Review

The synthetic approach to the study of spatial memory: Have we properly addressed Tinbergen’s “four questions”?

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A B S T R A C T

In 1963, Niko Tinbergen suggested that to truly understand the behavior of an animal, the ultimate causes (e.g., adaptive value, evolutionary history) as well as the proximate mechanisms (e.g., neurobiology, development) that result in the production of the behavior must be understood in an integrated framework. We examine whether the study of spatial memory in food storing birds has adequately addressed Tinbergen’s questions and highlight the work of Sara Shettleworth, who has made a tremendous contribution to this area of study, and whom this issue honors. Our conclusion is that while the study of food caching and spatial memory in birds has been a very good model of a program of research that has addressed Tinbergen’s questions, additional work remains.

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3. Have Tinbergen’s questions been addressed? ................................................................................................ 284

In a well-known paper, Niko Tinbergen (1963) suggested that to fully understand the behavior of an animal, four questions must be answered. Two of Tinbergen’s questions address the proximate causes of behavior and emphasize mechanisms within an animal that are responsible for the behavior. Researchers who are interested in the development, neurobiology, and mechanisms of learning, as they relate to behavior, are addressing proximate questions. The other two questions address the ultimate causes of behavior and focus on why an animal has evolved the aforementioned mecha-
anisms to produce behavior. Ultimate questions include questions about the potential adaptive value and evolutionary history of the behavior.

At the time that Tinbergen's article was published, the study of animal behavior was divided into two relatively isolated fields. Ethologists, like Tinbergen (Lorenz, 1970–1971; Tinbergen, 1952; von Uexkull, 1957) focused on the behavior of a wide range of animals in the natural environment to better understand how animals survived. That is, ethologists emphasized the exploration of questions of function and evolutionary history (e.g., Lorenz, 1970–1971). In contrast, another set of researchers tended to examine how a limited number of species learned to solve problems in laboratory environments, primarily as a model for understanding human behavior (e.g., Pavlov, 1927; Skinner, 1938; Thorndike, 1898, 1911; Watson, 1913). The emphasis for this later group of researchers tended to be on how mechanisms of associative learning led to the production of behavior. By suggesting that behavior could be analyzed at different levels, Tinbergen's paper offered a way to recognize the different types of questions ethologists and researchers examining associative learning were generating, as well as their different methodologies.

While the two groups used different methodologies, they often focused on how simple stimuli were linked with specific behaviors, either through innate mechanisms, in the case of ethologists (e.g., sign stimuli and fixed-action patterns) or learning mechanisms (instrumental or respondent conditioning procedures). For those examining associative learning, in the decade that followed the publication of Tinbergen's paper, two developments, one in psychology and one in ethology, helped set the stage for increased integration in the study of how animals learn and remember.

In psychology the influence of behaviorism was starting to wane (Bolles, 1970; Seligman, 1970; Shettleworth, 1972) and there was renewed interest in exploring the idea that there were important cognitive mechanisms (e.g., attention, memory, representations) that could be effectively studied in non-human animals (e.g., Roitblat et al., 1984). This emphasis on cognition inherently suggested that animals possessed knowledge about their environment and that this knowledge affected the expression of learned behavior. At the same time, the field of behavioral ecology was emerging among behavioral biologists, with its emphasis on the adaptive value of behavior (Kamil and Sargent, 1981; Krebs and Davies, 1997; Maynard Smith, 1982; Shettleworth, 1984; Stephens and Krebs, 1986; Wilson, 1975). Many of the optimization models of behavioral ecology demonstrated that if an animal possessed knowledge about its environment (e.g., the distribution of food), the knowledge could significantly enhance the animal's reproductive success. Thus, an enhanced interest in an animal's knowledge emerged simultaneously in biology and psychology.

As a result of these (and other) developments, the past 40 years have seen important changes in how animal learning, memory and cognition are studied. Researchers in both psychology and biology became interested in blending the methodologies and questions of each discipline within the framework of cognition (Kamil, 1988, 1998; Shettleworth, 1993, 1998). One of the effects of this synthesis has been a significant increase in the range of animals studied and techniques used. Among psychologists, this has led to the application of procedures developed for the study of learning to exploring the role of cognition in settings defined by problems animals face in the world outside of the lab. Sara Shettleworth has been a leader in the development of such techniques, ranging from her early work on reinforcement and the organization of behavior in hamsters (Shettleworth, 1975, 1978a,b,c, 1981; Shettleworth and Juergensen, 1980) to optimal foraging theory (Hamm and Shettleworth, 1987; Shettleworth, 1985, 1989; Shettleworth et al., 1988; Shettleworth and Plowright, 1989), from spatial memory (Hampton and Shettleworth, 1996a,b; Shettleworth and Krebs, 1982, 1986; Shettleworth et al., 1990) to her later major integrative textbook (Shettleworth, 1998). In this review, we will concentrate on work investigating the spatial memory of seed-caching birds in two passerine families, chickadees and tits (Paridae) and related work by others with jays and nutcrackers in the family Corvidae. Our goals in this review are to highlight the contributions of Sara Shettleworth's work to this literature, while showing the value of having multiple laboratories working on parallel problems with varying methodologies. Finally, we hope the review will show that while much work has been done to address Tinbergen's four questions regarding spatial cognition, gaps in our knowledge still remain.

