

Spatial Learning and Memory in Birds

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Spatial learning and memory · Cognitive ecology · Foraging

Abstract

Behavioral ecologists, well versed in addressing functional aspects of behavior, are acknowledging more and more the attention they need also to pay to mechanistic processes. One of these is the role of cognition. Song learning and imprinting are familiar examples of behaviors for which cognition plays an important role, but attention is now turning to other behaviors and a wider diversity of species. We focus here on work that investigates the nature of spatial learning and memory in the context of behaviors such as foraging and food storing. We also briefly explore the difficulties of studying cognition in the field. The common thread to all of this work is the value of using psychological techniques as tools for assessing learning and memory abilities in order to address questions of interest to behavioral ecologists.

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Introduction

Tinbergen [1963] delineated four types of questions concerning an animal's behavior: its function, mechanism, ontogeny and evolution. Behavioral ecologists, by

focusing on functional questions, have been hugely productive in furthering our understanding of many behaviors. Of late, however, some have attempted to integrate function and mechanism [for example: physiology e.g., Kullberg et al., 2002; endocrinology e.g., Van Duyse et al., 2002; cognition e.g., Uy et al., 2000; immunology e.g., Norris and Evans, 2000]. In this brief review, we address one of these burgeoning areas, specifically the role of cognition in behavior [for an articulate formulation for the advantages of such integration see Yoerg, 1991].

Learning and memory, which underpin a great deal of behavior, allow plasticity in response to changing situations, both social and ecological. However, there are few behaviors for which we have a substantial understanding of the role learning and memory plays or of their neural substrates. The most familiar and fully elucidated examples are song learning in passerines and imprinting in precocial birds [see reviews in Catchpole and Slater, 1995; Bolhuis and Honey, 1998]. The impressive bodies of work on these two behaviors have focused, by and large, on one, or a few species in spite of, in the case of song learning, the striking interspecific variation in the flexibility of when and what songs are learned. We know little of whether the mechanistic processes underlying song learning or imprinting do or do not differ among species [but see MacDougall-Shackleton and Ball, 1999; ten Cate, 2000].

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Variation in Cognitive Abilities

Inter- and intra-specific variation in cognition have been postulated on a number of occasions and ever more frequently by behavioral ecologists. The general assumption is that cognition, like morphological and other behavioral traits, has been, and continues to be, acted on by natural selection. However, Macphail and Bolhuis [2000; see also Bolhuis and Macphail, 2001] have criticized this supposition. They claim that natural selection has acted solely on the peripheral nervous system (by which they mean neural regions involved in perception of stimuli) and not on 'higher learning areas'. The foundation of their argument has two parts: the first is that Darwin thought that differences in intelligence among animals would be quantitative, not qualitative. The second is, in fact, the extension of this thought on which almost all of psychological research has been founded since Darwin's time, i.e. that the same rules for learning and memory are applied irrespective of the organism or the context in which the learning and memory is to be used. The view that natural selection should be able to 'reach' and affect any part of an animal's morphology or behavior, including cognitive abilities (we do not wish to use 'intelligence' as Macphail and Bolhuis [2000] do, as it tends to be defined 'in the eye of the beholder' and, usually, it is then taken to mean a specific cognitive ability or group of abilities) is the general standpoint of the behavioral ecologist [for a clear exposition of the background and differences between these two views, see Shettleworth 1998]. This focus on qualitative differences does not exclude the possibility that natural selection has also brought about quantitative differences in cognitive abilities as championed by Macphail and Bolhuis [2000]. Suffice it to say that when Macphail and Bolhuis [2000] and Bolhuis and Macphail [2001] appeared, they were met by a stinging volley of responses [for example, see Dwyer and Clayton, 2002; Flombaum et al., 2002; Hampton et al., 2002; MacDougall-Shackleton and Ball, 2002]. However, in spite of all the rhetoric, at this stage neither side of the argument can muster substantive support.

