Introduction

Integrating ecology, psychology and neurobiology within a food-hoarding paradigm

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Many animals regularly hoard food for future use, which appears to be an important adaptation to a seasonally and/or unpredictably changing environment. This food-hoarding paradigm is an excellent example of a natural system that has broadly influenced both theoretical and empirical work in the field of biology. The food-hoarding paradigm has played a major role in the conceptual framework of numerous fields from ecology (e.g. plant–animal interactions) and evolution (e.g. the coevolution of caching, spatial memory and the hippocampus) to psychology (e.g. memory and cognition) and neurobiology (e.g. neurogenesis and the neurobiology of learning and memory). Many food-hoarding animals retrieve caches by using spatial memory. This memory-based behavioural system has the inherent advantage of being tractable for study in both the field and laboratory and has been shaped by natural selection, which produces variation with strong fitness consequences in a variety of taxa. Thus, food hoarding is an excellent model for a highly integrative approach to understanding numerous questions across a variety of disciplines. Recently, there has been a surge of interest in the complexity of animal cognition such as future planning and episodic-like-memory as well as in the relationship between memory, the environment and the brain. In addition, new breakthroughs in neurobiology have enhanced our ability to address the mechanisms underlying these behaviours. Consequently, the field is necessarily becoming more integrative by assessing behavioural questions in the context of natural ecological systems and by addressing mechanisms through neurobiology and psychology, but, importantly, within an evolutionary and ecological framework. In this issue, we aim to bring together a series of papers providing a modern synthesis of ecology, psychology, physiology and neurobiology and identifying new directions and developments in the use of food-hoarding animals as a model system.

Keywords: food hoarding; memory; seed dispersal; neurogenesis; hippocampus; cognition

1. INTRODUCTION

Many animals experience changing environments, which may present challenges for obtaining sufficient energy reserves at some times, while food is abundant at other times. These changes can take place from a daily time scale to a seasonal one. While some animals have solved the seasonal problem by evolving either migratory behaviour or hibernation/aestivation during the food shortage periods, some species have evolved to store food for later consumption (Vander Wall 1990). This behaviour is variably referred to as food hoarding, food caching or food storing and these terms will be used interchangeably in this special issue. Food-caching animals can store large amounts of food during the periods of food abundance and then use these caches during periods of food shortage (Vander Wall 1990). These species can be generally divided into two categories: larder hoarders and scatter hoarders. Larder hoarders (e.g. acorn woodpecker Melanerpes formicivorus, Eastern chipmunk Tamias striatus) accumulate food caches in one larder that is usually defendable against competitors. Scatter hoarders, on the other hand, store food in multiple locations scattered throughout their home ranges. It is precisely because scatter-hoarding species use multiple locations over fairly large areas that they have stimulated much interest in a broad interdisciplinary group of scientists: ecologists are interested in plant dispersal and its effects on populations and communities; psychologists and physiologists are interested in how the motivation to hide food is integrated and contrasted with the well-studied motivation to eat; comparative psychologists are interested in the cognitive strategies used to safeguard and retrieve the caches; neurobiologists are interested in how the brain processes these cognitive mechanisms; and evolutionary biologists are interested in the evolution of brain and behaviour and in the coevolution of plants and animals. All of these topics will be considered in

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One contribution of 10 to a Theme Issue 'Integrating ecology, psychology and neurobiology within a food-hoarding paradigm'.
this special issue of the Philosophical Transactions of the Royal Society B, starting off with a brief historical overview of the development of this field (Brodin 2010).

