ANIMAL BEHAVIOUR, 2006, ■■, ■■–■■
doi:10.1016/j.anbehav.2005.08.020

REVIEW

The behaviour and evolution of cache protection and pilferage

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(Received 10 January 2005; initial acceptance 22 February 2005;
final acceptance 25 August 2005; published online ■ ■ ■; MS. number: RV-57R)

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. 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 behaviours in cachers, 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.

In group-living animals, those individuals that cache food may gain a disproportionate share of the resources, compared to nonstorers, because it is quicker to cache food items than it is to consume them (Clarkson et al. 1986; Jacobs 1992). Andersson & Krebs (1978) 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. If not, pilferers (competitors who steal others' caches) 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 (reviewed in Vander Wall & Jenkins 2003). Food pilferers are known to be both heterospecifics (grey jays, *Perisoreus canadensis*, and Steller's jays, *Cyanocitta stelleri*: Burnell & Tomback 1985) and conspecifics (grey squirrels, *Sciurus carolinensis*: Richards 1958; pinyon jays, *Gymnorhinus cyanocephalus*: Bednekoff & Balda 1996a; Mexican jays, *Aphelocoma ultramarina*: Bednekoff & Balda 1996b; Clark's nutcrackers, *Nucifraga columbiana*: Bednekoff & Balda 1996b; western scrub-jays, *Aphelocoma californica*: Clayton et al. 2001; common ravens, *Corvus corax*: Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002; pocket mice, *Chaetodipus* spp.: Leaver & Daly 1998).

Recently, two models have been proposed to explain the evolution of caching despite high levels of cache pilferage. In a model specific to the Paridae (tits and chickadees), Smulders (1998) posited that, provided individuals form small groups within a population, even if a storer's caches are pilfered by close associates, the caching genotype would spread because, in times of food scarcity, storers would be better off than the average nonstorer in the population as a whole. Vander Wall & Jenkins (2003) proposed an alternative model based on the caching behaviour of solitary rodents. 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.

Central to the models of both Smulders (1998) and Vander Wall & Jenkins (2003) is a degree of specificity as to the identity of the pilferer. While Smulders (1998) asserted that it must be an immediate associate of the storer, and therefore a conspecific, Vander Wall & Jenkins (2003) necessitated the thief to be a food-storer. In the wild, however, caches might often be stolen by individuals that are both heterospecifics and nonstorers (e.g. great tits, *Parus major*, stealing the caches of marsh tits, *Poecile palustris*, Gibb 1954; Eurasian jackdaws, *Corvus monedula* stealing rook, *Corvus frugilegus*: caches, personal observation). We might therefore expect storers

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0003–3472/06/$30.00/0

to engage in behaviours that serve to reduce cache loss. Indeed, caching behaviour 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.

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 (eastern woodrats, *Neotoma floridana*: Reichman 1988; grey squirrel: Hadj-Chikh et al. 1996) and handling time (white-breasted nuthatches, *Sitta carolinensis*: Woodrey 1990; grey squirrels: Jacobs 1992; American crows, *Corvus brachyrhynchos*: Cristol 2001). Importantly, several studies have predicted that when experiencing high levels of cache pilferage, storers will reduce caching and eat instead (Sherry 1985; McNamara et al. 1990; Lucas & Walter 1991).

In the Eurasian nuthatch, *Sitta europaea*, storers often experience substantially more cache pilferage after competitors have observed a caching event (Carrascal & Moreno 1993). 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 (Blem & Pagels 1984), without impeding metabolic rates and flight costs (Lima 1986; Lucas & Walter 1991; Witter & Cuthill 1993; Pravosudov & Grubb 1998; Pravosudov & Lucas 2001). As such, 'consumption' behaviour should be used in conjunction with, and not as a replacement for, generating external reserves.

Social Context

Social context (presence or absence of competitors) appears to be pivotal to the expression of cache protection behaviours. Several species have been observed to cease, reduce or delay the onset of caching behaviour in the presence of potential thieves (Table 1). While these behaviours might reduce pilferage, if observers are constantly present, individuals that abstain from caching in their presence, or that wait for them to become inattentive, will forfeit the ability to exploit ephemeral food resources. Thus, caching rates should be reduced only when the available resource is of little value to the storer, or when there are likely to be other opportunities to cache when observers have left the scene. If not, the level of cache loss that would be experienced from pilferage might not outweigh the benefit accrued from even limited recovery of high-value items.

