



Cache protection strategies of a scatter-hoarding rodent: do tree squirrels engage in behavioural deception?

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Behavioural deception has been studied experimentally primarily in captive-raised primates and corvids, and only in a laboratory setting. Here we show that free-living eastern grey squirrels, *Sciurus carolinensis*, caching food in the presence of conspecifics perform behavioural deception by covering additional empty sites where nothing has been cached. Such deceptive caching (1) occurred in two distinct populations, (2) occurred more often in the close presence of conspecifics and (3) reduced the probability of cache pilferage by surrogate (human) cache pilferers. In an additional experiment, in which we attempted to elicit deceptive behaviour by pilfering caches, deceptive caching appeared as one behaviour in a suite of pilferage-avoidance responses. To our knowledge, this is the first study to show evidence of behavioural deception by a rodent, and the first to use an experimental approach to studying deceptive behaviour in the wild.

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Behavioural deception involves the use of false signals to modify the behaviour of a receiver in a way that benefits a sender, at some cost to the receiver (Semple & McComb 1996). Although observed in numerous species, especially primates, behavioural deception is often only poorly documented with anecdotal observations (Mitchell & Thompson 1986; Whiten & Byrne 1988; Semple & McComb 1996; but see recent work with corvids, reviewed in Dally et al. 2006a). Deception can be accomplished in a variety of ways, from withholding information to tactical deception (Whiten & Byrne 1988), in which acts that normally convey accurate information are used in other, misleading contexts. Our limited knowledge of behavioural deception is due largely to its low frequency of occurrence, which is consistent with theoretical predictions that higher frequencies of deception would result in strong selection for detection strategies by the receiver (Semple & McComb 1996; but see Mitchell 1988). Here, we show that eastern grey squirrels, *Sciurus carolinensis*, engage in a type of behavioural deception: they cover

empty cache sites in the presence of conspecifics, apparently to reduce the risk of immediate cache pilferage.

Food hoarding is an evolved strategy that requires that the individual hoarder can retrieve enough food to pay the cost of hoarding. The hoarder should also have a greater probability of recovering its stored food than other foragers (Andersson & Krebs 1978; Smith & Reichman 1984; Stapanian & Smith 1984; but see Smulders 1998; Vander Wall & Jenkins 2003). Many food-hoarding animals are therefore faced with balancing the trade-off between the obvious benefits of cached food and the potential costs of cache pilferage (Andersson & Krebs 1978; Smith & Reichman 1984; Vander Wall 1990).

Compared to larder hoarders, which store food in central caches and vigorously defend them, scatter hoarders invest little in defence, and reduce pilferage by spacing caches far apart (Vander Wall 1990; Jenkins & Peters 1992; Jenkins et al. 1995). Although the dispersion of scatter hoards reduces the risk of cache pilferage, numerous studies show that cache pilferage remains a persistent problem for scatter hoarders and may regularly result in significant losses for some species (Vander Wall & Jenkins 2003). However, even in the face of high pilferage rates, scatter hoarding may persist as a viable strategy because

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of opportunities for reciprocation of cache pilferage (Vander Wall & Jenkins 2003). Vander Wall & Jenkins (2003) showed (via modelling) that scatter hoarding can be an evolutionarily stable strategy when pilfering is common, as long as all scatter hoarders are also pilferers. Although little is really known about pilfering behaviour in most species, Gerhardt (2005) observed that North American red squirrels, *Tamiasciurus hudsonicus*, pilfered 26% of the cones they ate, but also lost 25% of the cones from their larders. Moreover, pilfering and pilferage rates varied between 1–100% and 1–84% per individual, respectively, suggesting that even in this larder-hoarding species, reciprocal pilferage may be common. Among scatter-hoarding tree squirrels, it is widely assumed that pilferage is common because of the overlapping home ranges typical of the genus (Steele & Koprowski 2001). Naïve animals are assumed to engage in area-restricted olfactory searches that allow them to recover cached nuts, at least at minimum threshold densities (Stapanian & Smith 1978, 1984).

