

The comparative cognition of caching

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The avian food-caching paradigm has greatly contributed to our understanding of a number of cognitive capacities. Although the early work focused on spatial memory, contemporary studies of the cognitive abilities of food-caching birds have a much broader scope, ranging from episodic-like memory and mental time travel to aspects of social cognition such as observational spatial memory of other birds' caches and elements of mental attribution. A major strength of using the food-caching paradigm to test for cognitive abilities lies in the combination of ethological validity coupled with rigorous experimental control. Thus, food-caching is a naturally occurring behavior, but one that birds will readily perform in the laboratory. And, unlike many of the standard psychological tests of animal memory, the birds do not need to be trained to cache or recover. Yet, the very fact that memory for food caches can be tested in captive birds allows a level of control that would be difficult, if not impossible, in the field. For example, we can control for the time elapsed between caching and the first opportunity to recover that cache, as well as whether or not the animal can use cues emanating directly from the caches at the time of recovery. And, we can test hand-raised birds that have spent their life in captivity, ones whose reinforcement histories are well documented and whose previous experiences can be experimentally manipulated.

Our current approach to the comparative cognition of caching capitalizes on an integrative knowledge of behavioral ecology and comparative psychology. An understanding of behavioral ecology allows one to pose questions about the selective pressures that drive the evolution of cognitive abilities in food-caching birds, and how a bird's decisions concerning both caching and cache-recovery are shaped by ecological factors. For example, reliance on cached food may be greater for those individuals that live in harsher environments, where access to food supplies is limited and unpredictable because failure to recover food caches in the winter may lead to death from starvation (Pravosudov & Grubb, 1997). The prediction, therefore, is that an individual living in harsh conditions should cache more food and/or show more efficient recovery of caches (e.g., fewer searches to find its cached seeds) than one that lives in a more temperate environment. Support for this claim comes from population differences in the caching behavior of black-capped chickadees (*Poecile atricapillus*). Alaskan chickadees that have to endure severely cold winters cache considerably more seeds and are much more efficient at cache recovery than chickadees from low elevation Colorado, even when the two populations are housed for 2 months in identical conditions in the laboratory (Pravosudov & Clayton, 2002).

In comparative psychology, the emphasis is on understanding general processes of learning, memory, and cognition, and the questions are often inspired by the logical structure of the task. Adopting a psychological approach allows us to ask questions about whether, and to what extent, food-caching birds rely on various cognitive abilities such as

whether a potential pilferer uses observational spatial memory to steal another bird's caches or whether it simply relies on olfactory cues to detect the hidden cache at a later date. In the case of the Alaskan and Colorado chickadees, the psychological approach inspired us to compare these birds' performance on other tasks that rely on spatial and non-spatial memory (Pravosudov & Clayton, 2002).

By combining the two approaches, we can use natural variations in food-caching behavior across different species, and even different populations of the same species, to investigate the cognitive mechanisms that might underlie caching and recovery decisions. Indeed, studies comparing the caching abilities and spatial memory capabilities of different species in relation to their ecological demands have been particularly productive for assessing species differences in cognition, especially the studies of Balda and Kamil on species of North American corvids, notably the Clark's nutcracker (*Nucifraga columbiana*), the pinyon jay (*Gymnorhinus cyanocephalus*), and the western scrub-jay (*Aphelocoma californica*), which differ in their reliance on caches of pine nuts and on their performance on a battery of spatial and non-spatial memory tasks (e.g. Balda & Kamil, 1989). Most of the comparative work on food-caching birds has been conducted on two families of birds, the *Paridae* (tits and chickadees) and the *Corvidae* (the crow family which includes ravens, jays, magpies, and nutcrackers), so we shall begin this chapter with a brief overview of the variations among species in caching in relation to ecological and cognitive demands. The main body of this chapter will focus on the role of cognition for caching and cache-recovery decisions in members of the *Corvidae*, however, because it is this family of food-caching birds that is known for its relatively

large brain to body size ratio and its complex cognition (see Emery & Clayton, in press, for a review).

Our approach to comparative cognition is also informed by an evolutionary perspective, because a knowledge of the evolutionary history of the species is of critical importance when interpreting species differences in cognitive ability, particularly for teasing apart the role of current ecological factors and the role of previous pressures imposed on their ancestors; and, to do so, one needs to know the evolutionary relatedness among those species (phylogeny). We shall therefore conclude this chapter with a discussion of why an understanding of evolution in general, and in particular the phylogeny of the species under study, are essential for how we interpret species differences in cognition.

To cache or not to cache

Many bird species hide food for later consumption and rely on memory to recover their caches, often several days if not months later, when supplies are less abundant (Vander Wall, 1990). Within the Corvids and the Parids, the amount of caching varies considerably, from species that do not cache at all to species that cache thousands of items per year. Food caching and recovery behavior is thought to have evolved in response to temporal food scarcity (Roberts, 1979). For example, the Clark's nutcracker can winter at higher latitudes and breed earlier in the spring than other corvids by relying on caches of pinyon seeds that it has made during the previous fall (VanderWall & Balda, 1981).