1. Ultimate causation: spatial memory as an adaptive specialization

1.1. Field observations and early experiments

A number of birds within the family Paridae and Corvidae cache food in scattered locations and later recover it (Paridae: Haftorn, 1956; James and Verbeek, 1983; Källander, 1978; Löhr, 1950; Stephens and Krebs, 1986, Corvidae: Bossema, 1979; Pravodusov, 1985; Swanson, 1951; Tomback, 1977; Turcek and Kelso, 1968; Vander Wall and Balda, 1977, see Robert, 1979 for a review). In an impressive feat of caching, Siberian tits (Parus cinctus) have been reported to spend the majority of their time during the late summer and early Fall caching more than 100,000 items (Pravodusov, 1985). Likewise, the Clark's nutcracker (Nucifraga columbiana) caches up to 33,000 pine seeds in thousands of locations in the spring and fall and later recovers these caches for the next 9–11 months (see Balda and Kamil, 1998 for a review). These impressive examples of caching and recovery suggested to some researchers that many food caching birds may have a memory for the location of stored food (e.g., Löhr, 1950). Opponents of this memory hypothesis argued that scatter hoarding birds may not be capable of remembering the location of a large number of cache locations. Instead, it was hypothesized that birds that engaged in caching may recover their caches randomly as they revisited different areas of their territory (e.g., Gibb, 1960; Haftorn, 1954, 1956) or use alternate strategies or cues that place less demand upon memory (e.g., Andersson and Krebs, 1978; see Vander Wall, 1990 for a review).

Several lines of field evidence suggested that at least some food storing birds, particularly Parids and Corvids, might use spatial memory to recover stored food and that such memory might be an adaptive specialization (for reviews see Sherry, 1992; Shettleworth, 1990, 1995). In Parids, wild marsh tits (Parus palustris) recovered their own caches more frequently than control seeds that had been placed in the environment by the experimenters (Cowie et al., 1981). Likewise, Tomback (1980) found that the proportion of caches recovered by Clark's nutcrackers (Corvid), as well as the spatial distribution of their recovery sites, strongly suggested the use of spatial memory. These studies and other related work led to experiments based on the framework proposed by Tinbergen (1963), that is studying cognition in a context in which the adaptive function of spatial memory would be clear. The first step was to experimentally ascertain whether spatial memory was used for cache recovery. This, in turn, required studies to be carried out under more controlled conditions where alternative explanations could be evaluated.

In passerine birds, Sherry et al. (1981) were among the first to systematically examine spatial memory using a cache/recovery task in a laboratory environment. Marsh tits (Parus palustris) were more likely to return to the quadrants in which they had stored food than to quadrants in which they had not stored food. Shettleworth and Krebs (1982) extended the work of Sherry, Krebs, & Cowie by looking at the spatial memory for individual cache sites, rather than for larger sites in which food had been stored. Marsh tits were able to
locate the majority of their seeds while only making a few search errors to incorrect locations. Likewise, Sherry (1984) found that black-capped chickadees (Parus atricapillus) spent a larger proportion of time at sites where they had cached seed than at sites where they had not cached seeds.

Work investigating spatial memory was also being carried out with nutcrackers, seed-caching members of the Corvid family. The initial studies by Balda (1980) with a Eurasian nutcracker (Nucifraga caryocatactes), Vander Wall (1982) and Kamil and Balda (1985) with Clark’s nutcrackers, like the work with Parids, had birds store and recover food in controlled laboratory settings. In the Kamil and Balda (1985) experiments, nutcrackers were better than chance during each recovery session, even when relatively few cache sites had been made available. Furthermore, when the nutcrackers made errors, they tended to make them at holes in which they had previously recovered seeds.

1.2. Comparative assessment of spatial memory

One important issue that was raised by the results of these initial studies with Parids and Corvids was whether the spatial memory abilities of these seed-caching birds were actually greater than those of non-cachers, as might be predicted if spatial memory had evolved as a result of selection for the ability to find food caches (Sherry and Schacter, 1987). Continuing their work with Parids, Krebs, Healy, and Shettleworth (1990) compared the spatial memory of food storing coal tits (Periparus ater) and non-storing great tits (Parus major) in two experiments in which the birds were rewarded for returning to sites where they had seen food earlier in a trial. The differences between storing and non-storing species were small, but coal tits were more accurate than great tits at returning to the site where a seed had been seen. Coal tits were also somewhat better than great tits at discriminating between sites that had contained a seed and sites that were empty, corroborating other work (e.g., Sherry, 1984; Shettleworth and Krebs, 1982) suggesting that species that are more dependent upon storing are less susceptible to the effects of interfering information on spatial memory than are species that store less food.

Related work with Parids, using different procedures, also showed small differences in spatial memory between storing and non-storing species (Healy, 1995; Krebs, 1990; Krebs et al., 1990a,b). Hilton and Krebs (1990) compared the spatial memory of four tit species, two storers – the marsh tit and coal tit – and two non-storers – the blue tit (Parus caeruleus) and the great tit – using an open-room analogue of the 8-arm radial maze. The apparatus consisted of eight stands that could contain hidden food that were arranged in a circle. Birds were initially forced to choose four of the eight stands and then, following a variable retention interval (30 s to 24 h), the birds were able to select from among all eight stands.

