



THE BEHAVIORAL AND EVOLUTIONAL CHANGES OF CACHE PROTECTION AND PILFERAGE

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ABSTRACT

Food-storing animals hide food in times of abundance and rely on memory to recover those caches several days if not months later when supplies are scarce. Food-storing animals use a range of cache protection behaviours, which may reduce the level of cache theft they experience from competitors. It is possible that many of these behaviours simply constitute a response to the presence or absence of a competitor. This review focuses on the different models that have been proposed to explain the evolution of food caching, specifically those models that describe how food caching might have evolved in an environment of cache pilferage. We discuss the use of cache protection behaviour in caches, and the success of these behaviours in bringing about a reduction in cache theft, before looking at the behaviours of prospective thieves that facilitate cache pilferage. Finally, we consider the insights these behaviours give us into the cognitive abilities of food-storing animals.

KEYWORDS: *Behaviours, Cache, Food, Pilferage, Storers.*

1. INTRODUCTION

In group-living animals, those individuals that cache food may gain a disproportionate share of the resources, compared to non-storers, because it is quicker to cache food items than it is to consume them. Food pilferers are known to be both hetero-specifics and conspecifics. In the wild, however, caches might often be stolen by individuals that are both hetero-specifics and non-storers. We might therefore expect storers to engage in behaviours that serve to reduce cache loss. Indeed, caching behavior is inherently geared to reduce pilferage, as items are concealed in a manner that makes them imperceptible to potential thieves once they have been cached.

1.1. Cache Protection Behaviours

Upon encountering a food resource, storers can either eat or cache the available items and thus maintain both internal (fat) and external (food caches) energetic reserves. Whether an item is cached or consumed may depend on factors such as its perishability and handling time. Importantly, several studies have predicted that when experiencing high levels of cache pilferage, storers will reduce caching and eat instead. Thus, to maximize their energetic gain, individuals cache significantly more food in the absence of observers, and spend significantly

longer feeding in their presence. The risk of cache theft therefore appears to play a crucial role in the trade-off between the generation of external and internal energetic reserves. While consuming potential caches prevents competitors from gaining access to them, the ability to generate internal energetic reserves is confounded by the amount of fat that an animal can store, without impeding metabolic rates and flight costs. As such, 'consumption' behavior should be used in conjunction with, and not as a replacement for, generating external reserves.

1.2. Aggressive Defense

Once an item has been cached, one of the simplest methods to prevent cache theft would be to prohibit potential thieves from gaining access to cache sites. This could be achieved in one of two ways. First, storsers could prevent competitors entering the area in which they have cached, or second, they could defend a single cache site. The latter tactic is most commonly seen in larder hoarders, the use of a single store making cache defense somewhat easier. That is not to say that this tactic is absent in scatter-hoarding species, individuals having been observed to drive potential thieves away from cache sites. Furthermore, several caching species clump caches together, perhaps to aid cache defense.

Preventing competitors from entering a territory is a tactic commonly seen in parid flocks, as groups of tits and chickadees prevent potential thieves entering the winter territory in which cached food is widespread. Aggression in these flocks, however, is not directed only at transient individuals, as within some flock dominant males often use aggression to exclude subordinates from preferred foraging and caching areas. Therefore, although aggression provides a useful tactic to prevent cache theft, it is successful only if the potential thief is subordinate in status relative to the storer. If not, the storer would stand little chance of protecting its caches, and would therefore have to rely on an alternative strategy.

The risk that a dominant competitor represents to food caches should be particularly pertinent to larder-hoarders. While the use of a single store might make cache site defense somewhat easier, subordinates risk losing the sum total of their caches during a single encounter with a dominant thief. The trade-off between cache defense and cache pilferage might function to facilitate the dispersal of at least some part of the larder hoard into more dispersed sites. Squirrels scatter-hoard items throughout their territory in addition to caching items in a central madden. This mix of caching patterns might represent a response to the trade-off between the need to maximize cache defense and the need to minimize cache pilferage. Whereas larder hoarding is common to mammals, many avian species generally scatter-hoard.

