

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36

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

Laura A. Kelley^{1,2} & Nicola S. Clayton¹

¹ Department of Psychology, University of Cambridge, Downing Street, Cambridge
UK CB2 3EB

² Current address: Centre for Ecology and Conservation, University of Exeter, Penryn
Campus, Cornwall TR10 9FE, UK

Keywords: cache protection, visual contrast, pilfering

37 **Abstract**

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

57

58

59 **Introduction**

60

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

70

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

84

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

95

94 **Methods**

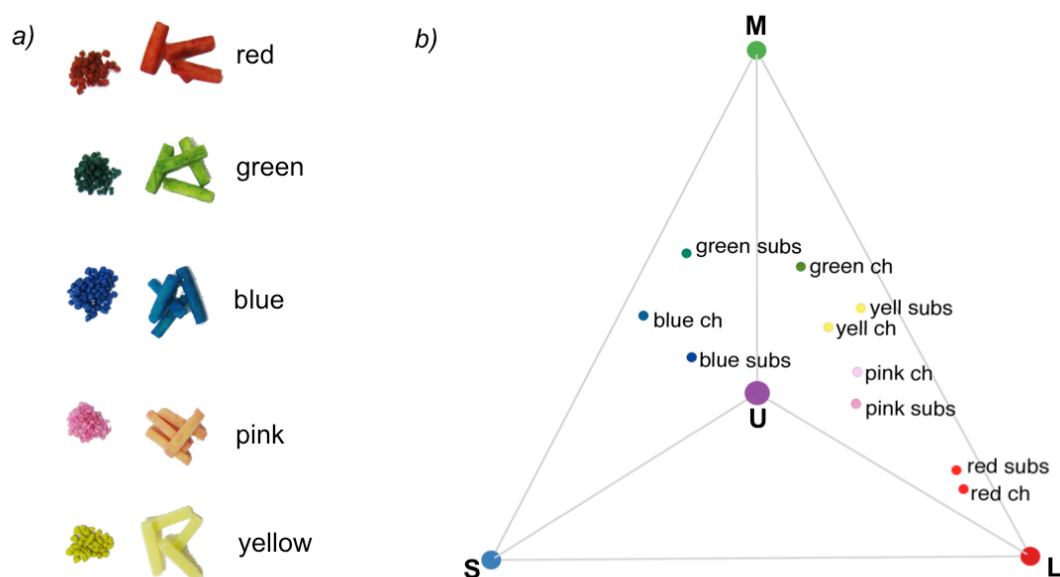
95

96 We tested three female and two male California scrub-jays that were all nine years
97 old. Birds were housed in indoor cages 4m long by 1m high by 1m deep and on a
98 12hr light:dark cycle. They were fed a maintenance diet supplemented with seeds,
99 fruit and wax worms. All food was removed from the cages one hour before testing to
100 ensure that it was not available for caching. Trials took place in the focal bird's home
101 cage, where birds could be separated using transparent or opaque cage dividers. In
102 the 'seen' condition, transparent dividers were used so that the focal bird could see
103 and hear a conspecific in a neighbouring cage. In the 'unseen' condition, opaque
104 dividers were used so that the focal bird could hear but not see the conspecific.

105 The focal bird was presented with two caching trays 25x6cm that contained a
106 2x8 array of ice cube moulds. Coloured aquarium gravel in five colours (Pettex
107 Roman gravel: Sonic Blue, Lemon Zest, Barbie Pink, Rosso Red and Ivy Green) was
108 used as a caching substrate. We used food dye (PME: pink, blue, yellow, red and
109 green) to approximately colour match batons of cheese (Tesco Value mild cheddar
110 cut into 15x5x5mm batons that weighed ~1g each) to each substrate. They had prior
111 experience of yellow cheese as an occasional component of their maintenance diet,
112 but they had no experience with the other coloured cheeses. We measured the
113 spectral reflectance of each substrate and cheese to confirm that each cheese was
114 closest in avian colourspace to the putative matching substrate (Figure 1b, see
115 Electronic Supplementary Material for full details of colour analysis). Green cheese
116 was more similar to yellow substrate than green substrate so the data from these
117 trials were analysed separately, but all other cheese and substrate matches were
118 appropriately colour matched.