Species differences in cache propensity are thought to correlate with differences in fluctuating food availability in the environments in which they live; the common assumption is that caching intensity is linearly related to the dependence on caches for survival. Those species that depend on their caches for survival tend to live in extreme environments where food availability follows a discrete seasonal pattern, such as at high altitudes in mountainous areas or high latitudes. Species living in more temperate areas, with a year-round availability of food, are usually less dependent on their caches for survival and they tend to cache less (see Andersson & Krebs, 1978; McNamara *et al.*, 1990). The Siberian jay (*Perisoreus infaustus*) is largely dependent on cached food for survival during the hostile winters of Siberia and it is a particularly prolific cacher that can store thousands of items a season (Ekman *et al.*, 1996). The same is true of willow tits (*Parus montanus*) and Siberian tits (*P. cinctus*) that occupy this harsh climate (Pravosudov, 1986). In contrast, the more southerly distributed Eurasian jackdaw (*Corvus monedula*) and magpie jay (*Calocitta formosa*) cache little, if at all. Similarly, within the Parids, species such as the blue tit (*P. caeruleus*) and the great tit (*P. major*) are also classified as non-storers. Species not only differ in the amount of food they cache, but also in the average time elapsed between caching and recovery. Some species of corvids, e.g. Clark's nutcrackers, are relatively long-term hoarders that recover their caches mainly in periods of food scarcity and they may have to remember the locations of their caches for months. Other species, such as the North Western crow (*C. caurinus*), only hoard for short intervals and they recover their caches within a day (James & Verbeek,

1983). Similarly, marsh tits (*P. palustris*) are thought to recover the majority of their caches within the first few days after caching (Stevens & Krebs, 1986).

The role of cognition in caching

What, when, and where to cache

At the initiation of every caching event, food-caching birds need to make complex decisions about the type and amount of food to cache, where to cache it, and when to cache it. These decisions may be directed by the animals' anatomy, physiology, and motivational state, as well as by ecological factors about the environment they inhabit. In order to make these decisions, animals also have to process complex information, and cognitive abilities may constrain these decision processes. The adaptive specialization hypothesis suggests that different environmental conditions may select for different cognitive abilities among species. By contrast, the general process view assumes that all food-caching species possess general learning and memory abilities that allow them to make these decisions; thus, one should not expect any variation in cognitive abilities to be directly related to caching. Figure 1 outlines some of the decisions a food-storer needs to make, the information required to make those decisions, and the potential cognitive abilities that might be used. In the following sections, we discuss these caching and recovery decisions in turn.

Insert Figure 1 here

The decision about what to cache is determined by a number of factors, such as the type of food available to the bird, anatomical adaptations for eating specific foods or caching in different substrates, and whether the species in question is a specialized or a generalized feeder. However, what is cached also determines what needs to be remembered. For instance, the Clark's nutcracker is a specialized cacher which eats and caches predominantly pine seeds (Vander Wall, 1990). Since seeds do not perish, there is no need to encode the time of caching. It therefore seems likely that the main information a nutcracker needs to remember is the location of the cache, although it does retain information about the cache size (Möller et al., 2001). By contrast, western-scrub jays cache perishable items such as beetle larvae as well as non-perishable seeds (Clayton & Dickinson, 1999b; Clayton et al., 2001). The rate at which a perishable item degrades depends on a number of ecological factors including the temperature and humidity of the environment, the type of substrate in which the food is cached, and the depth and location of a cache within a particular substrate. Caches that consist of invertebrates will degrade rapidly in the heat and more slowly in cold. The problem for the food-storer is not only to learn how quickly a particular food type degrades, but also to update this information in a flexible manner, based on the ecological conditions that occur in the interim between caching the food and recovering it. Elsewhere, we have argued that such flexible deployment of information relies on a declarative memory system (Clayton et al., 2003a).

The type and amount of food items which are cached, rather than eaten, are not randomly selected; the decision to cache rather than eat is based on the size and quality of the item,

its composition, and its perishability, as well as the cacher's motivational state at the time of caching. Scrub-jays have been shown to select the highest quality peanuts based on visual assessment and handling (Langen, 1999). Magpies (*Pica pica*) and jackdaws (*Corvus monedula*) will eat small pieces of bread, but cache large ones (Henty, 1975). Eurasian jays (*Garrulus glandarius*) preferentially cache large acorns, which are undamaged, and without a cavity between the kernel and the shell (Bossema, 1979). Motivational state at the time of caching can have important consequences on the decision of whether or not to cache, and what to cache. In one experiment, western scrub-jays were prefed either powdered peanuts or dog-food kibbles, which could be eaten but not cached, and were then given the opportunity to cache whole peanuts or dog-kibbles. Prefeeding on powdered peanuts selectively reduced caching levels of peanuts, but not dog-food kibbles, and vice versa (Clayton & Dickinson, 1999a). Clayton and Dickinson therefore argued that caching behavior is controlled by two independent systems: one for feeding and one for caching. The control exerted by the different systems appears to be mediated by the incentive value of specific items rather than by a general motivational state.

Many corvids demonstrate marked seasonal patterns in caching intensity. For example, Eurasian jays cache significantly more acorns in the autumn than the spring and summer (Bossema, 1979; Clayton et al., 1996). Clark's nutcrackers and pinyon jays commence caching in late August when pinyon seeds are mature, and begin to recover them in early winter (Vander Wall, 1990). In some species at least, the preference for what to cache also changes seasonally. Thus, independent of food availability, laboratory-housed

Eurasian jays prefer to cache worms in the spring, and nuts in the autumn and winter (Clayton et al., 1996).

