Review

Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals

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Understanding the survival value of behaviour does not tell us how the mechanisms that control this behaviour work. Nevertheless, understanding survival value can guide the study of these mechanisms. In this paper, we apply this principle to understanding the cognitive mechanisms that support cache retrieval in scatter-hoarding animals. We believe it is too simplistic to predict that all scatter-hoarding animals will outperform non-hoarding animals on all tests of spatial memory. Instead, we argue that we should look at the detailed ecology and natural history of each species. This understanding of natural history then allows us to make predictions about which aspects of spatial memory should be better in which species. We use the natural hoarding behaviour of the three best-studied groups of scatter-hoarding animals to make predictions about three aspects of their spatial memory: duration, capacity and spatial resolution, and we test these predictions against the existing literature. Having laid out how ecology and natural history can be used to predict detailed cognitive abilities, we then suggest using this approach to guide the study of the neural basis of these abilities. We believe that this complementary approach will reveal aspects of memory processing that would otherwise be difficult to discover.

Keywords: Paridae; Corvidae; Rodentia; neuroecology; comparative cognition; food storing

1. INTRODUCTION

(a) *Neuroecology of food hoarding*

In his seminal work, Tinbergen (1963) laid out four ways in which we can approach the study of behaviour: causation, survival value, ontogeny and evolution. He emphasized that each way of approaching behaviour answered a different type of question about ‘why’ a type of behaviour occurs. This separation of ‘levels of analysis’ is very important in order to reason and communicate clearly about one’s ideas and research in behaviour (e.g. Sherman 1988). Mixing up levels of analysis may cause one to try to answer a particular kind of question (e.g. a mechanistic one) with an answer about another level of analysis (e.g. function or survival value). However, this does not mean that insights into the survival value of a behaviour cannot be useful in the study of the mechanisms behind the behaviour. Tinbergen (1963) himself stated that ‘Zoo-physiology derived, and again derives much of its inspiration and guidance from knowledge or hunches about survival value’ (p. 423). A relatively recent

approach to the study of behaviour, termed ‘neuroecology’ (Kotrschal & Palzenberger 1992; Krebs & Clayton 1996; Bolhuis & Macphail 2001), starts from this viewpoint: that knowledge about evolution and survival value (so-called ultimate questions) can help us to elucidate mechanistic and ontogenetic (so-called proximate) issues and vice versa. In our opinion, the aims of neuroecology are twofold. On the one hand, it aims to understand the evolution of behaviour and nervous systems, and especially the selective pressures that have driven this evolution; and on the other hand, it aims to understand the neural basis of natural behaviours. For both of these, it draws inspiration from knowledge about the survival value of the behaviour in question to guide investigations. In this paper, we focus on how we can use information about the ecological, adaptive function of behaviour to guide the study of the underlying cognitive and neural mechanisms and to inspire the kinds of studies to perform (see also Sherry 2005).

One field in which the neuroecological approach has been used extensively is in the understanding of the neural and cognitive mechanisms involved in the retrieval of scattered caches by food-hoarding animals. Food hoarding is the gathering and storing of food items for later use. Typically, this can take two forms

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(although they are probably extremes on a continuum): larder hoarding and scatter hoarding (Vander Wall 1990). Larder hoarding means that all the stored food is kept in one, defended location, while scatter hoarding is the behaviour in which animals hide different items in different places, which are widely distributed across their home range. This latter behaviour raises the question of how this food is retrieved for later consumption. The neuroecological approach to answering this question is to first try to understand the adaptive significance of the behaviour (scatter hoarding and cache retrieval), and the conditions under which it could evolve. Then, this knowledge about survival value and evolution can be used to guide the research into the underlying mechanisms. In 1978, Andersson & Krebs addressed the question of the evolution of food-hoarding behaviour through game theoretical modelling. They came to the conclusion that the behaviour can only be adaptive if the individuals who do the hoarding in the first place have an advantage over other (cheating) individuals in retrieving this food. They concluded that this would probably not be difficult for animals that either live solitarily (and therefore can defend their territory against potential thieves) or larder-hoard, as they only have one location to defend against possible thieves. For social animals that scatter-hoard, however, having an advantage over other individuals in the group (or at least in the population; Smulders 1998) is more of a challenge. This insight from the ultimate explanations that whichever mechanisms underlie the ability to retrieve these items have to give an advantage to the individual that did the hoarding, constrains the mechanisms that we should consider as possibly being used by the animals. Even though the term was not yet in use at the time, this is a perfect example of the neuroecological approach. One possible solution that fits the constraints set out by the ecological model is that the individuals could remember the exact locations of their caches, providing them with information that is not available to the other members of the group. Other mechanisms are also possible, however, and have indeed been identified (e.g. Shettleworth & Krebs 1982; Brodin 1994b). This example also makes clear that insights from ultimate explanations cannot *determine* what the exact underlying mechanisms will be; they can only constrain the number of possible explanations that we consider.

The hypothesis that memory might be used for cache retrieval was soon tested in food-hoarding marsh tits (*Poecile palustris*), black-capped chickadees (*Poecile atricapillus*) and Clark's nutcrackers (*Nucifraga columbiana*) and in many species since then. Marsh tit caches in the field disappear faster than artificial caches placed only 10 cm away (Cowie *et al.* 1981), and a later study showed conclusively that they are retrieved by the same bird that hoarded them in the first place (Stevens & Krebs 1985). In the laboratory also, the evidence suggested strongly that these birds and their close relatives, the chickadees, use memory to retrieve their caches, at least over a period of several days (Sherry *et al.* 1981; Sherry 1982, 1984; Shettleworth & Krebs 1982). For Clark's nutcracker, a member of the corvid family, both field and

laboratory evidence also strongly suggested that these birds remember where they have hoarded food in the past (Tombback 1980; Vander Wall 1982), and there are a number of studies in mammals that show the use of spatial memory in relocating their own caches, at least over relatively short intervals (red foxes *Vulpes vulpes* (Macdonald 1976), grey squirrels *Sciurus carolinensis* (McQuade *et al.* 1986; Jacobs & Liman 1991), yellow pine chipmunks *Tamias amoenus* (Vander Wall 1991), Merriam's kangaroo rats *Dipodomys merriami* (Jacobs 1992), thirteen-lined ground squirrels *Spermophilus tridecemlineatus* (Devenport *et al.* 2000), deer mice *Peromyscus maniculatus* (Vander Wall 2000) and western flying squirrels *Glaucomyx volans* (Winterrowd & Weigl 2006)). It is important to emphasize again that a number of these studies showed that animals can and do also utilize visual and olfactory cues as well as site preferences, in addition to spatial memory, when relocating caches, and that they tend to do this flexibly depending on environmental conditions, which can change the relative importance of these cues (e.g. Shettleworth & Krebs 1982; Briggs & Vander Wall 2004; Winterrowd & Weigl 2006; Male & Smulders 2007b). Heavy reliance on only one type of cue might render animals ill equipped to recover caches in adverse conditions, which tend to coincide with periods of low food availability (heavy snow, prolonged drought), making flexibility of cue utilization in cache recovery potentially highly adaptive.

(b) *The search for cognitive and neural adaptations*

The realization that scatter-hoarding animals can and do use memory to retrieve their caches quickly led to the next hypothesis: that memory abilities in these animals were somehow selected for and adaptively specialized. The reasoning was that if an animal benefits from remembering where its food is stored, natural selection would act to improve this memory (Kamil & Yoerg 1982; Kamil 1983, 1984; Sherry & Schacter 1987; Krebs 1990; Krebs *et al.* 1990; Shettleworth 1993). Since the ancestors of the hoarding species presumably already used spatial memory to relocate food, mates, etc., the adaptations are most likely to be ones of degree: i.e. we expect quantitative, rather than qualitative, changes in memory to have occurred in these lineages. According to this hypothesis, these adaptations should have led to hoarding animals having better spatial memory than (closely related) non-hoarding species, and to those animals that in their ecology and natural history rely more on caches, having a better spatial memory than those that rely on these caches less.