2. THE CHALLENGES OF CACHE RETRIEVAL

For those species that engage in the behaviour, food caching appears quite crucial for survival and overall fitness (e.g. Hitchcock & Houston 1994; Pravosudov & Lucas 2001). Of course, caching would not be adaptive if the animals could not retrieve their food later. Questions about how these animals find their caches have therefore attracted much attention. For larder hoarders, the solution is trivial: all the food is in one (usually well-defended) location. Scatter hoarders, however, are known to make impressively large numbers of caches. Individual Clark’s nutcrackers (Nucifraga columbiana) have been estimated to store up to 100 000 seeds during one autumn season (Vander Wall 1990). Assuming that each nutcracker puts a few seeds per cache, these birds might need to find around 20 000 individual cache locations in order to retrieve these seeds. Parids (tits and chickadees) are even more impressive cachers than nutcrackers when it comes to the amount of cached food. While it is debatable whether parids actually remember all of their caches, they clearly cache more food items than any corvid. Several European tits species have been reported to make anywhere from 100 000 to 500 000 individual caches per year. Because parids only cache one item per cache site, they may be facing up to 500 000 cache sites to re-locate (Haftorn 1956; Pravosudov 1985; Brodin 1994).

Initial studies (e.g. Haftorn 1956) assumed that food caches were communal property shared by all individuals within social groups. A seminal paper by Andersson & Krebs (1978) provided strong theoretical arguments that food caching should evolve only when individuals making caches have an advantage over other individuals in retrieving their own caches. If this were not the case, some animals (‘cheaters’) would be able to benefit from the hoards, without paying the costs of the hoarding behaviour itself. In other words, Andersson & Krebs (1978) argued that food caching should not be altruistic, but selfish. Some more recent theoretical studies have suggested that there must be mechanisms allowing food-caching individuals to find their own caches more successfully compared with other individuals. This has resulted in an intensive research effort into the mechanisms of cache retrieval, most of which has focused on memory as the main cache retrieval mechanism (Shettleworth 1995).

3. MEMORY FOR CACHE RETRIEVAL

The evidence gathered over the last 30 years has made it very clear that all scatter-hoarding animals studied to date can and do use memory at least in part to retrieve their caches (Shettleworth 1995, 2003; Sherry 2006). So, what kind of information is it exactly that is stored to allow future recovery of these caches? Initial studies suggested that food-caching birds always rely on spatial cues (i.e. position relative to distant landmarks) over local cues (such as colours and patterns adjacent to the cache site), whereas non-caching species do not prioritize these cues and rely equally on all of them (Brodbeck 1994; Clayton & Krebs 1994; Brodbeck & Shettleworth 1995). Such results have been explained on an adaptive level of analysis by the higher reliability of spatial cues, which usually do not change over time, unlike colour cues. Later studies, however, showed that food-caching birds do not always prefer spatial cues and that cue use may be more complex than previously thought (LaDage et al. 2009). All studies showed that food-caching birds memorize both spatial and non-spatial cues suggesting that both types are important (Brodbeck 1994; LaDage et al. 2009), but more research is needed to better understand how and when some specific cues are preferred. Gould et al. (2010) provide a discussion of studies focused on what food-caching animals use to remember cache locations and how this has expanded our understanding of spatial navigation in general.

Another question is how long the memory for cache sites lasts (Smulders et al. 2010). Some food-caching corvids have been well documented in their impressive use of long-term memory (Vander Wall 1990). Clark’s nutcrackers, the champions of long-term memory, have been shown to accurately retrieve their caches more than 200 days after caching in laboratory conditions (Balda & Kamil 1992). Food-caching parids, on the other hand, remain a point of controversy. It is clear that these birds (as well as their close relatives, the nuthatches) consume food many months after it was hoarded (Haftorn 1956; Nilsson et al. 1993; Brodin & Ekman 1994). Long-term retrieval is, therefore, not controversial. The mechanisms they employ to retrieve these caches, however, are. The handful of laboratory studies (Hitchcock & Sherry 1990; Brodin & Kunz 1997; Male & Smulders 2007a), as well as a single field study (Brodin 1994), that have examined the question suggest that these birds can only use memory for up to a few weeks. Some researchers (including one of us, T.V.S.: Smulders & Dhondt 1997; Smulders et al. 2010; also Brodin 2005), think that this represents the situation in nature, and that food-caching parids do not need to use memory for long-term cache retrieval, as

