

Western scrub-jays conceal auditory information when competitors can hear but cannot see

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Western scrub-jays (*Aphelocoma californica*) engage in a variety of cache-protection strategies to reduce the chances of cache theft by conspecifics. Many of these strategies revolve around reducing visual information to potential thieves. This study aimed to determine whether the jays also reduce auditory information during caching. Each jay was given the opportunity to cache food in two trays, one of which was filled with small pebbles that made considerable noise when cached in ('noisy' tray), whereas the other one contained soil that made little detectable noise when cached in ('quiet' tray). When the jays could be heard, but not seen, by a competitor, they cached proportionally less food items in the 'noisy' substrate than when they cached alone in the room, or when they could be seen and heard by competitors. These results suggest that western scrub-jays know when to conceal auditory information, namely when a competitor cannot see but can hear the caching event.

Keywords: western scrub-jays; social cognition; cache protection; corvids

1. INTRODUCTION

Many animals hide food for future consumption (Vander Wall 1990). These caches are susceptible to pilfering by other individuals, both heterospecifics and conspecifics. To reduce this cache pilferage, several species engage in cache-protection strategies to reduce the likelihood that their caches are stolen. Many of these strategies are now established in a variety of species, such as covering up cache sites with leaves so they are inconspicuous, reducing the frequency of caching when competitors are around, and aggressively defending them (reviewed in Dally *et al.* 2006). In addition, there are several cache-protection strategies that may be restricted to corvids, such as ravens and jays, which are the only food-storers known to use observational spatial memory to remember the location of caches made by others (Bugnyar & Kotrschal 2002; Watanabe & Clayton 2007). To defend against theft using observational spatial memory, corvids use protection strategies such as re-caching food when an

observing competitor leaves (Bossemma 1979; Emery & Clayton 2001), caching far away from an observer (Bugnyar & Kotrschal 2002; Dally *et al.* 2005), caching behind an object (Bugnyar & Kotrschal 2002; Dally *et al.* 2005) or caching in the shade (Dally *et al.* 2004). These latter strategies suggest that the cacher reduces the quality or amount of visual information available to potential pilferers.

Auditory information might provide another source of information to potential pilferers. In birds, many examples of the use of auditory information are available, for instance keeping quiet if a predatory threat is detected nearby (Marler & Slabbekoorn 2004). The aim of this study was to investigate whether western scrub-jays (*Aphelocoma californica*) know when to conceal auditory information as a cache-protection strategy. To reduce auditory information available to conspecifics, scrub-jays should preferentially cache in a substrate in which caching is relatively silent when a competitor is near but not in visual contact, but should be indifferent to whether a substrate is silent when caching alone, or when seen as well as heard during caching.

To test this hypothesis, scrub-jays were allowed to cache in three different situations: (i) alone: so that no competitor could see or hear the caching event; (ii) seen and heard: a competitor could see and hear the caching event; and (iii) heard but not seen: a competitor could hear the caching event but its view was obscured by an opaque barrier. In each condition the cacher was provided with two caching trays, which were placed such that they were both equidistant from the competitor's cage. One of the trays was filled with a substrate of small pebbles that made noise when cached in ('noisy' tray), whereas the other tray was filled with a soil substrate that made little, if any, detectable noise ('quiet' tray).

2. MATERIAL AND METHODS

The subjects of this experiment were eight (four males and four females) sexually mature hand-raised western scrub-jays that had prior experience with the cache-recovery paradigm. The birds were housed in pairs in cages measuring 2 m wide × 1 m deep × 1 m high, and were maintained inside on a 12 L : 12 D cycle on a maintenance diet supplemented with nuts, seeds, dog biscuits, various fruits, wax worms and meal worms. The maintenance diet was removed from the home cage 2 h before an experimental trial, ensuring that the jays were mildly hungry during caching. All the caching trials took place in the cacher's home cage and jays were provided with 50 waxworms. The jays could be separated by cage dividers, placing each jay into a 1 m × 1 m × 1 m compartment of the home-cage for testing.

During the 'alone' condition, all but the experimental birds were removed from the home-cages in the room and placed in a near-by aviary, and the test bird could see all the remaining empty cages. In the 'seen and heard' condition, transparent dividers ensured that the competitor had visual access to the caching bird. In the 'heard but not seen' condition, the jays were divided by opaque dividers so the competitor could only hear but not see the cacher. The birds received trials in the 'alone' condition first, in order to establish a baseline preference for caching in the two trays. In the 'seen and heard' and 'heard but not seen' conditions, the jays received only one caching trial, and no opportunity to recover the caches they had made, so that they were neither punished nor rewarded for caching in the particular trays. The order of these conditions was counterbalanced.