One of the key decisions a caching bird has to make is where to cache. Corvids may reduce their memory load by caching next to landmarks or in locations which increase the likelihood of successful recovery. For example, pinyon jays tend to cache on the south side of trees which receive half the snow cover of other locations and which are the first to melt in the spring (Balda & Bateman, 1971). Eurasian jays prefer to cache along the edges of substrates, next to conspicuous landmarks (Bossema, 1979) and Clark's nutcrackers make most of their caches within 5 m of large objects (Vander Wall, 1982). A featureless landscape is not likely to be selected as a suitable caching environment and, indeed, most corvids cache in areas which contain multiple landmarks. The large vertical landmarks may also serve to constrain the view of the cache site from other birds, and thus act as barriers protecting the cache site from potential pilferers.

The number of food items that can be carried away and cached depends on morphological adaptations such as pouches. Species that are capable of carrying large amounts of food items at once tend to cache at larger distances from their feeding grounds than species that are more limited in their transport capacities. Clark's nutcrackers can transport around 100 seeds up to 22 km away, held in their large, sublingual pouch (Vander Wall & Balda, 1977), whereas pinyon jays can only transport about 40 seeds, 8-10 km away (and usually only 1 km) in their oesophagus. As scrub-jays have no specialized food-carrying structures, they are limited in the amount of food items they can carry (about 3

seeds), and most of their caches are made within 1 km of the food source (Vander Wall, 1990). It seems therefore that the decision where to cache is partly determined by morphological constraints rather than cognitive decisions. However, in the Eurasian jay, the amount of food transported correlates with the distance it is carried. A larger number of acorns (3-5) is carried for over 100 m, but 1 acorn is only carried 20 m (Bossema, 1979). So, for Eurasian jays, the decision of how far to cache from the food source varies between caching episodes and it is not only dependent on a morphological limitation.

Social aspects of caching: for my eyes only

Another factor that affects caching decisions is the potential for pilfering by other birds (Vander Wall & Jenkins, 2003; Emery & Clayton, 2001). When a bird is observed during a caching episode, the observer may return later to pilfer the cache. In response, food-storers will develop strategies to prevent their caches from being pilfered, ones which may or may not involve complex cognitive processes (Emery et al., in press). There is substantial variation in social structure among different caching species and consequently in the social cognitive demands related to caching. For instance, solitary species like the Eurasian jay and the Clark's nutcracker are less likely to be observed while caching than birds that live in social groups. Group structure can vary from colonies consisting of many, often unrelated individuals (e.g., the rook, *Corvus frugilegus*) to smaller family units, such as cooperative breeders (e.g., the Florida scrub-jays, *Aphelocoma coerulescens*). Cooperative breeding is a complex, strongly hierarchical social system in which several, usually related birds help raising the offspring of one dominant breeding

pair. Pilfering of caches within such groups is not necessarily detrimental to a particular food-storer because the recovered food may be used to feed the communal young, provided the pilferer is not an intruder. The caching behavior of these birds may thus require the ability to recognize certain individuals, and surely to distinguish intruders from group members.

Food-storers that live in large groups have to balance the benefits of being in a social group with the costs of pilfering by conspecifics (Andersson & Krebs, 1978). Any member of a social group may either be a storer or a stealer and each role may require a number of different cognitive abilities. For example, if pilferers are unable to obtain another's caches aggressively (e.g., if they are subordinate to the cacher), then they may employ cognitive strategies which are independent of aggression. An example may be remembering the location of a storer's caches so that they can be recovered when the storer has departed the scene. Pilferers may also employ 'deceptive' strategies, such as concealing themselves when observing another caching or observing at a distance, to increase the opportunity of recovering more caches and to reduce retaliatory aggression. Similarly, individuals storing food may employ cognitive counter-strategies to outwit potential pilferers, such as caching out of sight (i.e. behind obstacles), caching at a distance, caching when pilferers are distracted, or re-caching in new places at the time of recovery.

There is a considerable amount of support from field observations that caching corvids do indeed employ these cognitive strategies. In common ravens it has been shown that

stomers will delay caching if other ravens are in the vicinity and wait until potential pilferers are distracted or have disappeared (Heinrich & Pepper, 1998; Bugnyar & Kotrschal, 2002). Ravens and Northwestern crows (Heinrich, 1999; James & Verbeek, 1983) make 'false' caches. They cache either non-edible objects or they probe the bill into the ground without burying an item of food. Ravens preferentially store food behind obstacles such that other ravens cannot see where the caches are being made (Bugnyar & Kortschal, 2002). Clarkson and colleagues found that magpies adjusted the density of their caches by spacing them farther apart and placing them farther away from the central food source if the risk of pilfering was high (Clarkson et al., 1986). Individuals of several corvid species return alone to caches they had hidden in the presence of conspecifics and re-cache them in new places (Bugnyar & Kotrschal, 2002; DeGange et al., 1989; Emery & Clayton, 2001; Goodwin, 1956; Heinrich, 1999).

In a pair of recent experiments, Dally, Emery & Clayton (submitted) examined which strategies western scrub-jays use to protect their caches from being pilfered. In the first experiment, the jays were provided with two caching trays: one located close to an observer and the other located as far as possible from the observer. The jays cached preferentially in the tray farthest from the observer, but only when they were observed; they did not discriminate between the trays when they were allowed to cache in private. Interestingly, the jays only re-cached food from the near tray, suggesting that they treated the food items in that tray as the most likely to be pilfered. In a second experiment, jays were provided with two trays at equal distance from the observer: one tray was located in the open and the other was located behind an opaque screen (i.e., hidden from the

observer's view). In test trials, the jays preferentially cached behind the opaque screen. To determine whether the jays feared the open (and so failed to cache there), control trials were run in which powdered (non-cacheable) food was provided. The jays did not spend any longer eating behind the barrier than in the open. Therefore, during caching, scrub-jays appear to process the presence of conspecifics, their distance from the cache sites, and whether the cache sites are in view.