119 In each trial the focal bird was presented with two trays that each contained a
120 different colour substrate. A food bowl that contained 30g of cheese that matched the
121 colour of one of the caching substrates was placed 10cm in front of the two trays.
122 The order of trials (cheese and substrate colours used) and location of each tray
123 relative to the food bowl (left or right) was randomised. The trays and food were left
124 in the cage for 30 minutes before being removed. The substrates were then sifted to
125 locate any cached items that were weighed to determine the amount of food cached
126 in each substrate. All birds cached in at least one seen and one unseen trial. Due to
127 husbandry issues the full number of trials testing every combination of substrates
128 could not take place, but every bird was presented with every colour of cheese in
129 each social condition. The proportional weight each bird cached across all trials in
130 each social condition (seen and unseen) was averaged and Wilcoxon's matched

131 pairs signed-rank tests were used to test for differences in the proportion of cheese
 132 cached in each condition. To test whether social status affected the amount of
 133 cheese cached in the matching substrate, the data were analysed using a
 134 generalized linear mixed model with a binomial (logit) distribution using the lme4
 135 package in R 3.3.0 [8, 9]. The response variable was the proportion of cheese
 136 cached in the matching substrate and we included social status (seen/unseen) as a
 137 predictor and individual bird as a random effect. All data are available from [10].



138

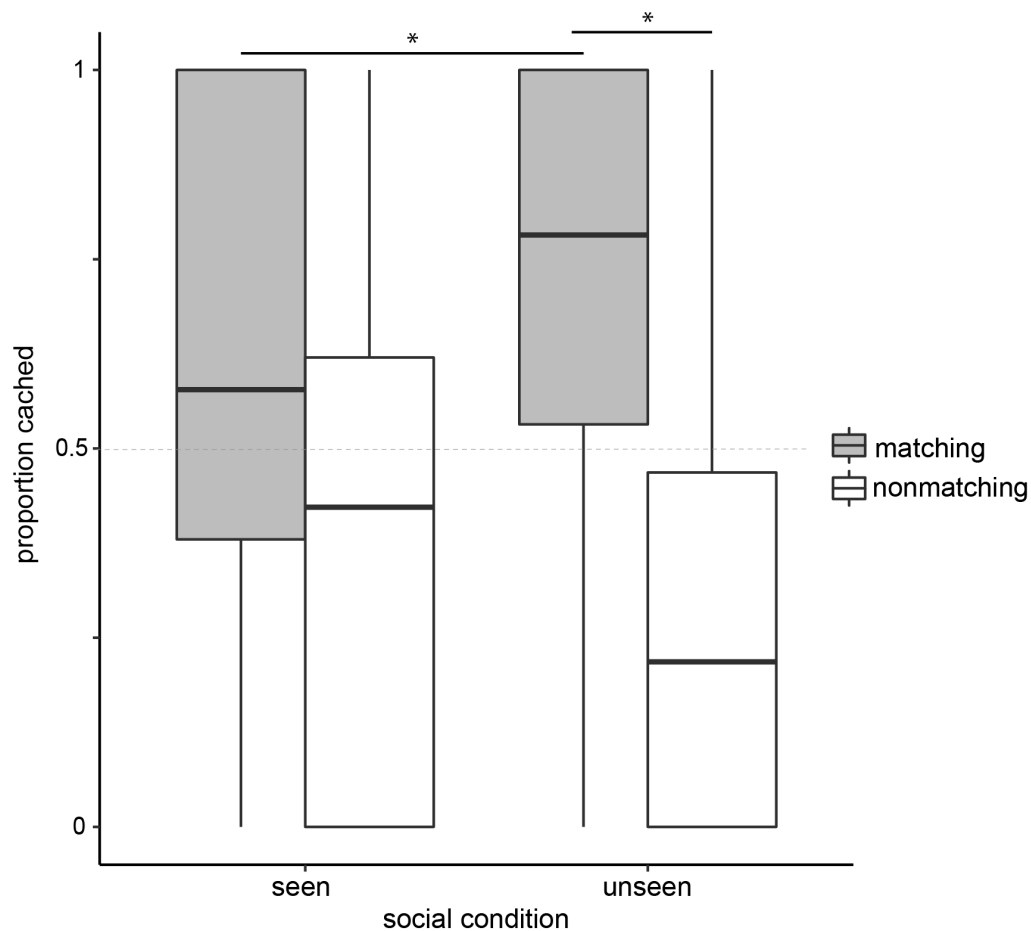
139 Figure 1a) The substrates (left) and cheeses (right) used in the experiment; b)
 140 tetrahedral plot showing the position of cheese (ch) and substrate (subs) colour in
 141 avian colour space. Labels at vertices represent the relative stimulation of U
 142 (ultraviolet), S (short), M (medium) and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

