

# Cache protection strategies by western scrub-jays (*Aphelocoma californica*): hiding food in the shade

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**In the presence of conspecifics, food-caching western scrub-jays (*Aphelocoma californica*) implement a variety of strategies to reduce the chances of cache theft. This experiment aimed to determine whether the jays could exploit an environmental variable, the level of ambient light, to reduce the transfer of visual information to potential pilferers. Each jay was allowed to cache non-degradable food in two trays, one of which was well lit, whereas the other was in shadow. In some trials the birds cached in private and in others they were observed; however, they always recovered their caches in private. When observed the jays preferentially cached in the shaded tray, whereas both trays were used equally when caching in private. By caching in shaded sites, the quality and transfer of visual information available to the observer may be reduced, thereby making the location of cache sites less certain. These results suggest that western scrub-jays may selectively cache in the shade as a strategy to reduce the chance of cache theft by observing conspecifics.**

**Keywords:** scrub-jay; social cognition; caching; cache protection; corvids

## 1. INTRODUCTION

Food-storing corvids, such as western scrub-jays, hide food for future consumption and rely on memory to recover their caches at a later date. These caches are susceptible to pilfering by other individuals, as a number of species commonly use spatial memory to recover caches that they have seen conspecifics make (Bednekoff & Balda 1996; Clayton *et al.* 2001; Bugnyar & Kotrschal 2002).

Field observations suggest that storers implement a variety of measures to reduce cache theft. These strategies include waiting until conspecifics have left or are distracted before caching (e.g. rooks, *Corvus frugilegus*; Simmons 1970; Källander 1978), or returning alone to caches previously hidden in the presence of conspecifics and re-caching them in sites unbeknown to the observer (e.g. western scrub-jays; Emery & Clayton 2001; Goodwin 1955; ravens, *Corvus corax*; Heinrich 1999). Furthermore, ravens will cache behind large objects in the presence of conspecifics. These objects may serve as barriers

concealing information about the location of caches from potential thieves (Bugnyar & Kotrschal 2002).

Although field observations are of enormous value in documenting the natural behaviour of these birds, an experimental approach is crucial for understanding the mechanisms underlying these behaviours and determining the effects of experience. Emery & Clayton (2001) tested whether it was the presence of an observer at caching, and the absence of one at recovery, that elicited the storer's recovery behaviour. Hand-raised western scrub-jays were allowed to cache either in private or while observed, and then recover their caches in private. Individuals that had prior experience (outside of the experiment) of pilfering another bird's caches subsequently re-cached food in new sites, but only when observed during caching. Because the two conditions were identical at the time of recovery, the birds had to remember whether or not they had been watched during caching to know when to re-cache during recovery, and whether to cache into new sites.

In the Emery & Clayton (2001) study, as in many of the field observations (e.g. Goodwin 1955), the birds' behaviour could be a response to the presence or absence of an observer during caching, coupled with a memory for their presence or absence at recovery. However, recent experiments have shown that when an observer is always present at the time of caching, jays use distance and barriers to reduce the probability of cache theft by conspecifics (Dally *et al.* 2005). For example, when given the choice of two caching trays, one 'near to' and one 'far from' an observer, the jays cached preferentially in the 'far tray', but not when caching in private. When given the choice of caching in a tray in view of a conspecific, or one hidden behind a barrier, the jays cached significantly more in the tray that was out of view, again not when caching in private. In both cases, during recovery, caches were re-cached only from the tray most at risk from pilfering (i.e. the 'near' tray and the 'in view' tray). These results suggest that the jays may have been attempting to minimize the transfer of visual information to the observer during the caching event.

In the field some cache sites would also be obscured by light intensity. For example, sites in shady spots would be far less visible than those in bright sunlight. The aim of this experiment is to test whether jays use shade as a cache-protection strategy. If jays act to reduce the visual information available to the observer at the time of caching, they should prefer to cache in shady sites when observed but not necessarily when caching in private. To test this hypothesis, the jays were allowed to cache both in private and when observed. In each condition they were provided with two caching trays that were equidistant from the observer's cage. One tray was well lit and the other was placed in the 'shade'.