It therefore follows that many scatter-hoarding species, including the eastern grey squirrels studied here, may be forced to tolerate various levels of pilferage (Vander Wall & Jenkins 2003, see also Smulders 1998). However, there are still numerous strategies that scatter-hoarding species such as tree squirrels might use to reduce pilferage, especially at the time of hoarding when pilferage rates may be highest as a result of visual detection by both conspecifics and other species (e.g. corvids). As reviewed by Dally et al. (2006a), many scatter-hoarding birds and some mammals modify their behaviour in response to the presence or the pilfering activity of conspecifics by modifying consumption or caching rates (Bednekoff & Balda 1996; Heinrich & Pepper 1998; Brotons 2000; Pravosudov & Lucas 2000; Emery et al. 2004), recovering and moving caches (Stapanian & Smith 1984; Emery & Clayton 2001; Bugnyar & Kotrschal 2002; Emery & Clayton 2004; Emery et al. 2004), spacing caches further apart or out of sight (Bugnyar & Kotrschal 2002; Dally et al. 2005), or shifting from scatter hoarding to larder hoarding (Jenkins et al. 1995; Preston & Jacobs 2001). However, limited information is available on the use of deception by food-hoarding species (Dally et al. 2005, 2006a). Only two hand-reared ravens have previously been reported to provide 'misinformation': one by caching inedible items (Heinrich 1999), and the other by leading conspecifics away from artificial food caches provisioned by experimenters (Bugnyar & Kotrschal 2004). Pigs also have been reported to lead conspecifics away from artificial food caches, but it is not known whether this is a case of deception or avoidance of food when dominant individuals are nearby (Held et al. 2002). Dally et al. (2006a) also mentioned personal observations of rooks, *Corvus frugilegus*, caching inedible items and/or making empty caches, but no details were given.

Here we report that eastern grey squirrels frequently cover empty sites in the course of caching food, either before or after the food item is cached. The results of this study strongly suggest that this behaviour functions to deceive potential pilferers that may be watching and to decrease the probability of losing caches to them. Our specific objectives in this study were to quantify the frequency of the

behaviour in two distinct populations and to conduct field experiments that test the conditions under which the behaviour occurs, its functional significance, its influence on potential cache pilferers, and whether the behaviour can be induced by simulation of cache pilferage.

METHODS

Study Sites

We report results from two sets of independently conceived studies, one in Wilkes-Barre, Pennsylvania, and another in New Britain, Connecticut, and Northampton, Massachusetts (hereafter, the PA and CT/MA sites, respectively). All studies in PA were conducted at Kirby Park (41°15'N, 75°53'W), a 48.5-ha park with an open 16.2-ha stand of mature oaks (*Quercus* spp.) and silver maples, *Acer saccharinum*, surrounded by urban development, open field and dense riparian woodland. The CT/MA studies were conducted on the campus of Central Connecticut State University (CCSU), the adjacent Stanley Quarter Park (41°42'N, 72°46'W), and the campus of Smith College (42°19'N, 72°38'W) and surrounding residential neighbourhoods. Observations and experiments were made in areas of maintained lawn, near or under deciduous trees or near woodlands.

When scatter hoarding a food item, grey squirrels typically first excavate a shallow pit by digging with the front paws, then, with the food item in their mouths, push the food item into the base of the pit, often with several obvious thrusts of the entire body, and finally cover over the site by dragging the paws along with soil and debris towards the body (<10 times). Covering often also includes 'patting' movements in which the front paws alternate to tamp down the soil, and squirrels may end a caching sequence by combing vegetation and debris towards themselves to further cover the cache site. The entire process usually takes less than 60 s. However, to cache a single item, a squirrel may excavate several sites before deciding on a suitable cache site.

Definitions

For the purposes of this paper we distinguish three types of caching behaviour observed during our studies: single, multiple and deceptive caches. Single caches were defined as those in which a squirrel excavated a single cache site, buried a food item, and covered only that cache site. Multiple caches involved caching events in which the squirrel excavated several cache sites (holes) in the process of caching a single item, placed the item in the last cache site, and then covered only that site. We define 'deceptive caching' as the covering of one or more excavated or unexcavated sites without food items in addition to the cache site where the food item is located.

We present evidence that this behaviour is best described as deceptive caching, because it serves to deceive potential conspecific cache pilferers about the location of cached food. Although we believe that the excavation of multiple cache sites may also serve to deceive conspecifics

(Dally et al. 2005), we make the distinction between deceptive and multiple caching to maintain a conservative estimate of deceptive behaviour (unused excavated sites may have simply been judged unsuitable). We have avoided the use of the term 'false cache' because it has been used to convey different meanings by different authors: a cache that contains an inedible item or is empty (Dally et al. 2006a), or behaviour in which animals place food in a cache site and then immediately move it to another site, but without covering the empty site (Stone & Baker 1989).

Observational Data

Observations in PA were conducted between 15 October and 21 December on 10 days in 1993 and 13 days in 1995. During each day we presented 9–47 squirrels with a single red oak acorn, *Quercus rubra*, and recorded whether the acorn was eaten or cached, and, if cached, the distance it was carried before it was cached. During these trials the squirrels were not marked but statistical independence was achieved within daily trials by presenting each animal with a single food item by following methods described previously (Smallwood & Peters 1986; Hadj-Chikh et al. 1996; Steele et al. 2001). We used red oak acorns because they are common at the site and because our previous studies had shown they are more likely to be cached than are other acorn types (Hadj-Chikh et al. 1996; Smallwood et al. 2001; Steele et al. 2006). In 1995, we recorded the distance to the nearest conspecific and the number of conspecifics within 20 m during each caching event.