The presence of observers is not always linked to the cessation or reduction of caching and sometimes increases caching levels (Eurasian jay, *Garrulus glandarius*: Bossema 1979; white-footed mouse, *Peromyscus leucopus*: Sanchez & Reichman 1987; western scrub-jays: Emery et al. 2004). Increasing the amount of caching, however, is a behaviour that is potentially disadvantageous. For example, if the resource is finite, it will not be possible to increase the cached reserve beyond a maximal level. Furthermore, this tactic provides a net benefit only if the energetic cost

Table 1. A summary of the cache protection behaviours used by food-storers

Strategy	Definition	Examples
Consumption	Eat items in the presence of competitors, and cache in their absence	Eurasian nuthatch: Carrascal & Moreno 1993
Enhanced caching	Cache more (to offset predicted cache loss) in the presence of observers	Eurasian jay: Bossema 1979; white-footed mouse: Sanchez & Reichman 1987
Reduction	Cache fewer items in the presence of observers than in their absence	Eurasian jay: Goodwin 1956; northwestern crow: James & Verbeek 1984; willow tit: Alatalo & Carlson 1987; Lahti & Rytkonen 1996; black-capped chickadee: Stone & Baker 1989
Cessation	Do not cache in the presence of potential thieves	Rook: Simmons 1968; grey jay: Burnell & Tomback 1985
Delay	Delay the onset of caching in the presence of potential thieves	Raven: Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002
Aggressive defence	Prevent potential thieves having access to cached items	Eastern chipmunk: Clarke & Kramer 1994
Spacing	Cache items at an 'optimal' density	Common magpie: Clarkson et al. 1986; kangaroo rat: Daly et al. 1992; Jenkins et al. 1995; marsh tit: Sherry et al. 1982; grey jay: Waite & Reeve 1995
Out of view sites	Cache 'out of view' of competitors	Raven: Bugnyar & Kotrschal 2002; western scrub-jay: Dally et al. 2005a
Difficult-to-see sites	Cache in 'hard-to-see' sites (e.g. 'shady', distant)	Western scrub-jay: Dally et al. 2004, 2005a; common magpie: Clarkson et al. 1986
Multiple moves	While caching in the presence of potential thieves, move caches around repeatedly	Western scrub-jay: Dally et al. 2005a, b; Eurasian jay: Cramp & Perrins 1994
Recaching	During recovery, in the absence of observers, move (specifically high-risk) items into new sites	Western scrub-jay: Emery & Clayton 2001; raven: Heinrich 1999; Eurasian jay: Goodwin 1955

of caching, or resultant level of pilfering, is minimal. If not, any energetic gain during recovery may still be less than the energetic costs of caching.

Some species show a propensity both to increase and to decrease caching rates in the presence of potential thieves. Both Eurasian jays and western scrub-jays cached more in the presence of observers in some studies (Eurasian jays: Bossema 1979; western scrub-jays: Emery et al. 2004), but not in others (Eurasian jays: Goodwin 1956; western scrub-jays: Emery & Clayton 2001; Dally et al. 2005b). This suggests that the use of this protection behaviour is not species specific, but is situation dependent. For example, the propensity to increase or decrease caching might depend on the specific social situation, or the perceived value of the potential cache. While the precise conditions under which different protection behaviours are used warrant further investigation, the behaviour of these birds suggests that the use of cache protection behaviours might represent a flexible response to the risk of cache theft, as opposed to an automatic response to the presence of a competitor.

Aggressive Defence

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, storers 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 (e.g. eastern chipmunks, *Tamias striatus*: Clarke & Kramer 1994), the use of a single store making cache defence 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 (Eurasian jays: Wilmore 1977; Bossema 1979; Goodwin 1986; western scrub-jays: Dally et al. 2005b; rooks: Goodwin 1986). Furthermore, several caching species clump caches together, perhaps to aid cache defence (coal tits, *Periparus ater*: Brotons 2000; grey squirrels: Spritzer & Brazeau 2003; common magpies, *Pica pica*: Clarkson et al. 1986).