## 2. METHODS

Nine sexually mature (four females and five males) hand-raised western scrub-jays were used. The jays had previously participated in a range of experiments (J. M. Dally, unpublished data), acting as both observers and pilferers. In these studies the caching trays were removed after the caching phase and on some trials the storer subsequently observed another jay pilfering their caches. This experience meant that re-caching behaviour could be expected. Birds were housed in cages measuring 2 m wide by 1 m high by 1 m deep, and were maintained inside on a 12 L:12 D cycle on a diet of mixed nuts, dog biscuits, various fruits, wax worms and mealworms. The maintenance diet was removed from the home cage the evening before an experimental day, ensuring that the jays were mildly hungry during caching.

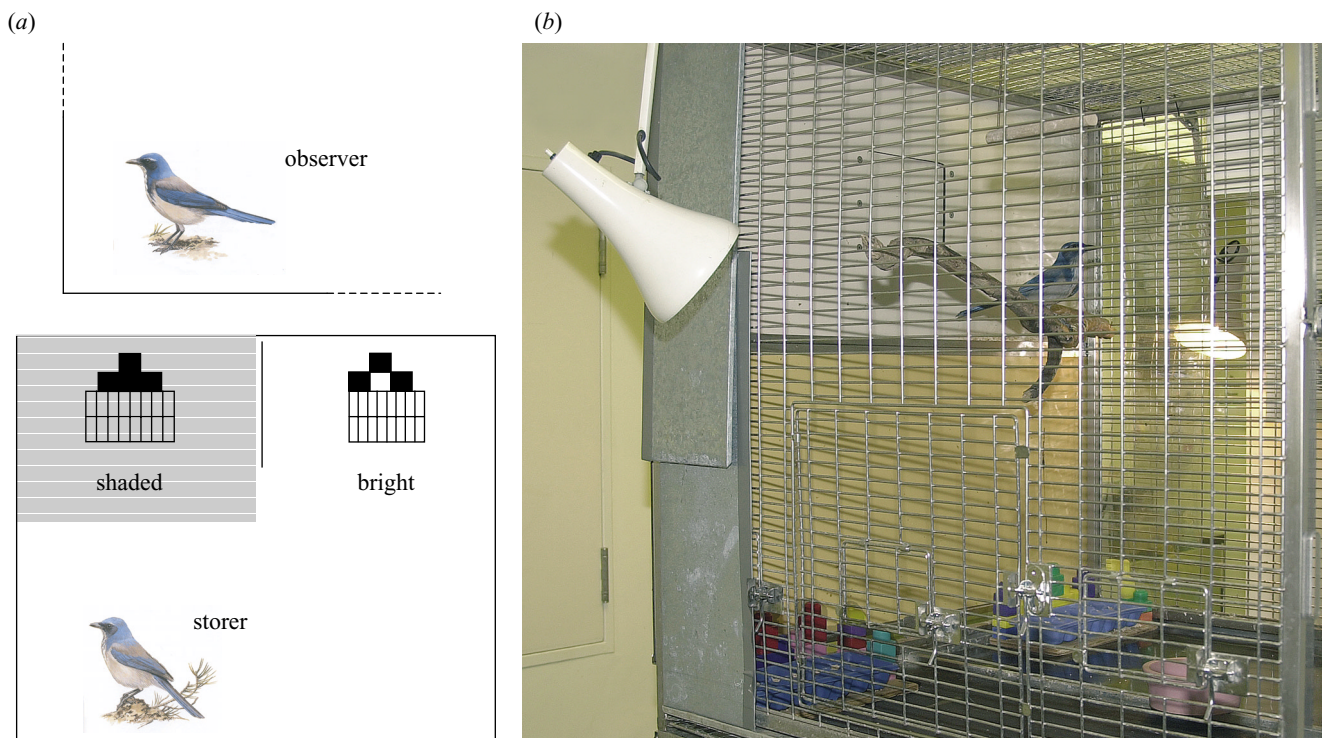


Figure 1. (a) The experimental set-up with the location of the 'shady' and well-lit 'sunny' cache sites in a storer's compartment, and the observer's cage. (b) The photograph shows a scrub-jay in one of the storer compartments, which contains two caching trays and a food bowl. A lamp was attached to the side of the compartment at a height of 54 cm above each caching tray. Note that only the lamp above the well-lit ('sunny') tray was switched on, resulting in a difference in illumination between the well-lit and shaded trays of 4 : 1 and a difference in temperature of 2 °C (see § 2). This difference in brightness cannot be detected from this photograph because of the use of flash photography.

The home cages were the site of all caching trials. Each jay was placed in a 1 m × 1 m × 1 m compartment of the home cage, and these were arranged side by side in rows of three, with an observer jay in the middle compartment and a storer in each of the two outer compartments (see figure 1). There were two caching conditions: 'in private' and 'observed'. During 'in private' trials, the observer's view was blocked by solid opaque dividers. Transparent dividers separated the observer from the 'observed' storer during 'observed' trials. The birds received two caching trials, one in each condition, as well as an additional trial in which they played the role of observer. The birds were moved from one compartment to another after each trial to counterbalance both the order in which the birds received these trials, and whether or not they cached in the cage to the left or right of the observer during the 'observed' condition.