There is much we need to know before we can comprehensively defend either side of this argument. Ironically, behaviors that have received considerable attention from behavioral ecologists over the past decade are not those to which we can currently look to provide us with much useful information with respect to interspecific (or intraspecific) variation in cognition. For example, although there is a vast literature on whether or not females choose mates and on what characters they might base their choice, the

question as to how it is that a female 'knows' which is a 'good' male remains largely unanswered. Does she have a physiological response to a good male and, for example, use a change in her heart rate on encountering him to tell her that he is of high quality? Something akin to this occurs in ring doves such that the visual and auditory stimulation from a male's display activates the female's hypothalamus, which eventually leads to stimulation of her ovaries [Barfield, 1971]. It is not clear, however, whether this is a mechanism of choice common to other animals. At least three other plausible alternative mechanisms of choice involve learning and memory to varying extents. The first is when the female visits some or all of the available males prior to mating, requiring her to remember what the male is like and/or where he is for successful relocation. There is evidence that prior experience may affect female choice [e.g., Rosenqvist and Houde, 1997; Uy et al., 2001] but one might expect either that females should not visit more males than they can remember, or, that they may go directly to a male with whom they have previously, successfully reproduced. We do not know if females differ in the number of males they can remember or whether such capacity varies across species. A second possible mechanism is that the female imprints on her father or her brothers. This seems at least plausible for those females whose fathers participate in rearing their offspring. One might then predict that females who visit multiple males do so until they find one that resembles the remembered paternal image [ten Cate and Vos, 1999; Plenge et al., 2000; Slagsvold and Hansen, 2001]. A third possibility is that a female does not directly assess a male but rather copies the choice of other females [e.g., Witte and Ryan, 1998; Reynolds and Jones, 1999]. Such a female needs only to learn to discriminate females from males and could then ignore inter-male variation. Such ignorance should lead to a long-term cost as females might eventually choose males of poor quality. This strategy might, then, be beneficial only to, or, especially to, females with no experience of their own. In subsequent matings or seasons, they may base their decisions on memories of their own past choices.

Although mate choice provides ample fodder for speculation on a role for learning and memory, investigations of foraging behavior have contributed more to our current understanding of variation in cognition and whether or not cognitive abilities might be matched to apparent cognitive demands. These contributions have been provided not least because of the amenability of foraging behavior to observation and manipulation in both the field and the laboratory. In addition, Optimal Foraging Theory (OFT)

provides a theoretical framework from which to make predictions about behavior, many of which were not met by the initially relatively simple, rule-of-thumb models. By incorporating aspects of learning and memory, including error making, models typically enabled far more accurate predictions of foraging behavior [for review see Stephens and Krebs, 1986].

One of the valuable lessons learned from testing OFT models was the advantages of using or modifying experimental paradigms that have been well developed and understood by experimental psychologists studying cognition. Skinner boxes, key or light pecking, infra-red beam breaking, operant conditioning and so on all seem a long way from any 'natural' behavior a behavioral ecologist might be interested in. However, through adaptations of apparatus and modifications to the specifics of the experimental design behavioral ecologists are profitably employing the wealth of knowledge of animal cognition supplied by psychology.

One well-developed attempt to integrate functional and mechanistic approaches to understanding behavior is the work on risk-sensitivity [e.g., Kacelnik and Bateson, 1997; Bateson and Kacelnik, 1998; Hurly and Oseen, 1999]. However, these data provide support in favor of the general processes view, in that of the variety of animals tested, they all made much the same decision when variability was in amount (more often risk-averse) or when variability was in delay (risk-prone), irrespective of their behavioral ecology. Rather, the most likely explanation to date for variation in species' preferences (for a variable or a fixed option) is that of body weight: small animals are more likely to respond to budget manipulations than are larger species [see Kacelnik and Bateson, 1996]. It has also proved difficult to reconcile the results from mechanistic studies with functional explanations [Bateson and Kacelnik, 1998].

Food Storing and Spatial Memory

In this regard at least, a more successful example is the deepening understanding we are gaining of the cognitive abilities underlying successful food storing behavior in songbirds through using variation in the behavior to make predictions about cognitive and neural differences among species. Storing excess food in their environment, rather than on their bodies as fat, is a behavior found across a diversity of taxa from invertebrates (e.g., ants and honeybees) to birds and mammals [see review in Vander Wall, 1990]. Within the songbirds, hoarding typically involves