146

147 Results

148 Caching rates were low in the seen condition and only took place in nine of 25 trials
 149 (36%) compared to 57 of 85 unseen trials (67%). There was no difference between
 150 the average weight of food each bird cached in each condition (mean±SE: seen=
 151 5.34±2.0g, unseen=5.20±2.6g; 66 trials, n=5, Wilcoxon $T=8$, $p>0.5$; ESM Table 1). In
 152 seen trials, birds did not prefer to cache in one substrate colour over another
 153 (pseudomedian=0.016, 95% CI [-0.49, 0.51], $Z=0.27$, $p=0.44$, $r=0.09$; Figure 2). In

154 the unseen trials, birds preferentially cached in the matching substrate
 155 (pseudomedian=0.47, 95% CI [0.23, 0.84], $Z=2.02$, $p=0.031$; Figure 2).
 156 Approximately 30% more food was cached in the matching substrate compared to
 157 the nonmatching substrate in the unseen condition, a medium to large effect ($r =$
 158 0.64). Overall, birds also cached a higher proportion of cheese in the matching
 159 substrate when they were unseen compared to when they were seen, although the
 160 effect size was small (GLMM $z=2.12$, $p=0.034$; $r=0.07$; Figure 2). In the three trials
 161 (all unseen social condition) where green cheese was offered with green and yellow
 162 substrates there did not appear to be a large difference in the proportion of cheese
 163 cached in matching or nonmatching substrates, perhaps due to the perceptual
 164 similarity of these colours (mean matching= 0.66 ± 0.17 , nonmatching= 0.34 ± 0.17 ;
 165 $n=3$).
 166



167
 168 Figure 2. Median, 25th and 75th centile of proportion of food cached in matching (grey)
 169 and nonmatching (white) substrates in seen and unseen conditions. Dotted grey line
 170 represents chance (proportion=0.5), asterisks indicate significant differences
 171 between groups.
 172

173 Discussion

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

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

202 The colours used in this study were easily discriminable to the birds, and
203 future work could use substrates with smaller differences between colours to
204 determine how carefully scrub-jays match their caches to substrate colour. Birds
205 appear to prioritise chromatic cues when foraging, as chromatic contrast is used in
206 object discrimination [20] and camouflaged prey generally minimise chromatic
207 contrast [21]. Varying the chromatic and achromatic contrast of food against
208 substrates would confirm that birds preferentially minimise chromatic contrast over
209 achromatic contrast, as we would expect in this context when potential pilferers were

210 other birds. It would be interesting to give scrub-jays experience of mammalian
211 pilferers to determine whether they adjust their caching behaviour in response to the
212 visual system of the potential pilferer. Mammals have dichromatic vision and are
213 more likely to use achromatic contrast when foraging [22], so minimising this would
214 reduce conspicuousness. There are fewer studies on cache protection strategies in
215 non-avian species, but we might expect that if caching mammals exhibit similar
216 strategies to birds, they would reduce achromatic contrast if conspecifics were the
217 primary pilferers. Our findings demonstrate that visual perception, alongside cognitive
218 abilities such as social intelligence, is important to consider when investigating the
219 evolution of caching strategies.

220

221 **Ethics**

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

224

225 **Data availability**

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

227

228 **Competing interests**

229 We have no competing interests.

230

231 **Author contributions**

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

236 **Acknowledgements**

237 We are extremely grateful to two anonymous reviewers for their comments that
238 greatly improved the manuscript and to Ben Longdon for assistance with analysis.

239 **Funding**

240 LAK received funding from the People Programme (Marie Curie Actions) of the
241 European Union's Seventh Framework Programme (FP7/2007-2013) under REA
242 grant agreement PIFI-GA-2012-327423.