Bugnyar and Kotrschal (2002) have suggested that caching and raiding ravens may present an example of tactical deception through their attempts to manipulate another individual's attention. This deception is either manifest as storer's attempts to prevent opponents from gaining opportunities to steal or to raider's attempts to gain opportunities to learn the location of the storer's caches. The investigators examined two forms in which another's attention may be manipulated: withholding information and directing another's attention away from the caches. During caching, storer's tended to withdraw from conspecifics, and were located at a greater distance from conspecifics during caching than during other activities, such as feeding and resting. Cachers moved their caches if an observer moved toward them and also protected their cache sites. Cache raiders also employed a number of strategies, seemingly to increase the potential for learning about cache sites and for stealing caches. If a storer was close to a cache site, then the observers delayed pilfering until the cacher moved away from the caches. These behaviors suggest that caching and raiding ravens appreciate the visual perspective of one another, and produce strategies and counter-strategies to influence the behavior of the other.

Cognition in cache-recovery

Remembering the 'what-where-and-when' of caching events: episodic-like memory

During the interval between caching and recovery, a bird needs to make several decisions that may or may not require complex cognitive processes. To successfully recover caches, food-storing animals need to form representations of the location of the cache site, the type and perishability of the cached item, and the social context during caching. Figure 2 outlines some of these recovery decisions, along with the information required and the potential cognitive abilities that might be used. Note that these representations may be based on purely spatial memories in animals which cache large numbers of a *single* food type over a wide area, or more complex declarative memories of which foods have been cached where and when in species which cache a *variety* of food items that differ in their levels of perishability.

Insert Figure 2 here

Vander Wall (1990) discussed several hypotheses of how animals may find their food-caches. First, animals may find hidden food through use of olfactory cues produced by the cache. Observations suggest that this is unlikely to be the case in corvids. Strong-smelling food items are not located with greater accuracy than non-smelling objects (James & Verbeek, 1983; Bunch & Tomback, 1986). Second, animals may find their

caches by following visual cues created during the act of caching, such as disturbance to the substrate or protuberance of the food itself. Balda (1980) smoothed over the soil in which Eurasian nutcrackers had previously made a cache, but the birds still searched in the correct sites, suggesting that the birds do not use direct visual cues. Third, the birds may find their caches through random search patterns. However, this cannot explain the exceptionally high success rates (50-99%) in recovering caches in several corvids (Bossema, 1979; Balda, 1980; Vander Wall, 1982; James & Verbeek, 1983, 1984). Finally, animals may remember the precise location of each cache site using spatial memory. There is ample evidence that birds find their caches using predominantly spatial memory (Vander Wall, 1990; Shettleworth, 1995).

What exactly is remembered about a cache location has been examined in several studies and there is now consensus that landmarks form a major contribution to spatial memory. Nevertheless, there seems to be variation among species in the type of cues used (such as local feature cues around the cache site, e.g., color and the shape of leaves) and more global position cues (such as the location of various trees and rocks). In memory tests in the laboratory, Eurasian jays tended to rely on global position cues, whereas non-storing jackdaws made more use of local cues in the same test (and the same difference between storsers and non-storsers was also found for species of tits; Clayton & Krebs, 1994). Clark's nutcrackers appear to use either local or global spatial cues, depending on which are available to them (Gould-Beierle & Kamil, 1998). Large landmarks provide more information to a caching animal than just the general location of a cache site. For example, Vander Wall (1982) allowed Clark's nutcrackers to cache in an arena

containing multiple objects. Between caching and recovery, the arena was extended by 20 cm to the right, and all objects in the right half were also moved by 20 cm. A large landmark in the left of the arena (rock) remained in place. The nutcrackers displayed errors in recovery accuracy for the caches the birds had made in the right-hand side of the arena, whereas the caches made in the left-hand side of the arena were recovered accurately. This pattern of results suggests that the nutcrackers calculate the actual distance between the cache site and a landmark. However, there are multiple landmarks present in most caching environments, and so cachers should possess the ability to calculate the relative distance between cache sites and two or more landmarks. Clark's nutcrackers can learn to find the half-way point between landmarks and transfer this 'rule' to changes in the distance between the landmarks (Jones & Kamil, 1997).

Corvids also appear to remember the specific content of their caches. When approaching cache sites containing large seeds, Clark's nutcrackers use a wide bill gape, but they use a small bill gape for caches containing small seeds (Möller et al., 2001). As noted earlier, when western scrub-jays were preferred powdered peanuts, they ceased recovering peanuts, but not dog-food kibbles, and vice versa (Clayton & Dickinson, 1999a). This pattern of results suggests that the jays had remembered the content as well as the locations of their caches. Further evidence that scrub-jays remember not only the content of their caches, but also the relative perishability of different foods has been provided by a series of experiments on episodic-like memory in western scrub-jays (see Clayton et al., 2001; 2003a; 2003b for a review). One important factor in accurate recovery of caches is the ability to differentiate caching actions from recovery actions. Western scrub-jays appear

to search selectively in those cache sites that still contain food, rather than in cache sites from which food items were recovered earlier (Clayton & Dickinson, 1999b).