Observations at the CT/MA sites were conducted on 7 days between 5 and 30 November 1995. On each day, 1–10 squirrels were observed (a maximum of 10 in CT and five in MA), each caching one to five acorns (some presented by us). Squirrels were not marked in 1995, but were either simultaneously in view or were found at distances far enough apart to ensure that we were studying different individuals on the same day. Squirrels were observed from a distance of 0.5–12 m, but usually from more than 5 m.

In both studies, researchers recorded the type of caching (single, multiple, or deceptive), the number of cache sites excavated, whether each site was covered, and the cache site where the acorn was located, using 7 × 35 binoculars when necessary to determine whether a squirrel still had an acorn in its mouth. When carrying an acorn, squirrels hold it in the front of the mouth with the incisors; hence, it is possible under close inspection (with binoculars) to see the acorn extending from the mouth. However, the complex sequence of behaviour involved in preparation of some false caches (including the excavation of the hole, sometimes the thrusting of the body into the hole in an apparent attempt to position a food item, and the covering of the empty cache site) result in a strong suggestion that a food item was indeed cached at the site. And since it is common for squirrels to excavate multiple sites in the process of searching for, as well as caching food, covering behaviour may hold particular significance for observers in indicating the likely location of cached food.

Experiment 1: impact of multiple and deceptive caching on cache pilferers

In previous studies, we observed conspecifics searching empty caches after squirrels performed deceptive caching (M. A. Steele, personal observation), but the opportunity for detecting both events in succession was rare enough to render evaluation of such pilfering attempts nearly impossible in the field. Thus, to experimentally test the effects of multiple and deceptive caching on the probability of successful pilfering, we used naïve human observers as surrogate cache pilferers. Despite the obvious concerns of using humans for this purpose, we concluded for several reasons that this approach was the most suitable method for testing the effects of deceptive caching in the wild. The olfactory acuity of human observers, although inferior to that of tree squirrels, is likely not relevant in this study because the hypothesized deception involves visual signals. Moreover, the visual acuity of tree squirrels is comparable to that of humans (Steele & Koprowski 2001 and references therein), and tree squirrels have been shown experimentally to rely primarily on spatial information for relocating hidden food (Lavenex et al. 1998). Consequently, we concluded that the use of human pilferers was a useful approach for evaluating the effect of deception on pilferage rates, and also a reasonable means by which to test behavioural modifications displayed by the caching subject in response to pilferage (see experiment 2, below). Finally, because animals in our study populations were well habituated to humans, human experimenters were unlikely to interfere with the animals' behavioural responses.

Experiment 1 was conducted at the PA site on 9 days in 1995, with a different naïve human observer (i.e. undergraduate student with no previous knowledge of the study) on each day. We presented squirrels with a single red oak acorn and recorded their caching behaviour as described above. After each acorn was cached and the squirrel had moved at least 5 m from the cache site, the observer was asked to retrieve the acorn based only on observations without the use of binoculars. We recorded whether the acorn was recovered and (for those found) the time to find the acorn. Observers were given 300 s to recover each acorn, before the trial was terminated. We used one-tailed Wilcoxon signed-ranks tests to compare mean search times because we predicted that search times would be shortest for single caches.

Experiment 2: does cache pilfering elicit deceptive behaviour?

We attempted to elicit deceptive caching by robbing caches of five squirrels between 30 January and 14 March 2004, and of 11 squirrels between 1 February and 3 May 2005, on the CCSU campus. A few squirrels had distinctive natural markings; the others were uniquely marked with small spots of black dye (Nyanzol-D or various brands of men's hair dye) applied with a plastic dropper from a short distance, without restraining the animals. Marking procedures were approved by CCSU IACUC (proposal no. 72). Dye marks were lost between years

when squirrels moulted, so statistical independence of observations was maintained only within years.