hiding one or a few items per cache site and perhaps as many as hundreds or thousands of cache locations. Food may not be retrieved for hours, days, weeks or months [see review in Sherry, 1985]. Field observations and experiments have been invaluable in demonstrating the logistic and scientific extent of the problem. The Paridae (tits and chickadees) provide a particularly clear example of the problem: small brown birds hide small brown seeds in many, many locations in large brown woods. The tracking of the storing behavior alone is a logistic nightmare, with accurate quantification of retrieval beyond our abilities at this stage. Field data have led us to believe that the birds retrieve a significant proportion of their stores: using radioactive seeds and detectors placed next to the hidden seed, Stevens and Krebs [1986] found that their marked marsh tits (*Parus palustris*) attempted to retrieve about 25% of their stores. Cowie et al. [1981] found that retrieval was quite accurate: cached seeds disappeared more rapidly than did seeds hidden by experimenters in sites 100cm from the cache. Investigating retrieval over longer periods of time than the few days that Cowie et al.'s study covered is problematic as a significant proportion of stores are removed by animals other than the cacher [but see Brodin, 1993 and Brodin and Ekman, 1994 for use of radio-ptilochronology to track birds eating tagged caches]. Ironically, prior to these experiments the sheer number of items stored and the impressive durations before retrieval had led most researchers to assume that it was implausible that these animals could be using memory to relocate stores. It is sadly, for those of us who would like to determine the birds' cognitive abilities on the spatial and temporal scales faced by them in the field, still the case that the most productive conditions under which to address questions of learning and memory in food storing are to be found in the laboratory.

Fortunately, both avian and rodent food storers will readily store in the laboratory [e.g., Barkley and Jacobs, 1998; Hitchcock and Sherry, 1990]. In laboratory tests Sherry [1984] showed that black-capped chickadees (*Parus atricapillus*) remembered both where they had stored food and what they had stored. This was subsequently also demonstrated in scrub jays (*Aphelocoma coerulescens*) by Clayton and Dickinson [1998] who also showed that these birds tracked when they had stored food. Although a number of animals had been shown to be able to time a range of durations, this was the first time that the 'what', 'where' and 'when' of an episode had been documented in a non-human animal. Prior to the results of Clayton and Dickinson, episodic memory had been considered a cognitive feature exclusive to humans. It seems

likely that behavioral ecologists could imagine instances other than food storing in which it might be advantageous for an animal to be able to remember all three components of an episode.

The demonstration that at least some food storing birds were able to remember locations of their caches was soon followed by the determination of an area of the brain heavily implicated in this memory ability. The hippocampus had, for several decades, been known to be involved in information processing and one strongly favored theory held that the hippocampus was especially responsible for spatial information processing [O'Keefe and Nadel, 1978]. Hippocampal lesions in black-capped chickadees resulted in the birds storing food but being unable to relocate their caches accurately. In motivation to retrieve and in mechanical ability these lesioned animals seemed to behave much as did control birds [Sherry and Vaccarino, 1989]. Additionally, lesions affected performance on spatial components of food finding tasks but not when color cues were used to mark locations of hidden food. Later, hippocampal lesions in homing pigeons and in laboratory pigeons also appeared to result in deficits specifically in spatial learning and memory [Bingman and Yates, 1992; Good and Macphail, 1994]. Functionally, then, the hippocampus appeared to enable successful cache relocation.

Variation in Hippocampal Volume

Structurally, the hippocampus of the food storer was also shown to be correlated not just with the presence of food storing but also variation in the degree to which food storing was exhibited. This was shown in several correlational studies: food storers have larger relative hippocampal volumes than do non-storing species [Krebs et al., 1989; Sherry et al., 1989, 1992] and the longer and more food is stored, the larger the hippocampus [Healy and Krebs, 1992a, 1996; Hampton et al., 1995; Basil et al., 1996; but see Volman et al., 1997]. Additional correlational studies have shown that hippocampal enlargement is also apparent in nonstoring groups that are heavily dependent on spatial learning and memory: in those brood parasitic cowbirds in which only the female finds and then relocates host nests, the females have a larger hippocampus than do their conspecifics males [e.g., brown headed cowbirds (*Molothrus ater*); Sherry et al., 1993]. In species in which both sexes relocate a potential host nest, there is no sex-specific difference but hippocampal volume in both sexes is larger than in a species that are not brood parasites [screaming and baywinged

cowbirds (*M. rufoaxillaris* and *M. badius*, respectively); Rebores et al., 1996]. In experienced migrants, too, hippocampal volume is larger than in those birds that have never migrated [garden warblers (*Sylvia borin*); Healy et al., 1996]. This effect is not seen in comparable age classes in a closely related resident species, the Sardinian warbler (*Sylvia melanocephala*). As migration distance is not correlated with an increased hippocampal volume, it is thought that the additional spatial demand comes from the need to return to specific breeding sites. The degree of philopatric precision that some species demonstrate is quite remarkable [e.g., Godard, 1991].