Scrub-jays form integrated memories of ‘what’ item was cached ‘where’ and ‘when.’

When caching perishable food, it would appear to be prudent to have learned something about the decay properties of the cached food; and, if two or more perishable foods are cached, then to learn their relative decay rates, so as to increase recovery efficiency.

Clayton and Dickinson (1999c) trained one group of scrub-jays (Degrade group) that wax worms were still fresh after a 4-hr retention interval between caching and recovery, but that the worms had degraded after a 124-hr retention interval. A second group of jays (Replenish group) always received fresh wax worms at recovery no matter what the retention interval had been. Less preferred peanuts were also available for caching and they never degraded. The Degrade group birds rapidly learned to avoid searching for wax worms at the 124-hr retention interval when they had perished. When tested in probe trials (in which the food and any odor cues had been removed) after caching both worms and peanuts in different parts of a trial-unique caching tray, the birds in the Degrade group searched in wax worm sites at the 4-hr retention interval, but they switched to searching in peanut sites at the 124-hr retention interval, suggesting that they had learned ‘when’ and ‘where’ wax worm and peanut caches had been made (Clayton & Dickinson, 1998, 1999b).

In natural situations, scrub-jays may need to remember about several caches that contain food items with varying perishability rates. Using a similar paradigm, but this time with

three different retention intervals and three different food types, Clayton et al. (2001) showed that scrub-jays can indeed learn about the relative perishability rates of two degradable foods. These studies provide convincing evidence that during cache recovery, western scrub-jays have remembered not only the location of their caches, but also the different food types located within individual cache sites, and the relative time since they were cached. This representation of the time since caching is essential for the efficient recovery of perishable food items and Clayton and colleagues have argued that western scrub jays use a flexible, declarative memory system (Clayton et al., 2001, 2003b).

Social aspects of cache recovery

Western scrub-jays have been shown to use cognitive social strategies during cache recovery. Emery and Clayton (2001) allowed hand-raised scrub-jays to cache either in private or while a conspecific was watching. Individuals that had prior experience (outside of the experiment) pilfering another bird's caches subsequently re-cached food in new cache sites, but only when they had been observed during caching. By contrast, those birds without pilfering experience did not move their caches to new sites, even though they had observed the caching behavior of others. The inference is that these birds engage in experience projection (i.e. the jays relate information about their previous experience as a pilferer to the possibility of future stealing by another individual and modify their recovery strategy accordingly). By focusing on the counter strategies of the storer when previously observed by a potential stealer, this experiment raises the intriguing possibility that this re-caching behavior is based on mental attribution.

A second experiment focused on the counter strategies of the storer when previously observed by a potential stealer. Scrub-jays that had previously observed some of their caches being stolen by a nonspecific subsequently switched recovery strategies from checking that their caches were still available to eating them. The birds also continued to re-cache, but they were more selective in their choice of re-cache location, moving caches to places inside their home cage which could not be accessed by other birds (Emery et al, in press).

Cache raiding may be interpreted as another form of recovery (of another's caches). For pilferers, the ability to locate caches made by others quickly and efficiently may be an important difference between successful pilfering and potential aggression from the storer. Therefore, pilferers may require a sophisticated observational spatial memory for learning about the precise location of another individual's caches. Note that, although parids have an excellent spatial memory for their own caches and they readily pilfer conspecific's food caches, the mechanisms they use do not appear to be based on observational spatial memory (Baker et al., 1988; Brodin, 1994; Bunch & Tomback, 1986; Hitchcock & Sherry, 1995). By contrast, corvids have been demonstrated to use observational spatial memory to locate and subsequently pilfer other's caches. Bednekoff and Balda (1996 a, b) tested the ability of pinyon jays, Clark's nutcrackers, and Mexican jays (*Aphelocoma ultramarina*) to remember where another bird had cached food, by examining their cache pilfering efficiency. The birds were allowed to observe another bird caching and were then given the opportunity to recover those caches either 1 day or

2 days later. All three species were accurate at recovering both self-made and observed caches after a 1-day interval. The asocial Clark's nutcracker was not able to recover caches made by another individual after a 2-day interval, but the other two species did (Bednekoff & Balda, 1996b). By contrast, ravens can only locate another's caches accurately when the duration between observing and pilfering is short (Bugnyar & Kortschall 2002). Because the cached food is often perishable in ravens, they may not require an elaborate observational spatial memory over an interval of similar duration as seed-caching corvids.

The flexibility required in this complex network of decisions that a caching corvid needs to make suggests that all of this information is processed using a declarative memory system (e.g. one that can be updated if new information comes available). Evidently, the cognitive processes involved in caching behavior are affected by a plethora of factors that may vary within individuals in different seasons, between individuals in different populations, and between species. These factors include temperature, food availability, food type, social structure, and habitat type. This variation in cognitive requirements is not likely to show a simple linear relationship with the amount of caching a species performs or with the amount of time elapsing between caching and recovery. Nonetheless such variation in caching and recovery behavior allows for comparative tests of different cognitive abilities in relation to prevailing ecological demands.