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 a flock dominant males often use aggression to exclude subordinates from preferred foraging and caching areas (black-capped chickadees, *Poecile atricapillus*: Baker et al. 1990; willow tits, *Poecile montanus*: Ekman 1979; Brodin 1994). 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 (e.g. eastern chipmunks: Clarke & Kramer 1994). While the use of a single store might make cache site defence somewhat easier, subordinates risk losing the sum total of their caches during a single encounter with a dominant thief. The trade-off between cache defence 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 midden (Dempsie & Keppie 1983; Gurnell 1984; Hurly & Robertson 1989). This mix of caching patterns might represent a response to the trade-off between the need to maximize cache defence and the need to minimize cache pilferage (Hurly & Lourie 1997; Gerhardt 2005).

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 (reviewed in Vander Wall 1990). This strategy might reflect the inability of woodpeckers to defend larder-hoards against pilferage from nocturnal rodents (Vander Wall 1990). 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 (Merriam's kangaroo rats, *Dipodomys merriami*: Daly et al. 1992; northwestern crows, *Corvus caurinus*: James & Verbeek 1983; Eurasian jays: Bossema 1979; grey jays: Waite 1988).

Two models have been proposed to predict how individuals should distribute their caches when cache loss is density dependent (Stapanian & Smith 1978; Clarkson et al. 1986). Although they generate two sets of predictions, both assert that caches should be uniformly distributed around a central food source. This propensity has been identified in a range of species (common magpies: Clarkson et al. 1986; kangaroo rats: Daly et al. 1992; Jenkins & Peters 1991; marsh tits: Sherry et al. 1982; fox squirrels, *Sciurus niger*: Stapanian & Smith 1984), but more impressively, individuals often redistribute caches (grey jays: Waite & Reeve 1995; Merriam's kangaroo rats: Jenkins et al. 1995) or adjust distribution patterns to maintain a uniform distribution (grey jays: Waite & Reeve 1992). Kraus (1983), however, argued that this 'optimal cache density' may not be achievable in the wild. Although storers remember the spatial locations of their own caches, the locations of the caches of competitors are unknown. Kraus (1983) therefore 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.

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 (Barnea & Nottebohm 1995). It therefore appears that cache spacing behaviour, 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. 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 storers 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 nonbreeders (Clarkson 1984). 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 (Birkhead 1991). 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.

Social Dominance

In the previous section, we suggested that storers might use information about their relative social status when implementing protective behaviours. 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 (Brodin et al. 2001). However, the results of studies that have investigated the caching rates of dominant and subordinate birds have been equivocal. For instance, Lahti & Rytkonen (1996) observed that, like mountain chickadees, *Poecile gambeli* (Pravosudov et al. 2003), subordinate willow tits cache more than their dominant counterparts. In contrast, Pravosudov & Lucas (2000) did not identify any differences in the caching rates of dominant or subordinate Carolina chickadees, *Poecile carolinensis*. Furthermore, a study by Lahti et al. (1998) on willow tits suggested that an individual's caching rate might depend on the immediate social environment. They found that dominant willow tits cached more than subordinates when in a group. 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 (Dally et al. 2005b).

Pilferer Identity

In some situations, observers might not represent a threat to cache safety, and any use of cache protection behaviours would therefore constitute unnecessary energetic expenditure. For example, storers might differentiate between the risks that conspecifics and heterospecifics represent to their caches. Steller's jays steal grey jays' caches, whereas Clark's nutcrackers do not. Thus, while grey jays cache as usual in front of a conspecific or a Clark's nutcracker, they cease caching in the presence of a Steller's jay (Burnell & Tomback 1985).

Field observations suggest that some corvids may differentiate between attentive and inattentive observers. For example, although in the presence of conspecifics ravens prefer to cache in 'out-of-view' sites (Bugnyar & Kotrschal 2002), when nearby conspecifics are preoccupied, storers do not implement cache protection strategies (Heinrich & Pepper 1998). Furthermore, Kalländer (1978) noted that caching rooks were not secretive if nearby rooks were also caching. However, if another rook landed near to a caching individual without a nut in its beak, the cacher would pick up its nut and cease caching until the newcomer left. This suggests that some corvids may base the use of cache protection strategies on the apparent attentional state of the observer as well as its identity.