Both of the storer's cages were differentially lit. Opaque metal screens were attached to the top and side of one half of the cage, and transparent sheets to the other. An anglepoise lamp was placed next to the transparent sheet to increase light levels on that side of the cage, and a second lamp was placed by the opaque screen but switched off. This resulted in a 'shady' and a 'sunny' side of the cage. The ratio of illuminance between the 'sunny' and 'shady' sites was 4 : 1. The temperature of the caching substrate was 28 °C on the 'sunny' side and 26 °C on the 'shady' side.

A Sony DCR-PC8E digital handycam recorded caching trials with input from three colour cameras (Sanyo, VCC-6572P). Each camera was positioned *ca.* 30 cm from the front of each cage. The jays' behaviour was recorded throughout the 15 min caching period. During this time the storers were given two caching trays and a 15 cm bowl containing 50 pine nuts.

The caching trays (6 cm × 25 cm), contained a 2 × 8 array of 2.5 cm ice cube moulds filled with corn kibble, with each of the moulds acting as a possible caching site. Each tray was attached to the centre of a wooden board (15 cm × 32 cm) and made visuo-spatially unique by attaching an arrangement of Lego bricks along one of the long sides. The trays were positioned in the cage equidistantly from both the observer and the food bowl. One tray was placed on the 'sunny' side of the cage and one on the 'shady' side.

At the end of the caching period, the trays and food bowl were removed along with any caches made in the storer's cage. The

experimenter then recorded the locations of the food items cached in either tray. Opaque dividers were then erected, and a retention period of 3 h followed before the trays were returned to the storer's cage, the storers were then able to recover their caches in private. During the recovery period, the experimenter recorded the number of caches recovered, and what proportion of these were eaten or re-cached. The trays were then removed and the maintenance diet returned to the cage.

The videos were scored to verify the number and location of caches and non-parametric statistics (Wilcoxon's matched pairs signed-rank test) were used to analyse the data, with condition ('in private' versus 'observed'), and tray ('sun' versus 'shade') as within-subject variables. Alpha was set at 0.05. As Mundry & Fischer (1998) have suggested that inflated *p*-values can result from the use of modern statistical programs to perform non-parametric statistics on behavioural data with low sample sizes, we performed all of our Wilcoxon tests by hand (Siegel & Castellan 1988).