In a series of studies using similar procedures with nutcrackers, pinyon jays, and Mexican jays, Olson et al. (1995) also showed that nutcrackers were able to tolerate much longer retention intervals than pinyon jays, scrub jays or Mexican jays during a comparable spatial DMSTS task.

In the case of the Corvids, the evidence supporting the hypothesis of better memory in seed-cachers has been stronger than that for tits (though see Bolhuis and Macphail, 2001). Clark’s nutcrackers, pinyon jays (Gymnorhinus cyanoccephalus) and Western scrub jays ( Aphelocoma californica) vary in their degree of dependence on stored food. Nutcrackers and pinyon jays are highly dependent upon the recovery of caches for survival; in contrast, the scrub jay caches, but it is also able to utilize other resources for survival during the winter (see Balda and Kamil, 1998). This allowed Balda and Kamil (1989) to examine the adaptive specialization hypothesis with these Corvids using procedures comparable to those of Kamil and Balda (1985). As predicted, Clark’s nutcrackers and pinyon jays were more accurate than scrub jays during cache recovery after a 7-day retention interval, but were not reliably different from one another (see also Bednekoff et al., 1997).

Kamil et al. (1994) also tested Clark’s nutcrackers, pinyon jays, scrub jays, and the Mexican jay ( Aphelocoma ultramarina) – a jay similar to the scrub jay in terms on its dependence upon cache recovery – on an open-room analogue of the radial maze task. Twelve sand filled holes were arranged in a circle in the floor of a small room. During an initial phase, four of the holes were open and each contained hidden food. The birds recovered the food from each of the four holes and a variable retention interval began. Following the retention interval, four additional holes were opened and the bird was allowed back into the room. All four species had comparable accuracies for searching in the new holes following short retention intervals, but pinyon jays and nutcrackers were more accurate than scrub jays or Mexican jays as the retention interval increased.

1.3. Alternative explanations for species differences in memory

At the same time that Shettleworth and Krebs (1986) were exploring the modularity of spatial memory in food storing birds, Kamil (1988) reasoned that, in using an ecological approach to comparative cognition, one must test species using a variety of paradigms. In particular, related food storing and non-storing birds needed to be examined on tests in which the species would be expected to show the predicted expectations regarding memory, as well as on tests in which a different pattern of results may appear. Kamil noted that species differences that appear for one type of task may be due to contextual variables specific to the task or to motivational factors. Thus, tests with different paradigms are important in further exploring potential differences in spatial memory.

Olson (1991) examined the ability of Clark’s nutcrackers, scrub jays, and pigeons to recall spatial information using a Delayed Non-Matching-To-Sample (DMTS) procedure similar to that described previously. Nutcracker’s performance was significantly better than that of the scrub jays and pigeons on this spatial task. In a second series of studies using similar procedures with nutcrackers, pinyon jays, scrub jays and Mexican jays, Olson et al. (1995) also showed that nutcrackers were able to tolerate much longer retention intervals than pinyon jays, scrub jays or Mexican jays during a comparable spatial DMSTS task.

Along the same lines, Hampton and Shettleworth (1996a,b) also tested chickadees and dark-eyed juncos on a non-spatial color matching task using procedures similar to those previously described. In contrast to the findings from the spatial study, the results from the non-spatial experiments did not show a correlation between the dependence on stored food and memory performance. Combined, the findings from Corvids and chickadees given non-spatial memory tasks ruled out explanations based on differences in memory broadly or the abilities of certain species to adapt to a laboratory environment (Kamil, 1988).
1.4. Geographical distribution, seed-caching and memory

It may be the case that food caching species that live in southerly environments are less dependent upon caching and recovery of stored food than more northerly food caching species.

To this end, Hampton et al. (1995a,b) examined the caching behavior of three North American Parids: bridled titmice, Mexican chickadees that reside in the south, and the black-capped chickadees that reside in the north. Hampton et al. (1995a,b) found that black-capped chickadees have relatively larger hippocampi, a brain structure involved in spatial memory (see below) than both Mexican chickadees and bridled titmice. Black-capped chickadees also cached more food than either the titmice or Mexican chickadees in laboratory environments. More recently, Pravosudov and Clayton (2002) compared food caching and memory in black-capped chickadees that ranged from Alaska to Colorado. The Alaskan chickadees cached more food and were more accurate during tests of spatial memory than their southerly counterparts. The results from both studies generally support the adaptive specialization hypothesis.

1.5. Evolutionary history of caching in seed storing birds

Recently, there has been interest in better understanding the phylogeny of food caching in Corvids (e.g., de Kort and Clayton, 2006). Consistent with Tinbergen (1963), de Kort and Clayton argued that evolutionary history must be considered when comparing the cognitive abilities or underlying neurological structure of related species. Specifically, when looking at a trait in a set of related species, it is important to know the status of that trait in the common ancestor. Often, it is assumed that the presence of specialized mechanisms for cache recovery is the derived trait and the absence of these characteristics in related species, the ancestral state, but this may not always be the case. Apparently similar adaptations may be due to convergent evolution rather than common descent. Modern comparative techniques in biology (see Harvey and Pagel, 1991) to approach this historical question use phylogenies based upon traits other than those being evaluated (to avoid circularity). With the emergence of powerful (and inexpensive) molecular techniques, these phylogenies are usually based primarily on analyses of DNA structure. The trait in question is then mapped onto the phylogeny and the resulting pattern analyzed to reconstruct the history of the trait in the clade being analyzed.