Observer identity does appear to influence a storer's use of cache protection behaviours, as storing corvids appear to tolerate cache theft from some individuals and defend their caches against others. Goodwin (1956) observed that while female Eurasian jays tolerated their partners stealing their caches, they directed aggression at other individuals that approached their cache sites. This finding was confirmed in a study by Dally (2004), which also found that, in western scrub-jays, partners defended each other's caches against pilfering conspecifics, suggesting that scrub-jays perceive individual birds as representing different levels of risk. If mates are not perceived as a threat to cache safety, storers should abstain from investing energy in the implementation of cache protection strategies in their presence. Heinrich & Pepper (1998, page 1087) observed in ravens that 'when a mated pair was working alone at a carcass, they sometimes walked with food and cached it nearby so that cache direction and often cache location could be observed'. This observation suggests that, at least in some corvids, the specific risk that an observer poses, not just the presence or absence of an observer, governs whether cache protection strategies are used.

THE EFFECT OF CACHE PILFERAGE

Several studies have investigated the effect of cache pilferage on a storer's caching strategy. For example, Lucas & Zielinski (1998) 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. This behaviour 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. In a study on black-capped chickadees, however, Baker & Anderson (1995) found that if storers experience complete cache pilferage the number of items they cached was unaffected. Although this finding initially seems somewhat at odds with Lucas & Zielinski's (1998) study, should these birds experience cache pilferage from some sites but not others, chickadees prefer to cache in the nonpilfered sites (Hampton & Sherry 1994). Taken together, these findings suggest that storers use cache protection behaviours only when at least some of their caches can be recovered later. More recently, Clayton et al. (2005) showed that western scrub-jays prefer to cache worms than peanuts. If over a series of trials, however, storers find that their worm caches are consistently pilfered, they stop caching worms and instead cache nonpreferred peanuts. In all these experiments, however, storers were reacting to cache loss, and their behaviour might have been different had they observed a thief stealing their caches.

Preston & Jacobs (2001) found that Merriam's kangaroo rats that observed 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. Similarly, Emery et al. (2004) found that after caching in the presence of an observer and observing half of their caches being pilfered, western scrub-jays recached 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.

THE BEHAVIOUR OF PILFERERS

Prospective thieves use several mechanisms to facilitate cache pilferage. For example, several species use random search to locate others' caches (Clark's nutcrackers: Kamil & Balda 1985; grey squirrels: McQuade et al. 1986; yellow pine chipmunks, *Tamias amoenus*: Vander Wall 1991). 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 (Merriam's kangaroo rats: Jacobs 1992; grey squirrels: Jacobs & Liman 1991; MacDonald 1997; ground squirrels, *Spermophilus tridecemlineatus*: Devenport et al. 2000) and birds (Siberian jays, *Perisoreus infaustus*: Ekman et al. 1996; Clark's nutcrackers: Tomback 1980; Kamil & Balda 1985; willow tits: Suhonen & Inki 1992).

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 (common magpies: Buitron & Nuechterlein 1985; ravens: Harriman & Berger 1986; yellow pine chipmunks: Vander Wall 2000; deer mice, *Peromyscus maniculatus*: Howard & Cole 1967; Howard et al. 1968; Vander Wall 2000; Merriam's kangaroo rats: Reichman & Oberstein 1977). 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 (Vander Wall 1993, 1995, 1998). Consequently, the impact of cache loss through the use of olfaction might vary as weather conditions change (Vander Wall 2000).

