



Object caching in corvids: Incidence and significance



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ABSTRACT

Food caching is a paramount model for studying relations between cognition, brain organisation and ecology in corvids. In contrast, behaviour towards inedible objects is poorly examined and understood. We review the literature on object caching in corvids and other birds, and describe an exploratory study on object caching in ravens, New Caledonian crows and jackdaws. The captive adult birds were presented with an identical set of novel objects adjacent to food. All three species cached objects, which shows the behaviour not to be restricted to juveniles, food cachers, tool-users or individuals deprived of cacheable food. The pattern of object interaction and caching did not mirror the incidence of food caching: the intensely food caching ravens indeed showed highest object caching incidence, but the rarely food caching jackdaws cached objects to similar extent as the moderate food caching New Caledonian crows. Ravens and jackdaws preferred objects with greater sphericity, but New Caledonian crows preferred stick-like objects (similar to tools). We suggest that the observed object caching might have been expressions of exploration or play, and deserves being studied in its own right because of its potential significance for tool-related behaviour and learning, rather than as an over-spill from food-caching research.

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1. Introduction

Food caching is known across the corvids, and was probably present in their common ancestor (de Kort and Clayton, 2006). Its high incidence supports cognitive research across the group in contexts such as spatial memory (e.g. Gibson and Kamil, 2009), object permanence (e.g. Bugnyar et al., 2007b), delay of gratification (e.g. Dufour et al., 2012), inferential reasoning by exclusion (e.g. Mikolasch et al., 2012), tool-use (e.g. Kenward et al., 2011), transitive inference (e.g. Bond et al., 2010), theory of mind (e.g. Bugnyar, 2011), episodic-like memory (e.g. Clayton and Dickinson, 1998), and future planning (e.g. Raby et al., 2007).

However, the specificity of the relationship between food caching and general cognition is still unclear (Grodzinski and Clayton, 2010); which one preceded the other and how did they co-evolve? The extent to which corvids cache food, and their reliance on these caches varies across species. For example, jackdaws (*Corvus monedula*) cache virtually no food (Healy and Krebs, 1992; Vander Wall, 1990) whereas Clark's nutcrackers (*Nucifraga columbiana*) rely almost exclusively on retrieving cached pine seeds

in order to survive the winter (Vander Wall, 1990). Using phylogenetic comparisons, de Kort and Clayton (2006) suggested that the common ancestor of all corvids probably was a moderate food cacher, implying that species like Clark's nutcracker became more specialised while others, like jackdaws, lost the propensity to do so.

Handling, exploring and caching inedible objects has also been reported, but their significance for cognitive, ecological, or developmental factors are largely unknown, which is surprising, given that food and object caching in corvids has been known since ancient times (Hertz, 1926).

We report experimental results on object-addressed behaviour in captive adult corvids and review the literature and ideas related to object manipulation and caching in corvids and other birds. Vander Wall (1990) defines food caching as the handling of food for later use, noting that a necessary condition is that it deters other organisms from consuming the food, which can include preparation, transportation, placement, and concealment of the food item. Because the objects are not consumed, we define object caching as insertion of an object into another object, substrate or crevice, and being left there. This definition does not require that the object is placed out of view of a human observer, but excludes casual abandonment of objects in random locations. Although such caches are often retrieved, retrieval is not a necessary component. Even if a cache gets pilfered or is forgotten, the act of caching, and the

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selectivity that may precede it, can be informative. There are good reasons to consider purpose, as in Vander Wall's definition, but it could be problematic to include it in the definition, as an observer may not be able to discern either the proximate or functional determinants of an act at the time of occurrence.

Prima facie object caching does not serve any obvious biological need. Ritter (1921) even suggested that it is a maladaptive consequence of the caching instinct. This explanation fits uneasily with current approaches to behavioural adaptation. While it is reasonable to expect that food and object caching are related, treating the latter as merely a non-functional over-spill of the former would be to jump to conclusions given the lack of research.

Among birds, object caching appears most prevalent in corvids. Eurasian jays (*Garrulus glandarius*) predominantly cache stones, which to a human observer resemble their main food source: acorns (Clayton et al., 1994). In contrast, common ravens (*Corvus corax*) prefer to cache colourful objects over objects that resemble food (Kabicher 1996, as cited in Bugnyar et al., 2007a). Scrub jays (*Aphelocoma coerulescens*) reduce their stone caching when they previously had simultaneous access to powdered peanuts and stones, but not to powdered peanuts, stones, or whole peanuts alone. As only whole peanuts could be cached and eaten, stone caching in this species seems to satiate by a combination of pre-feeding and stone pre-caching, suggesting that it is governed by both hunger and caching motivation, to some extent acting independently of one another (Clayton and Dickinson, 1999).

