



# No evidence of temporal preferences in caching by Western scrub-jays (*Aphelocoma californica*)<sup>☆</sup>

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## ABSTRACT

Humans and other animals often favour immediate gratification over long-term gain. Primates, including humans, appear more willing to wait for rewards than other animals, such as rats or pigeons. Another group displaying impressive patience are the corvids, which possess large brains and show sophisticated cognitive abilities. Here, we assess intertemporal choice in one corvid species, the Western scrub-jay (*Aphelocoma californica*). These birds cache food for future consumption and respond flexibly to future needs. Cache-theft and cache-degradation are time-dependent processes in scrub-jay ecology that might necessitate sensitivity to delays between caching and retrieval. We adopt a caching paradigm with delays of up to 49 h. Across two experiments we find no evidence of a preference for earlier recovery. We highlight the possibility that, although scrub-jays can discriminate between the present and the future, they may not understand how far into the future an event will occur.

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## 1. Introduction

Tradeoffs between rewards at different points in time are ubiquitous in many animals' choices about mating, cooperation, parental investment, and foraging. In an uncertain world, gains expected in the future may never bear fruit. Future gains and losses should therefore be underweighted relative to those available in the present. Indeed, many animals choose smaller, more immediately available rewards over larger, more delayed rewards, including pigeons (Ainslie, 1974; Green et al., 2004), monkeys (Addessi et al., 2011; Tobin et al., 1996), rats (Green et al., 2004; Richards et al., 1997), and humans (Green and Myerson, 2004; Kirby et al., 1999). This behaviour is commonly described in terms of 'temporal discounting' of future rewards; here we adopt the theoretically neutral term 'intertemporal choice'.

Investigation of human intertemporal choice has focused primarily on monetary decisions. For example, "Would you prefer \$54 today, or \$55 in 117 days?" (taken from Kirby et al., 1999). A robust feature of human intertemporal choice is dynamic inconsistency; people are especially delay-averse as the prospect of gratification becomes more immediate. For example, many people prefer \$50 immediately to \$100 in six months, but would opt for \$100 in a

year over \$50 in six months, despite the difference in delay and reward between the options being identical across the two choices. This pattern of preference is best described mathematically by a hyperbolic function (Green et al., 2004; Rachlin et al., 1991).

While humans will sometimes wait 25 years for a large (hypothetical) sum of money (Green et al., 1996), rats and pigeons are typically intolerant of delays beyond a few seconds (Green et al., 2004). Several primate species show a greater propensity to wait for a larger pay off (Addessi et al., 2011; Amici et al., 2008; Beran, 2002; Stevens and Muhlhoff, 2012; Tobin et al., 1996). Indeed, chimpanzees were *more* delay-tolerant than humans under similar task conditions in one study (Rosati et al., 2007; though see also Paglieri, 2013, for discussion of methodology).

Species differences in intertemporal choice have been attributed to a range of factors including metabolic rate (Tobin and Logue, 1994), brain size (Tobin et al., 1996), and the demands of an animal's ecology (Addessi et al., 2011; Stevens et al., 2005a,b). Corvids, like the great apes, exhibit impressive cognition across a range of physical (Bird and Emery, 2009; Taylor et al., 2007; Weir and Kacelnik, 2006) and social (Bugnyar and Heinrich, 2005; Emery and Clayton, 2001; Ostojic et al., 2013) domains, underpinned by large brains for their body sizes (Jerison, 1973). Corvids also seem to show delay tolerance comparable to that seen in great apes: carrion crows (*Corvus corone*) and common ravens (*Corvus corax*) waited for up to 320 s for a preferred reward in a delayed exchange task (Dufour et al., 2012; though see also Wascher et al., 2012 for limitations). Emery and Clayton (2004) argue that similarities in corvid and great ape psychology are the product of convergent evolution, driven by similar ecological challenges of both a physical and social nature.

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Many corvids cache food for consumption at a later date. Caching inherently involves an intertemporal choice (Stevens, 2010): *eat now or cache for later?* In one species of caching corvid, the Western scrub-jay (*Aphelocoma californica*), this behaviour is mediated by separate motivational drives to eat and to cache (Clayton and Dickinson, 1999). The latter system is relatively inflexible, eliciting persistent caching in the absence of any feedback at recovery (de Kort et al., 2007). However, when given a choice of food or caching location, scrub-jays show sensitivity to the conditions of cache-retrieval, avoiding locations that have been pilfered (de Kort et al., 2007), and selectively caching food items that will be highly valued at recovery (Correia et al., 2007). This behaviour depends on input from the general satiety system governing feeding, and on prospective cognition.

Correia and colleagues manipulated subjects' motivational states using specific satiety – the decrease in incentive value of one food type following consumption of that food type. Subjects were given the opportunity to cache, and then recover, two food types: peanuts and kibble. Pre-feeding ensured specific satiety for one food type during caching, and for the other during recovery. As found previously (Clayton and Dickinson, 1999), the birds cached fewer of the items that they were satiated on in trial 1. Importantly however, on trials 2 and 3, the birds were able to overcome their current desires and switch to caching the food they would want at recovery as opposed to that they want at the present time when caching. Another food-caching corvid, the Eurasian jay (*Garrulus glandarius*), can cache for two different future motivational states (Cheke and Clayton, 2012).

