

Review

Problems faced by food-caching corvids and the evolution of cognitive solutions

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The scatter hoarding of food, or caching, is a widespread and well-studied behaviour. Recent experiments with caching corvids have provided evidence for episodic-like memory, future planning and possibly mental attribution, all cognitive abilities that were thought to be unique to humans. In addition to the complexity of making flexible, informed decisions about caching and recovering, this behaviour is underpinned by a motivationally controlled compulsion to cache. In this review, we shall first discuss the compulsive side of caching both during ontogeny and in the caching behaviour of adult corvids. We then consider some of the problems that these birds face and review the evidence for the cognitive abilities they use to solve them. Thus, the emergence of episodic-like memory is viewed as a solution for coping with food perishability, while the various cache-protection and pilfering strategies may be sophisticated tools to deprive competitors of information, either by reducing the quality of information they can gather, or invalidating the information they already have. Finally, we shall examine whether such future-oriented behaviour involves future planning and ask why this and other cognitive abilities might have evolved in corvids.

Keywords: food-caching birds; social intelligence; episodic memory

1. INTRODUCTION

(a) *Caching: from compulsion to complexity*

Caching, or hiding, food items for later consumption is widespread among birds and mammals (Vander Wall 1990), and in the corvid family in particular (de Kort & Clayton 2006). The complexity of caching behaviour serves as a successful paradigm to investigate features of cognition, which we shall discuss below. However, it seems to be underpinned by a motivationally controlled compulsion to cache, as revealed by the ontogeny of caching and also by evidence from adult caching behaviour (see later). Young ravens, *Corvus corax*, have a predisposition to move objects around with their beaks, press them visibly towards large objects and then also to insert them into crevices and ultimately to cover them (Bugnyar *et al.* 2007a). Similarly, young western scrub-jays, *Aphelocoma californica*, start manipulating objects in a structured sequence: picking up objects from the ground, moving them around, placing them elsewhere, pecking an object into the ground and later hiding and immediately retrieving objects (Salwiczek *et al.* 2009). Until young ravens and scrub-jays finally develop their full caching behaviour, placing items out of sight for later consumption, food and time are probably wasted and such tentative caching behaviours do not fulfil any obvious function except for the caching experience they may provide. This, together with

their structured, sequential development, suggests that the propensity to cache may be pre-programmed (Pollok *et al.* 2000; Bugnyar *et al.* 2007a; Salwiczek *et al.* 2009).

This does not mean, however, that caching behaviour develops devoid of cognition. Indeed, similarly to what has been found in titmice (Clayton 1992, 1994; Haftorn 1992), further improvements of caching efficiency in corvids, including cache-protection strategies, require experience (Emery & Clayton 2001; Bugnyar *et al.* 2007a). Young storsers need to learn what makes a good cache site, how to cache different food items (e.g. killing or paralyzing prey before caching) and how to deal with the risk of pilfering. After they have mastered their techniques, adult corvids incorporate many factors into their caching decision-making, as detailed in the next sections. This scenario, where an initially compulsive behaviour gradually becomes more flexible and influenced by experience and cognition, is quite straightforward, but the compulsive basis of caching is not restricted to young birds.

In adult western scrub-jays, caching has been shown to be motivationally controlled, such that pre-feeding decreases the subsequent number of cached items and pre-feeding on a specific food type decreases its subsequent caching (Clayton & Dickinson 1999a). In addition to the effect of the feeding system, Clayton & Dickinson (1999a) showed that caching also depends on a 'caching system': after eating and caching a specific type of food, caching of that food type is reduced compared with the caching amount after only eating the food in a non-cacheable powdered form. The influence

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of a 'caching system' is further supported by the fact that having the opportunity to cache stones (while also eating the food in powdered form) reduced the subsequent caching amount of that food to the same low level as after caching and eating it. Indeed, when food items are unavailable, western scrub-jays store inedible items such as stones (Clayton & Dickinson 1999a), as do Eurasian jays, *Garrulus glandarius* (Clayton *et al.* 1994), and ravens (Heinrich & Smolker 1998; see also Bugnyar *et al.* 2007b).

If, as seems likely, there is no benefit for caching such items, this suggests that the basic propensity to cache does not depend on the outcome of caching. Supporting such a claim, scrub-jays continue to cache at consistent rates even when caching is never rewarded and do not reduce their caching as long as they have only one choice of what or where to cache (de Kort *et al.* 2007). However, when given more than one food type or caching location, these jays quickly learn to stop caching those types of foods or in those locations that were not rewarded (Clayton *et al.* 2005; de Kort *et al.* 2007; see also Hampton & Sherry 1994). Indeed, while caching starts as, and continues to be based on, a compulsive tendency, many factors in the bird's physical and social environment influence this behaviour, making it rich, plastic and complex.