de Kort and Clayton (2006) used this technique by combining several studies of the phylogeny of Corvids and then mapping caching behavior onto the resulting single phylogeny. de Kort and Clayton’s model indicated that it is quite likely that the common ancestor of all Corvids would be classified as a moderate cacher. Since contemporary Corvids include both species that cache very little (e.g., jackdaws, Corvus monedula) and species that cache a great deal (e.g., nutcrackers), this implies that there have been a number of transitions in caching behavior in the history of the Corvids. The analysis of de Kort and Clayton suggests that the transition from moderate to specialized cacher may have occurred on five occasions, while transitions from moderate caching to little or no caching may have occurred twice.

2. Proximal causation and spatial memory

2.1. Neurobiological mechanisms of spatial memory

2.1.1. Behavioral assessments of modularity and spatial memory

While the hypothesis that memory is an adaptive specialization was being tested in Parids and Corvids, the issue of spatial memory as a modular system was also being evaluated. The ability of food storing Parids and Corvids to remember the location of hidden food, as demonstrated by the results from both Shettleworth and Krebs (1982) and Kamil and Balda (1985), for example, raised the question of the modularity of their superior memory performance. Was their performance limited to specific spatial locations in three-dimensional space, limited to spatial information, or part of a more general memory system (see Sherry and Schacter, 1987; Shettleworth, 1985)? That is, even if the memory of some Corvids and Parids is an adaptive specialization resulting from the ecological demands for retrieving stored food, did selection act on memory in a very narrow sense or in a broader way and did different brain regions specialize in processing spatial information.

Shettleworth and Krebs (1986) reasoned that one way to examine whether the memory for food caches differs from memory for other kinds of information (spatial or otherwise) would be to examine whether or not the memory for recalling the locations of cached food is different from the memory used to recall food items in a different context. Shettleworth and Krebs (1986) and Shettleworth et al. (1990) compared the ability of black-capped chickadees and coal tits to remember where they had stored food with their recall for where they had encountered food during an excursion. In an initial study, Shettleworth and Krebs (1986) had birds encounter both “storage” and “window-shopping” trials. During the storage trials the birds were released into a room that had 60 storage sites (a block of wood with a hole in the center). The birds were allowed to place seeds in up to six sites. During recovery the birds were allowed to search the blocks of wood, but cloth flaps covered the holes. During window-shopping trials the birds were released into the room, and allowed to observe the location of sunflower seeds that could be seen behind small windows, but not eaten. The recovery phase for these trials was similar to that described for the storing trials. Following a 2 h retention interval the birds were released back into the room and allowed to search for and consume the seeds, which were no longer protected by the windows. Both black-capped chickadees and coal tits were better at discriminating between sites that had stored seeds than sites that they had visited (but not stored seeds) than discriminating between sites in which they had seen seeds from those that they had visited (but also not stored seeds).

Additionally, like Shettleworth and Krebs (1986) did with Parids, Olson et al. (1995) examined nutcrackers, pinion jays, scrub jays, and Mexican jays birds on memory tests in which the relationship between memory and dependence upon stored food might not be predicted to hold. Specifically, these birds were tested on a non-spatial matching-to-sample task similar to that used by Olson (1991) that required the birds to remember the color, rather than the spatial location of the sample stimulus. The results revealed no relationship between memory performance and the dependence upon stored food.

2.1.2. Neuroecology

While the aforementioned research with Parids and Corvids revealed that spatial memory was strongly associated with dependence on the recovery of stored food, there was also a second movement to explore the neurobiological substrates of spatial memory in birds. This movement, referred to as the “neuroecological” approach (Macphee and Bolhuis, 2001), has been favored primarily by those researchers taking a modular view of memory (Hampton et al., 2002, see Healy et al., 2005).