There have been a number of studies that have tested this hypothesis in a range of different tasks and different species. Many findings have been broadly consistent with the predictions that animals that rely more on caches perform better on a range of spatial memory tasks than species that do not hoard or rely less on their caches (e.g. Balda & Kamil 1989; Clayton & Krebs 1993, 1994b; McGregor & Healy 1999; Biegler *et al.* 2001). However, a number of studies have also resulted in findings that were

inconsistent with these predictions (e.g. Hilton & Krebs 1990; Healy & Krebs 1992a,b; Healy 1995; Gould-Beierle 2000; reviewed by Shettleworth 1995; Bolhuis & Macphail 2001; Macphail & Bolhuis 2001; Bolhuis 2005). To some, the failure of some studies to conform to the predictions is a fatal blow to the hypothesis of adaptive specialization in cognition (Bolhuis & Macphail 2001). However, we will argue in this paper that there may not have been reasons to predict differences in those studies in the first place, based on the detailed ecology and natural history of the species in question.

The fact that the memory for hoarded food is primarily spatial in nature suggested that one of the brain structures involved in this memory might be the hippocampus (O'Keefe & Nadel 1978) or its avian homologue, the hippocampal formation (HF). This was therefore taken as the starting point in investigating the neural basis of the memory for cache locations. Sherry & Vaccarino (1989) showed that lesions of the HF in black-capped chickadees resulted in a deficit in cache retrieval in the laboratory, thereby replicating findings from Eurasian nutcrackers (*Nucifraga caryocatactes*; Krushinskaya 1966). Sherry and his colleagues also found that songbirds in food-hoarding (sub-) families had a larger HF than birds in non-hoarding (sub-) families (Krebs *et al.* 1989; Sherry *et al.* 1989). These findings, combined with findings on species and sex differences in hippocampal volume that related to differences in the use of spatial information in other contexts, led to the hypothesis that just like cognition itself, the neural structures underlying cognitive processes can be adaptively specialized (Sherry 1989; Krebs 1990; Sherry *et al.* 1992; Krebs *et al.* 1996). Most studies that were published in the next decade supported this view, showing a larger HF in hoarding than in non-hoarding species (Healy & Krebs 1993; Healy *et al.* 1994), and a larger hippocampus/HF in species that rely more on stored food than in those that do less so (Healy & Krebs 1992c, 1996; Jacobs & Spencer 1994; Hampton *et al.* 1995). Finally, intraspecific studies have also shown that populations of the same species that rely more on hoarded food have a larger HF than populations that rely less on hoarded food (Pravosudov & Clayton 2002; Roth & Pravosudov 2009). For a detailed discussion of the use of volume as a measure of neural adaptation, and for the controversies in this field, see also Roth *et al.* (2010).

(c) *Oversimplification of the problem*

We believe that many of the inconsistencies in the literature that we mentioned in the previous section result from an oversimplistic approach to the idea of adaptive specialization in brain and cognition (see also Healy *et al.* 2009). Often little attention is paid to the details of the ecology and natural history of the species under study. The large majority of studies in the literature make the implicit assumption that all scatter hoarders will be equivalent in their neural and cognitive adaptations. This would imply that comparisons of scatter hoarders to non-hoarders or to larder hoarders (Jacobs & Spencer 1994; Volman *et al.*

1997) will always result in the same outcomes. At best, scatter hoarders have been split into 'less specialized' and 'more specialized' hoarders (Healy & Krebs 1992c, 1996; Brodin & Lundborg 2003; Garamszegi & Eens 2004; Lucas *et al.* 2004; de Kort & Clayton 2006). This still implies that there is only a single dimension along which scatter hoarders have undergone cognitive and neural adaptation, and that some species will just be further along that dimension than others. The other assumption that has been made is that the adaptation would be evident in all tests of spatial memory, regardless of the demands or details of the task (Kamil 1988). However, spatial memory is a multi-dimensional trait (McGregor & Healy 1999; Biegler *et al.* 2001). Having 'good' spatial memory can mean many different things. It could mean having a very high spatial resolution memory for locations (McGregor & Healy 1999), it could mean having a longer lasting memory (Biegler *et al.* 2001), or it could mean having a larger memory capacity. It is possible that some food-hoarding animals have an adaptive specialization in only one of these aspects of spatial memory, which might not be tested in all (if any) of the laboratory tasks employed. It is also possible that some of the species being compared have adaptive specializations in aspects of their spatial memory system owing to other selective pressures, independent of food-hoarding behaviour. These two possibilities could explain those studies in which no differences were found in memory performance between hoarding and non-hoarding species: the tasks used in those studies may not have tapped into the specific adaptations undergone by the species under study or they may have tapped into aspects that have been adapted for other purposes. In the rest of this review, we will examine the different ways in which spatial memory is used by different scatter-hoarding animals and use this to make predictions about the adaptive specializations one would expect in the cognition of the species in question. Later, we will outline how this information could be used to guide the study of the underlying neural mechanisms. Throughout this paper, we focus on the three groups of animals that have been best studied in this context: Paridae (titmice and chickadees), Corvidae (jays and crows) and Rodentia (rodents).

2. USING ECOLOGY TO PREDICT SPECIFIC MEMORY ADAPTATIONS

In the rest of this paper, we will set out which improvements in cache memory function (longer duration, higher capacity and finer spatial resolution) we believe may have been selected under different ecological circumstances, and we try to make some predictions about as-yet-untested adaptations. Depending on the survival value of the cache-location memory, and the context in which it is used, different aspects of memory would be expected to be acted on by natural selection. Our reasoning is based on the assumption that memory is costly, and that improved memory, along any dimension, is more costly than 'regular' memory (Dukas 1999). As such, we would expect a close match between the ecological needs of the

animals and the actual cognitive mechanisms observed. Any animals whose ancestors were selected to have an improved aspect of their memory, but which do not currently have that need any more, would therefore be expected to revert to a less-specialized version of that aspect of memory, owing to the cost of maintaining an otherwise useless system.

(a) *Memory duration*

We know that many food-hoarding animals use memory to retrieve their caches at a later time. However, how long this memory lasts from the time it is encoded may differ between species, depending on the ecological function of cache retrieval and the specific conditions under which they retrieve their caches. When we discuss the duration of a memory trace, we mean that this trace is maintained (e.g. by spontaneous replay during sleep (Wilson & McNaughton 1994) or waking (Karlsson & Frank 2009) or other mechanisms) without retrieving the cache and either leaving the item in place or rehoarding it (Grubb & Pravosudov 1994). Maintenance could happen by travelling through the area where caches are located, and then triggering the memories for the cache locations, which are thereby reconsolidated (Nader *et al.* 2000a,b). Brodin (2005b) has already discussed this issue to some degree for Paridae and Corvidae. Here we discuss for each of the three groups of animals what we predict their needs for memory duration to be and what is known about the longevity of their memories.

(i) *Paridae*

For how long do tits and chickadees need to remember their caches? To answer this question, we first need to know how long after hoarding tits typically retrieve the food. When marsh tits in England hoarded seeds from a feeder in a fixed location in the field, the seeds disappeared from their hoarding sites (i.e. were retrieved) within 3 days of being hoarded (Cowie *et al.* 1981; Stevens & Krebs 1985). This suggested to the authors that these animals do not keep items hoarded for more than a few days, and they would therefore have no need to remember them for much longer than that. However, this observed pattern was probably an artefact of the way in which the seeds were presented. When Brodin (1992) presented 50 seeds from a single feeder to willow tits (*Poecile montanus*) in the field in Sweden, the retrieval times were comparable to those of the marsh tits in England. However, when the 50 seeds were presented from five different locations, separated by at least 100 m, the retrieval time became four to five times longer. The findings therefore suggest that other food-hoarding parids may also retrieve caches after much longer intervals than just a few days. Classic field studies of stomach contents in winter confirm this suspicion: all species of food-hoarding tits studied consume items in winter that can only be available from caches made many months earlier in the year (Haftorn 1954, 1956a,b; Gibb 1960).