If a food item is to be cached for later consumption, then the storer would benefit from remembering where it is. In addition, it might be beneficial to remember such things as how deep the item was stored, to be able to quickly decide whether the food has been pilfered when it is not immediately found at recovery. For some food types, the type of substrate they are stored in may influence the rate of decay, and so may determine how soon these caches need to be recovered before the food perishes. In order to make informed decisions of when to recover a cached item, a storer may require a memory of when caching has occurred. For storers that cache different types of food, the content of caching is very likely to be important in this respect, especially so if they cache a variety of perishable items that decay at different rates. In §2, we shall see that some storers remember what they have cached, where and when and use this information, together with information about decay times of different types of food, to retrieve those items that are still edible. Another factor in the storer's physical world is the weather both during and since caching. A wet ground, for example, could increase the decay rate of certain types of food and the probability that smell-oriented cache pilferers will steal it (e.g. Vander Wall 1995), making it beneficial to retrieve them earlier in such conditions. Weather is unpredictable, and coping with its effects would require continuous flexibility and integration of new information. Similar and even greater unpredictability is what storers need to cope with on another front, that of their social worlds.

When food items are regularly being cached, there is little surprise that other individuals might try to scrounge as many of those items as they can. Cache-pilferage is indeed a great problem for storers and may require attention to others' presence when making caching decisions. Therefore, it may be

important for the storer to acquire some information of other individuals in its vicinity to assess, and act to minimize, pilfering risk. Such information may include who is watching and whether it is a potential competitor for the food (either conspecific or heterospecific), as opposed to the storer's mate with whom they may share the caches or a heterospecific which feeds on other types of food altogether. It could also be advantageous for the storer to use information about the level of threat posed by specific individuals, such as whether the observer is dominant or subordinate, a talented pilferer or a less adept individual or a young one (who would perhaps not pilfer). In some cases, the observer may have food preferences which make it more or less likely to return to pilfer the type of food that is being cached.

Food-storing corvids face many challenges in hiding and retrieving their caches and in protecting their caches from competitors and pilfering others' caches themselves. These challenges may have been the driving force behind the evolution of highly advanced cognitive abilities in corvids: episodic-like memory, planning for the future and perhaps even the ability to attribute mental states to other individuals, or theory of mind. In this paper, we shall review the different problems that storers and pilferers need to cope with and discuss their cognitive consequences. We shall also discuss why corvids may have evolved especially advanced abilities.

2. COPING WITH THE PERISHABILITY OF CACHED FOOD

For caching to be adaptive, cached items have to be successfully retrieved. If the retrieval proportion is not high enough to offset the time and effort involved in caching, and the investment of not consuming food right away, it would be more beneficial not to cache at all. At first sight, it might seem that all a storer would need in order to successfully recover such a high proportion is to remember where the caches were hidden (or cache in specific locations where it also looks for food). Indeed, there is much evidence for the use of spatial memory to find caches (reviewed in Shettleworth 1995; Clayton 1998), peaking perhaps in the Clark's nutcracker, *Nucifraga columbiana*, and its ability to remember and return to a very large number of different cache locations (Tomback 1980; Bednekoff & Balda 1997). Some species can also remember which caches they already recovered, so as not to return to empty ones (Shettleworth & Krebs 1986; Clayton & Dickinson 1999b).

While cache location is critical to their recovery, storers may benefit also from remembering when each item was cached, and which food has been cached where. First, the continuous risk of caches being pilfered means that the older the cache the higher the probability that it is already empty. This may affect optimal retrieval times, as well as increase the discounting of cache locations that have been found empty at recovery, if only a short while had passed since caching. In species that cache different types of food that decay at different rates, a second reason to remember when caching had occurred and

integrate this information with a memory of what had been cached may be to ensure that items are recovered before they decay.

Cached (and dead) invertebrates become inedible much faster than nuts by virtue of the fact that they perish, and it would be maladaptive for a bird caching both types of food to wait too long until recovering such invertebrates as opposed to the nuts. Some short-term hoarding corvids such as magpies, *Pica pica*, and western scrub-jays cache such types of food regularly (Birkhead 1991; Curry *et al.* 2002, respectively), and Eurasian jays cache less of a perishable than a non-perishable food and recover it sooner (Clayton *et al.* 1996). Thus, we might expect those species to encode different features of caching to enable a correct and timely recovery.

In a series of laboratory experiments, Clayton, Dickinson and colleagues have shown that jays form an episodic-like memory of caching events, remembering their 'what, where and when'. Jays remember where they had cached each of two types of food, as well as the location and food type they had already recovered. This is evident when they use this information to search for a preferred food type (their food preferences were altered through specific satiety; Clayton & Dickinson 1999b; see also Clayton *et al.* 2001b). In addition, after experiencing the relative short time it takes for wax moth larva ('wax worms') to decay, and that peanuts do not decay, jays searched preferentially for peanuts when allowed to recover after a long time (after worms had already degraded) and for the preferred worms when the time elapsed since caching was short enough for worms to stay fresh (Clayton & Dickinson 1998, 1999c). This suggests that they remember when and where they cached each type of food. Together with their ability to quickly learn the decay rates of at least two different food types (Clayton *et al.* 2001b), their episodic-like memory enables these jays to recall when perishable items were cached and return to those locations before they degrade.