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individual advantages can be guaranteed based on individual niche segregation for both foraging and food caching (Haftorn 1956; Pravosudov 1986; Brodin 1994; Lins et al. 1994). Others (including the other one of us: VVP) disagree with this viewpoint and take the more cautious standpoint that absence of evidence is not evidence of absence. There are several potential reasons why parids might not show long-term memory in the laboratory, while corvids would. One possibility is that the motivation to retrieve caches in a captive environment is different between parids and corvids, especially after long intervals. It is also possible that the two groups of birds manage their memories differently. In the wild, parids are always foraging close to their caches. In the laboratory, however, these birds are completely removed from the caching area for a long period of time and therefore may actively discard these memories as not needed. Many corvids (including and especially Clark’s nutcracker), on the other hand, routinely cache food far from their normal daily foraging (Vander Wall 1990) and thus laboratory environments in which these birds are removed from the areas with caches for the duration of the retention interval may be more naturalistic specifically to corvids. There is also some field evidence from a species that caches and forages similar to parids, Eurasian nuthatch (Sitta europaea), which suggests the possible existence of long-term memory. Nuthatches were observed to retrieve sunflower seeds for up to 98 days after these seeds were cached (Nilsson et al. 1993). More importantly, nuthatches retrieved most caches specifically during more severe weather conditions. Such ‘prudent’ behaviour suggests that they were not randomly retrieving their caches by just foraging in their regular microhabitats, but intentionally sought out their caches, a behaviour that may be explained by long-term memory. However, other explanations are possible too, and more studies are clearly needed to better understand the longevity of cache site memories.

4. ADAPTIVE SPECIALIZATION OF MEMORY AND THE HIPPOCAMPUS
It has been well established that almost all food-caching species use spatial memory, at least in part, for cache recovery (Shettleworth 1995) and, therefore, food-caching species present a great model to investigate a variety of proximate questions about memory and its underlying neural mechanisms in a naturalistic system. Most importantly, food-caching animals are extremely convenient for studies of spatial memory in controlled laboratory settings because they regularly cache food and recover previously made food caches using spatial memory (Shettleworth 1995). Thus, unlike the traditional laboratory rodent model, spatial memory and the relationship between memory and its underlying neural mechanisms can be tested by using an unforced, natural paradigm of memory-based food caching and retrieval. One of the brain areas that are known to be involved in spatial memory processing in both mammals and birds is the hippocampus (O’Keeffe & Nadel 1978; Shettleworth 2003; Sherry 2005; Smulders 2006). Using food-caching black-capped chickadees, Sherry & Vaccarino (1989) and Hampton & Shettleworth (1996) showed that hippocampal lesions impair spatial but not colour memory, and these findings seem to establish causal relationship between the hippocampus and spatial memory in food-hoarding birds. While other brain areas are undoubtedly involved in spatial memory function as well, the involvement of the hippocampus is undeniable, and this is where the field has focused its efforts to date.

An important idea that was proposed early on is that memory in food-caching species is under intense selection pressure because cache retrieval is essential for survival, and, as a result, memory and its underlying neural mechanisms in food-caching species should be adaptively specialized compared with memory in non-caching species (Krebs et al. 1989, 1996; Sherry et al. 1989; Sherry 2006). This adaptive specialization hypothesis, which extends to both memory and underlying neural mechanisms, predicts that food-caching species should have better spatial memory compared with non-caching species, a prediction that has been tested quite extensively (Shettleworth 1995). Results of behavioural tests appeared inconclusive, as some studies have reported that caching species indeed perform better on spatial memory tasks while a few studies failed to support superiority of food-caching species (reviewed by Shettleworth 1995; Bolhuis & Macphail 2001; Macphail & Bolhuis 2001). A potential cause of these apparent discrepancies is discussed by Smulders et al. (2010).