The caching sites were plastic ice-cube trays (25 cm × 6 cm) consisting of a 2 × 7 array of 2.5 cm cube moulds, each of which was a potential cache site. The moulds were filled with soil ('quiet' tray) or small pebbles ('noisy' tray). The jays had no experience with these substrates prior to the baseline trials. The trays were mounted onto a wooden board (35 cm × 15 cm), with a

visuo-spatially unique construction of Lego bricks attached to one of the long sides of the tray.

At the end of each 30-min caching period, the trays and food bowl were removed along with any caches made elsewhere in the cacher's cage. The experimenter then recorded the locations of the food items cached in either tray. Only in the 'alone' condition were the trays returned after 90 min of food restriction with the stored items in place. After 15 min the trays were exchanged for the maintenance diet.

Repeated-measures analysis of variance (ANOVA) were used to analyse the effect of condition (within-subject variable) on total number of items cached and proportions cached in the 'noisy' tray. The assumptions of sphericity and normally distributed data were not violated for either ANOVA. To break down possible main effects, tests of within-subject contrasts were used, in which the 'alone' and 'seen and heard' conditions were compared with the 'heard but not seen' condition. For the 'alone' condition, averages were taken over the trials in which food was cached in the trays. A paired-samples *t*-test was used to compare the average number of items cached in the 'noisy' and 'quiet' tray to determine a preference in the 'alone' condition. Alpha was set at 0.05 for all the experiments, and mean and s.e. are reported throughout. One bird failed to cache during the entire experiment and was excluded from the analyses. We recorded the number of items cached in the 'noisy' tray as a proportion of the total number of all the items cached ('noisy' tray + 'quiet' tray + 'out of tray'). Caches made outside the trays are considered to be quiet, as most of these caches were placed under the rubber floor mat lining the bottom of the cage. There was no substrate outside the trays.

3. RESULTS

In the 'alone' condition the jays cached a mean of 5.5 ± 1.1 items in the 'noisy' tray, and only 2.0 ± 0.6 items in the 'quiet' tray (paired-samples *t*-test: $t_6 = 3.978$; $p = 0.007$). In total, a mean number of 15.8 ± 3.5 items were cached, and there was no significant difference between the number of items cached in the 'alone' (13.1 ± 4.3), 'seen and heard' (14.9 ± 4.1) and 'heard but not seen' (19.3 ± 4.3) conditions (repeated-measures ANOVA: $F_{2,12} = 1.17$; $p = 0.34$).

The proportion of items cached in the 'noisy' tray was 0.58 ± 0.11 in the 'alone' condition and 0.66 ± 0.15 in the 'seen and heard' condition, whereas it was only 0.15 ± 0.01 in the 'heard but not seen' condition (figure 1). Indeed, there was a significant effect of condition on these proportions ($F_{2,12} = 5.29$, $p = 0.022$), and the contrasts revealed that the proportion cached in the 'noisy' tray in the 'alone' ($F_{1,6} = 7.69$, $p = 0.032$), and 'seen and heard' conditions ($F_{1,6} = 10.80$, $p = 0.017$) were both significantly higher than in the 'heard but not seen' condition. Table 1 provides the individual data for each bird in each condition.

4. DISCUSSION

Western scrub-jays cached proportionally less in the 'noisy' tray when a competitor could hear but not see the caching event ('heard but not seen'), compared with when no competitor could see or hear the caching ('alone') or when a competitor could both see and hear the caching event ('seen and heard'). This finding suggests that these birds differentiate between these conditions not only on the basis of when a competitor can and cannot see, but specifically only reduce sound when the competitor relies on hearing alone.