The memory that does this is thought to involve an integrated *what–where–when* structure (Clayton *et al.* 2001b): at recovery, the sight of each tray elicits a memory of *where* caching had occurred, which elicits a memory of *what* was cached in that location, and (probably independently) a memory of *when* caching occurred in that location. In addition to outlining the minimal structure of how these different features are bound in memory, this specific structure seems to make evolutionary sense. It is reasonable to assume that memory for the where of caches is the most primitive of the *what–where–when* trio, since memory for location is the only feature necessary for reliably recovering one type of non-perishable food, and is also extremely widespread (e.g. Shettleworth 1995). When western scrub-jays (or their ancestors) started caching different types of food with different decay rates, remembering the when and what of caching could have evolved separately, but each of those features could only be beneficial to remember if it could be integrated with the existing where, or else it would not improve recovery success.

Using the *what–where–when* of caching seems highly beneficial as a guide for recovering the right

cache at the right time. However, from a psychological point of view, is it comparable with human episodic memory? In order to make this question tractable and productive, it is necessary to avoid Tulving's (2005) more recent requirements such as the subject being consciously aware that the past memories are her own and that she re-experiences the event when remembering. Therefore, Clayton & Dickinson (1998) related to Tulving's (1972) earlier definition, requiring memory of the *what–where–when* of an event to outline the borders of 'episodic-like' memory. These three features must be bound to one another in some way to make each event distinguishable from similar events, as is indeed the case in scrub-jays (Clayton *et al.* 2001b). The jays' ability to incorporate new information about the decay rate of different food types that is received *after* caching (Clayton *et al.* 2003) further confirms that they indeed create a unique *what–where–when* memory for each caching event. There is still some debate as to whether this information is coded using episodic recall of the previous caching events or semantic knowledge about what happened where and when, of which birthdates are the classic example for we have no episodic memory of our birth and yet we know where and when it happened. Consequently, some researchers (e.g. Suddendorf & Busby 2003; Zentall 2006) have argued that the jays could learn the relations between the *what*, *where* and *when* information and the correct recovery decisions using semantic memory.

Scrub-jays show further flexibility in the sort of rules that may be learned. Just as they learn that food can decay, scrub-jays can quickly learn that food is inedible after a short interval but will 'ripen' later on (de Kort *et al.* 2005). Further evidence for such flexibility in the type of decay rule that may be learned comes from a study showing *what–where–when* memory in magpies. Zinkivskay *et al.* (2009) allowed magpies to simultaneously cache two colours of otherwise similar food pellets, and then recover either later during the same day or on the next day. While one colour was available and edible during the same-day recovery, the pellets of the other colour were replaced before recovery with inedible beads of similar colour. The edible and inedible colours were switched in trials when recovery occurred the next day, and the magpies quickly learned to search for caches of the edible colour according to the different recovery times. Magpies and scrub-jays are thus not limited to learning rules that necessarily occur in their natural worlds, and their use of *what–where–when* memory may be quite flexible in incorporating new, and even arbitrary, information. Such plastic behaviour in the face of new information and ever changing conditions is also exhibited to a great extent when caching corvids cope with the challenges of their social world discussed in the next section.

Although we suggest that episodic-like memory in corvids could be a mechanism that has evolved to cope with food perishability, there is now evidence that other animals such as rats and Rhesus monkeys can form *what–where–when* memories (Roberts 2006; Hoffman *et al.* 2009). Such evidence raises the possibility that similar memory mechanisms have

evolved to solve different ecological problems in different species. In this respect, it will be interesting to find out in which animals there is binding of the what, where and when (in pigeons, e.g. the memory of these components is not bound or integrated; Skov-Rickette *et al.* 2006). In particular, the specific way in which these components are bound might suggest the sort of problem it has evolved to solve.

3. COPING WITH COMPETITION: CACHING, PILFERING AND CORVID THEORY OF MIND

Storing food at times of plenty for later consumption at times of need could be very beneficial, but this benefit critically depends on the actual retrieving and consumption of stored food. The importance of correct retrieval has led to using spatial memory to find caches, and some corvids have evolved episodic-like memory enabling recovery of different types of food at appropriate times. However, even if storers can recover at the right place at the right time, they might find that the cached food is no longer present. Pilferage, the loss of cached food items to other individuals, is indeed one of the more serious problems storers have to deal with, and in this section, we will discuss how this social challenge has led storers and pilferers to ever more sophisticated behavioural strategies. It must be noted from the start that we are not trying to make a very general point of how sociality was a driving force for cognition, but rather we attempt to outline the specific social challenges that arise from caching and pilfering, and their relation to corvid social cognition.

Pilferage proportions may be quite high, ranging between 2 and 30 per cent per day, at least for artificial caches (reviewed in Vander Wall & Jenkins 2003). If the pilferage rate is high enough for the average non-storer to do better than the average storer, caching behaviour may be selected against (Andersson & Krebs 1978; Smulders 1998). This notion has led to emphasizing spatial memory and other mechanisms that help the original storer recover more quickly and in a more efficient way, giving them a recovery advantage over potential pilferers (see Shettleworth 1995). However, in addition to spatial memory, corvids have evolved a variety of cache-protection strategies to reduce the pilferage risk (see Dally *et al.* 2006a for an in-depth review in corvids, and Clayton *et al.* 2007 for scrub-jays in particular).