Scrub-jays are therefore able to dissociate from the context of the present and cache in accordance with a future desire to eat. This has been considered evidence of a capacity for future planning (Cheke and Clayton, 2010; Raby and Clayton, 2009), which has traditionally been thought unique to humans (Suddendorf and Corballis, 1997, 2007 but see Corballis, 2012; for full discourse see also Suddendorf and Corballis, 2008; Clayton et al., 2008). Representation of future rewards is an important mechanistic consideration for the study of intertemporal choice. At its simplest, a choice between eating and caching is governed by competition between the eating and caching drives, with no representation of the delay. This is an intertemporal choice, but not one that is sensitive to any temporal contingencies. Control of caching by predicted future drives implies representation of the consequences of intertemporal caching decisions. Scrub-jays are thus sensitive to delay-dependent fluctuations in the incentive values of cached food, as noted by Correia et al. (2007).

Western scrub-jays face two key ecological challenges that necessitate sensitivity to delays between caching and recovery. First, scrub-jays are versatile food-cachers. Unlike specialist cachers such as Clark's nutcrackers (Balda and Kamil, 1989), scrub-jays cache all year round and store a range of different food types (Curry et al., 2002). Degradation of dead invertebrates is considerably faster than that of nuts and seeds, and is likely to depend on seasonal variations such as humidity and temperature. Scrub-jays keep track of their caches and target recovery to items that are currently edible depending on the delay between caching and retrieval using 'episodic-like memory' (Clayton et al., 2001, 2003; Clayton and Dickinson, 1998; de Kort et al., 2005). They can also keep track of different foods that perish and ripen at different rates (de Kort et al., 2005). Work with another versatile cacher amongst the corvids, magpies (*Pica pica*), has also shown some aspects of episodic-like memory (Zinkivskay et al., 2009). It seems likely that sensitivity to the future incentive value of food when caching (Correia et al., 2007) would incorporate degradation and ripening. Since these are time-dependent processes, some representation of the delay between caching and retrieval would be required.

Second, scrub-jays also need to contend with cache theft, and exhibit a range of strategies to protect their stores (Dally et al., 2004, 2006a,b; Stulp et al., 2009). Some of these strategies appear highly cognitive (Emery and Clayton, 2001; Thom and Clayton, 2013). The continuous risk of pilferage should affect optimal delays between caching and retrieval (Grodzinski and Clayton, 2010): the earlier an item is recovered and eaten, the less time it has to be stolen. Scrub-jays may therefore be expected to cache with the intention of recovery in the near future. Indeed, scrub-jays typically retrieve caches more quickly than Clark's nutcrackers (Pravosudov and de Kort, 2006), despite no substantial differences in long-term spatial memory between the two species (Bednekoff et al., 1997).

In this study, we examined intertemporal choice patterns in scrub-jay caching behaviour. Experiment 1 assessed distribution of caches across three trays associated with different delays between caching and recovery. Experiment 2 tested the motivation to cache in a single tray depending on delay-to-recovery, using a shorter minimum delay than Experiment 1. Experiment 2 also introduced opportunity costs, allowing more time to recover after short delays than longer ones. In both experiments, a tendency to cache fewer items when the delay between caching and retrieval is long would indicate preferences consistent with 'temporal discounting' over long delays in scrub-jay caching.

## 2. Experiment 1

In Experiment 1, the birds were given the opportunity to cache mealworms across three trays, each associated with a different delay: 1 h/25 h/49 h. Mealworms are high-value food items that degrade quickly. For each mealworm, the birds had to choose (1) whether or not to cache and (2) where to cache (i.e. when to recover). We had two main predictions. First: the eating system would be delay-sensitive, and so would drive differential caching between the trays. Second: any detectable differentiation would follow a hyperbolic pattern, as seen in other species (e.g. Green et al., 2004), so the biggest difference in caching would be seen between shorter delays.

### 2.1. Materials and methods

#### 2.1.1. Ethics statement

Work was conducted under UK Home Office project licence PPL 80/2519.

#### 2.1.2. Subjects and housing

Eight hand-raised Western scrub-jays participated as subjects in this study. In both experiments, all birds had previous experience with caching and recovery (e.g. Clayton and Dickinson, 1998). Birds were fed on a maintenance diet of fruit, vegetables, mixed nuts, grains and seeds, bread, dog biscuits, and cuttlefish bone. The birds had ad libitum access to water at all times. Subjects were pair-housed in 2 m<sup>3</sup> home cages, kept at 21 ± 1 °C on a 12:12 h light-dark schedule.

#### 2.1.3. Apparatus and testing conditions

Birds were given 40 mealworms to cache across three trays. One bird had previously refused to cache mealworms, and so was given 30 'wax worms' (wax moth larvae) per trial instead. The worms were held in an open opaque plastic bowl in the centre of the cage floor. The three trays were placed equidistant from the bowl, against the sides of the cage.

Caching trays each consisted of an ice cube tray attached to a wooden base. Each tray was a 2 × 7 formation of potential caching sites – individual cube moulds filled with corncob caching substrate. Formations of Lego® blocks around one or two sides of the wooden base were added to aid the birds' recognition of their trays.

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