The hippocampal formation in birds appeared to be a likely brain structure involved in spatial memories, since it had been implicated in the spatial memory of mammals (O’Keefe and Nadel, 1978). The hippocampus and parahippocampal regions form the hippocampal formation of food storing birds; the complex is located in the dorsal medial cortex. To the extent that spatial memory is linked to the hippocampus, this part of the brain should be larger in birds that have a greater demand on spatial memory. Indeed, comparisons have generally indicated that the hippocam-
pus is relatively larger in species that have a greater dependence on spatial memory for survival (Basil et al., 1996; Garamszegi and Eens, 2004; Hampton et al., 1995a,b; Healy and Krebs, 1992, 1996; Krebs et al., 1989; Lucas et al., 2004; Sherry and Vaccarino, 1989). Although a large proportion of studies have shown a positive relationship between performance on spatial memory tasks, food dependence, and the size of the hippocampus (see Healy, 1998 for a review), Bolhuis and Machpail (2001) have called some of this evidence into question. Bolhuis and Machpail point out that during some tests of spatial memory, the species with a greater dependence for cache recovery (and thus the species predicted to perform better on tests of spatial memory), did not always perform better than related species that are less dependent upon cache recovery for survival. Likewise, Pravosudov and de Kort (2006) found evidence indicating that the ratio of the hippocampus to the size of the telencephalon for some Corvids may not always be correlated with dependence upon stored food. In particular, they found the size of the hippocampus relative to the telencephalon to be larger for scrub jays than either pinyon jays or Clark’s nutcrackers. The discrepancy may be due to the fact that the scrub jay is an ecological generalist, caching a variety of food items that have different degrees of perishability. Much evidence has shown that the scrub jays remember what, when and where about different types of food in their environment, whereas other species may only remember where they have cached food. A second premise of the neuroecological approach has been that damage to the hippocampal formation may have a greater impact on birds that are more dependent upon spatial memory than on birds that are less dependent on cache recovery for survival. Using an experimental approach some researchers have tested this prediction. Several studies have indicative that lesions of the hippocampus result in deficits in spatial memory during cache recovery tasks (birds made more errors to previously visited locations) but did not impair caching behavior more broadly. Krushinskaya (1966) found that Eurasian nutcrackers (Nucifraga caryocatactes) were unable to accurately relocate the caches they had made when the hippocampus was lesioned, but continued to cache and search for stored food. Likewise, Sherry and Vaccarino (1989) made bilateral lesions to the hippocampus in black-capped chickadees and found similar results. Chickadees continued to make and search for caches, though they were less likely to find them during recovery. Importantly, chickadees with hippocampal lesions were still able to use other cues that identified the location of food during a non-spatial associative learning task. Hampton and Shettleworth (1996a,b) extended this work outside the domain of cache recovery using a comparative approach. They examined black-capped chickadees and dark-eyed juncos on a delayed matching-to-sample procedure in an operant chamber. Chickadees have a larger hippocampus relative to their total body size than juncos. Hampton and Shettleworth (1996a,b) reasoned that if the hippocampus was involved in spatial memory, chickadees should act more like non-storing juncos following hippocampal lesions. They found that chickadees were more resistant to interference for sample locations on previous trials than were non-storing juncos. Following lesions to the hippocampus, chickadees responded like juncos and were more susceptible to interference than they were prior to the lesions.

2.1.3. Seasonal changes in the hippocampus

In many environments the demand for remembering the location of stored food may change during the course of a year. The demand on spatial memory for food storing birds is likely to be stronger during the fall and winter when other food resources in the environment are no longer present. The evidence cited above generally indicated a positive relationship between spatial memory and dependence upon cache recovery. It may also be the case that selection has favored changes in the composition of the hippocampus that are associated with seasonal patterns. Smulders et al. (1995, 2000) found that black-capped chickadees have a larger hippocampus relative to telencephalon size in October, than they do at other times of the year. Likewise, Barnea and Nottebohm (1994) have found that there are more new neurons in the hippocampus of black-capped chickadees during October than during other times in the year. Other studies have not found seasonal differences associated with the hippocampus, however. For example, Hoshooley and Sherry (2004) failed to find seasonal variations in the volume or total number of neurons in the hippocampus of black-capped chickadees.

2.1.4. Photoperiod

Changes in photoperiod have been shown to correspond with changes in caching behavior. Shettleworth et al. (1995) reported that black-capped chickadees maintained on a shorter “winter like” daylight cycle in a laboratory cached more food than birds kept on a long “summer like” daylight schedule; the same relationship appears true for marsh tits (Clayton and Cristol, 1996). Notably, Clayton and Cristol (1996) also found that tits that had encountered a short daylight cycle performed better on a test of spatial memory than those birds maintained on a long daylight cycle. However, manipulations of photoperiod have not been associated with changes in hippocampal volume in black-capped chickadees (MacDougall-Shackleton et al., 2003).

2.2. Corticosterone and spatial memory

In people, long-term elevated levels of corticosterone have been associated with reduced hippocampal volume and a deficit in spatial memory, whereas short-term elevations appear to improve memory performance (McEwen, 2000; Sapolsky, 1996). Stress associated with caching and recovering a limited and unpredictable supply of food may induce stress and impact spatial memory. In 2000, Saldanha et al. examined whether corticosterone impacts spatial memory in food storing birds. They gave mountain chickadees short-term doses of corticosterone prior to caching or recovery in the laboratory. Chickadees that were treated 5 min prior to retrieval had a better spatial memory than untreated controls. In related work, Pravosudov and Clayton (2001) maintained one group of mountain chickadees on a limited and unpredictable diet and another group on an ad lib diet. Chickadees that were maintained on the unpredictable diet displayed better performance during a test of spatial memory compared to birds given the ad lib diet. Both groups of birds showed comparable performance during a non-spatial task, however, indicating that both groups had similar levels of motivation. Birds given an unpredictable diet also show elevated levels of corticosterone in their blood plasma (Pravosudov and Clayton, 2001), though hippocampal structure remains unchanged during these tasks (Pravosudov and Clayton, 2002). Pravosudov et al. (2003) also implanted mountain chickadees with time-release corticosterone pellets that resulted in moderate elevations of corticosterone compared to the high, and perhaps unnatural, levels used by Saldanha et al. (2000). Birds that received the treatment were still more accurate in both cache recovery and one-trial spatial associative learning tasks compared to controls.