Our experiments were conducted by teams of three to five people, with the entire team present throughout all parts of the experiment. One person provided nuts, a second narrated the behaviour of the focal animal (and that of the experimenters) into a hand-held tape recorder, and a third served as the pilferer during the pilfering trials of the experiment. If another squirrel approached us during an experiment, one of the team members (but not the pilferer) presented the animal with a nut so that it did not interfere with the subject's behaviour. In this experiment, we presented squirrels with peanuts in intact shells. For each subject, we first presented peanuts until 5–12 of the nuts were cached (prepilfering trials, Table 1; these trials were considered to begin with the first nut cached). Following presentation of each nut, the squirrel was observed from approximately 5 m until the nut was eaten or cached, and it was then presented another nut as soon as it resumed foraging behaviour. After the last nut in this first series was cached and the squirrel resumed foraging, the designated pilferer attempted to recover that nut from the cache site in the presence of the squirrel that buried it. We then presented the squirrel with another series of nuts ($N = 4\text{--}16$ per squirrel), for which we attempted to pilfer the previous nut cached before presenting another nut (pilfering trials). We recovered 33% (19/58) and 54% (50/92) of the nuts in 2004 and 2005, respectively. For five squirrels (two in 2004 and three in 2005), we followed pilfering trials with a third series of 1–21 nuts for which we did not attempt cache pilferage (postpilfering trials). Trial order was reversed for one squirrel in 2004: after caching one nut, it received 12 nuts in pilfering trials and 16 nuts in postpilfering trials. We report data only for squirrels with at least four nuts in both pilfering and nonpilfering trials. We used one-tailed statistical tests because we specifically hypothesized that more pilferage-averting behaviour would occur during trials when pilfering was attempted than when pilfering was not attempted.

We used statistical tables to determine P values by hand, avoiding the problems of statistical software that may use inappropriate approximations for P values for small sample sizes (Emery et al. 2004). All statistical tables were from Siegel & Castellan (1988).

RESULTS

Observational Data

Based on more than 500 trials with more than 52 free-ranging grey squirrels, we observed 255 caching events over 2 years at the PA site. These caching frequencies (of about 50%) were comparable to those reported for red oak acorns in previous studies (Hadj-Chikh et al. 1996; Steele et al. 2001). We also observed 49 caching events by at least 15 free-ranging grey squirrels in November 1995 at the CT/MA sites.

Deceptive caching was infrequent, occurring in 13.8% and 13.2% of all caching events in 1993 and 1995 at the PA site, respectively, and 22.3% of all caching events at the CT/MA sites (Fig. 1a). The remaining caching events were more or less evenly divided between single and multiple caches. There were many days on which deceptive caching was not observed at all (Fig. 1b, c). At the PA site in 1993, the frequency of deceptive caching increased significantly through the autumn (i.e. after 30 September) as energy demands increased and food availability declined (Spearman rank correlation: $r_s = 0.804$, $N = 10$, $P < 0.005$; Fig. 1b). No such pattern was evident in 1995 ($r_s = 0.104$, $N = 13$, $P > 0.25$; Fig. 1c).

More squirrels were sighted within 20 m of the focal animal when deceptive caching occurred than when deceptive caching did not occur, suggesting that the presence of conspecific competitors influenced the behaviour (Fig. 2a). This difference was significant on days on which at least one deceptive caching event was observed (Kruskal–Wallis test: $H_2 = 7.65$, $P < 0.05$). A similar, but marginally nonsignificant pattern was observed for all experimental trials

Table 1. Comparisons of grey squirrel behaviour in trial series with and without attempted pilfering by observers

Trial series	2004			2005		
	Prepilfering	Pilfering	Postpilfering	Prepilfering	Pilfering	Postpilfering
Number of squirrels	5	5	2	11	11	3
Number of nuts taken	6.6±1.5	8.9±1.7	9.5±2.5	8.8±0.4	8.5±0.8	11.7±5.0
% Nuts cached*	98.0±2.0	88.9±3.4	87.5±12.5	94.4±2.7	84.7±5.0	97.9±2.1
% Cached nuts with extra sites covered (deceptive caching)	0.8±0.8	11.6±4.7	0±0	7.6±2.9	9.3±4.3	0±0
% Nuts cached out of sight or in an inaccessible location	0.8±0.8	8.3±4.6	4.2±4.2	7.8±2.9	20.5±6.3	4.9±2.9
% Cached nuts with time spent out of sight	17.8±5.6	26.0±4.3	11.3±3.0	35.3±7.0	45.7±8.0	27.3±10.3
Number of sites excavated/cached nut	4.7±1.1	3.4±0.3	2.9±0.1	4.4±0.7	4.7±1.0	2.3±0.4
Time to cache nut (s)	70.8±10.7	64.2±7.0	59.0±1.0	78.6±14.7	98.5±14.3	36.2±5.9

Experiments with each animal were initiated with nonpilfering trials (prepilfering) and then followed by trials in which pilfering was attempted (pilfering); for some animals, a second set of nonpilfering trials (postpilfering) followed the pilfering trials. The same human observers, including pilferers, were present during both nonpilfering and pilfering trials. Data are means ± SE. Most squirrels were tested on only 1 day. For squirrels tested on 2 days (two in 2004, one in 2005), percentages were calculated separately for each day, and then averaged for that squirrel's contribution to the overall mean.