If food caching is associated with intense selection pressure for the mechanisms of cache retrieval such as memory, mechanisms mediating this memory should be under selection pressure as well. As a result, it has been predicted that food-caching species should have a relatively larger hippocampus compared with non-caching species (Krebs et al. 1989, 1996; Sherry et al. 1989; Sherry 2005, 2006). There have been a number of studies testing this hypothesis and while most of them provided solid support, some did not. Such inconclusiveness in studies of memory and the hippocampus comparing caching and non-caching species has spurred criticisms of the entire adaptive specialization hypothesis (Bolhuis & Macphail 2001; Macphail & Bolhuis 2001; Bolhuis 2005; Brodin 2010; Roth et al. 2010a).

The article by Smulders et al. (2010) as well as that by Roth et al. (2010a) provide a discussion of the problems associated with the current approach to linking the hippocampus to the adaptive specialization hypothesis. Smulders et al. (2010) argue that the comparisons to date have used an oversimplified approach by looking for a single cognitive adaptation that applies to all aspects of spatial memory and across all food-hoarding species. This ignores the complexity underlying differences in food-caching behaviour among different species. In their paper, they lay out a more nuanced approach to the adaptive specialization hypothesis that may point the way for future studies.

While that may be one of the problems, there may be different ways to address the adaptive specialization hypothesis as it relates to the hippocampus. One way would be to compare multiple lineages while carefully
controlling for phylogeny (Smulders et al. 2010), but this approach may not eliminate potential problems associated with differences in memory between the lineages that are not related to the food-caching behaviour. Consequently, failure to support the adaptationist hypothesis using multiple lineages comparisons might not be conclusive proof against this hypothesis, as it is impossible to take into consideration differences between all lineages in all other memory-related behaviours (not associated with food caching and retrieval).

Another approach might be to document that selection on memory is indeed capable of producing differences in mechanisms such as the hippocampus (Roth & Pravosudov 2009). This approach might involve comparisons of multiple populations of the same species that differ in their reliance on food caching as differences between populations of the same species will almost always be much smaller than differences between species (Pravosudov & Clayton 2002; Roth & Pravosudov 2009). Such comparisons, of course, will only provide correlative support (Smulders 2006; Smulders et al. 2010) and so they should be followed by additional research establishing the heritable basis of differences between the populations and artificial selection experiments. If it can be demonstrated that selection for better memory can be followed by hippocampal enlargement, it would provide experimental support to the adaptive specialization hypothesis.

Another potential problem with most neuroecological studies concerns the fact that almost all studies used only hippocampal volume as the main neural measure (Krebs et al. 1989; Sherry et al. 1989; Shettleworth 2003). In other words, the assumption in these studies is that better memory is associated with an enlarged hippocampal volume, but no other measures of hippocampal anatomy were used. It appears, however, that volume measurements are highly sensitive to a variety of factors and they may be quite unreliable when volumetric data from multiple sources are pulled together for comparative analyses. An article by Roth et al. (2010a) in this issue provides a thorough discussion of all the benefits and pitfalls associated with using brain volume as the main currency. It appears that it may be necessary to move to more detailed analyses of the brain involving neuron numbers, neurogenesis and neuronal connections, which may better reflect brain functional abilities (Roth et al. 2010a).

5. MECHANISMS UNDERLYING HIPPOCAMPAL MEMORY PROCESSING

Because the hippocampus of food-hoarding animals needs to process large numbers of memories with high accuracy and for relatively long periods of time, it is the ideal system in which to study the mechanisms that underlie hippocampal memory processing. The study of a system that presumably works close to its maximum capacity in a natural environment may yield general principles of memory processing that might not be discovered using traditional laboratory animal models. The fact that the animals do not need to be trained on a somewhat unnatural task, but perform the behaviour naturally, also avoids the many confounds possible with artificial laboratory tasks. We briefly discuss three physiological phenomena that are related to hippocampal memory processing: sleep, glucocorticoid hormones and neurogenesis.