### 3. RESULTS

#### (a) Caching

The jays cached a median of two items (inter-quartile range (IQR) = 8), and there was no significant difference between the number of items cached on 'observed' (median = 2, IQR = 5) and 'in private' trials (median = 3.5, IQR = 12;  $n = 9$ ,  $T = 15$ ,  $p > 0.5$ ). As figure 2 shows, however, there was a significant difference in the number of items cached on the 'sunny' and 'shady' sides of the cage when observed ('sun' median = 0, IQR = 2; 'shade' median = 5, IQR = 9.25;  $n = 6$ ,  $T = 21$ ,  $p = 0.016$ ), whereas 'in private' no significant differences were found ('sun' median = 3, IQR = 8.75; 'shade' median = 4, IQR = 13.25;  $n = 8$ ,  $T = 21$ ,  $p = 0.38$ ).

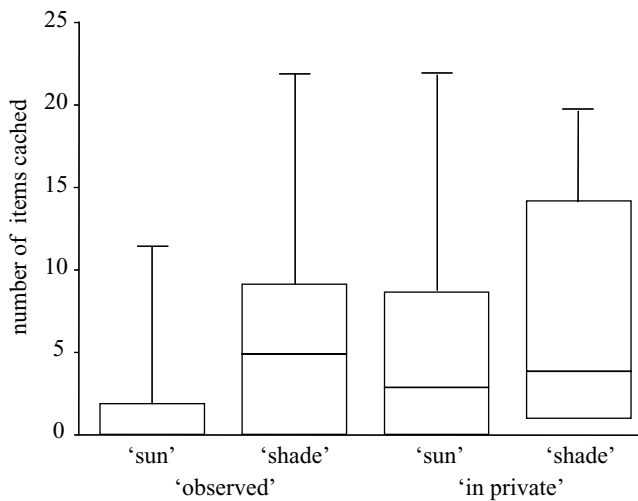


Figure 2. A box and whisker plot showing the median number, 25th percentile, and 75th percentile of items cached in the 'sunny' and 'shady' trays for both observed and in private conditions.

#### (b) Recovery

The jays recovered a median of 0% of their caches (IQR = 0.2). The low levels of recovery (three birds in the 'observed' condition and two in the 'in private' condition) meant that it was not possible to detect any differences between the proportion of items recovered after the 'observed' (median = 0, IQR = 0.61) and 'in private' trial (median = 0, IQR = 0.07). There was no significant difference in the proportion of items recovered from either the 'sunny' or 'shady' sides of the cage when observed ('sun' median = 0.31, IQR = 0.81; 'shade' median = 0, IQR = 0.04;  $n = 3$ ,  $T = 4$ ,  $p = 0.38$ ). The low level of recovery after caching in the 'in private' condition meant a statistical comparison of the proportion of items recovered from the 'sunny' (median = 0, IQR = 0.05) and 'shady' (median = 0, IQR = 0.02) sides of the home cage was not possible.

Low levels of recovery also meant that statistical analysis of the proportion of items recovered and then eaten or re-cached was not possible. Items were eaten from both trays during both 'observed' ('sun' median = 0.25, IQR = 0.5; 'shade' median = 0.5, IQR = 1) and 'in private' caching conditions ('sun' median = 0.55, IQR = 0.9; 'shade' median = 0.5, IQR = 1). However, the pattern of re-caching behaviour differed between caching conditions. When birds had cached in private they moved approximately equal amounts from both trays ('sun' median = 0.45, IQR = 0.9; 'shade' median = 0.5, IQR = 1). By contrast, when they had been observed during caching, birds selectively moved only those items that had been cached in the sunny tray ('sun' median = 0.75, IQR = 0.5; 'shade' median = 0, IQR = 0).

#### 4. DISCUSSION

These results demonstrate that social context and environmental variables affect a jay's choice of cache site. Although jays cached preferentially in the shaded tray when observed during caching, both trays were used

equally when caching occurred in private. We suggest that this differentiation in site use may stem from the potential threat posed by the observer. By caching only in the shaded tray in the presence of possible thieves, the level and quality of information available for visual transfer, and thus the chance of cache theft, is reduced.