(a) *Cache protection*

Hiding food items in many, dispersed, locations helps scatter hoarders, such as food-caching corvids, reduce the probability that their caches will be found by the other animals foraging in the same area (e.g. Sherry *et al.* 1982; Stapanian & Smith 1984; Clarkson *et al.* 1986; Male & Smulders 2007a,b, 2008). Corvids will also readily defend their caches against pilfering attempts (Bugnyar & Kotrschal 2002a; Dally *et al.* 2005a), making dominants those most able to pilfer in the presence of the storer. This is the expected relation between dominance and scrounging in non-caching contexts (if competitive differences are

strong, see Barta & Giraldeau 1998), where scrounging in the presence of the original 'producer' of the food is the only option. Caching, however, opens the opportunity that scroungers (pilferers) can avoid such aggression by pilfering in the producer's (i.e. the storer's) absence, if they can remember where another individual has cached. Ravens use observational spatial memory in order to return to caches they saw others make and pilfer them only after they leave, avoiding aggression at least in some cases (Bugnyar & Kotrschal 2002a). To cope with such pilfering techniques, it may not be enough for storers to scatter and defend their caches. In addition to these strategies, some corvid species protect their caches by acting in ways that manipulate the information available to pilferers. First, some species preferentially cache when they are in private, rather than in the presence of potential pilferers (e.g. grey jays, *Perisoreus canadensis*, Burnell & Tomback 1985; ravens, Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002a). While western scrub-jays sometimes increase the amount of items cached in the presence of observers (Emery *et al.* 2004), they employ other, more complex strategies to prevent or reduce the information that a potential pilferer (equipped with observational memory) may gain.

For example, scrub-jays preferentially re-cached in new places those food items that they had been observed caching, but not those cached 'in-private' (Emery & Clayton 2001). However, only storers with previous experience as pilferers were able to make this distinction, suggesting that when storing they can project their experience of being a thief to make decisions based on another's expected behaviour, something never before shown in non-humans. After (pilfering-experienced) storers witnessed their caches being pilfered by the individual who observed caching, they re-cached more items from the pilfered tray than from another ('intact') tray and did this preferentially in other locations in the cage or in the other tray (Emery *et al.* 2004). Consequently, scrub-jays re-cached more when caching had been observed (Emery & Clayton 2001; Emery *et al.* 2004), and in locations where pilfering was witnessed (Emery *et al.* 2004). Relocating items that are at high risk of being pilfered will cause observers who witnessed only the original caching event to be misinformed about the food's present location and will thus reduce the risk of pilferage. Indeed, when there is no reason to misinform the observer, such as when caching had been observed by their partner, with whom they share their caches, storers do not return to re-cache (Dally *et al.* 2006b).

Behaving differently when observed by the partner is not the only way in which storers are sensitive to observer identity. For storers to optimize cache protection, it may be beneficial to keep track of 'who knows what' about their caches. A first indication towards this is the different response of scrub-jays and ravens to conspecifics with different knowledge states about their caches, suggesting that they can at least track 'who was watching when' (Dally *et al.* 2006b). Ravens retrieved a higher proportion of caches when paired with an individual who had observed them cache, compared with the proportion they retrieved

when paired with a non-observer (Bugnyar & Heinrich 2005). In addition to distinguishing observers from non-observers, scrub-jays act differently towards two observers who witnessed two different caching events, re-caching more from the tray which the jay present at recovery also observed during caching (Dally *et al.* 2006b). The above strategies reduce pilfering by acting after caching has been completed (e.g. by re-caching to invalidate the observer's information). Storers can also act during caching itself to limit the information available to observers.

When observed, western scrub-jays preferentially cache in trays placed in the shade compared with those placed in well-lit areas (Dally *et al.* 2004), and in trays placed far from the observer compared with those placed closer to it (Dally *et al.* 2005b). Ravens tend to be further away from other individuals during caching than at other times (Bugnyar & Kotrschal 2002a). Thus, storers act to decrease the quality of the information available to the observer (Dally *et al.* 2005b). When it is possible to altogether deny others of visual information by caching out of view, ravens preferentially cache behind objects that prevent observers from seeing (Bugnyar & Kotrschal 2002a; see also Bugnyar & Heinrich 2005) and scrub-jays prefer a tray that is out of view compared with an equidistant tray in view of the observer (Dally *et al.* 2005b). Scrub-jays do not make these distinctions when the observer's view is blocked completely and caching is performed 'in-private' (Dally *et al.* 2004, 2005a), or when caching in far or close trays is observed by the jays' partner (Dally *et al.* 2006b). Thus, jays do not simply prefer to cache in those locations that happen to deprive observers from information. Rather, they incorporate the pilfering risk (and aversity) specific to each caching event and act only when it is relevant.

At recovery, they use this information again, preferentially moving to new places items at high risk of being pilfered (i.e. those cached in trays in view or close to the observer, Dally *et al.* 2005b; or those cached in well-lit areas, Dally *et al.* 2004). Moreover, during recovery in front of an observer who had seen the original caching, they move each item many times before re-caching and make 'false' caches by probing in new sites with their bill after the food item has already been placed in another site (Dally *et al.* 2006a,b).