*Nuts that were taken but not cached by squirrels were eaten.

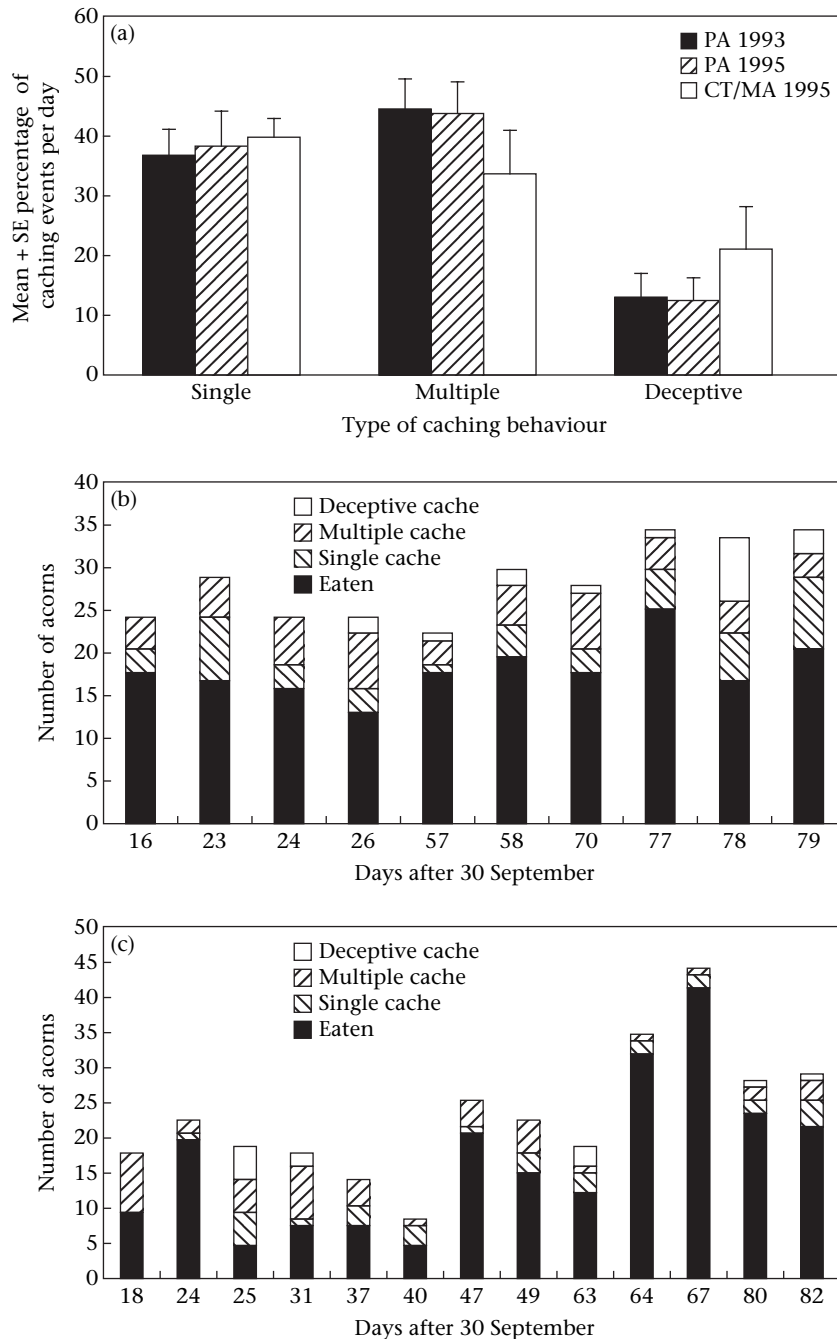


Figure 1. Frequency of deceptive caching in two independent populations of grey squirrels. (a) Summary of single, multiple and deceptive caching events at both study sites. Frequency of single, multiple and deceptive caching events per experiment in (b) 1993 and (c) 1995 at the Pennsylvania (PA) site.

($H_2 = 5.77, P < 0.10$). The mean distance to the nearest conspecific was also shortest for those caching events in which deceptive behaviour was performed (Fig. 2b). However, this pattern was not significant for all trials ($H_2 = 0.586, P > 0.70$), nor for the subset of days on which deceptive caching was observed ($H_2 = 0.604, P > 0.70$; Fig. 2b), primarily because of the variation in distances to conspecifics during trials in which single caches were made. This result may suggest that the specific behaviour of conspecifics, rather than just the presence of conspecifics, may trigger

deceptive behaviour. Sample size was too small to test these patterns at the CT/MA site.