Having established that tits and chickadees can indeed retrieve their caches months after hoarding them, the question then becomes whether any of these birds retrieve caches using memory that lasts

for many months. Several authors have suggested that, because tits and chickadees store items mostly in their normal foraging niches, they will be very likely to find them during future foraging, and hence would not need memory that lasts for many months to gain the benefit of retrieving these caches (Haftorn 1956c; Gibb 1960; Pravosudov 1986; Suhonen & Alatalo 1991; Brodin 1994b, 2005b; Lens *et al.* 1994; Smulders & Dhondt 1997; Smulders 1998). This mechanism would work fine for long-term hoarding, in which the main purpose of the behaviour is to have food generally available at times of the year when food is naturally scarce, as long as immediate retrieval of items is not of the utmost importance. Tits and chickadees also use caches in the short term (hours to days). All throughout winter, they hide items when food is relatively abundant, and retrieve them when they need to eat. This day-to-day use of caches has been the basis of a number of theoretical models of short-term energy balance in these birds, and its adaptive value is generally accepted (McNamara *et al.* 1990; Grubb & Pravosudov 1994; Brodin 2000; Pravosudov & Lucas 2001). In order for caches to be useful on a short time scale, however, they have to be immediately accessible, something that is only possible if the bird knows exactly where to find them. The ecology of these birds therefore suggests to us that they should have an accurate memory lasting a few days up to a few weeks, but that a longer lasting memory may not be necessary. There are those who would argue that not using a memory strategy for longer term retrieval opens the system up to cheating strategies (*sensu* Andersson & Krebs 1978). However, we have theoretically shown that flock territoriality and niche separation can keep this risk down (Smulders 1998), in which case the benefit of longer term memory may be outweighed by its costs.

All laboratory studies that have explicitly explored the duration of memory for food caches have come to similar conclusions, independent of the tit species studied: the evidence suggests a maximum memory duration of two to four weeks (Hitchcock & Sherry 1990; Healy & Suhonen 1996; Brodin & Kunz 1997; Male & Smulders 2007b). Circumstantial evidence from the field is consistent with this estimate: Brodin (1994a) used the disappearance rates of naturally hoarded items, and compared them with those of items hidden by the experimenter in previously emptied willow tit hoarding sites. This showed that items hoarded by willow tits had a higher disappearance rate (presumably because the bird that had hoarded them retrieved them by memory) until approximately 42 days after hoarding. After this, the disappearance rates were the same (presumably owing to random foraging by all the birds, including those that had made the caches). This puts an estimated upper limit of six weeks on the duration of spatial memory of willow tits in the field, which is on the same order of magnitude as the laboratory estimates. Although there are potentially alternative explanations for these data (Pravosudov & Smulders 2010), the fact remains that there is currently no positive evidence for cache memory in tits lasting longer than six weeks, unlike in some corvid species (see below). Based on what

we currently know about parid winter ecology, there is also no indication that different species of food-hoarding tits would have a need for different memory durations, although further ecological findings may change that prediction.

Should food-hoarding tits have longer lasting spatial memory than non-hoarding species? Many animals (including hoarding and non-hoarding tits) have a need to remember the locations of food sources, predators, territory boundaries, potential mates, etc. In most of these cases, these memories will be reinforced by repeated experience of the information (e.g. by foraging in the same locations on a regular basis). We see no *a priori* reason to believe that this kind of memory should differ between hoarding and non-hoarding species. Memory for food caches, however, is different, in that the birds only visit these locations once (when hoarding the cache) and then need to remember its location at retrieval (equivalent to one-trial learning; Brodbeck *et al.* 1992; Clayton & Krebs 1993). This distinction might predict that food-hoarding tits need a higher spatial resolution memory for locations that were experienced only once when compared to their non-hoarding relatives (see later). Whether this memory needs to be longer lasting in hoarding than in non-hoarding tits is currently unclear.

A number of studies that have compared memory performance in hoarders and non-hoarders in this family have included aspects of memory duration on time scales that are relevant to cache retrieval. The fact that hoarding coal tits (*Pariparus ater*) have a longer lasting working memory than non-hoarding great tits (*Parus major*) (Biegler *et al.* 2001) does not speak directly to the duration of cache memories, although longer lasting working memory could translate into better memory consolidation and therefore potentially longer lasting long-term memories. Hilton & Krebs (1990) compared coal tits and marsh tits (both hoarders) with blue tits (*Cyanistes caeruleus*) and great tits (both non-hoarders) on an avian analogue of the 8-arm radial arm maze at different retention intervals. The data suggested (the effect was just short of significance) that the two food-hoarding species' reduction in performance with increasing retention interval (up to 24 h) was shallower (and therefore memory duration longer lasting) than that of the two non-hoarding species. However, studies using a one-trial associative memory design that had a range of retention intervals up to 24 h did not find any evidence (or even non-significant trends) of better performance of food-hoarding tits at the longer retention intervals (Healy & Krebs 1992a; Clayton & Krebs 1993). No studies to date have compared memory duration between hoarding and non-hoarding tits at intervals longer than 24 h though, so the jury remains out on whether having a one-trial memory duration of several weeks is an adaptive specialization of food-hoarding tits or not.

(ii) *Corvidae*

Whereas most food-hoarding parid species studied to date seem to have a similar ecology and use caches

in a similar manner (both short and long term), the same cannot be said for the *Corvidae*. Based on our current knowledge, this family of birds is much more diverse in its hoarding and retrieval strategies than the *Paridae* (reviewed by Vander Wall 1990). Many corvids that scatter-hoard food do so predominantly in the autumn and recover their caches throughout the winter, sometimes even into spring. This applies to many temperate jay species (e.g. Eurasian jay *Garrulus glandarius*, blue jay *Cyanocitta cristata*, pinyon jay *Gymnorhinus cyanocephalus*), as well as the nutcrackers (i.e. Clark's nutcracker and Eurasian nutcracker *N. caryocatactes*). These species typically collect nuts (e.g. acorns, beech nuts, pine nuts) at the time of year when they are most abundant, and eat them throughout winter and sometimes into the next spring. These jays and nutcrackers hide the nuts by burying them in the soil or under lichens or moss, although appropriate holes and crevices are also used (Vander Wall 1990). They do not naturally forage by digging holes in the soil. Therefore, they would most likely never find their caches during the course of normal foraging, like the parids can. Randomly digging (even in a restricted area) would take too much time and energy. The prediction, therefore, is that all these species that retrieve their caches after many months should have good long-term memories. There is one possible exception to this rule, and that is the grey jay (*Perisoreus canadensis*), which forms food boluses that are stuck to tree trunks, branches, foliage, etc. They are consumed at least several months after hoarding, and are important for the energetic state of the birds in winter (Waite 1990). Because these birds hoard their long-term caches in places where they might theoretically find them while foraging throughout winter (like the *Paridae*), it is possible that they do not require long-term memory to retrieve these items months after hoarding, but this prediction remains to be tested experimentally.