One exciting possibility is that corvids incorporate an attribution of others' knowledge or ignorance into their flexible use of cache-protection strategies. While unequivocal evidence for such 'theory of mind' (Premack & Woodruff 1978) in non-humans is especially challenging to obtain (Heyes 1998; Penn & Povinelli 2007; Lurz 2009), there is accumulating evidence that corvids are flexible and adjust the use of cache-protection strategies in ways consistent with the knowledge state of an observer (see above; also see Dally *et al.* 2006a). All of the cache-protection strategies discussed so far were concerned with ways to prevent or limit a potential pilferer's visual information and to make invalid the information it already gathered. However, if corvids are using 'theory of mind' to attribute knowledge states to

others, we may expect that they will not be limited to the visual modality. First evidence towards such flexibility comes from western scrub-jays, who conceal auditory information from potential pilferers only when it is relevant to do so. Stulp *et al.* (2009) provided the jays with two trays: one with little pebbles as substrate, which create noise when cached in, and another with soil that does not create much noise. The proportion of caches jays made in the 'quiet' tray was higher when a potential pilferer was present and could hear them from an adjacent cage, but could not see them, than when the other jay could see as well as hear them, or when they cached in private.

(b) Pilfering strategies

Storing activity causes high-quality food to be available in the ground, in crevices in tree bark and in other locations, and individuals can gain from pilfering others' caches as well as from storing and recovering their own. The simplest (and probably most primitive) way to do so is to randomly search for caches—for example, digging to appropriate depths in the ground and exploring crevices in tree bark. Storers using spatial memory to locate their caches have a recovery advantage over pilferers (Shettleworth 1995) that allows the evolution of caching in the face of such simple pilfering (Andersson & Krebs 1978, but see Smulders 1998; Vander Wall & Jenkins 2003 for alternative theoretical models, less relevant for corvids). This, however, does not prevent pilfering from evolving as well.

The next step for pilferers could have been to follow storers and try to kleptoparasitize their food when they attempt to hide it. However, as we discussed, such a strategy is most likely open only to dominant individuals (e.g. Bugnyar & Kotrschal 2002b). A better pilfering mechanism is to observe storers while they cache, encode where the cache is and use this spatial information to return later and pilfer the cached food. The ability to locate caches made by others using observational spatial memory has been shown in Mexican jays, *Aphelocoma ultramarina* (Bednekoff & Balda 1996a), Pinyon jays, *Gymnorhinus cyanocephalus* (Bednekoff & Balda 1996b), ravens (Bugnyar & Kotrschal 2002a; Scheid & Bugnyar 2008) and western scrub-jays (Clayton *et al.* 2001a; Watanabe & Clayton 2007). In the latter, pilferers can even mentally rotate a caching tray to correctly locate caches when the tray is rotated 180° by the experimenter (Watanabe & Clayton 2007).

The connection between social living and the evolution of social cognition is well known from primate studies (e.g. Byrne & Whiten 1988), and it is interesting to consider the evolution of observational memory in the light of social structure and reliance on cached food (Bednekoff & Balda 1996a; Scheid & Bugnyar 2008). Species with some level of sociality who are either specialized cachers (such as pinyon jays) or moderate cachers (such as Mexican jays, ravens and western scrub-jays; see de Kort & Clayton 2006, but see Pravosudov & de Kort 2006) are excellent at locating others' caches. In contrast, Clark's nutcrackers,

who are specialized cachers but are mostly solitary, and jackdaws, *Corvus monedula*, who are highly social but do not cache, are not able to do as well (Bednekoff & Balda 1996a; Scheid & Bugnyar 2008, respectively). Thus, it seems that alone neither specializing in caching nor social living are enough for excellent observational memory to develop (Bednekoff & Balda 1996a; Scheid & Bugnyar 2008).

The best predictor for observational memory in pilferers may be the frequency of encountering caching conspecifics (or heterospecifics) throughout each species' evolutionary history and during ontogeny. For example, while western scrub-jays are less social than other corvid species, with pairs defending their territories against other pairs, groups of unpaired individuals flock together through these territories (Curry *et al.* 2002), allowing ample opportunity for pilfering and subsequently cache-protection strategies to become beneficial. In addition to their excellent observational memory, however, pilferers may evolve other behavioural strategies to cope with the variety of cache-protection strategies discussed above. For example, subordinate ravens delay pilfering until the storer has left (Bugnyar & Kotrschal 2002a), and after food had been cached by an experimenter they delay pilfering when paired with a non-observer, while quickly pilfering it when paired with a dominant who co-observed the caching (Bugnyar & Heinrich 2005).