Experiment 1: impact of multiple and deceptive caching on cache pilferers

Both multiple- and deceptive-caching events reduced the probability of acorn recovery and increased the time for acorn recovery by human pilferers (Fig. 3). For paired comparisons (within each observer), the percentage of

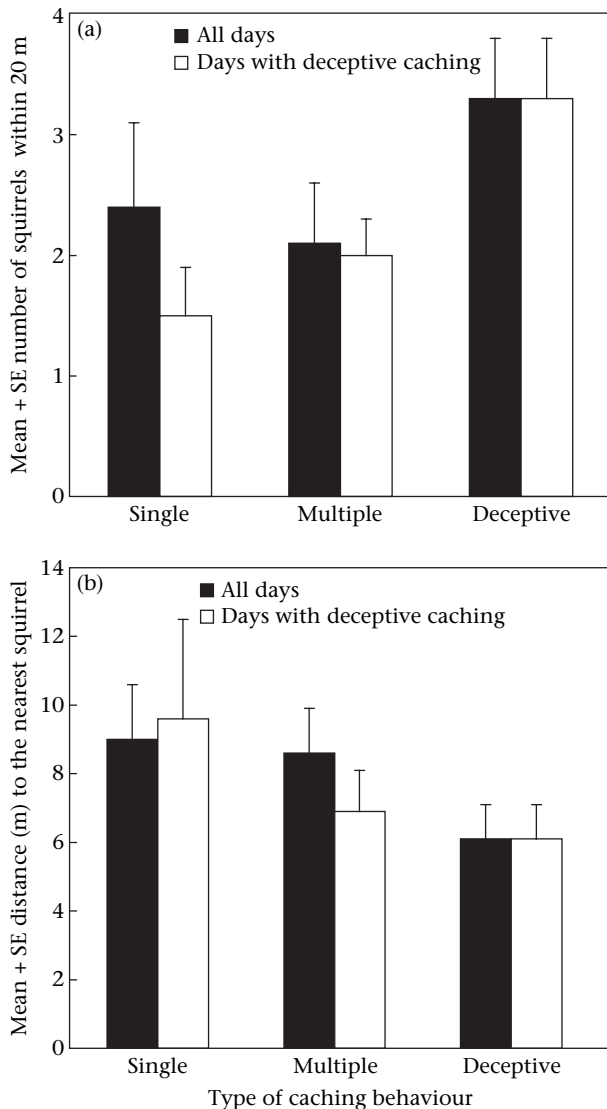


Figure 2. Study animal's proximity to other squirrels when caching (PA site, 1995). (a) Number of other squirrels within 20 m of the study animal. (b) Study animal's distance to the nearest squirrel when performing single, multiple and deceptive caches.

acorns recovered was significantly higher (one-tailed Wilcoxon signed-ranks test: $T = 37$, $N = 9$, $P = 0.049$; Fig. 3a) and time to recover was significantly shorter for single caches than for the other two cache types combined (for all acorns: $T = 38$, $N = 9$, $P = 0.037$; Fig. 3b). The proportion of acorns recovered also differed significantly across cache types (Kruskal–Wallis test: $H_2 = 6.79$, $P < 0.05$) and was lowest for those trials in which deception was performed (Fig. 3a). For those acorns that were recovered, the time to recovery took, on average, more than twice as long after multiple- and deceptive-caching events than after single-caching events (Fig. 3b). A three-way analysis, however, was not possible because only a single acorn was recovered following deceptive behaviour. This result further supports our hypothesis that deceptive caching would reduce pilferage success at the time of caching. When all acorns were considered, search time differed significantly across