Correlations between hippocampal growth and the onset of food storing during development [Healy and Krebs, 1993; Healy et al., 1994] were shown to have a causal basis by two experimental studies in which experience of food storing was manipulated in hand raised, juvenile marsh tits and mountain chickadees (*Poecile gambeli*) [Clayton and Krebs, 1994a; Clayton, 2001]. Hippocampal growth occurred only when the birds were allowed food storing experience. Other experiments also show that it is not food storing per se that causes hippocampal enlargement but rather spatial experience, such as a food finding task as provided to young marsh tits by Clayton [1995]. The requisite experimental manipulations have not been carried out in any of the other groups showing hippocampal enlargement.

Implicit, for a behavioral ecologist, in the finding that hippocampal enlargement is correlated with, or causally related to, an apparently higher than usual demand for spatial learning and memory is that the enlargement is beneficial to its bearer. Unfortunately, incontrovertible support for this assumption has been difficult to obtain. It was naïvely, with hindsight, thought that an enlargement as substantial as that seen in the food storer's hippocampus would confer an easily demonstrable psychological advantage over nonstorsers. A number of experiments showed this not to be the case [e.g., Hilton and Krebs, 1990; Healy and Krebs, 1992b, c; Healy 1995]. Several experiments showed that food storers preferred to use spatial rather than featural (e.g., color, shape) cues to return to food locations, whereas nonstorsers divided their preferences between these two cue types [e.g., Brodbeck, 1994; Brodbeck and Shettleworth, 1995; Clayton and Krebs, 1994b]. However, even though hippocampal lesions affect spatial memory and not memory for featural cues [Hampton and Shettleworth, 1996a], the results showing variation in cue preference do not shed much light on what, if any, advantage was conferred by an enlarged hippocampus.

To date, only a small handful of studies do appear to show some advantage. Hampton and Shettleworth [1996b] showed that food storing black-capped chickadees (*P. atricapillus*) performed better than did nonstoring dark eyed juncos (*Junco hyemalis*) on an operant spatial-non-matching-to-sample task in which birds had to choose between two pecking keys having pecked at one of them 5, 15, 30 or 60 s previously (in the 'sample phase'). The bird was rewarded for pecking at the key that they had not pecked in the sample phase. Chickadees achieved higher scores than the juncos at each of these intervals. Similarly, McGregor and Healy [1999] tested storing coal tits (*Parus ater*) and nonstoring great tits (*P. major*) in an operant task in which birds had to peck at an image on a touch screen and, following a retention interval, choose this image from one, two or three alternatives. The most striking result from this experiment was that nonstorsers made mistakes after much shorter durations (approx. 20 s) than did storsers (approx. 60 s). This result was confirmed in a test by Biegler et al. [2001] who compared the same species on an operant task which assessed the birds' ability to remember an increasing number of items, over an increasing retention period and with alternative images placed in varying proximities to the sample image (in this experiment the bird was rewarded for choosing the image that was not that seen in the sample phase). Biegler et al. found that coal tits did not differ from great tits in their spatial accuracy or in the number of items remembered, but were able to remember one item for significantly longer periods of time than could great tits.

These few studies demonstrate what has long been clear to psychologists which is that it is inordinately difficult to demonstrate cognitive differences among species, even in a relationship like that of food storing and spatial memory that appears to point to a rather specific cognitive ability. Amassing the current evidence has been at the cost of testing the animals under anything approaching 'natural' conditions: they are wild birds but tested over long periods in laboratory cages and the stimuli (small squares), the durations (seconds) and the distances among stimuli (a few centimeters) are all conspicuously far from those they would face in the real world. This, for the moment at least, appears to be an insurmountable problem. The control over extraneous variables that can be exerted in the laboratory environment allows us to be somewhat confident that these birds differ in their cognitive abilities. It can only be presumed, at this stage, that the differences in performance seen in non-matching-to-sample tasks such as these are representative of the varia-

tion in cognitive abilities required for their real world environment. An alternative interpretation is that of Macphail and Bolhuis [2000] and Bolhuis and Macphail [2001] who presume that such an avenue of research is flawed from the outset and inevitably doomed to failure.