Pilferers that use observational memory might benefit from observing others from a concealed position. This 'scrounging from the scrub' strategy may be beneficial for pilferers in several ways. First, given that storers tend to cache when (they perceive themselves to be) in private, hiding from foraging storers may increase the probability that they will cache in the first place, and thus the overall quantity of caches a pilferer observes (Bugnyar & Kotrschal 2002a). Second, if the storer is unaware of having been observed during caching, it is also less likely to, for example, cache far from the observer or in the shade (which would limit the observer's information) or return later to re-cache the hidden items in a different location (which would make the information invalid). Thus, observers can increase pilfering success by improving the quality of information they gather as well as ensuring its validity (Bugnyar & Kotrschal 2002a). A third possible benefit in hiding is to prevent future aggression. Scrub-jays are aggressive towards non-partner pilferers when they witness them pilfering (Dally *et al.* 2005a), and remember which individual observed them cache in which location (Dally *et al.* 2006b). Thus, when finding a cache empty, they may be able to retaliate and direct their aggressiveness towards the individual that had observed them cache in it. This might depend on observers tracking 'who was caching where', or something similar, so that post-pilfering aggressiveness will be beneficial for the aggressor. Hiding while observing can prevent such post-pilfering aggressiveness, if it exists.

(c) *The coevolution of caching and pilfering*

From the above discussion of cache-protection and pilfering, the emerging picture is that of an

evolutionary arms race between storing and pilfering strategies (see also Bugnyar & Kotrschal 2002a; Dally *et al.* 2006a; Emery & Clayton 2008). Spatial memory allows a recovery advantage for storers over random pilferers, and storing to remain adaptive (Andersson & Krebs 1978). Observational spatial memory may evolve when pilferers regularly encounter others caching, increasing pilfering success and preventing aggression. The existence of non-random pilfering which relies on observing caching, in turn, creates a selective advantage for avoiding being seen while caching, as well as acting to decrease the quality of information available to observers (e.g. by caching far from them) or making observer information invalid by re-caching in private (see above). Such cache-protection strategies create a selective advantage for pilferers who can avoid them, for example, by observing from a hidden position, as we have discussed.

The above scenario is, of course, only one possible avenue for a storer–pilferer arms race to take place. There are, however, a few general factors that are likely to influence such an arms race's onset, rate and the level of strategy sophistication. First, pilferers' observational memory is key for the onset of an arms race of cognitive abilities (Bugnyar & Kotrschal 2002a). The straightforward reason is because it markedly improves pilfering success, making it more advantageous for storers to evolve a counter measure, even if the cognitive mechanism and behavioural flexibility involved are costly to produce or to maintain. In addition, as long as pilferers use other tactics such as randomly searching, all pilferers have similar knowledge states about all caches (i.e. they do not know about any of them). Once pilferers use observational memory, however, pilfering risk becomes cache specific, depending upon other's knowledge about it (which depends on whether caching was observed, and how well). This creates the possibility for a variety of cache-protection strategies to evolve that are concerned with tampering with pilferers' knowledge, as well as mechanisms allowing great flexibility of applying those strategies selectively when they are relevant (see above). It is still an open question whether corvids (and non-humans in general) can attribute knowledge or ignorance to others (i.e. whether they have 'theory of mind', see Heyes 1998; Penn & Povinelli 2007; Emery & Clayton 2008; Lurz 2009). If they do, it is not impossible that the selective pressure necessary for the evolution of corvid theory of mind has come about when pilferers started to differ in knowledge states regarding different caching events.

Second, the fact that individuals act as storers as well as pilferers may have enabled shortcuts that accelerated the evolution of advanced strategies and counter-strategies (Emery & Clayton 2008). Consider the effect of pilfering experience in western scrub-jays on their ability to specifically re-cache in locations where caching had been observed (Emery & Clayton 2001). A capacity to predict high pilfering risk from the presence of an observer by using one's own experience as pilferer suggests that jays may be able to imagine another individual's point of view (Emery & Clayton 2008). 'Putting themselves in another's shoes' would open the door for using many

cache-protection (and pilfering) strategies without (or with less) trial and error, or the need for innate strategies and counter-strategies to evolve. Ravens can differentiate between knowledgeable and ignorant competitors both as storers and pilferers (Bugnyar & Heinrich 2005), and it would be interesting to see whether they too use experience in one role to make decisions in another.

Third, the profitability of producing and scrounging should affect the relative frequency of these two foraging strategies in the population (Caraco & Giraldeau 2000), and this may have had an accelerating effect on the evolution of ever sophisticated storer and pilferer strategies. When producing becomes very profitable, for example, the relative frequency of producing compared with scrounging will rise. With respect to the storer–pilferer arms race, if a new and successful cache-protection strategy spreads in the population, this will make caching more profitable and the population will shift towards more caching (and less pilfering). In such a population, where individuals tend to cache rather than pilfer, any pilfering strategy that can increase pilfering success will have a great advantage. That is, on top of the advantage that it would anyway have, it will have an additional advantage because the producer–scrounger game will have made caching so common. When the new pilfering strategy becomes popular, the population will also shift to a new equilibrium with a higher frequency of pilfering, adding to the selection advantage of the next cache-protection strategy. Such a scenario may accelerate the arms race between storer and pilferer strategies and perhaps enable strategies that would otherwise be too costly to evolve.

4. IS CACHING PERFORMED WITH THE FUTURE IN MIND?

We have discussed how caching, recovery and related behaviours are affected by the need to cope with food perishability and competition. Indeed, we have seen that caching is sensitive to its consequences regarding both food decay and pilfering, i.e. to the success of recovery (Clayton *et al.* 2005; de Kort *et al.* 2007), and to the risk that caches will be pilfered after the storer leaves (see §3). It thus seems intuitive to assume that corvids may have the future (i.e. recovery) in mind when they cache and when they act to protect their caches. While the benefit of caching is indeed based on future food consumption, however, evidence for future planning has taken more than intuition to achieve.