These observations illustrate cases where cached objects are not used later, but when caching may still serve a future function, given that the animal learns from the behaviour. In other cases, cached objects may indeed be retrieved and used. Wild grey jays (*Perisoreus canadensis*) and Siberian jays (*P. infaustus*) cache materials, such as feathers and deer hairs, retrieved for nest construction (Lawrence, 1968 and references therein). Object caching is not exclusive to the corvid family. Loggerhead shrikes (*Lanius ludovicianus*) have been reported caching twine and a small root on barbed wire in the wild (Burton, 1999). Possibly as a display towards females, adult male shrikes add inedible objects to their food caches, which increase their conspicuousness. They continue to do this after their young have hatched, which led some authors to believe it also aids in territorial demarcation and defence (Yosef and Pinshow, 2005). Two captive marsh tits (*Parus palustris*) who only had access to powdered food, unsuitable for caching, used a sticker to collect it; when food was unavailable they stored this sticker. This may be interpreted as caching potential tools when being deprived of cacheable food, either redirecting their caching motivation non-functionally or perhaps preparing the tool for later use (Clayton and Joliffe, 1996).

Similarly to the Eurasian jays, four woodpecker species have been observed caching objects, which one could consider as a non-functional, redirected food caching behaviour expressed when no cacheable food is available, with some birds wedging acorn-sized pebbles into drilled holes (Kilham, 1963, 1974; Orcutt, 1884; Ritter, 1921). Red-headed woodpeckers (*Melanerpes erythrocephalus*) sometimes use wet pieces of wood to seal holes leading to large food caches inside tree trunks. After drying, these seals become well camouflaged and difficult to remove, preventing pilferage by conspecifics and other birds, which regularly occurs with open caches (Hay, 1887; Kilham, 1958). This type of object caching provides an example of potential ecological function.

In several bird species, object caching precedes proficient food caching during development. Marsh tits cache objects as soon as they reach nutritional independence, but stop doing so after about two weeks, regardless of food caching experience (Clayton, 1992, 1994). Recently fledged loggerhead shrikes wedge inedible objects into crevices a few days before they do so with food; a behaviour which eventually develops into their distinctive impaling of prey

(Smith, 1972). Young, nutritionally dependent, jackdaws also cache objects and food pieces (A.M.P.v.B., pers. obs), but in contrast to marsh tits, this is unlikely to be for practise as they do not frequently cache food as adults.

In New Caledonian crows (*Corvus moneduloides*), caching has structural parallels with tool-use. The ontogeny of both food and object caching in ravens and tool-oriented behaviour in New Caledonian crows (hereafter 'NC crows') begins with basic object combinations, later followed by functional insertions. Juveniles of both species spend similar amount of time (increasing with age) manipulating objects. Non-functional object combinations increase with age and are higher overall for NC crows, but decrease in ravens. Thus, NC crows appear to have greater motivation for object interaction, which might be instrumental in learning tool-use (Kenward et al., 2011). Woodpecker finches (*Cactospiza pallida*) also rely strongly on tool-use to obtain invertebrates and, albeit little studied so far, exhibit behaviours that resemble food and object caching (Eibl-Eibesfeldt, 1970; Eibl-Eibesfeldt and Sielmann, 1962).

Object caching has been suggested to be a type of play (Burghardt, 2005; Heinrich and Smolker, 1998; Hertz, 1926; Kilham, 1974). In many situations object caching meets Burghardt's five criteria: limited immediate function, endogenous "voluntary" component, structural or temporal differences with "serious" performance, repeated but not rigidly stereotypical performance, and relaxed competition from other motivational systems (Burghardt, 2005; Graham and Burghardt, 2010). Object caching develops in parallel with the different phases of object permanence in ravens and scrub jays (Bugnyar et al., 2007b; Salwiczek et al., 2009). Initially, young ravens place items in contact with larger objects, later they stick them into crevices, and in the final stage they cover them with substrate. This applies both to food and non-food items, although the former is accompanied by more visual (checking laterally and looking up) and manipulative acts. As the fledgling ravens grow older, caching as well as pilfering attempts increase, but only in relation to food. Individuals become more skilled in securing food caches by moving away from conspecifics and caching behind barriers. The behaviour in relation to inedible objects, however, remains unchanged (Bugnyar et al., 2007b). Similarly, adult ravens employ more strategies to protect their caches from a pilfering experimenter than from a merely inspecting one if they cache food, but not when they cache objects (Bugnyar et al., 2007a). The authors therefore suggested that by playfully caching objects, young ravens learn about the pilfering behaviour of their conspecifics and acquire skills needed to protect their food caches later in life.

In sum, proximate explanations for object caching in birds are: (1) a form of *object play*; (2) a *side-effect* of food-caching motivation directed towards food-like objects when cacheable food is unavailable; (3) a motivation present only as a passing *developmental stage*. Ultimate explanations include: (1) *acquiring proficiency* in food caching, tool-use, or social interactions; (2) *storing materials* for nest building; (3) *courtship*; (4) *aiding in territory defence*. It might well be that object caching serves various functions, and is governed by diverse motivational systems in different species.

It is possible that, in addition to functions related to object caching itself, as discussed above, adult corvids cache objects as part of a general explorative behaviour helpful in developing knowledge of the physical affordances of their surrounding environment, for broad ranging future benefits. Object caching may, for instance, support physical innovativeness. Corvids are known for their behavioural flexibility and for being both neophobic and neophilic (Greenberg and Mettke-Hofmann, 2001; Jönsson et al., 2012). After an initial fearful response, they can spend extensive periods of time exploring novel objects. Some of this may relate to their life history. Corvids are large-brained and long-lived, mostly opportunistic generalists, which do not migrate over long distances. In general they are very successful in coping with, and adapting

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