Choice of Model System

Do these problems of testing cognition then restrict behavioral ecologists interested in the cognitive abilities of their animals to donning white coats and learning apparently impenetrable psychological jargon? We would argue that the second question is most easily answered and in the affirmative. Psychologists, after all, have a proven track record in testing questions concerned with cognitive abilities. We would answer the first question with a more cautious 'not necessarily'. One time honored approach to this problem familiar to geneticists working on *Drosophila*, to developmental biologists working on *Caenorhabditis elegans*, and to psychologists testing pigeons and rats, is the use of a model animal, chosen mainly for its logistic benefits. The domestic chick, for example, has proved to be a useful model not only in the classic imprinting and passive avoidance paradigms but also in addressing questions in spatial learning [e.g., Cozzutti and Vallortigara, 2001], navigation [e.g., Zimmerman et al., in press] and in signaling [e.g., Guilford et al., 1987; Marples and Roper, 1996; Rowe, 2002]. In many cases, however, there is a specific species we would like to investigate (e.g., food storsers) but where it is difficult to test the animals in a suitable laboratory setting, or, where having tested them in the lab, one would like to extend the findings to the field. Nonetheless there is both increasing interest and success in investigating cognition in animals or in situations that have not commonly been tested in the past, e.g., spatial learning in sticklebacks (*Gasterosteus aculeatus*) [Girvan and Braithwaite, 1998], and pigs (*Sus scrofa*) [Mendl et al., 1997], Mullerian mimicry in insectivorous wild birds [Speed et al., 2000], training a range of endangered vertebrates in predation avoidance [Griffin et al., 2000].

Unfortunately, few animals present themselves as obvious candidates for subjects in field tests of cognition. A non-exhaustive list of the desirable features for this purpose is that the animal (1) is individually identifiable, or can be marked; (2) can be excluded from interference by others for the course of the experiment; (3) can be easily observed; (4) will readily learn to use appropriate experimental equipment; (5) can be tested at relatively frequent,

regular intervals. Various invertebrates fulfill these criteria and have proved to be useful test subjects, e.g., symmetry learning in honey bees [Giurfa et al., 1996], in bumble bees [West and Laverty, 1998], navigation in desert ants [Collett and Zeil, 1998]. Invertebrates are also much more easily brought into and tested in a laboratory setting than many vertebrate species [see reviews in Collett and Zeil, 1998; Weiss, 2001].

Testing Cognition in the Field

It is much less easy to find a vertebrate that is quite so amenable to our requirements. However, over the past decade we have been investigating the cognitive abilities of wild, free-living rufous hummingbirds (*Rufus selasphorus*) because this species does meet these criteria for field studies of cognition. These birds are fiercely territorial and can be individually marked, learn within an hour to feed from artificial food sources, feed every ten minutes or so, and hold territories encompassing open fields and so are readily followed by eye. Rufous hummingbirds migrate between northern Mexico and the Rocky Mountains in Canada and en route have previously proved useful in addressing questions in optimal foraging [e.g., Hixon et al., 1983; Gass and Sutherland, 1985; Wolf and Hainsworth, 1990]. Although they are also tractable laboratory subjects [e.g., Brown and Gass, 1993; Garrison and Gass, 1999], we have been exploiting the logistic advantages to testing cognition in rufous hummingbirds in the field to probe the hypothesis that there may be an advantage to the territorial males of remembering flowers they have recently emptied. Male hummingbirds do remember and avoid visiting recently emptied flowers [Healy and Hurly, 1995], they return to flowers they did not empty, whether or not these flowers have changed visually in the interim [Hurly and Healy, 1996, 2002], and they prefer to visit flowers they have never seen rather than flowers seen previously but which they had not visited [Henderson et al., 2001]. The birds pay more attention to spatial cues than to visual cues when returning to rewarding flowers, and which spatial cue is used depends on the proximity of other flowers. When other flowers are 40 cm or closer, the birds learn a rewarded flower's location in relation to those flowers. When other flowers are further than 40 cm from the rewarded flower, the bird learns the location of the rewarded flower in relation to the larger, surrounding non-floral cues such as bushes, trees, etc. [Hurly, 1996; Healy and Hurly, 1998]. Thus far we have confirmed and extended earlier findings from the laboratory showing the

predominant role of spatial cues over visual cues during foraging decision making by territorial rufous hummingbirds [Miller et al., 1985; Sutherland and Gass, 1995]. We also have some insight into how hummingbirds might encode flower locations with respect to surrounding landmarks. This confirmation of laboratory results by field data may engender some comfort to those who are confined to testing their animals in the laboratory.