But, it is crucial that the study species are carefully selected in order to allow the correct comparisons to be drawn. For instance, within the old world corvids, the jackdaw has a

relatively small hippocampus and it is also one of the few species that caches little or no food (Healy & Krebs, 1992). The jackdaw is often presented as the typical example of a non-storing species and is used as a baseline to test for a relationship between spatial memory and relative hippocampus size in other species of corvid. However, if all of its close relatives cache, then it may be more parsimonious to assume that the common ancestor of the corvids also cached, in which case caching behavior in jackdaws has been secondarily lost. So, within these corvids, *loss of caching* in jackdaws might be seen as the adaptive specialization. What needs to be explained then is not why most species cache, but rather why the non-storing species lost this trait (de Kort & ten Cate, in press; Wiens, 2001) and whether it had consequences for related cognitive abilities such as spatial memory and episodic-like memory. Indeed, the evolutionary history of a group of related species is a factor that has often been neglected in comparative cognition, yet it may have far-reaching consequences, as we shall explain below.

Why evolution matters

The adaptive specialization hypothesis assumes that brain and behavior, just like any other aspect of an organism, are shaped through natural selection. In much the same way as different demands of foraging have selected for different beak shapes in the Darwin's finches, different cognitive demands have selected for different brains and behavior. The capacity and longevity of cache location memories have led a number of authors to hypothesize that the increased visuo-spatial demands of remembering the locations of so many scatter-hoarded food caches are associated with an enlargement of the

hippocampus (e.g., Krebs 1990). According to the adaptive specialization hypothesis, food-caching animals should not only have larger hippocampal volumes (relative to overall brain and body size) than their non-caching counterparts, but they should also outperform non-caching species on tests of spatial memory. By contrast, there should be no difference on non-spatial memory tasks. Indeed, a number of studies have suggested that species that are dependent on stored food are more accurate at retrieving caches than non-storing species (Kamil et al., 1994; Olson et al., 1995), and that the hippocampus is larger in birds that cache large amounts than in those that cache little or none at all (Basil et al., 1996; Healy & Krebs, 1996). These results were interpreted as supporting the adaptive specialization hypothesis (Healy & Braithwaite, 2000; Shettleworth, 2003).

Recently, the adaptive specialization hypothesis has been criticized on the grounds that there is no conclusive evidence that there are adaptive specializations in the brain that are related to ecological demands (Bolhuis & Macphail, 2001; Macphail & Bolhuis, 2001; Papini, 2002). These critics maintain the general process view: namely, that the mechanisms of learning and memory are fundamentally the same across species. Their critique resulted in a lively debate (Dwyer & Clayton, 2002; Bolhuis & Macphail, 2002; Hampton et al., 2002; Shettleworth, 2003).

A crucial point raised by Papini (2002), but which has largely been ignored in the field of comparative cognition, is the concept of homology/homoplasy. Homology refers to a similarity in certain traits between species based on common ancestry, while homoplasy refers to similarities that evolved independently as a result of common selection

pressures. Homology and homoplasy are relative concepts and therefore their categorization depends on the taxonomic level of the comparison and the definition of the trait under study. Consider the wings of birds, bats, and bees as an example. As forelimbs, wings are homologous between birds and bats because they derived from those of their common reptilian ancestor. As wings (i.e., forelimbs to fly with), they are homoplasous because these structures evolved independently in birds and bats, even though they have the same function. Wings of bees are homoplasous in any level of comparison to both those of birds and bats.

The distinction between homology and homoplasy is important because it allows for an assessment of whether a comparison between species is meaningful with respect to a given hypothesis. Food caching probably developed independently in the parids and corvids (Papini, 2002). Therefore, enhanced spatial memory in these two groups is a case of homoplasy and not of homology. Thus, although the current behavior pattern (caching) appears similar, the underlying ways to solve the problem may differ. Consequently one does not necessarily expect to find a similar relationship between caching propensity and size of the hippocampus when these two groups are compared (Brodin & Lundborg, 2003).

Spatial memory is a trait present in all vertebrates and the vast majority of invertebrates, having most likely arisen as early as when organisms began to engage in active locomotion. Spatial memory is thus not confined to food caching animals and it is certainly a homologous trait across all families of birds that cache food. At this level,

there is no reason to compare species for differences in spatial memory, just as one would not compare them for the presence or absence of having feathers. The adaptive specialization hypothesis tests for specific enhanced spatial memory capacities in food-storing species in relation to their natural history (caching), whereas the general process hypothesis looks for similarities among species. The adaptive specialization hypothesis thus focuses on homoplasies, whereas the general process hypothesis focuses on homologies. At this point, it is important to emphasize once more that homoplasy/homology are relative concepts. For instance, when the adaptive specialization hypothesis is tested using the relationship among caching, enhanced spatial memory, and enlarged hippocampus, it is implicitly assumed that caching is a homoplasious trait. However, one must consider what traits were likely to be possessed by the common ancestor of the species being compared. As stated at the end of the previous section, within the Corvidae, it is likely that the common ancestor already possessed spatial memory as an adaptive specialization. Consequently, all species within that group are derived from a species that already had the adaptive specialization and it is therefore a homologous trait.

Below, we outline five historical scenarios about the ancestor of corvids, based on a hypothetical phylogeny of the five species illustrated in Figure 3. We contrast two different starting points: one in which the ancestor was a cacher and one in which the ancestor was a non-cacher. Note that, in the absence of a detailed phylogenetic analysis, it is not clear which of these scenarios is the most plausible. For each scenario, we make predictions about whether or not the presence or absence of caching behavior is

correlated with two aspects of cache recovery: namely, accuracy of spatial memory and hippocampal size. Although it need not be the case, for simplicity, we assume that hippocampal size and performance on spatial memory tasks (referred to here simply as ‘spatial memory’) go hand in hand; they are thus treated as one trait.