One phenomenon that is known to have an important influence on memory consolidation and hippocampus is sleep. Biomedical researchers have focused on the relationship between sleep and memory for quite a while, but debates continue on whether and/or how sleep might affect memory and neurobiological processes in the brain. Roth et al. (2010b) provide a review of research on the relationship between sleep, memory and the brain and argue that the food-caching paradigm may present a great model to advance our understanding of such a relationship. No research to date has investigated sleep in food-caching animals, and taking advantage of the food-caching system may provide novel insights into the role of sleep in memory consolidation.

There are also endocrine factors that modulate plasticity in the hippocampus. Hormones are well known to affect memory function but most research on hormones, memory and the brain has been done on mammals, mostly laboratory rodents. Gonadal (testosterone and oestradiol) and glucocorticoid (corticosterone and cortisol) hormones in particular appear to have strong effects on memory performance, usually in a dose-dependent fashion (de Kloet et al. 1999; McGaugh & Roozendaal 2002; Janowsky 2006; Luine 2008). Food-caching species again provide a convenient model to investigate the relationship between hormones and memory using a naturalistic memory-based paradigm in species with naturally changing hormone levels. For example, in many food-caching birds, baseline corticosterone levels are highest during the winter when naturally available food supplies are most unpredictable but energy demands are the highest (Pravosudov 2005). Moderately elevated corticosterone levels, which appear to be triggered by limited and unpredictable food supply in the winter (Pravosudov et al. 2001), enhance spatial memory, probably resulting in improved cache recovery and increased survival (Pravosudov 2003). Further research connecting various naturally changing hormones to memory and brain processes using food-caching species might advance our understanding of both causal relationships between hormones, memory and the brain as well as fitness consequences of variation in hormone levels.

Finally, adult hippocampal neurogenesis is another phenomenon that has been linked to memory use and has received much attention (Gould et al. 1999; Leuner et al. 2006). Neurogenesis consists of neuron production and survival, and memory use has been suggested to modulate adult neurogenesis rates (Gould et al. 1999; Leuner et al. 2006). Demonstrating that specifically memory and/or learning affect hippocampal neurogenesis rates has proved to be challenging because other variables such as environment complexity and even physical exercise also directly affect neurogenesis rates (van Praag et al. 1999, 2000). A pioneering study by Barnea & Nottebohm...
(1994) showed that adult hippocampal neurogenesis rates vary seasonally in food-caching black-capped chickadees (Poecile atricapillus), with the highest peak during the autumn. These birds usually cache most food during the autumn. and Barnea & Nottebohm’s (1994) findings have been used to suggest a direct relationship between food caching, associated spatial memory use and hippocampal neurogenesis (Barnea & Nottebohm 1994). We will devote a little more attention to this landmark study, because the exact interpretation of the results strongly determines how one thinks about the role of adult neurogenesis in learning and memory.

The Barnea & Nottebohm (1994) study served as an impetus for more investigation into hippocampal neurogenesis, but, unfortunately, has often been interpreted as directly linking food caching to new neuron incorporation rates (Pravosudov 2007). However, the results of that study on seasonal variation in hippocampal neuron incorporation rates do not provide enough data to warrant such a strong conclusion, as the data can be interpreted in a number of alternative ways. Part of this variability in interpretation is the result of not actually knowing when (and for how long) the hoarding peak occurred in their population of birds. They assumed that the peak of hoarding was in October as based on Odum (1942). However, in other populations of the same species, the peak of hoarding has been found to be in September (Brodin 2005). Barnea & Nottebohm (1994) found that birds injected with cell division marker in October had more new neurons six weeks after the injection. They did not measure cell proliferation rates or survival of these new cells prior to the six week period, and, therefore, their results might be explained either by increased neuron production rates in October or by increased new neuron survival rates in the six week period after the injection (i.e. into November–December), or both.