It has been hypothesized that social status may also have an impact on spatial memory for food storing birds and this relationship is mediated by corticosterone. Subordinate individuals live in a more unpredictable environment. A subordinate may recover food but be supplanted by a more dominant individual. Subordinate individuals may engage in more food caching as a result of the increased unpredictability of obtaining food in their environment. These same birds may also have a higher level of corticosterone that facilitates...
spatial memory. The evidence for a relationship between social status, caching and corticosterone has not generally been supportive of this position, however (Pravosudov et al., 2004). Both Pravosudov and Lucas (2000) and Lundborg and Brodin (2003) failed to find a reliable difference in food hoarding behavior between dominant and subordinate individuals in willow tits (Parus montanus) and Carolina chickadees (Poecile carolinensis), respectively. Likewise, Pravosudov et al. (2004) found that subordinate mountain chickadees cached less, had a poorer spatial memory, and lower levels of corticosterone than their more dominant counterparts.

2.3. Maturation, caching experience, and the content of memory

The study of the development of caching in food storing birds has been limited primarily to Parids. Clayton (1994) has done some of this work primarily with Marsh tits. Food storing begins around the age of 35 days for Marsh tits, and a sudden burst appears around 44 days (Clayton, 1992). A similar pattern appears for Coal tits (Clayton and Lee, 1998). The increase in caching for Marsh tits appears to be based on age rather than experience, as birds that are prevented from storing and retrieving quickly learn to do so after day 44.

Dimmick (1993) has also found that accuracy of cache recovery improves for nutrcrackers during the first 3 years of the bird’s development, though the effects of experience were not separated from age. More recently, Stafford et al. (2006) have found that young, inexperienced pinyon jays were just as accurate as 3-year-old birds with at least 3 years of caching experience. Thus, cache recovery accuracy appears to be fully developed at a relatively young age in pinyon jays.

Much of the formative work on spatial memory in food storing birds was dedicated to characterizing and comparing the memory of related species. More recently, researchers examining the spatial cognitive abilities of animals have placed an emphasis on exploring the content of the spatial memory that allows an animal to return to a previously visited location.

2.4. Landmarks and bearings

Animals can use objects in their environment as landmarks to determine their position or the position of hidden objects (Kamil and Cheng, 2001). Objects in close proximity to a goal can be used as beacons (see Shettleworth, 1998 for a review). If a hidden goal is located some distance from an object, the animal needs to determine a bearing between the landmark and the goal to accurately return to the goal location (Cheng, 1988, 1989, 1994). The bearing indicates the distance and direction of the goal from one or more landmarks. Vander Wall (1982) had Clark’s nutcrackers cache pine nuts in an oval arena that contained objects (e.g., rocks) that could be used as landmarks. Following caching, the birds were removed from the arena and the boundary of one end of the arena was extended 20 cm away from the center of the arena. Likewise, the objects at that end of the area were also displaced by 20 cm in the same direction. The birds tended to search near the displaced visual cues during recovery, that is, 20 cm away from their caches at the end of the arena that had been elongated. Thus, nutcrackers had encoded the location of their caches relative to the objects inside the arena and the arena boundary. In related work, Cheng and Sherry (1992) trained chickadees and pigeons to find food that was hidden on a tray. The location of the food was fixed between an object on the tray and one edge of the tray. During testing, the object was shifted perpendicularly, in parallel, or diagonally, relative to the edge of the tray. Search by both species tended to be displaced in the parallel, rather than the perpendicular direction, regardless of the movement of the landmark, suggesting that an edge can served as a cue about where to search.

Vander Walls’ (1982) study also indicated that nutcrackers may prefer to use objects or cues that are close to cache sites (rocks, edge of arena) compared to objects or surfaces that are farther away (outside the arena), when encoding and returning to the location of hidden food. Indeed, Bennett (1993) found that European jays (Garrulus glandarius) weigh landmarks that are more proximal to a goal more heavily than those that are farther away. The interplay between the use of local and more distal/global cues has received much attention in food storing birds. For example, Herz et al. (1994) allowed chickadees to cache seeds in small holes in the “branches” of radically symmetrical artificial trees in a small enclosure. Cues that had different color and shape features were placed on the walls of the enclosure (distal cues) or near individual cache sites (local cues). Removal of the distal cues had a larger impact on search accuracy than did the removal of the local objects. Gould-Beierle and Kamil (1996) used procedures similar to those used by Cheng and Sherry (1992) and found that searching by nutcrackers was influenced both by local cues (objects near the goal) as well as by more distal information provided by the position of the tray in the room. In a follow-up study, nutcrackers, pinyon jays and scrub jays were equally adept at using local objects and more distal information to search for a goal (Gould-Beierle and Kamil, 1998). The finding suggests that, although these birds differ in their spatial memory, their ability to utilize either type of information is comparable.

Another important issue related to the nature of the spatial memory of seed-storers is whether or not birds that are more dependent upon spatial memory weigh spatial cues more heavily than non-spatial cues during caching and recovery. In a well-known series of studies, Brodbeck (1994) and Brodbeck and Shettleworth (1995) trained food storing chickadees and non-storing juncos to find food from one of several feeders. The correct feeder could be defined by the compound of its global position on the wall, its position relative to the other feeders in the array, and the feature cues (e.g., color) provided by the feeder. During tests of competition, when different sets of these cues were placed in conflict, chickadees, the birds more dependent on spatial memory, tended to weigh spatial cues more heavily, whereas juncos tended to weight the non-spatial cues more during search. These results have also been replicated using an operant version of the task (Brodbeck and Shettleworth, 1995, see also Shettleworth and Westwood, 2002). Similarly, Clayton and Krebs (1994) found that food storing Marsh Tits and Eurasian jays (Garrulus glandarius) weighed spatial cues more heavily than feature cues compared to their non-storing counterparts, the Blue Tit and Jackdaw (Corvus monedula), during one trial associate learning tests in which feature cues were placed in conflict with spatial information.