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 (Clark's nutcrackers: Vander Wall 1982; Kamil & Balda 1985). 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 (kangaroo rats: Daly et al. 1992), and no evidence that parids are capable of the same (black-capped chickadees: Hitchcock & Sherry 1995; willow tits: Brodin 1994). In a study by Baker et al. (1988), black-capped chickadees received the opportunity to observe a conspecific make three food caches. Either 6 min or 2 h later, the observer received the opportunity to steal these 'observed' caches, along with three 'unobserved' caches that had been made by the experimenter prior to the recovery period. 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 (Baker et al. 1988; Preston & Jacobs 2001), 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 (Smith et al. 2002). Bednekoff & Balda (1996a, b) tested the ability of pinyon jays, Clark's nutcrackers and Mexican jays to recover items they had observed other birds cache. Subjects were allowed to cache items themselves, and during a separate event observe a conspecific caching. Either 1 or 2 days later, the birds were given the opportunity to recover their own caches in addition to those they had seen a conspecific make. All three species were highly accurate at recovering both sets of cached items 1 day after caching. Unlike the other two species, however, Clark's nutcrackers were significantly less accurate at recovering their conspecifics' caches after a 2-day interval (Bednekoff & Balda 1996b). Subsequent studies showed that western scrub-jays (Clayton et al. 2001) and ravens (Heinrich & Pepper 1998) 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. Indeed, an experiment by Bugnyar & Kotrschal (2002) found that ravens were able to use observational memory only when short time periods had elapsed between the caching and pilfering events.

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 (Bednekoff & Balda 1996b). In social species (e.g. pinyon jays, Mexican jays, rooks), 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 (Balda et al. 1996).

THE 'EVOLUTIONARY ARMS RACE'

Bugnyar & Kotraschal (2002) suggested that the capacity for observational spatial memory in corvids represents the catalyst for an 'evolutionary arms race' between cachers and the pilferers, a 'race' in which the participants would be expected to develop opportunities for social learning, such as being unobtrusive as observers, and to engage in strategies to counter the risk of cache pilferage. The concept of an arms race, however, is equally applicable to those species that suffer a high degree of cache loss to pilferers using olfaction. The propensity for chipmunks (Briggs & Vander Wall 2004) and blue jays, *Cyanocitta cristata*: (Johnson et al. 1997) to cache preferentially in ash substrates might represent a response to just such a threat. Vander Wall (2003) suggested that the odour of ash might mask the odour of the cached food items. If this were the case, potential thieves would be unable to use olfactory cues to locate others' caches. The findings of Briggs & Vander Wall (2004) appear to support this hypothesis, showing that while pilfering chipmunks are able to use olfactory cues to locate caches made in sandy substrates, they are unable to do the same when items are cached in ash.

Before discussing the behaviours that corvids use to combat the risk of cache theft from observational spatial memory, we discuss why cache pilferage poses a particular problem in these species. Previously, we described two models that purported to show that caching could evolve in a population despite high levels of pilferage. However, the criteria on which these models are based are not applicable to food-caching corvids. For example, Smulders' (1998) model requires that, within a population, each individual has a separate foraging niche, but this foraging strategy is specific to parids (e.g. willow tits: Brodin 1994; crested tits, *Lophophanes cristatus*: Lens et al. 1994). Furthermore, the model developed by Vander Wall & Jenkins (2003) is based on solitary rodents, yet many corvid species are colonial (e.g. rooks: Wilmore 1977) or semiterritorial (e.g. western scrub-jays: Curry et al. 2002). For these reasons, corvids might be expected to be particularly sensitive to the risk of cache theft, and to use protective behaviours to lessen cache loss. Although the ensuing discussion of protective behaviours is biased towards corvids, this is not necessarily because there is no evidence that parids and mammals do not use these behaviours, but rather because there are no comparable data on these groups.

Storers

Out-of-view sites

One of the most effective ways to increase cache safety is to cache in sites that an observer cannot see, and therefore prevent competitors from using observational spatial memory to facilitate cache theft. Unlike caching cessation or reduction, caching in sites that prevent the transfer of visual information would allow storers to continue to exploit an ephemeral food resource. Bugnyar & Kotrschal (2002) found that ravens cached selectively behind large obstacles in the presence of conspecifics, positioning the obstacle between themselves and the would-be thief. Similarly, when presented with caching locations that were either behind barriers or 'in-view' (and equidistant from the observer), scrub-jays consistently cached in out-of-view sites (Dally et al. 2005a). The scrub-jay results did not appear to arise from a preference for solitude, or a fear of conspecifics, because the jays divided their time equally between in-view and out-of-view locations, eating in both, when given powdered (noncacheable) food. In addition, unlike the raven study, the results could not be explained by a preference for these birds to cache near a landmark.