Insert Figure 3 here

(1). The common ancestor was a cacher; therefore, caching is a homology in corvids. Thus, the non-caching species lost the ability or motivation to cache.

Scenario A: Retain.

Non-caching species did not lose the associated traits for caching such as a preference to use large landmarks when remembering food locations and other features that allow for enhanced performance on spatial memory tasks (including hippocampal volume changes), because there was no counter selection against such traits. According to this scenario, no relationship between hippocampus size and performance on spatial memory tasks is expected.

Scenario B: Co-opt.

Rather than necessarily retaining the trait for spatial memory, a second scenario is that the trait was co-opted for other cognitive tasks in some of the descendants (e.g. western scrub-jays may have co-opted spatial memory to also encode timing of caching, i.e. episodic-like memory). This scenario also makes no prediction about the relationship between caching and spatial memory and hippocampus size.

Scenario C: Too costly.

According to this scenario, the adaptations underlying spatial memory and hippocampal size are too costly to maintain in those species that do not cache. Selection pressure will therefore result in non-cachers having reduced hippocampal volumes and less accurate performance on spatial memory tests. This scenario might be named the adaptive despecialization of non-cachers.

(2). The common ancestor was not a cacher; therefore, caching is a homoplasy in corvids. According to this hypothesis, not all species of corvids develop the ability to cache.

Scenario D: Spin off.

The enhanced performance on spatial memory tests and the enlarged hippocampal size is a consequence of a general increase in cognitive capacities, as opposed to one that is specifically related to caching behavior. Thus, no clear relationship between size of hippocampus, spatial memory, and caching is predicted. Note that the prediction is the same as in Scenario A, but the evolutionary trajectory differs.

Scenario E: Adaptive specialization.

According to this scenario, only those species that developed caching behavior evolved an enhanced spatial memory and increased hippocampal size. This scenario has the same prediction as Scenario C, but the evolutionary trajectory differs fundamentally in

suggesting that the difference between cachers and non-cachers results from an adaptive specialization of cachers as opposed to an adaptive despecialization of non-cachers.

According to Scenario E, the extant caching species would have independently developed the caching behavior and the associated enhanced spatial memory and hippocampal enlargement, as shown in Figure 3. Thus, pinyon jays and clark's nutcrackers might show differences in some aspects of the hippocampal enlargement and enhanced spatial memory. One might argue that the better performance of the clark's nutcracker at accurate cache recovery over long retention intervals (e.g. Balda & Kamil, 1992), but the better spatial performance of the pinyon jay (and scrub-jay for that matter) on the radial arm maze (Gould-Beierle 2000), constitute support for this claim.

The take-home message from this analysis is that an assumption based purely on the caching behavior of current-day corvids may lead one to predict that a non-caching species has an inferior spatial memory and reduced hippocampal volume when compared with a caching species; but this assumption may be incorrect. Distinguishing among the five scenarios is not possible without using phylogenetic techniques to establish the evolutionary history of the corvids, and thus whether or not the ancestor was a cacher. Below, we will discuss two other examples that may gain relevance if these evolutionary processes are considered.

Comparison of corvid species for spatial capacities

The consensus from a series of comparative studies of memory in food-caching corvids is that species with the highest dependence on cached food generally perform the best on tests for spatial memory (e.g. Balda & Kamil, 1989; Kamil et al., 1994). However, there were some notable exceptions that have been notoriously difficult to interpret (Bolhuis & Macphail, 2001). In one study, four corvid species were compared for their spatial memory in an analogue of the radial maze (Gould-Beierle, 2000). In light of the adaptive specialization hypothesis, the results were surprising; a less dependent species (the western scrub-jay) performed better at the task than a species highly dependent on caching (the Clark's nutcracker), whose performance was about equal with that of the non-storing jackdaw. And, the western scrub-jay performed equally to the pinyon jay, which, like the nutcracker, is also highly dependent on caching. As pointed out by the author, the four species are not equally related. The new world jays (the pinyon jay and the western scrub-jay) are more closely related to each other than they are to the other two species (Hope, 1989; Cibois & Pasquet, 1999). Although the western scrub-jay does not cache large quantities of food, the common ancestor that it shares with the pinyon jay may have done so. The scrub-jay may still have the capacity to perform well in this particular memory test, because its ancestor evolved the capacity to do so in relation to efficient recovery of large numbers of cached seeds, and the capacity was maintained even though the selection for intensive caching may have been reduced. In other words, the scrub-jay shares this trait (as shown by the capacity to perform well on the radial-arm memory task) with the pinyon jay through homology. The ancestor of the jackdaw and

the nutcracker may never have evolved this specific trait, and consequently these species do not perform as well as the two jay species. Although the caching behavior of the nutcracker is similar to that of the pinyon jay, efficient cache recovery may be homoplasous in these two species, which means that they both need enhanced spatial memory for accurate cache recovery, but the specific way in which they solve the problem may differ.