Food storing birds may also encode the relative relationships between two or more objects and a goal. Kamil and Jones (1997) trained nutcrackers to find a goal that was halfway between two upright landmarks. During testing the birds encountered different inter-landmark distances than they had encountered during training. The nutcrackers continued to search accurately halfway between the two landmarks rather than at a fixed distance from one or both of the landmarks that had been encountered during training. The finding suggested that nutcrackers can encode the relative geometric relationship between landmarks, and that they do not just rely on fixed bearings. That is, they learn a rule about where to locate food (i.e., halfway between two landmarks). In subsequent work, Kamil and Jones (2000) found that while nutcrackers were able to learn a variety of geometric rules, they showed better performance when the rules were based on directional, rather than distance, information (see also Jones et al., 2002; Spetch et al., 2003).

The memory of a cache location for nutcrackers, in particular, appears to include information from multiple landmarks (Kamil and Cheng, 2001). Nutcrackers use multiple landmarks to iden-
tify the location of a hidden goal (e.g., Vander Wall, 1982; Basil, 1993). Likewise, during recovery of hidden caches, nutcrackers often approach the cache location from a direction that is different from the one they used to make the cache (see Kamil et al., 1999). The use of multiple landmarks is important, given that the nutcrackers need to return to small hidden caches. The addition of multiple bearings between the landmarks and the goal reduces search accuracy by increasing the number of directional references to the goal, precisely the directional information that nutcrackers appear to favor (Kamil and Jones, 2000).

2.4.1. “Snapshot” memory

Bossema and Pot (1974) compared the routes used by individual Eurasian jays in making caches with the routes used when recovering caches. The same routes tended to be used more often than would be expected by chance. They suggested that the birds took a ‘snapshot’ of the scene from the cache site when they cached, then matched what they saw to the snapshot during recovery. Kamil et al. (1999) found this interpretation unconvincing. They argued that the same path could be used during both caching and recovery for a variety of reasons. Therefore, they conducted an intensive videotape study of movement patterns by nutcrackers during caching and recovery. Like Bossema and Pot (1974), Kamil et al. (1999) found that the birds tended to frequently use the same path during caching and recovery, but differing paths and body orientations were also often used. Kamil et al. (1999) were able to determine that consistency of direction had no effect on recovery accuracies. Nutcrackers were equally accurate regardless of the path used, which argues directly against the snapshot hypothesis.

2.4.2. Cognitive maps

The flexible use of egocentric and geocentric information by animals has suggested that animals may encode the information into a representation, or map (see Shettleworth, 1998, for a review), that later can be used to direct behavior. An important test of such a map would be that it could be used to develop new and efficient routes to a goal. Such a representation would seem particularly useful in the case of food storing birds, given the large number of sites they need to visit. Gibson and Kamil (2001a,b) found that a nutcracker was able to form a novel route to get to a goal when it was presented with landmark information that had been encoded into memory but had not been encountered at the goal. Likewise, Gibson et al. (2007) have found that pigeons are able to form relatively efficient routes when connecting different points on a computer screen, potentially indicating the use of a map-like representation. Clearly, these results are suggestive, but more work remains to be done.

2.4.3. Egocentric mechanisms

There are many situations in which animals must orient or navigate in the absence of any landmarks, or in homogenous or unfamiliar environments. Under such conditions, “dead reckoning,” estimating the direction and distance using self-motion cues, is often employed to allow the animal to update its position relative to a starting point after each leg of the journey. Ants, rodents, and some birds have been shown to use dead reckoning in determining their position (see Shettleworth, 1998; Gallistel, 1990 for reviews). Recently, both nutcrackers (Gibson and Wilks, 2008) and pigeons (Shettleworth and Sutton, 2005) have been shown to be able to use self-motion cues to identify the direction needed to travel to a hidden goal. While the ability to estimate position in the absence of landmarks is particularly useful when traveling in homogeneous or unfamiliar environments, one limitation of dead reckoning is that errors in estimated position can accumulate during a journey and lead to large inaccuracies in search. Many animals may also utilize familiar objects in their environment to return to a hidden goal.

2.4.4. Sun compass

Several studies have shown that chickadees (Duff et al., 1998) and some Corvids are sensitive to manipulations that involve using the sun as a compass to assist with navigation (Balda and Wiltschko, 1991; Wiltschko and Balda, 1989; Wiltschko et al., 1999). For example, Wiltschko et al. (1999) examined the ability of Clark’s nutcrackers and pinyon jays to use a sun compass in a cache recovery paradigm. When the bird’s clock was shifted 6 h between caching and recovery, pinyon jays shifted their search in accordance with the use of a sun compass. The Clark’s nutcrackers search behavior was influenced less by the clockshift than the pinyon jays or scrub jays in previous work (Wiltschko and Balda, 1989). However, the relatively low level of dependence on the sun compass in this study may also be attributed to the fact that directional information from landmarks in the vicinity of the arena may have provided conflicting information about the location of food (see Kamil and Cheng, 2001).