More recently, we have shown that hummingbirds may, like scrub jays, remember when they last visited a location. Remembering the time of a previous visit is as useful as remembering where the flower was if the animal is to avoid revisiting a flower before it has refilled with nectar. In a field experiment territorial birds were provided with eight flowers, four of which were refilled ten minutes after he had emptied them and the others refilled after 20 min. Such a replenishment schedule is termed a Fixed Interval (FI) schedule. As expected, if the birds were matching visits to an expectation of reward, birds visited the FI(10) flowers much more frequently than the FI(20) flowers [Henderson et al., submitted]. More impressively, the distribution of visits peaks just after 10 min for FI(10) flowers and not long after 20 min for the FI(20) flowers. The timing of visits to the two groups of flowers (randomly located in the array of eight) also differed from each other so the birds were not simply visiting any flower on any one visit nor timing visits to be spaced by about 20 min. In this experiment, the males tested had exclusive access to the flowers. In an earlier test of timing abilities in hummingbirds, however, Gill [1988] presented male long-tailed hermit hummingbirds (*Phaethornis superciliosus*) off their lekking territories with either two or three feeders that offered sucrose solution according to an (FI) schedule of either 10 or 15 min. Typically, more than one bird used a feeder although one of them tended to become the predominant visitor. Not only did the principal user visit the feeder more frequently, he often returned to the feeder prior to the scheduled refill (a timing loss). Delaying return by too long, however, left him vulnerable to the possibility that another male would empty his feeder (a competitive loss). Faced with these opposing timing pressures, at least one male's typical return time lengthened over the course of three days from returning too soon to matching very closely the FI(10) schedule. By doing so he more than doubled his success rate. The ability to time intervals in this way, then, may be valuable for nectivorous animals, whether or not they are territorial. Just how many such intervals one of these birds can concurrently keep track of is not clear.

There are two general mechanisms for keeping track of temporal information: phase timers, such as circadian rhythms, which enable the animal to return to a location at the same time each day (i.e. events spaced about 24 h apart) and interval timers. These latter enable the bird to set a timer from the occurrence of a particular event, irrespective of when during the day this event occurred [Gibbon et al., 1997]. Both of the hummingbird studies would implicate the use of an interval timing mechanism and, like the animals in laboratory time-place studies (usually pigeons or rats), the rufous and long-tailed hermit hummingbirds, are able to time at least one or two intervals concurrently [e.g., Crystal and Miller, 2002]. The rufous hummingbird results extend what we know of animal interval timing abilities from laboratory experiments in that the birds appeared to be tracking eight different locations and timing intervals of 10–20 min. The intervals in the lab, used to date at least, have not been greater than eight minutes [e.g., Carr and Wilkie, 1998] and the number of locations usually not more than four [e.g., Carr and Wilkie, 1997; Pizzo and Crystal, 2002].

All of the experiments referred to here [and those by other workers e.g., testing hummingbirds of various species; Valone, 1992; Sandlin, 2000a, b] show that hummingbirds are a particularly useful group to investigate questions of cognition in the field. They are, of course, not the only animals that are useful in this way but it can be rather more difficult than might be assumed at first to find animals that are suitable for this kind of investigation on the relevant logistic criteria.

Hormones and Cognition

There are many pitfalls awaiting the behavioral ecologist wanting to know more about the cognitive abilities of their animal. Using an appropriate testing paradigm (i.e., one that suits the animal's perceptual and mechanical abilities) and controlling for extraneous variables (such as temperature, time of day, season, age, prior experience and so on) are among the most obvious. A number of other mechanistic processes additionally impinge on an animal's performance in a cognitive task. One of especial relevance to the study of spatial learning and memory, at least in mammals, is the role of hormones in performance. Male mammals consistently outperform their conspecific females on spatial tasks [review in Jones et al., 2003]. This difference appears not to be correlated with body size differences or speed of movement but rather with the level of androgen to which the animal is exposed (specifi-