Difficult-to-see sites

Several species cache predominantly in distant sites in the presence of observers (willow tits: Lahti et al. 1998; coal tits: Brotons 2000; common magpies: Clarkson et al. 1986; grey squirrels: Spritzer & Brazeau 2003). These sites are potentially more difficult for observers to see, thereby reducing the accuracy with which they might pilfer the storer's caches. Storers, however, might always cache in sites furthest from competitors, regardless of whether the potential pilferers are observing the caching event, because the further away the cache site the longer it will take the potential pilferer to reach it. Thus, the use of the distance tactic might be based on what the observer can see, or on a fixed rule. In an experiment where an observer's view was or was not blocked by a metal screen, scrub-jays maximized the distance between the observer and the cache site only when the observer was visible (Dally et al. 2005a). This finding suggests that, at least in scrub-jays, storers behave in a way that reduces the visual information available to other birds. Together with evidence from studies on ravens (Bugnyar & Kotrscha1 2002) this result suggests that the caching behaviour of corvids is flexible, and that corvids may be constantly calculating the position of moving observers in order to select optimal cache sites.

At first glance, the increased energetic costs of transport appear to make the use of a distance strategy costly. Heinrich & Pepper (1998), however, argued that if a food supply is infinite, the energy expended does not significantly detract from the store available. If, in comparison, food supplies are limited, storers appear to offset the energetic costs of transport by caching specifically high-value items in distant sites (grey jays: Waite 1992; Eurasian jays: Chettleburgh 1952; willow tits: Jokinen & Suhonen 1995; crested tits: Jokinen & Suhonen 1995; Merriam's kangarro rats: Leaver & Daly 1998).

The preference for caching in sites that may be harder for an observer to see is not limited to a propensity to cache in distant locations. When given a choice of 'shady' and 'well-lit' sites, western scrub-jays cache predominantly in shady sites when observed by a conspecific, but show no preference when the view of their competitor is obscured (Dally et al. 2004). While shade represents one method of reducing the clarity of the visual information available to potential thieves, it is possible to imagine a variety of others such as fog or dense vegetation. Indeed, observations suggest that rooks cache predominantly in long grass in the presence of potential thieves (N.J. Emery & N.S. Clayton, personal observation). Furthermore, if competitors are near by but out of sight, it might also pay storers to reduce the occurrence or amount of any acoustic information that may alert potential thieves to the caching event.

In each of the scrub-jay experiments we have described thus far, storers cached a few items in the less preferred sites ('near', 'in-view' and 'well-lit' sites). It is possible that there may be an advantage in not hiding all the caches in one place, because caching some items in the presence of an observer may focus its attention away from other caches and thus increase the protection of the majority. One way in which it might be possible to test this assumption would be to allow storers to have simultaneous access to both preferred and less preferred food items and to high- and low-risk caching sites. If caching items in high-risk sites functions to distract the observer, then storers should cache preferred food items in low-risk sites and the less preferred food items in high-risk sites. In this way, storers may increase the likelihood that the more valued items are available for later recovery, as pilfering should be focused on the sites containing the nonpreferred food. However, this tactic would be expected to occur only if there was a limited capacity of low-risk sites.

Multiple moves

In some situations it may not be possible to prevent or reduce the visual information available to observers. For example, if cache sites are equidistant to nonstationary observers it would not be possible to use a distance strategy, nor would storers be able to cache in out-of-view sites reliably. In this situation, storers appear to respond by moving items around multiple times (Eurasian jays: Cramp & Perrins 1994; western scrub-jays: Dally et al. 2005a). For example, in an experiment where observers could move in and out of the view of a storer, western scrub-jays repeatedly moved items that the observer had seen cached, movement that occurred specifically in view of the observer. The jays must therefore have remembered whether the observer had been present during each caching event, in order to move those specific caches around (Dally et al. 2005a).