How can we explain the reduction in the proportion of items cached in the 'noisy' tray in the 'heard but not seen' condition? A preference for either substrate due

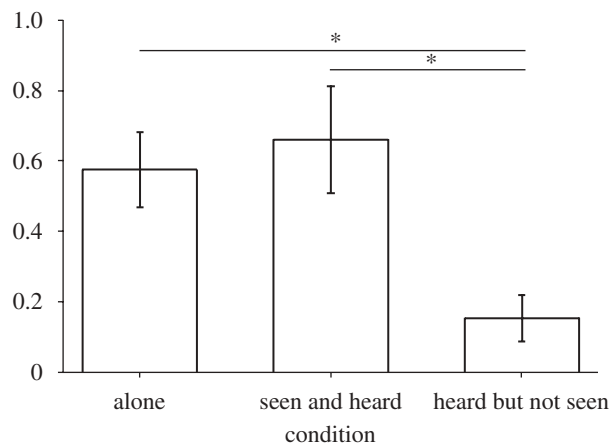


Figure 1. The proportion of items cached in the 'noisy' tray in the three different conditions (mean \pm s.e.). The 'heard but not seen' condition was significantly different from both other conditions. * $p < 0.05$.

to simple associative learning can be ruled out because the jays had no prior experience with the two particular substrates used, and as the jays had no opportunity to recover the caches they had made, they were neither rewarded nor punished for caching in the trays in either the 'seen and heard' or the 'heard but not seen' conditions. Furthermore, we cannot explain the jays' behaviour in terms of an exclusive preference to cache in the 'quiet' tray since there was a significant preference for the 'noisy' tray in the 'alone' condition. Additionally, the preference to cache in the 'quiet' substrate was only manifest in the 'heard but not seen' condition.

The jays' decision of where to cache was also not based on the absence or presence of a competitor by itself because the jays showed a preference to cache in the 'noisy' tray in both the 'alone' and 'seen and heard' condition (in which, respectively, no competitor and a seeing and hearing competitor was present). The jays only cached differently in the condition in which the competitor could hear the caching event but not see it ('heard but not seen' condition).

Similar reasoning leads us to reject the hypothesis that the bird reacts solely to a competitor, independent of its state. As there is a difference between the conditions with a competitor (seeing and hearing versus hearing alone), the mere presence of a competitor is not pivotal to the expression of the cache-protection strategy of reducing auditory information. We conclude, therefore, that jays are sensitive to both visual and auditory information that a competitor may use to detect the location of their caches, and consequently the cachers only reduce sound when the competitor relies on hearing alone.

Another explanation for our results, not mutually exclusive, is that the caching jays reduced making sound in order to be able to listen to the activities of the competitors behind the partition. We cannot exclude this interpretation, but consider it more likely that the jays were primarily concerned with the protection of their food rather than the behaviour (which has to be inferred by listening) of the observer.

Table 1. The number of items cached in the ‘noisy’ tray (N), ‘quiet’ tray (Q) and ‘out of tray’ (O) and the proportion of items cached in the ‘noisy’ tray in the three different conditions per jay. For the ‘alone’ condition, averages are reported.

bird	alone		seen and heard		heard but not seen	
	proportion in ‘noisy’	no. of items (N; Q; O)	proportion in ‘noisy’	no. of items (N; Q; O)	proportion in ‘noisy’	no. of items (N; Q; O)
1	0.75	(3.0; 1.0; 0)	0.68	(17; 0; 8)	0.29	(7; 0; 17)
2	0.30	(5.7; 1.4; 12)	0.92	(11; 1; 0)	0.45	(10; 4; 8)
3	0.33	(11.0; 3.8; 18.5)	0.20	(6; 2; 22)	0.16	(4; 2; 19)
4	0.33	(6.5; 4.3; 9)	0.83	(10; 1; 1)	0.17	(6; 9; 20)
5	0.50	(2.0; 2.0; 0)	1	(21; 0; 0)	0	(0; 7; 14)
6	1	(4.0; 0; 0)	1	(2; 0; 0)	0	(0; 0; 6)
7	0.83	(6.3; 1.3; 0)	0	(0; 2; 0)	0	(0; 2; 0)

Our findings are comparable to those found in the studies of Melis *et al.* (2006) and Santos *et al.* (2006), in which chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*) concealed auditory information in a competitive situation. In comparison with these studies, we did find an effect after only one trial (in contrast to Melis *et al.* 2006) and we included an additional control condition (the ‘alone’ condition, in contrast to Santos *et al.* 2006) to exclude the possibility of a baseline preference for always being silent, except when observed. Consequently, we argue that food-caching western scrub-jays conceal auditory information if—and only if—the competitors can hear, but cannot see the cachers. In short, western scrub-jays know when to be as quiet as a mouse.

These experiments comply with the UK Home Office regulations concerning animal research and welfare, as well as the University of Cambridge regulations on the use of animals. We thank Chris Bird for advice and discussion.

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