3. Have Tinbergen’s questions been addressed?

By emphasizing the importance of questions about both causal and proximate influences on behavior, Tinbergen (1963) laid out a framework in which biological and psychological questions could be integrated. Sara Shettleworth’s work in many areas, including spatial memory in food storing birds, has been at the forefront of the application of this synthesis to animal cognition. Collectively, the research of the past 30 years on spatial memory in food storing birds has clearly addressed Tinbergen’s questions and demonstrated the utility of Tinbergen’s approach, though additional work remains.

Tinbergen’s questions about the ultimate causes of behavior have undergone different levels of investigation. One the one hand, questions about the function or adaptive value of food caching and spatial memory in food storing birds have been well addressed. A substantial amount of work has revealed that spatial memory is an important aspect of the recovery of food items by food caching birds. The comparative work indicates that Corvids, and to a lesser extent Parids, birds that are more dependent upon the recovery of hidden food have better spatial memories than related birds that do not have the same pressures for recovering food. The body of literature on the adaptive function of food caching in Corvids and Parids has also occurred in parallel with comparable work using rodents (e.g., Jacobs, 1992; Gibbs et al., 2007). The fact that similar patterns of results have been reported for diverse lineages enhances the validity of our current understanding of the adaptive value of food caching and evolution of memory in animals. There remain a few notable areas where work on questions about adaptive value of spatial memory may be extended. First, the number of species examined in studies of spatial memory in food storing birds has been confined to a limited number of Corvids and Parids. Future work should be conducted to broaden our understanding in a larger array of species, including other families that cache (e.g., the Sittidae) to further bolster arguments about adaptive function. Second, relatively little work has been done in the field to examine what the impact of spatial memory is on the fitness of the animals being studied. Do individuals that have a better spatial memory fare better than conspecifics that have poorer spatial memory?

Questions about the evolutionary history of food caching in Corvids and Parids are less well understood. Although work such as that of de Kort and Clayton (2006) has provided important information, much remains to be done. For one thing, the phylogeny of Corvids will undergo some revision in coming years as more molecular-based phylogenetic research is carried out. In addition, mapping spatial memory onto phylogenies will prove difficult because it is a quantitative trait rather than a qualitative one. An example of the possible complexities can be found in the comparative work on spatial memory by Kamil, Balda and their col-
leagues. While nutcrackers and pinyon jays have performed very similarly in comparative tests of spatial memory during caching (Balda and Kamil, 1989) and radial-maze analog procedures (Kamil et al., 1994), nutcrackers dramatically outperformed pinyon jays during operant DMTS procedures (Olson et al., 1995). This suggests that selection acted somewhat differently on spatial memory in the two evolutionary lines.

The study of the causal mechanisms of food storing behavior and spatial memory has been important and continues to be an exciting and active area of investigation. Early work investigating neural mechanisms was important in establishing that the hippocampus is an important center for spatial memory in food storing birds. More recently researchers have become interested in examining what environmental factors may impact spatial memory. For example, unpredictable food supplies, demanding environments, and social status all appear to be factors that have some influence on caching, and perhaps spatial memory. The role of corticosterone has been also examined as a common mechanism for these effects. Researchers also have examined how the structure of the hippocampus changes across seasons and whether or not photoperiod plays a role. This line of work appears to have a promising future. Much work will need to explore whether seasonal variation in caching and recovery in individual birds is associated with changes in hippocampal structure to rule out alternative explanations for season variation (e.g., Pravosudov, 2007). Thus, basic behavioral work on the time-course of individual birds caching and recovering in the field needs to be done (e.g., Pravosudov, 2006).

Our understanding of the content of spatial memory has advanced tremendously in the past decade. We have learned much about the nature of the objects in an environment that food storing birds use to establish bearings from to later return to hidden food, as well as additional cues that can provide directional information such as a sun compass. We are beginning to understand how different types of spatial cues are weighted by different species and how these cues interact with each other to direct behavior. Much research has also been done to investigate how animals may represent spatial information in memory and whether or not their representations are consistent with a cognitive map. Finally, the work on development of spatial memory in food storing birds has been informative and interesting. Additional work remains to be done to examine, for example, how the use of different types of spatial cues may change across development.

The study of the spatial memory systems of food storing birds has had a major influence on the field of animal cognition. Part of this influence has been to increase the range of species being tested in the study of cognitive mechanisms in non-human animals. Another impact has been the emphasis on the importance of testing predictions about the adaptive function of cognitive traits using a comparative approach. The study of spatial memory in food storing birds has interfaced with research investigating the neurobiology of memory and has lead to an extensive movement to explore the content of spatial memory in non-human animals. While many interesting ideas about spatial memory and food storing remain to be explored, the corpus of work is one of the prime examples a field that has made much progress in addressing Tinbergen’s questions.


Bennett, A.T.B., 1993. Spatial memory in a food storing corvid: I. Near tall landmarks tested in the study of cognitive mechanisms in non-human animals. While many interesting ideas about spatial memory and food storing remain to be explored, the corpus of work is one of the prime examples a field that has made much progress in addressing Tinbergen’s questions.

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