First, there are several theoretical arguments that suggest that planning for the future might be involved here. Human episodic memory and planning for the future are considered to be achieved using shared mechanisms (Atance & O'Neill 2001; Klein *et al.* 2002). If the existence of one of these abilities suggests the other in birds as well, we can expect at least scrub-jays and magpies to show some future planning based on the evidence for episodic-like memory in these species (see above). In addition, caching may require future planning because it is inherently directed at fulfilling a future motivation to consume the cached food.

Perhaps, then, storers can do so independent of current motivation. However, the studies mentioned above were not designed to distinguish between using future planning and simpler accounts based on motivation and behavioural cues at the time of caching.

The first unambiguous evidence that non-humans can plan for the future, according to Shettleworth (2007), comes from a study conducted on western scrub-jays (Raby *et al.* 2007), in which the jays were first trained that breakfast (powdered pine nuts) is only available in one of two compartments. In the evening after six such morning trainings, the jays were allowed to cache pine nuts in either compartment for the first time and chose to cache predominantly in the compartment they will be hungry in the next morning. In a second experiment, both compartments contained food in the morning trainings—but of different types (peanuts or dog kibbles). In the evening of the test, jays were allowed to cache both types of food in either compartment, and preferentially cached the different type of food from the one that will be available in each compartment at breakfast. An associative learning account is ruled out because the jays never had the chance to experience the consequences of caching these foods in either compartment. These experiments show that the jays can base their decisions of where and what to cache on their future needs, challenging the Bishof–Köhler hypothesis that only human can do so (see Suddendorf & Corballis 1997). While an action to fulfil current needs does not exclude that planning for the (near) future is involved, behaviours that fulfil future rather than current needs are viewed as the ultimate proof for thinking about the future (Raby & Clayton 2009). Therefore, the next step was to test whether jays can act on their future needs even when these are directly opposed to their current ones.

To do this, Correia *et al.* (2007) used specific satiety (e.g. Clayton & Dickinson 1999a) to contrast scrub-jays' motivational state at caching (for eating pine seeds or dog kibbles) with the motivational state they were trained to expect at recovery. Birds from the 'Different' group were pre-fed one type of food just before caching (say pine seeds) and the other (kibbles in this example) just before recovery. According to their current motivational need at caching (having been pre-fed pine seeds), these birds should cache (and eat) more of the kibbles (see Clayton & Dickinson 1999a, and experiment 1 in Correia *et al.* 2007). However, in the second and third trials they cached more pine seeds, reflecting their future motivation for pine seeds at recovery which they were exposed to in the first trial (having been pre-fed kibbles before recovery). Birds from the 'Same' group were pre-fed the same food before caching and recovery. As expected from their similar current and future motivational states, these birds continued to cache the non-pre-fed food.

The jays' remarkable ability to switch after only one trial to caching the food they are currently sated on (i.e. against current motivation) suggests that caching is inherently directed towards needs that will be present at the future time of recovery. In humans, prospective cognition may be done by imagining oneself

in another time (Gilbert *et al.* 2002), and it is still an open question whether animals can travel mentally in time (e.g. Suddendorf & Corballis 1997; Suddendorf & Busby 2003; Tulving 2005; Zentall 2006; Roberts 2007; Raby & Clayton 2009). However, mental time travelling is not necessarily the only way to plan for the future. Rather, it is possible that animals as well as humans can make decisions based on semantic propositions about the future without imagining themselves in that future (see Raby & Clayton 2009 for a detailed discussion). Caching is definitely a realm where future planning *could* be beneficial because it will assist in adjusting current caching according to future conditions and needs, which are what gives caching its adaptive value in the first place. Caching species may have evolved capacities of varying degrees for such forward thinking, depending on whether such adjustments are beneficial in their specific niche. For example, specialized cachers that predominantly cache one type of food, such as Clark's nutcrackers and pinyon jays mentioned above, might benefit less than species that cache a variety of food types such as scrub-jays and magpies from a mechanism allowing them to act according to future needs that are different from current needs. On the other hand, it is not at all clear whether future planning in scrub-jays is an adaptive specialization for caching or whether it has evolved for different reasons and is used, perhaps among other behaviours, in caching (see discussion below). This is clearly a key question for future research. Another interesting question regarding caching 'with the future in mind' is its apparent contrast with caching as a compulsive behaviour (during development as well as in adult caching; see §1).

5. WHY CORVIDS? CONCLUDING REMARKS

In the previous sections, we have discussed how different features of caching behaviour are related to episodic memory, social cognition and prospective cognition. In addition to these cognitive abilities, corvids are also exceptional in the physical cognition realm. The New Caledonian crows are excellent tool users and manufacture tools in the wild (Hunt 1996). They have recently been shown to understand something about their physical world as they choose the right diameter and length of stick suitable to retrieve a piece of food (Chappell & Kacelnik 2002, 2004), with one individual spontaneously making a hooked tool out of a straight piece of wire when that was needed (Weir *et al.* 2002). Recently, it has been shown that even corvids that are not habitual tool users in the wild will readily use tools under laboratory conditions (e.g. rooks, *Corvus frugilegus*: Seed *et al.* 2006; Bird & Emery 2009).