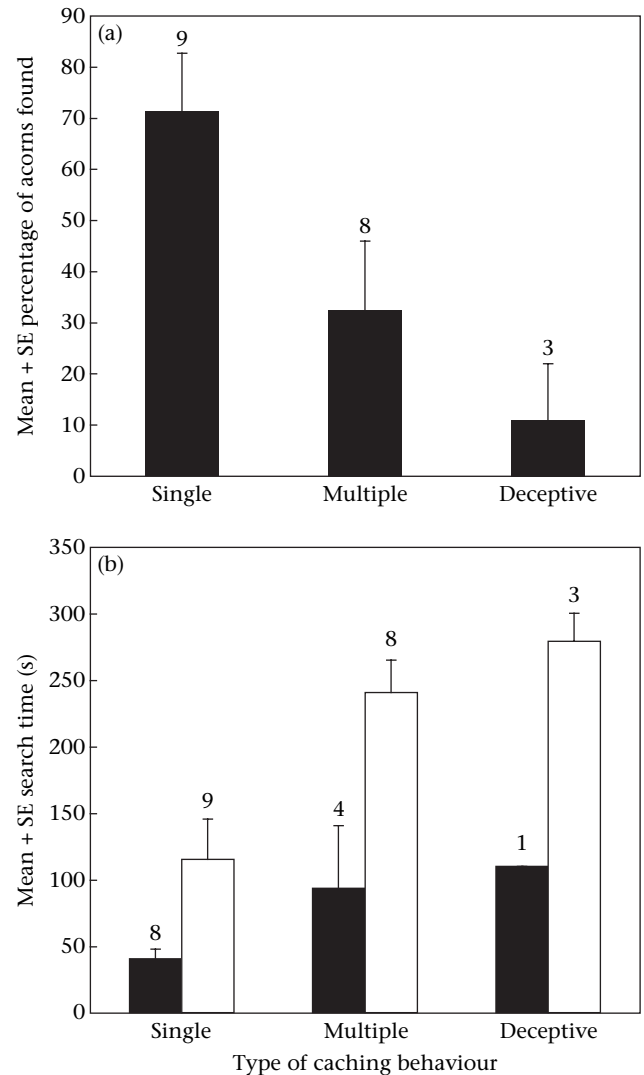


Figure 3. Ability of naive human observers to locate squirrel caches. (a) Mean percentage of acorns found. (b) Mean search time for recovered acorns (■) and for all acorns (□); acorns not recovered were assigned a search time of 300 s, the maximum time allowed for each observer to locate a cache. Sample sizes for the number of observers (above bars) varied because squirrels did not perform each type of caching for each naive observer.

cache types (Kruskal–Wallis test: $H_2 = 9.26$, $P < 0.01$), and again, was shortest for single caches (Fig. 3b).

Experiment 2: does cache pilfering elicit deceptive behaviour?

In 2004 and 2005, we conducted 385 additional trials with five (2004) and 11 (2005) individually marked squirrels from which we attempted to experimentally elicit deceptive behaviour on the CCSU campus: 219 trials with no attempt to pilfer caches and 166 trials during which cache pilfering was attempted. Grey squirrels adjusted their behaviour when experiencing the loss of cached food to human pilferers by displaying three kinds of pilferage-averting behaviour: (1) covering sites where nothing had

been cached (deceptive caching); (2) caching nuts in sites that were either out of view of or inaccessible to observers (behind obstacles, under bushes, in tree nests and cavities, in stumps and in muddy areas); and (3) eating nuts rather than caching them (Table 1; also see [Supplementary Material, Tables S1 and S2](#)). For each squirrel, we compared the combined percentages of these behavioural acts during pilfering and nonpilfering trials (Fig. 4; also see [Supplementary Material, Fig. S1](#)). Nonpilfering trials included both pre- and postpilfering trials to allow for adequate sample size; because the behavioural effects of pilfering could continue into the postpilfering trials, combining pre- and postpilfering trials makes our test of the effects of pilfering conservative. In both 2004 and 2005, squirrels performed significantly more pilferage-averting behaviour when pilfering was attempted than when pilfering was not attempted (one-tailed Wilcoxon signed-ranks test: 2004: $T = 15$, $N = 5$ squirrels, $P = 0.031$; 2005: $T = 56$, $N = 11$ squirrels, $P = 0.021$; Fig. S1). In 2004, small sample sizes precluded separate statistical analysis of each behaviour. In 2005, squirrels cached a significantly higher percentage of nuts at sites that were either out of view of or inaccessible to observers ($T = 31$, $N = 8$ squirrels, $P = 0.039$) in pilfering trials than they did in nonpilfering trials. Nut consumption and deceptive caching also occurred at higher frequencies when cache pilfering was attempted, although these differences were not statistically significant (nut consumption: $T = 25$, $N = 7$ squirrels, $P = 0.055$; deceptive caching: $T = 16.5$, $N = 7$ squirrels, $P < 0.406$). Three other measures potentially related to deceptive behaviour (movement out of sight of the observer during caching, the number of sites excavated and caching time) all had higher mean values