While most jays and nutcrackers studied to date seem to require a long-term memory to retrieve their caches throughout winter, most crows and magpies are believed to be more opportunistic hoarders, hoarding food from temporarily abundant sources, and retrieving it within the next few hours or days (Vander Wall 1990). Often, the food that is hidden is perishable. For example, north-western crows (*Corvus caurinus*) hide food (clams and other intertidal prey) at low tide, to recover it at high tide (James & Verbeek 1984). These species do not show a seasonal hoarding peak and do not retrieve caches many months after they have been hoarded. Again, there are exceptions to this rule. Rooks (*Corvus frugilegus*), for example, hoard large quantities of walnuts when they are ripe, and consume these caches for months afterwards (Waite 1985). Like with many corvid caches, these nuts are buried, and it is therefore very likely that some form of memory is required for retrieving them over all intervals. Finally, one other species that is worth mentioning is the jackdaw (*Corvus monedula*), a small crow that has been referred to as one of the only corvid species that does not scatter-hoard to any extent (Simmons 1968; Henty 1975), although it may larder-hoard (Vander Wall

1990). This makes the jackdaw a potentially interesting comparison with the scatter-hoarding corvids. One would expect that memory duration would not be as long as the long-term hoarders, and it would not be expected to be specialized with respect to cache retrieval. Whether it is shorter than that of opportunistic hoarders depends on how long the opportunistic hoarders need to remember their scattered caches. This information is currently still unavailable.

The ecology of food-hoarding corvids predicts that many jays and nutcrackers, as well as rooks (and some other crows), should have long-term spatial memories for their cache locations. Other crows and magpies (as well as potentially grey jays), on the other hand, would not be expected to be able to remember their cache locations for longer than a few days to weeks at most. To date, no studies have looked into memory duration for the latter category of birds. However, there are clear data for some species in the former group. Clark's nutcrackers tested in four groups, each with a different retention interval between hoarding and recovering, performed well above chance levels from 11–285 days (Balda & Kamil 1992). In the field as well, recovery patterns of these birds suggest the use of long-term memory in the retrieval of their caches (Tombback 1980). Bednekoff *et al.* (1997a) compared nutcrackers with pinyon jays, western scrub jays (*Aphelocoma californica*) and Mexican jays (*Aphelocoma ultramarine*) and found that while the nutcrackers and pinyon jays had better cache-recovery performance overall, there was no difference between the species in how retention interval affected their performance, and all four species still performed above chance after 250-day intervals. These results are consistent with the predictions we made from the ecology of these species.

(iii) *Rodentia*

Most studies of food-hoarding mammals focus on the Sciuridae (squirrels) and Heteromyidae (pocket mice), many species of which are avid scatter hoarders. The time scale over which different species retrieve their scattered caches varies enormously. Scatter caches are very short lived, less than a day, in eastern chipmunks *Tamias striatus*, who mostly rely on larder hoarding (Clarke & Kramer 1994). Yellow pine chipmunks, in contrast, scatter-hoard in the autumn, but move most of their food into larders over winter. Grey squirrels make thousands of scatter caches in the autumn for use over the winter months (e.g. Thompson & Thompson 1980). And finally, Merriam's kangaroo rats scatter-hoard extensively and rely on food caches during long periods of drought, which can last up to several years (Leaver 2000), although so far, they have only been shown to retrieve their own caches for up to 12 days in the field (Daly *et al.* 1992). What are the mechanisms these animals can use to retrieve their caches after these different intervals? Most rodents bury their caches, and like in corvids, we would argue that random digging, even in a restricted area, is too costly a strategy for substantial cache retrieval. This is again in contrast to the parids,

which are likely to find caches through random searching of normal foraging microsites. Rodents do have another strategy, however, that allows them to detect buried caches without having to dig them up: they can smell them (Vander Wall 1998, 2000). This strategy increases the risks of pilferage by other rodents, although as long as this pilferage is mutual, it may not be a problem for the evolutionary stability of the behaviour (Vander Wall & Jenkins 2003). In principle then, this strategy could allow rodents to retrieve their caches without needing to remember them. However, grey squirrels often retrieve their caches through snow, which masks olfactory cues (Lewis 1980). Similarly, dry conditions in the deserts in which Merriam's kangaroo rats live make the localization of caches using olfactory cues difficult (Vander Wall 1995, 1998). On the other hand, there is some evidence that heteromyid rodents have evolved a more sensitive sense of smell that helps them locate caches in arid environments (Vander Wall *et al.* 2003). Without knowing how much individual species rely on olfaction to retrieve their caches, therefore, it is difficult to make specific predictions about their use of memory, and how long it should last. If winter conditions really prevent the use of olfaction in cache retrieval (Lewis 1980), then squirrels at least would be predicted to rely on memory for retrieval of caches throughout winter. Whether a similar prediction can be made about drought for desert rodents depends on whether they really cannot use olfaction in dry conditions.

To our knowledge, there are no direct tests of the limits of cache memory duration in any rodents. However, a number of studies have probed memory at different retrieval intervals. The only study directly addressing the duration of memory for caches made by grey squirrels themselves was conducted by Jacobs and Liman in 1991. They allowed squirrels to bury 10 hazelnuts in an arena, then allowed them to retrieve their own 10 caches plus 10 caches made by other squirrels after a retention interval of 2, 4 or 12 days. In all cases, squirrels retrieved significantly more of their own caches than those of other squirrels, with no evidence of deterioration of memory over time, indicating that they do remember the location of their own caches accurately, at least up to 12 days, and probably beyond. The only other study addressing the duration of memory for caches in grey squirrels was conducted by Macdonald in 1997. Four wild squirrels were tested on a number of cache arrays buried by the experimenter in a 1 m radius. All of the squirrels had accurate memory of cache locations up to 21 days, and one squirrel, which was tested at longer intervals than the others (42 and 62 days), also showed accurate retrieval at these intervals. This is notable because the squirrels in this study were not able to check or manage these caches, since they were removed between learning and retrieval trials. In the same study, Macdonald also compared the performance of grey squirrels with European red squirrels (*Sciurus vulgaris*) and found that the red squirrels' retrieval time increased (i.e. accuracy decreased) after 17 days. Since European red squirrels are also exclusive scatter hoarders (Gurnell 1987), it is not clear why this should be the case. Further study into

the differences in hoarding ecology between red and grey squirrels is needed to understand these differences. While this study shows that squirrels in the genus *Sciurus* are capable of remembering cache locations for relatively long periods of time, it is important to consider that the squirrels in this study probably benefited from the rehearsal of cache location during the learning phase. Whether caches they make themselves (and to which they only have a single exposure) can be remembered for that long remains to be tested.

Vander Wall (1991) conducted laboratory studies of spatial memory for caches made by yellow pine chipmunks. He tested recovery 4 and 35 days after animals were allowed to hoard 200 seeds in an arena. There were no seeds present during recovery trials, so it was not possible for the animals to use olfactory cues to relocate caches. The chipmunks 'recovered' more of their own caches than those made by other chipmunks, with no evidence of a decrease in performance over time. However, when he tested the chipmunks' ability to recover caches made with wet seeds, which give off strong olfactory cues, recovery was better than recovery of their own caches with no olfactory cues. This study shows that while the chipmunks do use spatial memory for cache recovery, they also use combined cues for cache recovery, rather than simply relying on one mechanism. The use and duration of spatial memory for cache recovery by yellow pine chipmunks has also been studied in the field by comparing the rates of recovery over a 3-month period of real caches made by the chipmunks themselves with artificial caches placed 30 cm away in an identical microhabitat (Vander Wall *et al.* 2006). At about half of these sites, the original hoarder was removed over the winter period. The researchers found that real caches were recovered 4.7 times more quickly than artificial caches at sites where the hoarder remained, and where the hoarder was removed, real and artificial caches disappeared at the same rate. They consistently found that the hoarder's recovery advantage decreased only slightly over a 30-day period, e.g. dropping from 78 per cent recovered on the first day following hoarding to 73 per cent within the first month. Chipmunks enjoyed the greatest recovery advantage in the first week. Spatial memory therefore provides an important advantage to yellow pine chipmunks in the field, and this advantage persists for more than 30 days.

It is clear that a lot of work remains to be done on better understanding the natural history and ecology of scatter-hoarding rodents and on their retrieval strategies over longer intervals. Only when we have this can we start comparing different species on their cognitive abilities, and eventually the neural adaptations that underlie these abilities (see later).