cally testosterone and estrogen) either during antenatal development or via postnatal circulation. Supporting data come from a range of experiments. For example, female rodents exposed to increased testosterone in utero, either experimentally or because they come from a male-biased litter, perform better on spatial tasks as adults than do unmanipulated females or those from female-biased litters [e.g., Williams et al., 1990; Williams and Meck, 1991; Roof, 1993]. Sex differences in spatial learning and memory in voles are only seen when the animals are tested in the breeding season when the males' level of testosterone (T) is high relative to the nonbreeding season [Galea et al., 1994, 1995]. These behavioral differences are also correlated with neural changes, particularly in the hippocampus [e.g., Gouchie and Kimura, 1991; Roof and Havens, 1992]. It is not currently known what relationship T has with spatial learning and memory in other animals but it is likely that there is some androgenic influence on performance. Other hormones (e.g., glucocorticoids, thyroid hormones), too, affect cognitive performance under a range of conditions, including stressful situations [review in Schantz and Widhom, 2001]. Knowing that several hormones are likely to affect cognitive performance, let alone other equally probable influences such as early experience [e.g., Juraska et al., 1984], ageing [e.g., Barnes, 1988], and disease [e.g., Berdoy et al., 2000], makes the task of demonstrating convincing differences among species in cognitive ability all the more difficult.

In summary, there is increasing interest in understanding the role that cognition, in this case specifically learning and memory, may play in the behavior of animals in the 'real world'. Imprinting and song learning are examples of behavior we now have a considerable understanding of but for only a very few species. It is, therefore, difficult to determine whether there is variation in these behaviors across species and if there is, whether or not this variation can be explained to any degree by the species' behavioral ecology. That such an attempt should be made is disputed by Macphail and Bolhuis [2000] and Bolhuis and Macphail [2001] who would claim that, backed by Darwin, they have shown that natural selection both should not and has not acted on parts of the brain that deal with processes 'higher' than those concerned directly with peripheral sensory information. We claim that the relevant data are not yet available to support such a view. We would suggest that one profitable way forward is for behavioral ecologists to explore systems that combine both a plausible biological scenario for a role of learning and memory and one that is logistically sensible. The first of these is much more straightforward than the second.

We have described one system that we believe has valuably profited from this approach, that which began with the behavior of food storing. One of the current difficulties with that system is in acquiring more accurate field data. In the interim, however, it is a system that is amenable to laboratory testing, both in assessing learning and memory performance as well as for neural experimentation. The data that have resulted from the investigation into this particular system, such as the demonstration that hippocampal volume is experience-dependent in food-storing species and that food storers remember when they've stored food, has opened up many unexpected exciting avenues. It seems likely that other such explorations will yield insights into the cognition of the animals under study that may not be predicted at the outset. The complementation of field data with laboratory data may be one way forward for some systems, especially those in which the animals are readily housed and tested. The hummingbird field data we have collected, for example, can be compared with data from similar experiments carried out in the laboratory [e.g., Brown and Gass, 1993]. Alternatively, for some animals/systems a 'halfway house' situation between the laboratory and the field might be achieved as was done in the assessment of cue use by sticklebacks from different environments [Girvan and Braithwaite, 1998]. Small, short-lived vertebrates and invertebrates, in particular, seem to lend themselves to these kinds of testing situations. An illustration that the integration of the two sources of data can be very productive comes from the demonstration that in the pest species *Helicoverpa amiger*, a noctuid moth foraging on economically important crops, oviposition preferences are learned

and relevant prior experience is correlated with host abundance: the more abundant a host, the more likely this moth is to prefer to feed and to oviposit on that host, rather than other equally favorable hosts [Cunningham et al., 1998, 1999; Cunningham and West, 2001].

In conclusion, we think that behavioral ecologists, armed as they are with the knowledge of the social and ecological demands placed on their animals, are well placed to take forward investigations into animal cognition. One specific rationale for doing so might be to provide data with which to answer, one way or another, the claims of Macphail and Bolhuis that natural selection has left untouched non-perceptual cognitive processes. A more general rationale might be to investigate the cognitive abilities of their animals in order to understand the underpinnings of decision making in many contexts (e.g., mate choice, nest choice, foraging and so on). We think one profitable methodological route to do this is for behavioral ecologists to plunder the riches of the psychological literature for the most suitable testing paradigms and that through this kind of integration the issue of what effect natural selection has had on cognition may be resolved.

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