of species differences in stimulus salience. As pointed out above, a priori the cognitive adaptation of food-storers, if any, does not necessarily need to be in memory rather than some other component of spatial information processing. In any case, the possibility that these results are evidence of differential memory cannot be so readily dismissed. There are at least three possibilities. (1) Food-storers selectively attend to spatial rather than color/local cues when both are available, whereas non-storers do not, or do so to a lesser degree. This is the mechanism dismissed as ‘mere’ stimulus salience by MacPhead and Bolhuis [2001]. (2) Food-storers discriminate better among spatial locations than do non-storers. Thus, even with no better spatial attention or spatial memory than non-storers, they perform better in a spatial test because they can more easily discriminate the correct stimulus from nearby distractors. This possibility has been tested for some Eurasian parid species, with mixed support [McGregor and Healy 1999; Biegler et al., 2001]. (3) Relative to color, food-storers remember locations better than non-storers, i.e., they do in fact have superior spatial memory as proposed by the simple adaptive specialization hypothesis. Note that this alternative is stated in a way compatible with the relative approach of Lefebvre [1996] outlined above. (4) A fourth possibility is that food-storers simply prefer to respond first to spatial cues when such cues conflict with other cues. However, Brodbeck and Shettleworth [1995] showed that, contrary to this hypothesis, chickadees still show a spatial superiority even when spatial and color cues are tested individually after exposure to a location-color compound, and further data of this kind are summarized below.

In a recent series of experiments with black-capped chickadees and dark-eyed juncos, Richard Westwood and I tested species differences in the division of attention, spatial memory, and spatial discrimination separately using an operant delayed matching to sample procedure [Shettleworth and Westwood, 2002]. Our first experiment tested for species differences in the division of attention. The idea here is to compare the animal’s memory for a particular type of cue when it has been presented alone (i.e., attention is undivided) vs. when it has occurred together with another cue that also needs to be remembered (i.e., attention must be devoted to both cues). A detrimental effect of dividing attention is evidenced in poorer performance in the compound cue than the simple cue case. The hypothesis suggested by the findings of Brodbeck [1994] and others is that when presented with spatial and color cues, chickadees will show a divided attention effect for color but not location, whereas for juncos performance with both features will be degraded.
somewhat under conditions of divided attention. Contrary to this hypothesis, however, neither chickadees nor junco showed a divided attention effect with spatial cues: they performed equally well on tests of memory for the location of a white square on the touchscreen whether or not a to-be-remembered colored disk had accompanied the square. At the same time, both species showed a substantial divided attention effect for color, performing worse on color tests when the location of the sample also had to be remembered.

In the next experiment [Shettleworth and Westwood, 2002, Experiment 2], the same birds now had only separate tests of spatial memory or color memory. Each individual performed both tasks on alternate days. Thus on Monday, for example, the sample stimuli were colored disks and the tests of memory consisted of asking the bird to choose between two side-by-side colored disks and rewarding it for pecking the one which was the same color as the sample. On Tuesday, each sample stimulus was a white square in any of 20 locations on the touchscreen, and in tests a bird had to choose between a square in that location and one in a different location. On Wednesday, memory for color was tested, and so on. To ask how memory for location compares to memory for color, we accustomed the birds to retention intervals up to 20 s long and then exposed them to alternating space and color days with randomly varying retention intervals of up to 40 s. Throughout the experiment, chickadees consistently performed better on spatial than color matching whereas juncos did not. However, this species difference was not statistically significant in an overall analysis of the data as required by the simple hypothesis that chickadees have absolutely better spatial memory than juncos. Rather, spatial performance was significantly better than color performance in the chickadees, whereas this was not the case for the juncos. This pattern is encompassed by the modified, relative, adaptive specialization hypothesis that spatial performance is better relative to performance on a control task in the chickadees than in the juncos.

Analyses of other relevant data from our lab follow the same pattern [Shettleworth and Hampton, 1998].

Chickadees may perform relatively better than juncos on spatial compared to color matching not because they have better memory per se but because they have better spatial discrimination ability. To address this possibility we [Shuttleworth and Westwood, 2002, Experiment 3] analyzed performance on all the spatial matching sessions in terms of whether the comparison stimulus was adjacent to (near) the sample or nonadjacent (far). If chickadees are capable of sharper spatial discrimination, they would be expected to perform especially well at the difficult near trials. Contrary to this prediction, chickadees performed better than juncos only on the far trials, which were, as predicted, substantially easier for both species [McGregor and Healy, 1999; see also Biegler, 2001]. We also performed a more detailed analysis of the effects of the positions of samples and distractors on matching accuracy using multidimensional scaling which showed that both species represent the stimuli on the touchscreen in a similar, Euclidean, manner.

