California scrub-jays reduce visual cues available to potential pilferers by matching food colour to caching substrate

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Abstract

Some animals hide food to consume later, however these caches are susceptible to theft by conspecifics and heterospecifics. Caching animals can use protective strategies to minimise sensory cues available to potential pilferers, such as caching in shaded areas and in quiet substrate. Background matching (where object patterning matches the visual background) is commonly seen in prey animals to reduce conspicuousness, and caching animals may also use this tactic to hide caches, for example by hiding coloured food in a similar coloured substrate. We tested whether California scrub-jays (*Aphelocoma californica*) camouflage their food in this way by offering them caching substrates that either matched or did not match the colour of food available for caching. We also determined whether this caching behavior was sensitive to social context by allowing the birds to cache when a conspecific potential pilferer could be both heard and seen (acoustic and visual cues present), or unseen (acoustic cues only). When caching events could be both heard and seen by a potential pilferer, birds cached randomly in matching and nonmatching substrates. However, they preferentially hid food in the substrate that matched the food colour when only acoustic cues were present. This is a novel cache protection strategy that also appears to be sensitive to social context. We conclude that studies of cache protection strategies should consider the perceptual capabilities of the cacher and potential pilferers.

Introduction

Many animals hide food to retrieve and eat later [1]. These food caches are susceptible to theft by other animals, but the cacher can reduce the likelihood of theft by using protective strategies such as reducing caching in the presence of others and covering up caching sites to reduce conspicuousness [reviewed in 2]. Some species of corvids such as jays are prolific cachers that employ a variety of additional cache protection behaviours, including caching in shaded areas, caching in quiet substrates and caching food that an observing conspecific has low motivation to steal [3-6]. Most strategies attempt to reduce the number of sensory cues that potential pilferers can use to locate caches.

Birds and other caching animals could attempt to minimise other visual cues available for potential pilferers. Many animals conceal themselves from the attention of predators by bearing patterns with colouration that allows them to blend into the visual background, a type of camouflage called background matching [7]. Effective background matching minimises the visual contrast between an object and the background it is viewed against. Visual contrast can arise due to differences in chromatic (hue and saturation) and achromatic (brightness) aspects of the object and viewing background. By selecting a caching substrate that is visually similar to the food being hidden, animals may reduce the likelihood of a pilferer detecting partially hidden caches or locating caches when rooting through substrate. Social environment may also affect the value of this strategy, for example if a potential pilferer directly observes caching then there may be limited use in concealing visual contrast when there is already plenty of information about cache location available.

We tested whether California scrub-jays (*Aphelocoma californica*) attempted to minimize the visual contrast of their cached food by selecting an appropriate caching substrate. Birds were given a coloured food and a choice of two substrates to cache in: one that was of a similar colour to the food (i.e. lower visual contrast) and one of a dissimilar colour (i.e. higher visual contrast). We also tested whether social context affected caching behavior, by allowing birds to cache when a conspecific potential thief could be both heard and seen (‘seen’) and when the conspecific could be heard but not seen (‘unseen’). We predicted that birds would only minimize colour contrast when a potential pilferer could not see the caching event, and that they would cache randomly in either substrate when they could be seen.

Methods

We tested three female and two male California scrub-jays that were all nine years old. Birds were housed in indoor cages 4m long by 1m high by 1m deep and on a 12hr light:dark cycle. They were fed a maintenance diet supplemented with seeds, fruit and wax worms. All food was removed from the cages one hour before testing to ensure that it was not available for caching. Trials took place in the focal bird's home cage, where birds could be separated using transparent or opaque cage dividers. In the 'seen' condition, transparent dividers were used so that the focal bird could see and hear a conspecific in a neighbouring cage. In the 'unseen' condition, opaque dividers were used so that the focal bird could hear but not see the conspecific.