With behaviours that suggest complex cognition in many areas, corvids are considered the most intelligent birds (together with parrots), comparable with non-human primates. Indeed, similarities between the challenges faced by corvids and primates suggest that their exceptional cognitive abilities may be a product of convergent evolution (Emery & Clayton 2004; Seed *et al.* 2009). The same principles could be extended to the possibility of convergent evolution of

cognitive abilities in other groups such as parrots and cetaceans, as well as to food-storing mammals (e.g. cache-protection strategies in squirrels Leaver *et al.* 2007). Here, we focus on the challenges corvids face and their possible relation to their cognitive abilities.

First, some corvid species are highly omnivorous, and the many types of foods that they feed on may have required them, like other generalist foragers, to use flexible foraging strategies. In addition, corvid species such as rooks and jackdaws have quite large social groups (for a review of social structures in corvids see Clayton & Emery 2007). The social-intelligence hypothesis (Humphrey 1976) holds that the need to cope with the politics of social lives was the driving force behind primate intelligence. The same argument may be applied to the evolution of corvid cognition. However, the evolution of social cognition is not explained by sociality *per se*, but it might be explained by a combination of some degree of sociality and the opportunity to use cognitive skills to outcompete rivals (Clayton *et al.* 2007), for example when protecting one's caches or pilfering others' caches (see Emery & Clayton 2004; Seed *et al.* 2009). Other features that may be related to corvid cognition (and also occur in primates) are their relatively long lives and large brains. Such ecological, life-history and physiological features are, of course, not enough to explain the evolution of complex cognition in corvids. Among other things, this is because one cannot be certain, for each of these features, whether it has contributed to driving the evolution of corvid intelligence or perhaps it was the other way round.

According to the adaptive specialization view, we should be able to explain the cognition of each species through the socioecological problems it currently faces and those it has faced in the past. As we have discussed in the previous sections, corvids flexibly incorporate many factors when caching, pilfering and recovering their caches. de Kort *et al.* (2006) argue that we should therefore not expect to find a simple relationship between cognitive abilities and, for example, the amount of caching performed by different species because the evolution of caching-cognition is likely to depend on the interplay between such factors. In the example given above, sociality alone is probably not enough to drive the evolution of pilferer observational memory. Rather, the combination between sociality and caching, particularly the probability that individuals will encounter others caching, may better do so.

de Kort *et al.* (2006) stress the importance of considering the evolutionary history of caching when assessing whether it is related to other traits. For example, to determine whether or not caching is related to increased hippocampal volume, it is not enough to compare these two traits in extant species because the predictions will also differ depending on whether the corvid ancestor was a cacher or not (de Kort *et al.* 2006). Similarly, to explore whether the complex 'cognitive tool box' of corvids (Emery & Clayton 2004) is linked to caching behaviour, and how, will require such evolutionary considerations.

It is most likely that caching is the primitive state in corvids (de Kort & Clayton 2006) and has therefore

played at least some role in the evolutionary history of corvid lineages. This becomes more clear when considering that together with tool-using, the caching paradigm is responsible for most of the experimental evidence we have for complex cognition in corvids. It is therefore reasonable to assume that it is indeed linked to their impressive cognitive tool-box (including episodic-like memory, prospective cognition and perhaps mental attributions). However, it is again less clear whether caching was the driving force behind the evolution of these cognitive traits, or perhaps it is complex cognition that pre-existed in the corvids, enabling some of them to apply it to caching behaviour (which allowed researchers to gather evidence for cognition). To resolve such issues a comparative approach is required: more data on the cognitive abilities involved in the caching behaviour of more corvid species will be needed in order to test which of these hypotheses is more likely.

There is, of course, still an open debate as to whether what looks like cognition cannot be explained by alternative mechanisms (e.g. Suddendorf & Busby 2003; Penn & Povinelli 2007; Clayton & Grodzinski 2010). Associative learning has been successfully ruled out by using individuals with known reinforcement histories for rigorously controlled experiments, containing no opportunity to learn the task at hand. However, this may not be enough in order to assess the possibility that innate rules of response dictate behaviour, rather than cognition. To do this, it may be productive to use the prediction that a cognitive appreciation of reality should be exhibited in many contexts, while this is less likely for an innate response rule evolved to solve a certain type of task. In the case of caching, it would be very interesting to see whether food-storing corvids can exhibit episodic-like memory, ability to plan for the future and seeming mental attributions in non-caching contexts.

There is an intriguing resemblance between the conceptual purpose of mindreading and the actual reality of caching. The very purpose of 'mindreading', or attributing mental states to others, may be to gain access to their intentions while keeping your own intentions from them (Whiten 1997). With that in mind, perhaps it is not surprising that evidence suggesting mental attribution in corvids comes from caching, where the purpose is to gain access to others' caches while keeping your own caches from them.

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