As the concluding part of this study, Robert Hampton [Hampton and Shettleworth, 1996a] performed hippocampal lesions on the same birds and retested each individual on the same separate spatial and color matching tasks. In every one of the eight birds that could be tested, spatial memory was impaired but color memory was unaffected, a compelling demonstration not only that the hippocampus is involved specifically in the spatial task in both species but that it plays a role in the very task for which chickadees show a relative advantage. The results of this lesion study are also consistent with a large body of literature on the effects of hippocampal lesions in other birds, primarily pigeons, on performance in a variety of laboratory spatial and visual memory tasks [Colombo and Broadbent, 2000; Hampton and Shettleworth, 1996b; but see MacPhail, 2002]. This series of studies, then, clearly shows that the chickadees’ preference to respond to spatial rather than color cues when both are relevant reflects a difference in spatial, relative to color, memory rather than a difference in spatial attention or discrimination ability, as compared to juncos. But of course this does not mean that analogous spatial preference in other species or settings reflects the same mechanism. In principle, this same kind of experimental analysis could be used with other species to tease apart attention, discrimination, and memory as well as to gather data appropriate for testing the relative hypothesis about species differences. However, other approaches to unraveling the relationships among food storing, memory, and hippocampal enlargement might be more productive.

**Alternative Approaches: 2. Within-Species Comparisons**

Whenever different populations of the same species inhabit somewhat different environments, within-species comparisons can be used to test functional hypotheses. In a recent ground breaking study Pravosudov and Clayton [2002] applied this approach by comparing memory and
brain in two populations of black-capped chickadees, one from Alaska and one from Colorado, where winters are comparatively milder. Birds from both areas brought into the laboratory in autumn and maintained in a standard way were given tests of food storing, spatial memory, and color memory, and their brains were examined. Consistent with the adaptive specialization hypothesis, chickadees from Alaska stored more food, performed better than Colorado birds on spatial but not color memory, and had relatively bigger hippocampi containing more neurons. This finding opens the way to more detailed study of hippocampal anatomy and possible seasonal and developmental changes in brain and behavior unconfounded by possible species differences in extraneous factors like sensory and motivational differences. Because experience can influence hippocampal development in food-storers [e.g., Clayton, 1996], an important question for such a research program would be the extent to which different developmental histories might contribute to behavioral and neural differences between populations. In principle, a research focus on one or two cases where a within-species comparison of brain and behavior is possible can provide a basis for better understanding of between-species differences, just as has been done so successfully with seasonal and sex differences in bird song learning [see review by MacDougall-Shackleton and Ball, 1999].

Concluding Remarks

A recurrent theme in Bolhuis and MacPhail's critiques of 'neuroecology' [Bolhuis and MacPhail, 2001, 2002; Macphail and Bolhuis, 2001] is that researchers in this area mistakenly confine answers to questions about the evolution and current function of behavior with answers to questions about causal mechanisms for behavior. Following Tinbergen [1963], they point out that these are different questions, and that at most the answers to functional questions can only provide clues to answers about causal questions. Now, it is absolutely correct that knowing, for example, that black-capped chickadees are under intense selection for successful retrieval of stored food does not tell us exactly how they actually manage to retrieve any food. The supposition based on natural history, experimental data, and modeling that food-storing is important to their winter survival and subsequent reproduction tells us only that they must have cognitive and neural mechanisms allowing them to retrieve their scatter-hoarded food. It certainly does not tell us whether they use memory, or their hippocampus, let alone exactly how these work, never mind how — if at all — memory or hippocampi differ among chickadee populations or species. But the great mass of evidence from comparative biology makes it seem more likely than not that in some behavioral, cognitive, and neural mechanism(s), they differ at least quantitatively and in an adaptive way from birds that store less or no food. From the viewpoint of evolutionary biology rather than the traditional comparative psychology of learning [e.g., Macphail, 1987], the onus is on those who claim no species differences. In fact, of course, both generality and specificity are part of the picture, and in studies of cognition and brain as elsewhere in comparative biology, neither should be emphasized too much at the expense of the other [for more discussion see Papini, 2002]. In the intellectual climate sketched at the beginning of this article, an attractive and plausible hypothesis is that food-storing birds possess an adaptation specific to spatial memory and its neural substrate. Many of the data resulting from attempts to test this hypothesis are consistent with it. This includes the recent more detailed investigations of population and species differences reviewed here. None of these findings would have resulted without the assumption that analyzing how animals learn in nature is not only fascinating but revealing of mechanisms that should be of central importance to the comparative study of cognition.

References


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