(b) Memory capacity

Many animals have to keep a large amount of information stored in memory upon which to act in the future. However, scatter-hoarding animals need to remember an especially large number of similar, but separate facts about cache locations, and potentially

contents as well (Sherry 1984; Clayton & Dickinson 1998, 1999). Different species of food hoarders may create vastly different numbers of caches, and hence the potential load on the capacity of their memory systems may vary substantially. Differences in memory capacity are very difficult to test in experimental settings, as the actual memory capacity of most animals is probably larger than can be practically tested. Therefore, most evidence is indirect. In this section, we explore this potential variation in the required memory load and the evidence that currently exists to back up the predictions made from this aspect of natural history.

(i) *Paridae*

To estimate how many items/locations a bird may have to keep in its memory at any one time, one of course first has to take into account the duration of that memory. If tits and chickadees remember all the caches they make within one season, this would mean they potentially have to remember hundreds of thousands of locations (Pravosudov 1985). But even if we are correct in our reasoning as set out in the previous section, and memory in tits and chickadees probably does not last much longer than about four to six weeks, this can still add up to significant numbers of locations that need to be remembered. Because tits are seasonal hoarders, this maximum amount would vary across the year (Pravosudov 2006), with estimates of well over 20 000 items during the hoarding peak itself (Pravosudov 1985; Brodin 2005a,b). And even if the memories of these 20 000+ items were not used for retrieval later in winter, they might be used to actively manage the cache dispersal process during the hoarding peak (Male & Smulders 2007c), because the local density of caches (their distribution pattern) plays a crucial role in the long-term survival of these caches (Sherry *et al.* 1982; Waite 1988; Waite & Reeve 1994; Male & Smulders 2007a, 2008).

Another prediction is that species that store more items across the year will most probably store more items in any given period, and therefore have more locations to keep in memory at any one time. The amount of food storing seems to depend less on the species involved, and more on the environment in which any particular population of food-storing tits finds itself. As such, populations from the same species that live at different latitudes hoard different amounts (e.g. crested tits *Lophophanes cristatus* (Brodin *et al.* 1994), black-capped chickadees (Pravosudov & Clayton 2002), willow tits (Brodin *et al.* 1996)), although these comparisons are very dependent on year-to-year changes in food availability (Brodin *et al.* 1996) and on the exact timing of the hoarding peak (Pravosudov 2006). Therefore, memory capacity demands will differ in different regions, in different years and at different times of the year. If maintaining a large-capacity memory system is expensive, we might predict that these birds would have evolved a flexible system that can expand its capacity on demand (Smulders 2006; see also Roth *et al.* 2010).

Is there any evidence for such plasticity in memory capacity, both within and across populations and

species? Psychologically, this is a very difficult variable to measure in laboratory conditions, especially at capacities that are ecologically realistic. The only attempts at comparing memory capacity between species of hoarding and non-hoarding birds have focused on working memory, which is believed to be a different system from long-term memory, at least in mammals (Rolls 2000; Squire 2004). In an operant touch-screen study in which they varied working memory duration (1–30 s), capacity (one to four items) and accuracy (distance on the screen), Biegler *et al.* (2001) found no evidence for a larger working memory capacity in coal tits compared with great tits.

Because of the lack of relevant psychological measures, we might consider looking for neural features that covary with a demand for higher memory capacity. At the time of year when most items are being stored, the HF of black-capped chickadees is larger (Smulders *et al.* 1995), containing more cells (Smulders *et al.* 2000) and incorporating more newly generated neurons (Barnea & Nottebohm 1994) than at other times of the year (see also Roth *et al.* 2010; Sherry & Hoshoooley 2010). Similarly, populations of black-capped chickadees that hoard more food have a larger hippocampus with more neurons than populations that hoard less food (Pravosudov & Clayton 2002; Roth & Pravosudov 2009). These correlations should be treated with caution, however, as demand for high capacity may covary with a demand for high spatial resolution (although it may not; see below), such that it is difficult to assign the differences in neuroanatomy to one or the other of the two aspects of spatial memory (or indeed any other correlating variables).

(ii) *Corvidae*

While there are not any studies looking directly at the limits of memory capacity in corvids, based on the distinction between long-term hoarders and opportunistic hoarders that was made earlier, one might predict differences in memory capacity between these two groups of corvids. Long-term hoarders store thousands of seeds during the hoarding peak, when food is abundant, whereas opportunistic hoarders may be storing significantly fewer items at a time. However, for a valid experimental comparison of memory capacity between species, the number of items to be remembered in the experiment would have to be quite large.

As the capacity of memory increases, the likelihood of interference might also increase. Information can be hard to retrieve from memory owing to memories that were created beforehand (proactive interference) or owing to memories that are created afterwards (retroactive interference). Bednekoff *et al.* (1997b) found that Clark's nutcrackers did not experience either proactive or retroactive interference among two sets of caches when recovering them. This demonstrates that they can robustly hold a number of cache sites, made at different times, in their memory simultaneously. However, on a task of remembering a list of spatial locations within a room that contained an experimenter-buried seed at each site, they did show

both proactive and retroactive interference among the lists of locations (Lewis & Kamil 2006). This suggests that the location of buried food that was hoarded by the bird itself versus food buried by an experimenter may be encoded differently, and thus affected differently by interference.

(iii) *Rodentia*

Like we have argued for birds, direct tests of memory capacity for cache sites in hoarding and non-hoarding rodents are needed in order to test the prediction that memory capacity increases adaptively with increased need. At one end of this continuum, species that rely almost exclusively on larder hoarding, such as banner-tail kangaroo rats (*Dipodomys spectabilis*), would not need to be capable of remembering a large number of spatial locations over time, and thus should not have as large memory capacity as Merriam's kangaroo rats, a closely related species that makes much greater use of scattered caches and for whom the fitness consequences of not remembering each cache location would be higher. Similar predictions could be made for various species of chipmunks that vary along the same continuum, and members of the genus *Sciurus*, which are scatter hoarders (e.g. Macdonald 1997), would be predicted to have a greater memory capacity than members of the genus *Tamiasciurus*, who are primarily larder hoarders, though some do also engage in scatter hoarding (e.g. Hurly & Robertson 1987).

In the same vein as our argument for parids, owing to the quasi-impossibility of actually measuring memory capacity in controlled conditions, we can also look at some neuroanatomical measures (with all the caveats expressed about this approach earlier). In grey squirrels, where we might expect memory capacity to vary seasonally (analogous to the argument made for the Paridae), there is no evidence of seasonal changes in cell proliferation, volume or the number of neurons in the hippocampus (Lavenex *et al.* 2000a,b). Of course, it remains to be seen whether squirrels only remember their caches for the duration of the hoarding peak (like we believe parids do) or whether they remember the locations of scattered caches all through winter (like nutcrackers and jays do). If they fit the latter pattern, no seasonal changes in memory capacity (and hence in its potential correlates in the hippocampus) would be expected. An interesting species to study in this context would be yellow pine chipmunks. These animals only scatter-hoard during the autumn, but move their caches into larders during the winter (Vander Wall 1990). We would therefore predict seasonal changes in memory capacity (and potentially in hippocampal anatomy) in this species.

Scatter-hoarding Merriam's kangaroo rats have a larger hippocampus than larder-hoarding bannertail kangaroo rats (Jacobs & Spencer 1994). Assuming that hippocampal volume is related to memory capacity, this is consistent with the predictions we made earlier. Barker *et al.* (2005) compared hippocampal neuron production in grey squirrels and yellow pine chipmunks, who the authors define as larder hoarders. This is slightly problematic since

yellow pine chipmunks are also extensive scatter hoarders in the autumn months, moving most of their scattered caches into larders for use over the winter (Vander Wall 1990). Grey squirrels did have more proliferating cells in their hippocampus, but these did not translate into a similar difference in the density of new neurons. It is unclear at this point what this result means for our hypothesis. A comparison of more closely related species that differ in their use of scatter hoarding, such as grey squirrels and American red squirrels, or yellow pine chipmunks and eastern chipmunks, would give us more revealing results.