Assuming the hoarding peak does not last for the six weeks after the injection, there are four possible scenarios that can be used to interpret their results: (i) increased neuron production rates caused by increased caching rates; (ii) increased neuron survival rates soon after neuronal birth as a result of intense learning of cache locations during food caching as opposed to memory use during cache retrieval; (iii) increased neuron survival rates later after their birth as a result of intense memory use during cache retrieval; and (iv) all of the above may provide a cumulative effect on increased neuron incorporation rates.

First, it is possible that intense food caching might be a trigger for higher neuron production, either because of increased physical activity or because of increased hippocampal activity. This interpretation of course is only possible if the peak of hoarding indeed overlapped with the injection period in October. Intense food caching may be a signal of forthcoming increased memory requirements and thus caching might trigger increased production of new neurons that might be fully incorporated into the neural circuits by the time these birds would need memory for cache retrieval.

Second, it is possible that neuronal survival, and not neuron production, was positively affected by continuing food caching in the early weeks after neuronal birth. Birds need to memorize cache locations as caches are made in order to retrieve them later and also in order to create optimal cache distribution that would minimize pilferage rates (Male & Smulders 2007b; Smulders et al. 2010), and it is possible that increased learning associated with creating optimal cache distribution results in increased neuron survival. Indeed, in the dentate gyrus of the rat hippocampus, new neurons are recruited to encode new spatial information specifically between one and three weeks after their birth (Tashiro et al. 2007). If it is the encoding of new memories that is important for this increased neuronal survival, then this explanation only works if hoarding intensity is still relatively high during the first weeks after injection. It is important to note that neurons appear to mature much faster in rats than in chickadees as a marker for mature neurons (NeuN) is expressed in more than 50 per cent of all newly generated hippocampal cells already at 21 days in rats (Brown et al. 2003), whereas in black-capped chickadees only about one-third of six-week-old newly generated cells expressed NeuN (Hoshioole & Sherry 2007). Such a potential later neuronal maturation in chickadees could shift forward the importance of learning on neuronal survival.

Finally, it is also possible that it is not food caching but memory retrieval during cache re-location that results in increased neuronal survival. If that is the case, survival of new neurons may be specifically affected by behavioural memory-based experiences relatively late after neuronal birth (i.e. in the final of the six weeks). In that case, the hoarding peak has probably passed, and increased memory retrieval associated with finding previously made caches may be responsible for the neuronal survival.

We favour the latter two explanations (neuronal survival either soon after neuron production or later on) because extensive research on neurogenesis in mammals suggests that various factors, such as enriched environment, physical exercise and memory use, often increase new neuron survival rates rather than neuron production rates (Leuner et al. 2006). However, we disagree on which of the two we deem more likely. T.V.S. hypothesizes that memory formation during the hoarding peak is most likely to influence neuronal survival during the first few weeks after neuronal birth, whereas V.V.P. thinks that memory retrieval during memory-based cache retrieval in November and early December might have contributed to the increased number of surviving new neurons in Barnea & Nottebohm’s (1994) study. What is clear is that the Barnea & Nottebohm’s (1994) study does not provide any data to resolve these issues and new studies are necessary.

Interestingly, Barnea & Nottebohm (1994) reported that neuronal incorporation rates of chickadees injected with cell division marker in August and in February–March were significantly lower compared with the October-injected birds. In some populations, black-capped chickadees may start caching intensively by the end of August and may cache most in September rather than in October (Brodin 2005). If Barnea & Nottebohm (1994) injected their birds in late August,
and the hoarding peak in their population matched that in the British Columbia sample of Brodin (2005), then this would argue against T.V.S.’s point of view that memory of making caches rather than their retrieval affects neuronal survival. Chickadees still cache intensely during September (six weeks after the injections) but are not likely to retrieve their caches at that time, and so reduced neuronal survival six weeks after the August injections would argue against the hypothesis that creating caches increases neuron survival. However, if the August injections happened even a week or two before the onset of the hoarding peak in the Barnea & Nottebohm (1994) study, then this information does not allow us to decide between the two opinions. Only a new study, in which the exact timing of the hoarding peak is known relative to when the birds are collected, can resolve this issue. Clearly, more research is needed to investigate the functional role of adult neurogenesis and its relation to hippocampus-based memory. Sherry & Hoshooley (2010) provide a review of research on seasonal changes in neurogenesis and how these changes may be related to seasonal changes in ecology.