The focal bird was presented with two caching trays 25x6cm that contained a 2x8 array of ice cube moulds. Coloured aquarium gravel in five colours (Pettex Roman gravel: Sonic Blue, Lemon Zest, Barbie Pink, Rosso Red and Ivy Green) was used as a caching substrate. We used food dye (PME: pink, blue, yellow, red and green) to approximately colour match batons of cheese (Tesco Value mild cheddar cut into 15x5x5mm batons that weighed ~1g each) to each substrate. They had prior experience of yellow cheese as an occasional component of their maintenance diet, but they had no experience with the other coloured cheeses. We measured the spectral reflectance of each substrate and cheese to confirm that each cheese was closest in avian colourspace to the putative matching substrate (Figure 1b, see Electronic Supplementary Material for full details of colour analysis). Green cheese was more similar to yellow substrate than green substrate so the data from these trials were analysed separately, but all other cheese and substrate matches were appropriately colour matched.

In each trial the focal bird was presented with two trays that each contained a different colour substrate. A food bowl that contained 30g of cheese that matched the colour of one of the caching substrates was placed 10cm in front of the two trays. The order of trials (cheese and substrate colours used) and location of each tray relative to the food bowl (left or right) was randomised. The trays and food were left in the cage for 30 minutes before being removed. The substrates were then sifted to locate any cached items that were weighed to determine the amount of food cached in each substrate. All birds cached in at least one seen and one unseen trial. Due to husbandry issues the full number of trials testing every combination of substrates could not take place, but every bird was presented with every colour of cheese in each social condition. The proportional weight each bird cached across all trials in each social condition (seen and unseen) was averaged and Wilcoxon's matched pairs signed-rank tests were used to test for differences in the proportion of cheese cached in each condition. To test whether social status affected the amount of cheese cached in the matching substrate, the data were analysed using a generalized linear mixed model with a binomial (logit) distribution using the lme4 package in R 3.3.0 [8, 9]. The response variable was the proportion of cheese cached in the matching substrate and we included social status (seen/unseen) as a predictor and individual bird as a random effect. All data are available from [10].

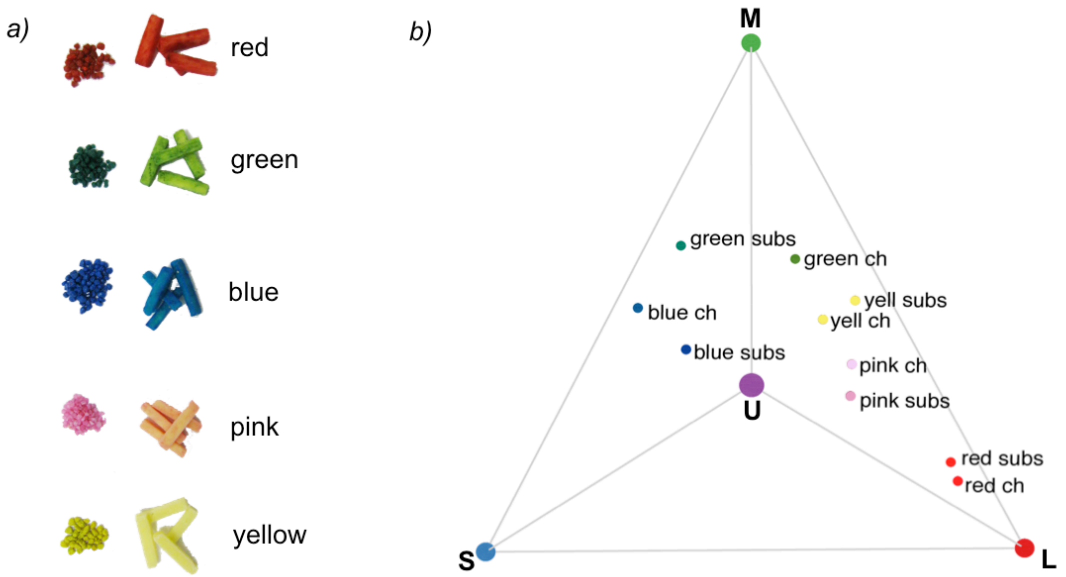

Figure 1a) The substrates (left) and cheeses (right) used in the experiment; b) tetrahedral plot showing the position of cheese (ch) and substrate (subs) colour in avian colour space. Labels at vertices represent the relative stimulation of U (ultraviolet), S (short), M (medium) and L (long) wavelength photoreceptor channels. The ultraviolet channel is represented by the top of the tetrahedron pointing out towards the viewer but is not shown here due to small variance in the amount of UV present in the cheeses and substrates.