(c) *Spatial resolution of memory*

In addition to how long they last, or how much information is stored, another aspect of spatial memory is how accurately the information is stored and can therefore be retrieved. The more spatially accurate the memories for cache locations are, the more efficient the process of cache retrieval will be. If a memory is stored (and retrieved) with such high spatial resolution that the animal can go straight to the location, without even having to search in the immediate area of where the item has been hoarded, it will save time that can be spent going to the next item or foraging for other food.

(i) *Paridae*

Because of the increased efficiency in cache retrieval, we would predict that high spatial resolution should be especially crucial when days are very short and/or temperatures are very low, and eating continuously during the few daylight hours available is essential for survival. In that way, no time is lost searching in the wrong places (even if those are just a centimetre away from the cache itself). If memory accuracy is a plastic trait that can change across the year within an individual, we would predict the highest accuracy when the days are shortest and/or coldest, as that is when time is most limited and most energy is needed. On the other hand, if memory accuracy is a fixed trait within an individual (possibly set by early experience or genetics), then we would predict that more northern populations (or species) that have to cope with shorter days (and lower temperatures) at least in the middle of winter, should have a more accurate spatial memory. Finally, hoarding species should also have a higher spatial resolution in their memories than non-hoarders, who may not need to relocate a given spot with pinpoint accuracy. As said before, in addition to being required for cache retrieval, spatial memory is also important in food-hoarding tits for distributing their caches during the hoarding season. However, we do not believe that pinpoint accuracy is crucial in this situation, as the goal is to avoid spatial clumps of caches, and we presume that a little bit of spatial slack makes no difference for this process.

Spatial memory resolution can be measured in a number of ways. One way is to place other items at different distances from the cache and see if the animal retrieves those items by mistake. This method assumes that these artificial caches mimic real caches

accurately, an assumption that is difficult to test. The results therefore should be interpreted with slight caution. Cowie *et al.* (1981) placed control caches 10 and 100 cm away from real caches made in the field by marsh tits. They found that the real caches usually disappeared before the 10 cm control cache, that the overall disappearance rate of real caches was significantly higher than for the 100 cm controls and almost significantly higher than the 10 cm controls. Taken together, this suggests that marsh tits have a memory accuracy of better than a 10 cm radius around the cache. This method of measuring spatial resolution has not yet been used to compare species, populations or different times of the year.

Many studies look at the number of mistakes made by birds during either cache retrieval or another spatial memory task. The number of mistakes made when the options available to the animal are discrete and limited (as they are in most laboratory tests with tits) is not necessarily a good measure of the spatial resolution with which an animal can retrieve a memory. There may be other reasons for investigating incorrect locations that are related to other failings of memory or to the motivation to explore the environment. Nevertheless, this approach has been used in some interesting comparisons. Pravosudov & Clayton (2002) found that black-capped chickadees collected from Alaska made fewer mistakes when looking for their caches in an indoor aviary than did chickadees collected from Colorado, which is much further south. Alaskan chickadees also made fewer mistakes than Colorado birds on two versions of a spatial one-trial associative memory task. This indicates that the chickadees from the more northern population may indeed have a more accurate spatial memory, which allows them to be more efficient at cache retrieval. Clayton & Cristol (1996) showed that marsh tits that had been on short photoperiods (10L:14D) in the laboratory for longer than 20 days made fewer mistakes on a spatial one-trial associative memory task than did birds on long photoperiods. The third prediction was that memory spatial resolution should be better in hoarding than in non-hoarding species. Studies using the same one-trial associative memory task as mentioned above have sometimes (Clayton & Krebs 1993), but not always (Healy & Krebs 1992a; Clayton & Krebs 1994a), shown species differences in the number of mistakes made. Food-hoarding species seem to remember where they have found food, whereas non-hoarding species only seem to remember where they have been (Clayton & Krebs 1994b). The interpretation of this finding is even more complex, as it depends on whether the food was visible or not in the first phase of the experiment. The discussion of what this might mean is not related to spatial resolution, and we will not go into this here.

Another approach to testing the spatial resolution of memory has been to use operant conditioning techniques. As mentioned before, these types of experiments mostly measure working memory, instead of the longer term memory that is necessary for retrieval in the field. Also, the size of the items to be remembered is very large, compared with the area within which they need to be remembered (the size of the

computer monitor). Nevertheless, one could argue that in order to store memories at high resolution for the long term, they first have to be processed at high resolution in working memory. McGregor & Healy (1999) showed that in a spatial-delayed matching-to-sample task, at a given retention interval (30 s), both hoarding coal tits and non-hoarding blue and great tits were affected by the proximity of distracters, but moving distracters from approximately 3 cm away to more than 8 cm away improved the performance of the coal tits more than it did the performance of the non-hoarders. This suggests that memory spatial resolution (at least at this scale) is higher for hoarders than for non-hoarders. The spatial-delayed non-matching-to-sample experiments by Biegler *et al.* (2001) showed that this difference in memory resolution is more pronounced at longer retention intervals (up to 20 s in their study).

(ii) *Corvidae*

Like for the Paridae, the argument about spatial memory resolution is that animals that have a greater need of retrieving their caches in as short a time period as possible would also have the greater need for a more accurate spatial memory for cache locations. This would include species/populations that live at high latitudes (short, cold days), high altitudes, or other environments where high efficiency of cache recovery is essential. Balda & Kamil (1989) showed that Clark's nutcrackers and pinyon jays, both species that rely heavily on caches throughout winter, were more accurate in recovery after 7 days than the scrub jays, although all three species were able to use spatial memory to relocate the caches they made. As mentioned earlier, Balda & Kamil (1992) had Clark's nutcrackers hoard and recover in groups that varied in the cache-recovery retention interval from 11 to 285 days. Interestingly, the error rate was approximately equal between groups with the shortest and longest retention intervals until the group with the longest retention interval had recovered about 75 per cent of their caches. After that, they started to make more errors. This suggests that there was a decay in the memory of certain cache sites and that the birds may have saved those for last, recovering the more robustly remembered sites first. A similar result was found when Kamil & Balda (1990) compared two groups of nutcrackers in recovery of caches: a control group that was allowed to recover in whatever order they chose and an experimental group that was forced to recover in only one-quarter of the room at a time. The experimental group showed lower initial recovery success than the control group, but this success level was constant across the four quarters of the room, whereas the success of the control group got worse over time. The birds in the control group again appeared to recover the caches that they remembered better, first. As they continued to recover, their success rate declined as they were trying to relocate sites that were not remembered as well. We can therefore conclude that memory accuracy is not identical for all memories. Some memories may be encoded in more detail than others, or some

memories may degrade more than others. One interesting aspect of this would be to look in more detail at the errors that are made as time recovering increases. The size and consistency of the errors might yield information about how the resolution of spatial memories is encoded. Comparative studies would also be beneficial. However, the variability in spatial resolution or detail of individual cache site memories, even within an individual, may confound comparisons, and differences between species may only be found when retention intervals are long enough and/or memory loads heavy enough.

Like in the parids, the spatial resolution of working memory in corvids has also been tested using operant conditioning techniques. During an operant-delayed non-matching-to-sample spatial task, nutcrackers maintained higher accuracy on much longer delays than pinyon, Mexican and scrub jays (Olson 1991; Olson *et al.* 1995). The argument has been made that differences in spatial memory accuracy among food-hoarding animals may be due to differences in perceptual ability, not spatial memory itself (Macphail & Bolhuis 2001). However, Gibson & Kamil (2005) tested fine-grained perceptual accuracy on an operant task in three species of corvids: nutcrackers, pinyon jays and scrub jays. Birds had to discriminate the distance between two circles on a computer screen, and were rewarded for pecking at circles that were closer than 50 mm, but not for pecking at circles that were further apart. All three species could accurately discriminate circles that were 40 mm apart from ones that were 60 mm apart. However, the discrimination gradients for the pinyon and scrub jays were sharper than for nutcrackers. What this means is that the two jay species were better at discriminating the distances between circles that were closer to the threshold. The results of this study do not support the idea that higher resolution spatial memory is purely due to higher resolution spatial discrimination abilities. On the contrary, the scrub jays have a more refined perceptual system for this task than do the nutcrackers, which is opposite of what would be expected based on most of the research on spatial memory differences.