Comparison between the parids and corvids

A well established technique used in comparative research addressing adaptive specializations is to test for a correlation between traits. The technique relies on the assumption that there is a positive relationship between the species best adapted to a certain selection pressure and a measure of the trait selected for (Pagel, 1997). Several studies show that there is a positive relationship between relative hippocampal volume and dependency on caching in both parids and corvids (Healy & Krebs, 1996; Basil et al., 1996; Healy & Krebs, 1992). However, Brodin and Lundborg (2003) presented a meta-analysis of these studies, combining the previously published data on parids and corvids, which they complemented with additional data from both parids and corvids. Based on this larger sample, the authors concluded that there is no relationship between food storing and hippocampal size. However, as we argued above, the common ancestor of the corvids, and possibly also the parids, was a food-storer. Therefore, the adaptive specialization tested for in this analysis has developed only twice; thus, the sample size in this analysis should be two, not the total number of species for which hippocampal size is

known. And, needless to say, with a sample size of two, one cannot conduct any meaningful statistical analyses.

Furthermore, as Felsenstein (1985) has argued, species are *not* independent data points in such a between-species comparison. All species are interrelated to some extent and one has to correct for this lack of independence in the data. Several statistical techniques have been developed to deal with this problem of non-independent data points (Harvey & Pagel, 1991). It is beyond the scope of this chapter to review them all, but suffice it to say that there is now general agreement that phylogenetic correction is required. There is an extensive literature that deals with the subject, and an important next step will be to integrate such methods into the study of comparative cognition. An obvious reason for the paucity of these types of analyses in the study of corvids and parids is that the tools required are missing. Unfortunately, there are no comprehensive modern phylogenies available for the food storing birds as yet. However, the fact that such information is missing is not a justification for ignoring the necessity to use it.

The discussion between the adaptive specialization hypothesis and the general process hypothesis is currently difficult to resolve. It is not possible to provide a convincing case that certain cognitive abilities are due to adaptation to specific ecological needs without looking at the evolutionary history of the species involved. The only way to resolve these problems is to reconstruct the evolutionary pathways of each species and to analyze the transitions that took place along the phylogeny of the species concerned. Evolutionary history cannot be reconstructed without reference to the phylogeny of the species in

question. To resolve this question, a modern comprehensive phylogeny for both corvids and parids will be required. An alternative solution, and one that circumvents the lack of a phylogeny, is to test several pairs of sister species (species that share a common ancestor) in which one of the pair does possess the trait and the other member of the pair does not. A problem with this approach is that it is difficult, if not impossible, to find a sufficient number of such sister-species pairs to allow meaningful statistical analyses.

Concluding remarks

The food-caching paradigm has been a productive combination of two traditionally separated fields of research: namely, behavioral ecology and comparative psychology. Current work has moved beyond just spatial memory to encompass other aspects of cognition. For instance, mental time travel has been considered a uniquely human trait (Suddendorf & Corballis, 1997), but several aspects of retrospective cognition have been investigated in food-caching corvids (Clayton & Dickinson 1998, Clayton et al., 2001, 2003 a, b), although the debate is still continuing (Roberts, 2002; Suddendorf & Busby, 2003; Clayton et al., 2003c). Similarly, the work on the social context of caching has opened new directions for testing various aspects of social cognition in non-primate animals (Emery & Clayton, 2001; Emery et al., in press). Tests of the strategies used by food-storers to protect their caches from theft by others allow for tests of various aspects of complex social cognition, including experience-projection, tactical deception, and other aspects of theory of mind.

The time is now ripe to place more emphasis on an evolutionary perspective to comparative cognition. So far, evolutionary thinking has been considered in the field of comparative cognition only from a theoretical perspective (Hauser & McDermott, 2003; Wasserman, 1993; Papini, 2002). Comparative psychology was warned in the 1950s that it should not be founded on laboratory studies of the white rat alone (Beach, 1950). By analogy, Ryan pointed out that comparative biology cannot be done without taking evolutionary history into consideration (Ryan, 1996). For the same reason, we suggest that the study of comparative cognition should not be conducted without due consideration to evolutionary history.

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Figure legends:

Figure 1: Some of the decisions a corvid has to make while caching (grey), the information it needs to process these decisions (white) and the potential cognitive abilities that might be used (black). Artwork by N. J. Emery.

Figure 2: Some of the decisions a corvid has to make while recovering caches (grey), the information it needs to make these decisions (white) and the potential cognitive abilities it might use (black). Note that the recovering individual does not need to be the same as the caching individual. Thus some of these recovery decisions could also be made by a pilferer, even an individual from a non-storing species (e.g. a jackdaw). Artwork by N. J. Emery.

Figure 3: A hypothetical phylogeny of five species of corvids (two Old World and three New World species), namely the food-caching Clark's nutcracker (CN), the non-caching jackdaw (JDW), the food-caching western scrub-jay (SJ) and pinyon jay (PJ) and the non-caching magpie jay (MJ). Note that the evolutionary trajectories are not based on any known data, but serve simply to illustrate five possible historical scenarios. Two of these scenarios are based on the assumption that the ancestor of these species was a non-cacher, while the other three scenarios are based on the assumption that the ancestor was a cacher. The five scenarios make different predictions about the relationship between (a) food-caching and (b) performance on spatial memory tasks and hippocampal size. Blank spaces indicate that there is no clear relationship between caching and memory and the

hippocampus, whereas '+' indicates that a particular species has gained the trait (i.e. enhanced spatial memory performance and increased hippocampal size) and '-' indicates that a particular species has lost the trait. 'O' refers to the case where a species may have co-opted the trait for a different function. For example, it is hypothesized that the western scrub-jay may have co-opted its spatial memory capabilities for use in episodic-like recall. See text for further details.