Results

Caching rates were low in the seen condition and only took place in nine of 25 trials (36%) compared to 57 of 85 unseen trials (67%). There was no difference between the average weight of food each bird cached in each condition (mean±SE: seen= 5.34±2.0g, unseen=5.20±2.6g; 66 trials, n=5, Wilcoxon T=8, p>0.5; ESM Table 1). In seen trials, birds did not prefer to cache in one substrate colour over another (pseudomedian=0.016, 95% CI [-0.49, 0.51], Z=0.27, p=0.44, r=0.09; Figure 2). In the unseen trials, birds preferentially cached in the matching substrate (pseudomedian=0.47, 95% CI [0.23, 0.84], Z=2.02, *p*=0.031; Figure 2). Approximately 30% more food was cached in the matching substrate compared to the nonmatching substrate in the unseen condition, a medium to large effect (r = 0.64). Overall, birds also cached a higher proportion of cheese in the matching substrate when they were unseen compared to when they were seen, although the effect size was small (GLMM z=2.12, p=0.034; r=0.07; Figure 2). In the three trials (all unseen social condition) where green cheese was offered with green and yellow substrates there did not appear to be a large difference in the proportion of cheese cached in matching or nonmatching substrates, perhaps due to the perceptual similarity of these colours (mean matching=0.66±0.17, nonmatching=0.34±0.17; n=3).