Finally, Kamil *et al.* (1993) used a cluster technique for recovery of caches in Clark's nutcrackers. When a bird made caches in sand-filled cups in a room, during recovery only a subset of holes were open. Clusters of six holes were opened, allowing a measure of spatial memory resolution for each individual cache site. Some were clusters that contained hoarded seeds (good) and some were clusters that contained no seeds (empty). The number of errors made when a bird was searching within a good cluster was significantly less than chance and the probability of recovering a cache on the first probe in a good cluster was significantly above chance. They also visited good clusters before empty clusters, as they were allowed to recover until all seeds were found. When they also carried out an experiment where clusters were opened that contained cache sites that were already retrieved by the bird at an earlier session, they made more errors within those clusters than they did in the good clusters. This demonstrates good accuracy at cache retrieval for nutcrackers. When this same technique

was used in a comparative study (Bednekoff *et al.* 1997a), nutcrackers and pinyon jays were more accurate in good clusters than scrub and Mexican jays at 10- and 60-day retention intervals, but when all retention intervals were combined (including 150- and 250-day intervals), each of the four species made fewer errors per cluster than expected by chance. However, when looking at the ability to discriminate between good and empty clusters, pinyon jays were the best and nutcrackers were the worst. All four species showed a decline in ability to make this discrimination as retention intervals increased. While nutcrackers may be highly accurate at retrieval within good clusters, they may not be as accurate at discriminating between good and empty clusters. There may also be species differences in the kind of accuracy they show, as the pinyon jays appear to be accurate both within good clusters and in discrimination between good and empty clusters. Further investigation of this idea would be of interest.

(iii) *Rodentia*

Just like for birds, better spatial memory resolution would allow rodents to save time at retrieval. The predictions for rodents are also similar, in that we expect greater accuracy in spatial memory for animals that rely more heavily on retrieving scatter caches for their survival, whether this is comparing populations that differ in latitude and therefore length and severity of winter, or species that differ in the extent to which they rely on scatter versus larder caches. We might also expect to find seasonal differences in accuracy in species that have seasonal reliance on food caches (such as sciurids), whereas we would not predict such differences in species such as kangaroo rats that rely less on seasonal production of seeds. As with memory capacity, there are very few comparative studies in rodents addressing these predictions, so we must instead focus on single species studies that tell us something about memory resolution during retrieval of scatter caches.

There are a number of studies looking at spatial memory resolution in actual cache retrieval. As mentioned earlier, Jacobs & Liman (1991) found accurate retrieval of 10 caches made by grey squirrels after intervals of up to 12 days and Devenport *et al.* (2000) showed that thirteen-lined ground squirrels (*S. tridecemlineatus*) also use accurate spatial memory to retrieve their caches. These researchers eliminated and/or moved visual cues and odour cues from both the seeds in the cache and the substrate around the cache to create decoy caches 40 cm from the original. Despite removal and/or displacement of odour or visual cues, the ground squirrels recovered 44 of their own caches within 5 days, and just one of 44 decoy caches in the 6-day study period, suggesting that the spatial memory resolution of these animals is better than 40 cm. Jacobs (1992) found that naive Merriam's kangaroo rats, allowed the same amount of time to search arrays buried by other kangaroo rats, were 28 per cent less successful than the average cache owner, and they also searched a greater number of cache sites in the same amount of time.

The results show that odour cues are probably important for cache pilferage, since naive individuals did have some success, but that the use of spatial memory is more efficient in terms of time and effort to retrieve caches. Vander Wall (1991) looked at the accuracy of cache retrieval in yellow pine chipmunks. He moved landmarks 20 cm in half of the hoarding arena to determine the effect on cache recovery after 4 days. He found that the chipmunks tended to search in the new 'correct' positions relative to the shifted landmarks, but that spatial memory resolution was not high. Chipmunks searched within 10 cm of the original cache site, and then engaged in extensive exploratory digging in the vicinity before pinpointing cache locations. He argues that since mammals have acute olfactory abilities compared to birds, it is likely that in natural circumstances they use a combination of spatial memory and olfaction (as well as small-scale visual cues such as marks left from digging) in order to pinpoint exact cache locations.

Other studies have looked at spatial memory resolution in food-finding tasks. Barkley & Jacobs (2007) found that Merriam's kangaroo rats had a much higher accuracy, in terms of visiting the sites more quickly, at relocating four cache sites after a 24 h delay than Great Basin kangaroo rats (*Dipodomys microps*), who rely much less on scatter hoarding. Furthermore, since both species performed similarly regardless of whether local cues were present, the difference in spatial memory did not seem to be due to differential use of localized cues. Macdonald (1997) tested grey squirrels' spatial memory resolution by giving three squirrels 4 days to learn the location of two nuts. She then tested them at 5, 10 and 20 days, providing a decoy cache at 2, 5, 10 or 20 cm from the original cache site. She also ran a control with no decoys present. In a total of 96 trials, only 13 decoys were taken (86% accuracy overall), 12 of which were at 2 or 5 cm away and one was 10 cm away. In a third experiment, she moved local landmarks 10 cm from their original location, and found that squirrels searched in the 'new' location over 88 per cent of the time, providing further evidence for the use of a high-resolution spatial memory (at least within 10 cm) in grey squirrels. These results must be interpreted with caution in terms of generalizing to memory for real cache locations because in this study, squirrels necessarily relocated the food several times in a row, whereas in a real hoarding situation, they would only experience it once. However, the results still indicate quite clearly that grey squirrels are capable of accurate spatial memory, which is an important trait for a species that is heavily reliant on hoarding.

3. UNDERSTANDING THE NEURAL BASIS OF MEMORY DURATION, CAPACITY AND SPATIAL RESOLUTION

The previous section has shown that we need to consider carefully how different animals use their spatial memory for hoarding and/or retrieval, and therefore in which aspects this memory might have been improved. The ecology and natural history of the

species involved can give us clues (Bolhuis 2005) and allow us to make specific predictions as to which animals (species, populations within species, or even individuals within populations under different environmental conditions) should have especially long-lasting, especially capacious or especially high-resolution spatial memory. In order to make good predictions, however, we need a more detailed natural history and ecological research on many species of hoarders. And making predictions is not enough, of course. Once the predictions have been made, they need to be tested in further comparative cognition studies, so that we can be sure that we have identified a number of species in which particular cognitive traits are especially enhanced and equally a number of comparator species in which this enhancement is not evident. Ideally, we would identify species with and without the enhanced function from as many independent clades as possible (parids, corvids, rodents, as well as potential other groups; Smulders 2006). In all cases, we believe that these enhancements will be quantitative in nature, and therefore will give us insights into the more general workings of the underlying processes.

Once we have identified the best sets of species to study, we can then use comparative neuroscience approaches to try and identify those features of neural organization or function that underlie the differences in cognitive traits between the species. Of course, two species, no matter how closely related (and indeed, the same could apply to two populations of the same species; Darwin 1859; Bolhuis 2005), will still differ in many aspects of their neural organization and function, and in many behavioural traits as well. This is why it is crucial to identify multiple sets of species, ideally from independently evolved lineages, that have the same cognitive trait difference (Smulders 2006, 2009). If the ancestors of these lineages share the same basic mechanisms for processing 'everyday' spatial memories, selection that leads to a quantitative change in that cognitive trait will probably act on the same aspects of the neural mechanisms underlying the trait (parallel evolution). Therefore, any neural feature differences that correlate with the quantitative cognitive feature differences across lineages are more likely to be mechanistically related to these cognitive features (e.g. Montagnese *et al.* 1993). Alternatively, one could study a number of species that all differ quantitatively in the cognitive feature, map both the variability in the cognitive trait and the variability in the putatively related neural trait together onto a cladogram and study whether the two covary in the phylogenetic tree (e.g. DeVogd *et al.* 1993).