Woodpeckers are a notable exception, however, as individuals cache large numbers of items in granaries. This strategy might reflect the inability of woodpeckers to defend larder-hoards against pilferage from nocturnal rodents. Scatter hoarding appears to reduce the proportion of caches that are lost, as a number of studies have found that widely spaced caches are more likely to survive than caches placed close to one another. Two models have been proposed to predict how individuals should distribute their caches when cache loss is density dependent. Although they generate two sets of predictions, both assert that caches should be uniformly distributed around a central food source.

Although storsers remember the spatial locations of their own caches, the locations of the caches of competitors are unknown. By caching items in a single direction from a food source, cache sites would share a common set of landmarks, and thus require a lower memory load than that needed to remember the locations of cache sites dispersed over a wide area.

There is also evidence, albeit limited, to suggest that storsers adjust the density at which they cache as a function of their social status. For example, territorial (breeding) common magpies make their caches closer together, and nearer to the food source, than non-breeders. This difference in cache spacing is thought to occur because magpie caches are most often stolen

by conspecifics. Thus, birds with exclusive territory use would experience less cache pilferage, a factor that would be reflected in their 'optimal' cache density. While the ecology of territorial and nonbreeding magpies might differ significantly, and therefore have implications for their use of cache sites, this finding highlights the need for further research on the sensitivity of food-storers to the risk of cache theft.

1.3. Social Dominance

The ability for dominant birds to pilfer others' caches successfully, is one that, in parids, has also been theorized to result in a preference for dominant animals to reduce investment in their own caches [1]. However, the results of studies that have investigated the caching rates of dominant and subordinate birds have been equivocal. However, when the dominants were removed, subordinate tits increased their caching rate significantly, suggesting that, in the presence of dominants, caching by subordinate willow tits might have been socially suppressed. A similar result has been found for western scrub-jays.

1.4. The Effect of Cache Pilferage

Several studies have investigated the effect of cache pilferage on a storer's caching strategy. if storers experience complete cache pilferage the number of items they cached was unaffected. Although, these birds experience cache pilferage from some sites but not others, chickadees prefer to cache in the non-pilfered sites. Taken together, these findings suggest that storers use cache protection behaviours only when at least some of their caches can be recovered later. In all these experiments, however, storers were reacting to cache loss, and their behavior might have been different had they observed a thief stealing their caches. conspecifics pilfering their caches switched from scatter hoarding to larder hoarding, thus making their caches easier to defend. The storers, however, had to experience cache theft before changing their caching strategy, as the presence of an observer during caching was not sufficient to stimulate the change. after caching in the presence of an observer and observing half of their caches being pilfered, western scrub-jays re-cached items in new sites around their home cage that they could defend from potential thieves. In addition, after a single pilfering trial, the jays switched their recovery strategy from predominantly recovering and replacing caches to predominantly eating them. This would be an advantageous strategy because uneaten caches remain susceptible to theft, whereas by eating high-risk items the birds are able to generate internal energetic reserves when the risk of theft is high.

1.5. The Behavior of Pilferers

Prospective thieves use several mechanisms to facilitate cache pilferage. For example, several species use random search to locate others' caches. However, as many animals use spatial memory to find their own caches, cache pilferage through exploratory digging should not impact significantly upon a single individual's food store. This is true of both mammals and birds. Although spatial memory is sufficient to offset cache loss through random search, it may not always confer a recovery advantage on the storer. For example, competitors often find the caches of others by smell. This pilfering mechanism, however, is generally successful only in wet conditions, as the strength of olfactory signals emanating from buried seeds is strongest when the seeds, or the surrounding substrate, are wet.

Consequently, the impact of cache loss through the use of olfaction might vary as weather conditions change. The use of olfaction to locate the caches of others is a pilferage behaviour that is not open to exploitation by granivorous birds, because their sense of smell is not sufficiently developed to detect buried seeds. The use of memory would give a potential thief the ability to find others' caches but there is only one anecdotal report to suggest that mammals are able to use observational spatial memory to pilfer caches, and no evidence that parids are capable of the same.