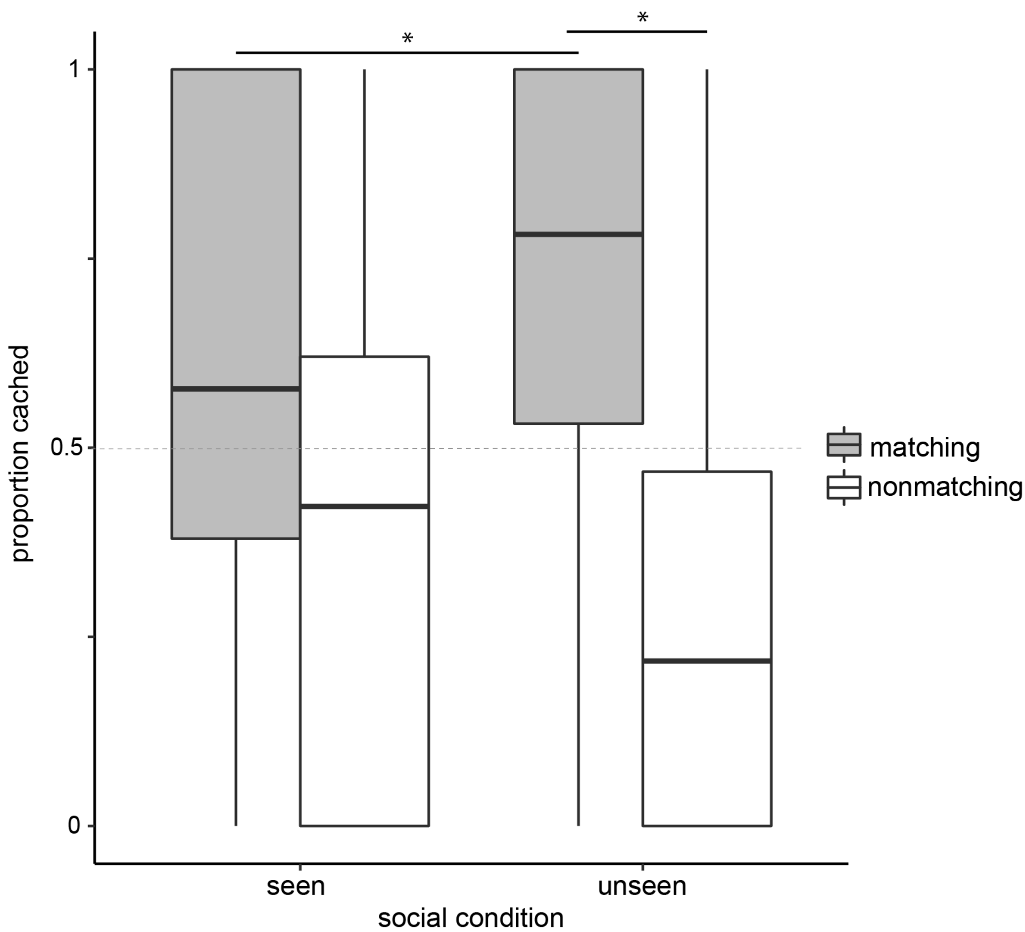

Figure 2. Median, 25^{th} and 75^{th} centile of proportion of food cached in matching (grey) and nonmatching (white) substrates in seen and unseen conditions. Dotted grey line represents chance (proportion=0.5), asterisks indicate significant differences between groups.

Discussion

Scrub-jays preferentially cached food in substrate that matched the colour of their food when a potential pilferer could not see them caching, but they cached randomly in either substrate when they could be seen. Birds cached proportionally more in the matching substrate when unseen due to a) caching much less in the non-matching substrate within trials and b) caching slightly more compared to the amount cached in the matching substrate when seen. As there is a much higher likelihood of theft when a caching event is observed, concealing visual contrast may be of limited efficacy in these cases. Instead, the cacher can stop or reduce caching [11], increase caching to offset predicted pilfering [12], move caches [13], or re-cache once the observer has left [14]. We did not observe reduced or increased levels of caching and birds did not appear to move caches around often, perhaps because there was limited space for hiding food. However, the focal bird may have cached in either substrate when observed to allow for the possibility of later re-caching into the matching substrate when the conspecific was no longer present [13].

When given the opportunity to cache without being seen, scrub-jays preferentially cached in the substrate that had lower visual contrast. In the wild, scrub-jays cache colourful fruits and berries as well as less colourful nuts and seeds, so colour matching between food and substrate may offer a valuable cache protection strategy in the wild. Reducing contrast is likely beneficial because brightly coloured food items can be detected from large distances and birds attend to chromatic contrast when foraging [15, 16]. Birds did not choose which caching substrate to use based on familiarity, as their usual caching substrate was beige. The ability to match food to caching substrate without prior experience or training suggests that this is a naturally occurring behaviour that is relatively plastic. Furthermore, the ability to use colour cues during caching is unlikely to be limited to scrub-jays given that magpies (*Pica pica*) can rapidly learn to discriminate between red and blue food types of differing nutritional value when retrieving caches [17], and many animals use colour cues (including contrast) during foraging [18, 19].

The colours used in this study were easily discriminable to the birds, and future work could use substrates with smaller differences between colours to determine how carefully scrub-jays match their caches to substrate colour. Birds appear to prioritise chromatic cues when foraging, as chromatic contrast is used in object discrimination [20] and camouflaged prey generally minimise chromatic contrast [21]. Varying the chromatic and achromatic contrast of food against substrates would confirm that birds preferentially minimise chromatic contrast over achromatic contrast, as we would expect in this context when potential pilferers were other birds. It would be interesting to give scrub-jays experience of mammalian pilferers to determine whether they adjust their caching behaviour in response to the visual system of the potential pilferer. Mammals have dichromatic vision and are more likely to use achromatic contrast when foraging [22], so minimising this would reduce conspicuousness. There are fewer studies on cache protection strategies in non-avian species, but we might expect that if caching mammals exhibit similar strategies to birds, they would reduce achromatic contrast if conspecifics were the primary pilferers. Our findings demonstrate that visual perception, alongside cognitive abilities such as social intelligence, is important to consider when investigating the evolution of caching strategies.

Ethics

Ethical approval was given by the UK Home Office (PPL no. 80/2519) and the University of Cambridge ethics committee.

Data availability

Data can be found at https://doi.org/10.6084/m9.figshare.4690015

Competing interests

We have no competing interests.

Author contributions

LAK designed and carried out the study, analysed the data and drafted the manuscript. NSC aided in experimental design, provided aviary facilities and commented on the manuscript. All authors gave final approval of the version to be published and agreed to be accountable for all aspects of the work.

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