One possible explanation for the unusually low recovery rate is that we used pine nuts, which are not as preferred as the wax worms that we have used in previous studies. Nonetheless, the pattern of re-caching was consistent with the prediction, that storers should preferentially re-cache those items to which the observer has had the greatest visual access and so are therefore most at risk of theft. Thus items were re-cached from both trays in the 'in private' condition, but only from the 'sunny' tray in the 'observed' condition.

The preference to cache in the 'shady' tray during the 'observed' condition could not be explained in terms of an aversion to the light source, because birds cached equal amounts in both trays during the 'in private' condition. The probability that cache sites were selected based on differential reinforcement can also be discarded as caches were not pilfered, and only a single trial was given in each of the two caching conditions.

In contrast to previous studies (e.g. Emery & Clayton 2001), it was not possible for the storer to use the presence or absence of an observer as a cue to caching behaviour. Although a preference for 'out of view' sites has been demonstrated in the presence of an observer, it is not clear whether the birds differentiated between what the observer could see, as opposed to what the storer saw. As such the observer may appear to be absent when the storer is behind the barrier. In this experiment the observer was always in view of the storer. The selective use of the shaded tray when observed during caching therefore raises the intriguing possibility that the jays may act to reduce the transfer of visual information, and therefore use shade as a cache protection strategy. Future studies will address the effect that this cache protection strategy may have on the recovery accuracy of the observer.

These results raise the intriguing question of whether the jays understand what an observer can and cannot see. They also add to the other strategies which scrub-jays use to protect their caches such as caching out of view, re-caching and caching at a distance from observers (Emery & Clayton 2001; Emery *et al.* 2004; Dally *et al.* 2005), which may provide convergent evidence for complex social cognition in scrub-jays.

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- Bednekoff, P. & Balda, R. 1996 Social caching and observational spatial memory in pinyon jays. *Behaviour* **133**, 807–826.
- Bugnyar, T. & Kotrschal, K. 2002 Observational spatial learning and the raiding of food caches in ravens, *Corvus corax*: is it tactical deception? *Anim. Behav.* **64**, 185–195.

- Clayton, N. S., Griffiths, D. P., Emery, N. J. & Dickinson, A. 2001 Elements of episodic memory in animals. *Phil. Trans. R. Soc. Lond. B* **356**, 1483–1491. (DOI 10.1098/rstb.2001.0947.)
- Dally, J. M., Emery, N. J. & Clayton, N. S. 2005 Cache protection strategies by western scrub-jays (*Aphelocoma californica*): implications for social cognition. *Anim. Behav.* (Submitted.)
- Emery, N. J. & Clayton, N. S. 2001 Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414**, 443–446.
- Emery, N. J., Dally, J. & Clayton, N. S. 2004 Western scrub-jays (*Aphelocoma californica*) use cognitive strategies to protect their caches from thieving conspecifics. *Anim. Cogn* **7**, 37–43.
- Goodwin, D. 1955 Jays and crows recovering hidden food. *Br. Birds* **48**, 181–183.
- Heinrich, B. 1999 *Mind of the raven*. New York: Harper Collins.
- Källander, H. 1978 Hoarding in the rook (*Corvus frugilegus*). *ANSER Suppl.* **3**, 124–128.
- Mundry, R. & Fischer, J. 1998 Use of statistical programs for non-parametric tests of small samples often lead to incorrect *P*-values: examples from animal behaviour. *Anim. Behav.* **56**, 256–259.
- Siegel, S. & Castellan Jr, N. J. 1988 *Nonparametric statistics for the behavioural sciences*. New York: McGraw-Hill.
- Simmons, K. E. L. 1970 Further observations on food-hiding in the corvidae. *Br. Birds* **63**, 175–177.