The birds recovered ‘observed’ and ‘unobserved’ caches equally well, suggesting that the experience of watching another individual did not provide the prospective thief with any recovery benefit. While there have been few studies investigating the use of observational spatial memory in parids and mammals, none of which have yielded positive results, corvids have been shown to be extremely proficient in recovering caches that they have watched others make. However, in monitoring the behaviour of others, individuals do not compromise their own foraging rates. Subsequent studies showed that western scrub-jays and ravens also have highly accurate observational spatial memory. Although common to corvids, the degree to which observational spatial memory has developed appears to vary across species. The variation between corvid species in their ability to exploit visual information gained by watching another bird cache might be a consequence of their social structure. In social species, the opportunity to observe another bird caching may be relatively frequent, whereas asocial species such as the Clark’s nutcracker would have few such opportunities. Increased social complexity might therefore have resulted in the selection for observational spatial memory.

2. LITERATURE REVIEW

Clayton showed that re-caching behavior is caused by, and not coincidental to, the presence of an observer during caching[2]. Western scrub-jays received the opportunity to cache either when observed by a conspecific, or in private, and recovered their caches in private. There were two main findings from this study. First, individuals that had been observed during caching re-cached food into new sites upon cache recovery. As recovery conditions were identical, the birds had to remember whether they had been watched during caching in order to know whether they needed to re-cache food items, and if so whether to cache specifically into new sites. Second, only birds that had previously been thieves hid their caches in new places; native birds did not do so.

Lahti & Rytkonen observed that, like mountain chickadees, *Poecile gambeli*, subordinate willow tits cache more than their dominant counterparts[3]. In contrast, they did not identify any differences in the caching rates of dominant or subordinate Carolina. Furthermore, a study by Lahti et al. on willow tits suggested that an individual’s caching rate might depend on the immediate social environment[4]. They found that dominant willow tits cached more than subordinates when in a group.

Kamil et al. suggested that the spacing of caches prolongs the time necessary for potential thieves to steal food items, and that this may be sufficient to make an area less attractive to thieving competitors[5]. The ‘optimal spacing’ strategy relies on the storer possessing and updating a memory for the spatial locations of cache sites. Unlike elevating or reducing caching rates, it cannot be ascribed to an automatic response to the presence of a competitor. In black-capped chickadees, however, items tend not to be cached ‘optimally’, but instead are clustered in sites in a preferred orientation from a food source. It therefore appears that cache spacing behavior, at least in some parids, might represent a compromise between the risk of pilferage and the need to remember the spatial locations of cache sites.

Andersson & Krebs proposed that food caching would become evolutionarily stable only if the storer had a significantly higher probability of recovering its own caches than a conspecific[6]. If not, pilferers would share the benefit of a cached resource without paying the energetic costs associated with caching, and caching would be unlikely to spread through a population. Nevertheless, somewhat paradoxically, cachers can lose up to 30% of their caches per day to pilferers.

Vander Wall & Jenkins proposed an alternative model based on the caching behavior of solitary rodents[7]. They suggested that because many pilferers are storers themselves, pilfered items, or the thief’s own caches, are made available to the original storer through reciprocal cache theft, and that this environment of reciprocal pilferage is conducive to the

evolution of long-term scatter hoarding. Lucas & Zielinski found that Carolina chickadees cached significantly more items when a quarter of their caches were consistently pilfered, compared to when their caches were left intact[8]. This behavior appears similar to the cases of enhanced caching described earlier, in which storers increase caching rates in the presence of observers. In both cases, elevated caching represents a response to either predicted or experienced levels of cache loss.