Moving caches multiple times may function to make their final position less clear to an observer than if they were left in their original cache site, as the memory for each new cache site would suffer interference from the memory of old cache sites. A potential cost of moving items repeatedly is that the accuracy with which storers recover their own caches may also be reduced. In this experiment, however, storers recovered caches that had and had not been moved with equal precision (Dally et al. 2005a).

Misinformation

One method for reducing cache theft would be to misinform competitors as to cache location. Consequently, use of observational spatial memory would not result in accurate cache theft. One method of misinformation would be to provide observers with incorrect information. There are several reports that corvids often make 'false' caches that contain either an inedible item such as a small stone or nothing at all (rooks: A.S. Seed, N.J. Emery & N.S. Clayton, personal observation; ravens: Heinrich & Pepper 1998; Heinrich 1999). Because corvids such as rooks and ravens transport food in their antelingual pouch, competitors cannot easily determine the type, or even the presence, of an item to be cached. Indeed, competitors are able only to observe the caching event, independent of whether it is a real or false act.

Recaching at recovery

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 recache them in new places unbeknownst to potential thieves (ravens: Heinrich 1999; Eurasian jays: Goodwin 1955). Emery & Clayton (2001) showed that recaching behaviour is caused by, and not coincidental to, the presence of an observer during caching. 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 recached 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 recache 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; naïve birds did not do so. This finding suggests that scrub-jays are capable of a high level of social understanding called experience projection (Emery & Clayton 2004), as individuals appeared to relate information about their previous experience as a pilferer to the possibility of future theft by another bird, and recached observed items accordingly.

Although a cache protection tactic in its own right, recaching 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 nonpreferred sites (e.g. in view of an observer or near the food resource). Because cache recovery always took place in private, the birds' recaching behaviour could not have been the result of behavioural cues shown by the observer (Dally et al. 2004, 2005). Instead, recaching strategies must have been based on a memory of the caching event, in addition to the presence or absence of an observer at caching.

Pilferers

Throughout this review, we have focused on caching behaviour. 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 (Emery & Clayton 2001; Dally et al. 2004, 2005a), 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. A study by Bugnyar & Kotrschal (2002), 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. Bugnyar & Kotrschal (2002) found that in the presence of storing conspecifics, ravens often changed their position relative to structures that would have otherwise blocked their view of a caching event. In addition, observers oriented themselves towards the location where caching occurred, yet remained at a distance from the storer, perhaps to avoid interrupting caching. Thieves were then able to use observational spatial memory to steal the storers' caches, although they waited until storers had left the cache site before attempting cache theft.

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 (i.e. partly occluded locations such as heavily leaved trees), a behaviour that might mean they are unnoticed by caching birds.

CONCLUSIONS

Food-storing animals use a range of cache protection behaviours (Table 1), 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. 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 recaching behaviours when alone at recovery, and that these behaviours are directed specifically towards those items cached in high-risk sites, shows that behavioural cueing is not sufficient to explain cache protection in this species. There is also evidence that the very implementation of cache protection strategies, at least in corvids, is under a high level of sociocognitive 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 (experience projection, Emery & Clayton 2001).

Unfortunately, as a result of a lack of comparable studies on parid 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 (e.g. recaching, out-of-view sites, multiple moves) 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 (e.g. Emery & Clayton 2001; Dally et al. 2004) and the raven (Bugnyar & Kotrschal 2002, 2004). 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.

Emery & Clayton (2004) proposed that the capacity for complex social cognition evolved convergently in corvids and apes. Indeed, the use of 'out-of-view' and 'difficult-to-see' protection behaviours in some corvids raises the possibility that, like great apes (Byrne & Whiten 1988; Hare et al. 2000; but see Karin-D'Arcy & Povinelli 2002), 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 ('out of sight, out of mind'). 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.

Acknowledgments

We thank Selvino de Kort, Scott Stevens and two anonymous referees for comments on the manuscript. N.S.C. was supported by grants from the National Institutes of Health, BBSRC, Clare College and the University of Cambridge. N.J.E. was funded by a Royal Society University fellowship. J.M.D. received financial support from Clare College, the University of Cambridge, the Sir Richard Stapely Educational Trust and the Sefton Educational Trust.

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