6. MOTIVATION FOR CACHING

The drive to forage for food and eat it when it is encountered is very strong. The evolutionary advantage of this is intuitively obvious. Nevertheless, food-hoarding animals very often do not consume the food they find, but instead hide it for future consumption. Under which circumstances are these animals more likely to hide the food than eat it? And what are the physiological mechanisms that underlie this motivation to hoard? We assume that these mechanisms would interact with the physiological mechanisms that regulate appetite and satiety, but the details have not been completely worked out. In their review of cognitive solutions to problems faced by food-hoarding corvids, Grodzinski & Clayton (2010) briefly touch on some of the behavioural and environmental factors that influence the motivation of corvids to hoard food. Grodzinski & Clayton (2010) emphasized the impulsive and probable genetic nature of food caching at least in birds and the idea that pre-feeding a particular food type leads to a decrease in motivation to cache that food type and an increase in motivation to cache alternative food types. Others have focused on the physiological mechanisms of hoarding motivation. Some studies on birds (parids in this case) have shown that moderate elevation in levels of glucocorticoid hormones usually associated with unpredictable food supply also increases the motivation to hoard food (Pravosudov 2003), while Keen-Rhinehart et al. (2010) summarize a large body of work on the physiological and neurobiological mechanisms that control hoarding behaviour in hamsters.

Clearly, there is still much unresolved about the motivation to cache. The natural peaks in caching intensity in many food-caching species in particular present challenges to our current understanding of motivation to cache food (Pravosudov 2006). For example, unpredictable and variable food has been proposed to motivate caching (Hurly 1992; Pravosudov & Grubb 1997), but most food-caching species cache most intensely when food is extremely abundant and predictable (Haftorn 1956; Pravosudov 1985; Brodin 1994). Variable and unpredictable food therefore cannot explain what causes these animals to cache food during autumn. On a physiological level, caching motivation may be partially explained by hunger levels and hormones associated with hunger/satiation (Keen-Rhinehart et al. 2010). These mechanisms may explain motivation for caching during the periods of food scarcity (e.g. winter), but, again, they cannot explain the most intensive caching recorded during the periods of extreme food abundance. Photoperiod is another factor that has been shown to trigger caching, at least in captivity (Krebs et al. 1995; Shettleworth et al. 1995; Clayton & Cristol 1996; MacDougall-Shackleton et al. 2003). This seems logical, as day length is predictably getting shorter during autumn. But at least some parids cache as intensively during the spring when day length is actually increasing (Pravosudov 1985), which would argue against the hypothesis that photoperiod is responsible for motivating these animals to cache (Pravosudov 2006). Finally, the motivation to cache based on pre-feeding some specific food types (Grodzinski & Clayton 2010) also fails to explain extremely high motivation to cache during intensive caching peaks in autumn and in spring, because during these peaks, birds cache and eat basically the same food type (e.g. pine seeds) and yet they continue to cache it until these food types are no longer available. Clearly, many questions remain about the environmental and physiological mechanisms that influence the motivation to hoard. This special issue brings together investigators from very diverse backgrounds to hopefully spark new ideas of how caching motivation can be studied at different levels of analysis.