Emery & Clayton proposed that the capacity for complex social cognition evolved convergently in corvids and apes[9]. Indeed, the use of ‘out-of-view’ and ‘difficult-to-see’ protection behaviours in some corvids raises the possibility that, like great apes, these animals understand what others can and cannot see. A simpler explanation, however, is that storers base their caching strategies on their own visual perspective as opposed to that of the thief. For example, when caching in sites that observers cannot see, storers may simply perceive conspecifics as absent.

A study by Bugnyar & Kotrschal, however, does not suffer from these constraints, and is presently the only study to look at the tactics that observers use when witnessing a caching event[10]. If pilferers have evolved a suite of behaviours that facilitate cache theft, we might expect prospective thieves to act in a manner that serves to increase the success of cache pilferage. For example, like pickpockets, an observer might attempt to distract a storer, and thus create an opportunity to pilfer caches undetected. Furthermore, we might expect pilferers not only to maintain a distance from storers, but also to observe caching events from discreet locations, a behavior that might mean they are unnoticed by caching birds.

3. DISCUSSION

Throughout this review, we have focused on caching behavior. The ability of corvids to use observational spatial memory to steal others’ caches, however, means that, in the ‘evolutionary arms race’ between storers and stealers, we might expect observers to increase their potential for stealing caches. In the scrub-jay experiments we described previously, the observer was housed in an adjacent cage, limiting its ability to steal caches immediately, or to move into a position that might be better suited to the observation of caching. It is possible that many of these behaviours simply constitute a response to the presence or absence of a competitor.

The implementation of cache protection behaviours is not limited to the initial period of caching. Several corvid species return alone to caches hidden in the presence of conspecifics, and re-cache them in new places unbeknownst to potential thieves. Emery & This finding suggests that scrub-jays are capable of a high level of social understanding called experience projection, as individuals appeared to relate information about their previous experience as a pilferer to the possibility of future theft by another bird, and re-cached observed items accordingly.

However, in corvids, there is evidence that these behaviours are used flexibly, depending on the specific social context of a caching event. A continuous theme throughout this review has been evidence that suggests that the degree to which storers use protective behaviours depends on the risk of future cache theft. The fact that western scrub-jays implement re-caching behaviours when alone at recovery, and that these behaviours are directed specifically towards those items cached in high-risk sites, shows that behavioral cueing is not sufficient to explain cache protection in this species.

Although a cache protection tactic in its own right, re-caching in western scrub-jays also occurs in conjunction with other protection behaviours. Its use is specific, however, being principally directed at items that have been cached in non-preferred sites (e.g. in view of an observer or near the food resource). Because cache recovery always took place in private, the birds’ re-caching behavior could not have been the result of behavioral cues shown by the

observer. Instead, re-caching strategies must have been based on a memory of the caching event, in addition to the presence or absence of an observer at caching.

4. CONCLUSION

Food-storing animals use a range of cache protection behaviours, which may reduce the level of cache theft they experience from competitors. There is also evidence that the very implementation of cache protection strategies, at least in corvids, is under a high level of socio-cognitive control, as storers relate their own experience of stealing others' caches to the presence of observers at recovery, and therefore the risk of future theft. Unfortunately, as a result of a lack of comparable studies on paped and mammal species there is a clear bias towards the study of cache protection in corvids in this review. It is essential that this bias is addressed before we can fully determine whether the suite of protective behaviours that have been identified in corvids are unique to these species, or whether they represent a more general ability of food caching animals.

Furthermore, within the field of corvid research, current studies of cache protection have focused almost exclusively on the western scrub-jay and the raven. It is therefore necessary to conduct comparative studies on other corvid species, before making wide-ranging assertions about the use of cache protection behaviours, and their basis in cognition, for corvids as a whole. Furthermore, although an observer is always present when storers cache in sites that might be difficult to see, it is still feasible to explain selective site use in terms of the storer's visual perspective. If these sites are harder for the observer to see, it is automatically harder for the storer to see the observer. The problem of how to differentiate between whether the storer is aware of the observer's or its own visual perspective is important. In this situation it is perhaps useful to look for convergent evidence for such a cognitive capacity.

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