243

244 **References**

- 245 [1] Vander Wall, S.B. 1990 *Food hoarding in animals*. Chicago, The University of
246 Chicago Press.
- 247 [2] Dally, J.M., Clayton, N.S. & Emery, N.J. 2006 The behaviour and evolution of
248 cache protection and pilferage. *Anim. Behav.* **72**, 13-23.
- 249 [3] Dally, J.M., Emery, N.J. & Clayton, N.S. 2004 Cache protection strategies by
250 western scrub-jays (*Aphelocoma californica*): hiding food in the shade. *Proceedings*
251 *of the Royal Society B* **271**, S387-390.
- 252 [4] Dally, J.M., Emery, N.J. & Clayton, N.S. 2005 Cache protection strategies by
253 western scrub-jays, *Aphelocoma californica*: implications for social cognition. *Anim.*
254 *Behav.* **70**, 1251-1263.
- 255 [5] Stulp, G., Emery, N.J., Verhulst, S. & Clayton, N.S. 2009 Western scrub-jays
256 conceal auditory information when competitors can hear but cannot see. *Biol. Lett.* **5**,
257 583-585.
- 258 [6] Ostojić, L., Legg, E.W., Brecht, K.F., Lange, F.L., Deininger, C., Mendl, M. &
259 Clayton, N.S. 2017 Current desires of conspecific observers affect cache-protection
260 strategies in California scrub-jays and Eurasian jays. *Curr. Biol.* **27**, R43-R56.
- 261 [7] Stevens, M. & Merilaita, S. 2009 Animal camouflage: current issues and new
262 perspectives. *Philosophical Transactions of the Royal Society B* **364**, 423-427.
263 (doi:10.1098/rstb.2008.0217).
- 264 [8] Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015 Fitting linear mixed-effects
265 models using lme4. *Journal of Statistical Software* **67**, 1-48.
- 266 [9] R-Core-Team. 2016 A language and environment for statistical computing.
267 (Vienna, Austria, R Foundation for Statistical Computing.
- 268 [10] Kelley, L.A. & Clayton, N.S. 2017 Data from: California scrub-jays reduce visual
269 cues available to potential pilferers by matching food colour to caching substrate.
270 *Figshare* <https://doi.org/10.6084/m9.figshare.4690015>.
- 271 [11] Lahti, K. & Rytönen, S. 1996 Presence of conspecifics, time of day and age
272 affect willow tit food hoarding. *Anim. Behav.* **52**, 631-636.
- 273 [12] Bossema, I. 1979 Jays and oaks: an eco-ethological study of a symbiosis.
274 *Behaviour* **70**, 1-116.
- 275 [13] Emery, N.J. & Clayton, N.S. 2001 Effects of experience and social context on
276 prospective caching strategies by scrub jays. *Nature* **414**, 443-446.
- 277 [14] Dally, J.M., Emery, N.J. & Clayton, N.S. 2005 The social suppression of caching
278 in Western scrub-jays (*Aphelocoma californica*). *Behaviour* **142**, 961-977.
- 279 [15] Schaefer, H.M., Levey, D.J., Schaefer, V. & Avery, M.L. 2006 The role of
280 chromatic and achromatic signals for fruit detection by birds. *Behav. Ecol.* **17**, 784-
281 789.
- 282 [16] Cazetta, E., Schaefer, H.M. & Galetti, M. 2009 Why are fruits colorful? The
283 relative importance of achromatic and chromatic contrasts for detection by birds.
284 *Evol. Ecol.* **23**, 233-244.
- 285 [17] Zinkivskaya, A., Nazir, F. & Smulders, T.V. 2009 *What-Where-When* memory in
286 magpies (*Pica pica*). *Animal Cognition* **12**, 119-125.
- 287 [18] Schmidt, V., Schaefer, H.M. & Winkler, H. 2004 Conspicuousness, not colour as
288 foraging cue in plant-animal signalling. *Oikos* **106**, 551-557.
- 289 [19] Spaethe, J., Tautz, J. & Chittka, L. 2001 Visual constraints in foraging
290 bumblebees: flower size and color affect search time and flight behavior.
291 *Proceedings of the Academy of Natural Sciences* **98**, 3898-3903.
- 292 [20] Osorio, D., Miklósi, A. & Gonda, Z. 1999 Visual ecology and perception of
293 coloration patterns by domestic chicks. *Evol. Ecol.* **13**, 673-689.
- 294 [21] Théry, M., Debut, M., Gomez, D. & Casas, J. 2005 Specific color sensitivities of
295 prey and predator explain camouflage in different visual systems. *Behav. Ecol.* **16**,
296 25-29.

297 [22] Hiramatsu, C., Melin, A.D., Aureli, F., Schaffner, C.M., Vorobyev, M.,
298 Matsumoto, Y. & Kawamura, S. 2008 Importance of achromatic contrast in short-
299 range fruit foraging of primates. *PLoS ONE* **3**, e3356.
300
301
302
303