7. FOOD CACHING AND COMPLEX COGNITION

Animal cognition has historically been an active area of research and most work on higher levels of cognition and animal intelligence has been focused on primates (Tomasello & Call 1997; Emery & Clayton 2004, 2005). However, recent work with some food-caching species, mostly birds in the family Corvidae (crows and jays), has provided interesting insights and comparisons, suggesting that at least some birds appear to be capable of complex cognition as well (Emery & Clayton 2004). Emery & Clayton (2004, 2005) have even suggested that complex cognition of food-caching corvids is similar to that of apes and may be a result of convergent evolution acting in similar socioecological environments. Many highly social species, however, are not known and/or have not been studied for their cognitive abilities and so there potentially remains a challenge to the purely social cognition hypothesis. If rich social environments were the main drive behind the evolution of complex cognition in corvids, we should expect to find similarly complex cognition in many similarly or even more social species of birds.
(e.g. long-tailed tits, Aegithalos caudatus; bee-eaters, Meropidae, etc.).

Maybe having a complex social system is only one component of the requirements for evolving complex cognition. Many corvids cache various types of food, which may perish at different rates. Cached insects, for example, may spoil within days if the ambient temperature is too high, while cached seeds and nuts may last for months. For species that cache both these types of food, the effective solution is to keep track of food types cached, locations and time elapsed since caching, or ‘what’, ‘where’ and ‘when’ (Clayton & Dickinson 1998). Western scrub-jays ( Aphelocoma californica), which cache multiple food types throughout the year, appear to do just that—they remember information about locations, food type and timing which allows them to efficiently manage their cached food (Clayton & Dickinson 1998). Such memory, called ‘episodic-like’, is quite complex and was previously thought to be a part of human cognition only. Further research revealed that food-caching corvids seem to recognize specific individuals and whether these particular individuals may be a threat to their caches (Clayton et al. 2007), learn whether and which food will be available in specific locations and then plan their future caching decisions accordingly (Correia et al. 2007; Raby et al. 2007), and project their own experience into their future decisions (Clayton et al. 2007). The question remains whether corvids are unique among birds and whether their complex cognition is mainly the result of their complex social environment. It is also possible that selection pressures associated mainly with food caching and with protection of food caches were the main drive behind the evolution of cognition in corvids. Food-caching non-corvids, such as some parids, for example, also manage their caches to prevent long-term loss (Male & Smulders 2007b) and appear to recognize potential pilferers, both conspecific and heterospecific (Pravosudov 2008). The article by Grodzinski & Clayton (2010) provides a thorough discussion on the evolution of complex cognition in food-caching corvids.

8. ANIMAL–PLANT INTERACTIONS

Scatter-hoarding behaviour has very likely evolved as a way to minimize cache loss to potential cache pilferers. Whereas larder hoarding may also be effective in preventing cache loss, it requires defending the larder. Scatter hoarding, on the other hand, allows caching more food as the cachers are not limited to defendable substrate for caches and no cache defence is necessary. Inadvertently, however, scatter hoarding may also have provided a path for coevolution of plants and seed-catchers who appear to serve as important seeds dispersers (Vander Wall 2010). Scatter-hoarding animals are not likely to recover all of their caches and therefore unrecovered cached seeds may germinate. Seed-bearing plants thus may greatly benefit from animals caching their seeds and natural selection may favour the evolution of seeds that may be preferred by caching animals specifically for caching. In other words, plants might benefit if animals cache their seeds rather than consume them. Natural selection should favour plants that increase their reproductive success via enhanced dispersal, and coevolution between seed-producing plants and seed-caching animals may provide a path for such enhanced dispersal mechanisms. Masting in particular appears to be one of the mechanisms plants may have evolved to disperse their seeds via food-caching animals (Vander Wall 1990). Vander Wall (2010) provides an interesting discussion on the relationship between seeds bearing plants, food-caching animals and seeds dispersal.

9. CONCLUSIONS

Unique characteristics of food-caching species, especially scatter hoarding and using memory for cache retrieval, make the food-hoarding paradigm an exciting model to address a multitude of interdisciplinary questions integrating ecology, psychology, physiology and neurobiology within an evolutionary context. A series of articles presented in this Theme Issue provide good examples of various applications of the food-hoarding paradigm along with promising future directions. Our hope is that this Theme Issue will promote more interest in using food-caching animals to address a variety of biological questions.

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