There are two caveats with comparative analyses as suggested above. Firstly, comparative analyses are per definition correlational. As such, they can only give us indications of potential underlying mechanisms, but they cannot test cause-and-effect relationships. In order to really understand the neural mechanisms that underlie a certain aspect of a cognitive trait, experimental manipulations are necessary, and their findings should feed back into other comparative analyses (Smulders 2006). This iterative approach is likely to give us insights into neural mechanisms that would

not have been obtained using traditional laboratory approaches. Secondly, measuring neural features can be expensive and time consuming, making it practically very difficult to do in a wide range of species. Only if high-throughput methods are available is this a feasible approach. Otherwise, it would be preferable to have a good candidate feature available already, in order to avoid wasting time and money. Identifying this candidate feature may be done from experimental approaches in single species. If that is the approach taken, the purpose of the comparative analysis is to investigate the generalizability of the conclusions, so that they can be applied to other species, including humans (Smulders 2009).

Having laid out the approach in theory, we will now give some examples of how this would work in practice. We would like to stress again the importance of basing the mechanistic studies on a solid basis of natural history and ecology. Without appropriate knowledge at this level, any predictions made are unreliable and findings uninterpretable. The first example deals with a better understanding of the neuronal features required for long-term memory storage. As we have outlined earlier, some species have a need for (and have been shown to have) longer lasting memories than others. One approach would be to pick one species that has especially long-lasting memory (e.g. Clark's nutcrackers), and start by investigating in detail which brain mechanisms are involved in this memory. For example, using immediate early genes (e.g. Smulders & DeVogd 2000), one could map out the brain regions activated when retrieving items after a few hours and compare this with the brain regions involved in retrieving items after a few months. This is likely to involve other areas in addition to the HF (Gould *et al.* 2001; Shiflett *et al.* 2002; Bolhuis 2005). Any differences between these two conditions are likely to point to differences in the brain areas involved in short-term and long-term memory retrieval. Focusing on the long-term mechanisms, one can then study the consolidation mechanisms using local pharmacological manipulations in these brain areas (e.g. Shiflett *et al.* 2003, 2004a,b) and hone in on a putative mechanism that is responsible for this long-term memory storage. The next step would then be to compare this mechanism (e.g. gene expression, connectivity pattern) between nutcrackers and other corvids that do not have long-term memory (e.g. northwestern crows; although the memory duration of most other corvids remains to be tested). Differences in the putative mechanistic trait would provide support for the idea that this trait has indeed been modified by evolution to obtain the long-term memory formation/retention that was selected for. If we then add comparisons between other species that have long-term memory and related species that do not (e.g. European jays versus magpies, hoarding tits versus non-hoarding tits, eastern chipmunks versus yellow pine chipmunks), and the pattern is upheld in all these comparisons, this would provide ever stronger evidence that this is an important trait in storing long-term memories in many vertebrates, including possibly humans. And because most traditional laboratory animal studies usually do not study memories at the

same time scale as is involved in remembering hoarded food, this trait may be a novel one which has not been studied before.

Another example might involve the study of which mechanisms allow animals to store and use memories of thousands of individual facts simultaneously. Inter-specific comparison may be confusing in this case because, as we outlined above, species that store more food (and therefore have more memories, at least for a while) are usually also the ones that have the most to gain from very efficient retrieval of food, and therefore of a high spatial resolution. Any differences we find in neural mechanisms could therefore be responsible for the increased capacity, increased accuracy or both. However, comparisons within species across different times of the year may provide a fruitful approach in this case. Because tits only remember their cache locations for a few weeks (or at least, such is our interpretation of the current evidence, consistent with our functional ecological predictions), their memory load (capacity) changes across the season: they will have the highest number of memories to store during the hoarding peak in the early autumn, compared with much lower numbers in mid-winter (Pravosudov 2006). On the other hand, we have predicted that the highest need for a very accurate memory would be in mid-winter, when time is very limited to obtain as much food as possible to survive the long, cold nights. As outlined earlier, there is some evidence to show that hoarding tits on shorter days have more accurate spatial memory (Clayton & Cristol 1996), and there is even some evidence for a putative mechanism: increased corticosterone levels, possibly triggered by an unpredictable food supply (Pravosudov *et al.* 2001, 2002; Pravosudov 2003). Using this system, one could then look for neurobiological features (or indeed endocrinological features, gene expression profiles, etc.) that vary across the season in a pattern consistent with either large-capacity memory (peak in early autumn) or high accuracy (peak in mid-winter). Once such putative mechanisms had been identified, they could then be tested in experimental settings, as well as by looking for similar patterns in other groups of hoarding animals.

It is clear from the previous paragraphs that a number of things need to be in place in order to proceed with the neuroecological approach to investigating neurobiological and cognitive mechanisms. Firstly, we need more information about the ecology and natural history of the different species of food-hoarding animals. Unless we know how much they hoard, at which times of the year, what the role of memory is in this process for particular species, etc., we will not be able to make meaningful predictions about the detailed aspects of their cognitive mechanisms. Secondly, we need to test these predictions and obtain more detailed information about the cognitive differences between species of food-hoarding (and closely related non-hoarding) animals. This would then allow us to identify the best sets of species to use for the question under investigation. Finally, laboratories that study food-hoarding birds need to adopt more sophisticated neuroscientific techniques in order to go beyond the simple measures of

hippocampal volume (see also Roth *et al.* 2010). Only by studying details of neural organization and function can we ever understand more general rules of how brains process memories.

4. CONCLUSIONS

The study of food-hoarding animals as a model for understanding cognitive mechanisms started with a prediction from a theoretical ecological model: if animals need an individual advantage in retrieving their caches, then specific memories for each of the cache sites might be one way of obtaining this result (Andersson & Krebs 1978). From the start, it was made explicit that the ecologically predicted functional feature (having an advantage over other animals) could be obtained using a number of mechanisms, and that memory was only one possibility. Later work has indeed shown that several other mechanisms can also play a role in providing individuals with this advantage. In this paper, we have argued that the logic of Andersson and Krebs needs to be followed through to understand the system in more detail. Once it is established that memory is used in a system, the ecology of the animals (i.e. the adaptive function that the memory serves in this particular species) needs to be investigated. This then allows us to make predictions about the properties this memory needs to have (long lasting, high capacity, high spatial resolution, etc.), after which these predictions can be tested behaviourally. Having particular memory properties says nothing about how (mechanistically) these properties are obtained. One can imagine a range of behavioural, cognitive and/or neural mechanisms that would allow animals to implement these properties. The predictions based on the adaptive function of the memory therefore do not allow us to determine the exact mechanisms involved, but they do constrain the number of possible underlying mechanisms, as whichever mechanism involved has to comply with the features that make the use of memory functionally adaptive in this system. At this stage, a range of comparative studies, combined with experimental approaches, can be brought to bear on elucidating the exact underlying mechanisms (Smulders 2006). In the ideal situation, the mechanisms underlying these functional adaptations will give us deeper insights into the general mechanisms underlying the cognitive trait in question. As such, the neuroecological approach is complementary to the more traditional neuroscience approach in more artificial laboratory situations. As envisioned by Tinbergen (1963), functional and mechanistic questions about behaviour, though logically distinct, can inform each other and as such speed up and enhance their study. Food-hoarding animals lend themselves superbly to this combination of approaches, and will continue to provide important new insights into the evolution of and the mechanisms underlying memory for years to come.

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