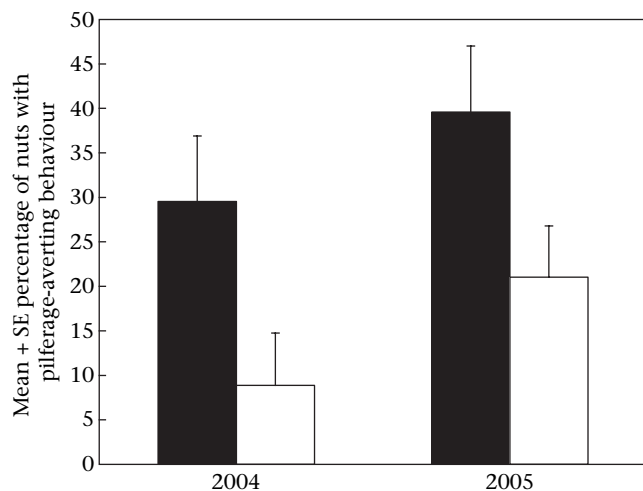


Figure 4. Responses to attempted pilfering. Mean \pm SE percentages of nuts for which squirrels performed pilferage-averting behaviour during trials when observers attempted to pilfer caches (■), compared to trials when pilfering was not attempted (□). Sample sizes were 5 and 11 squirrels in 2004 and 2005, respectively. For the five animals for which both prepilfering and postpilfering trials were conducted, results of pre- and postpilfering trials are combined. For squirrels tested on 2 days (two squirrels in 2004, one squirrel in 2005), percentages were calculated separately for each day, and then averaged.

during pilfering in 2005 (Table 1). Movement out of sight was significantly higher in pilfering than in nonpilfering trials in both years (2004: $T = 15$, $N = 5$ squirrels, $P = 0.031$; 2005: $T = 25$, $N = 7$ squirrels, $P = 0.039$).

DISCUSSION

Our results show that free-living eastern grey squirrels perform behavioural deception in the presence of conspecifics by covering excavated but empty cache sites (or open ground adjacent to cache sites). Moreover, we observed that deceptive behaviour occurred more often in the presence of conspecifics (<20 m away), and reduced the probability of cache pilferage by surrogate (human) cache pilferers. Finally, we found that a suite of pilferage-avoidance behaviours, including deceptive behaviour, increased significantly as a result of experimental cache pilferage. We were unable, however, to significantly increase deceptive behaviour by itself when simulating cache pilferage. Additional studies are needed to specifically determine the proximate factors that trigger this behaviour.

Although scatter hoarding results in the dispersion of individual food stores that are probably less defensible (Stapanian & Smith 1978, 1984; Vander Wall 1990) but also less attractive (Kraus 1983) to pilferers than larder hoards, there is also substantial evidence that scatter hoarders are susceptible, sensitive and responsive to the activity of cache pilferers. Indeed, much of the specific behaviour associated with scatter hoarding, such as cache site selection, optimal spacing of caches and frequent movement and management of scatter hoards (Stapanian & Smith 1984; Vander Wall 1990; Preston & Jacobs 2005), is likely to decrease the chances of cache pilferage. Moreover, several recent studies indicate that some scatter-hoarding species are able to modify hoarding behaviour in a way that probably reduces pilferage (Jenkins et al. 1995; Heinrich & Pepper 1998; Emery & Clayton 2001; Bugnyar & Kotrschal 2002; Vander Wall & Jenkins 2003; Emery et al. 2004; Dally et al. 2005, 2006a; Preston & Jacobs 2005), and results of our study provide support for the hypothesis that preparation of multiple cache sites (multiple caching) may serve to 'confuse' potential pilferers (Fig. 3; cf. Dally et al. 2005). Other studies suggest more advanced cognitive strategies for deterring pilferage (Heinrich 1999; Emery & Clayton 2001, 2004; Bugnyar & Kotrschal 2002; Emery et al. 2004; Bugnyar & Heinrich 2005; Dally et al. 2005, 2006b). Heinrich (1999) reported caching of nonfood items by a hand-reared raven, and Dally et al. (2006a) anecdotally reported similar behaviour from rooks, although it is unclear to what extent such behaviour involved deception. Our study, however, is the first to offer evidence of behavioural deception by a scatter-hoarding rodent, to analyse a behaviour that functions as a deceptive signal in the wild, and to elicit pilferage-averting behaviour in free-ranging animals by simulating competitor activity.

Deceptive caching appears particularly relevant to the natural conditions in which eastern grey squirrels are typically caching and retrieving food stores. Individuals of

this species, like other members of the genus *Sciurus*, have overlapping home ranges and often converge on dense food patches when scatter hoarding (Steele & Koprowski 2001). During autumn mast conditions, squirrels rapidly disperse nuts and acorns away from such patches as they scatter-hoard these items (Stapanian & Smith 1984; Vander Wall 1990; Steele et al. 2001). Considerable overlap in caching areas occurs between individuals (Steele & Koprowski 2001; M. A. Steele, unpublished data); hence, pilfering by conspecifics is thought to be common during the caching period and later during the cache retrieval period (Stapanian & Smith 1984; Vander Wall & Jenkins 2003). At our PA site, for example, caches of red oak and pin oak, *Quercus palustris*, acorns usually remain at their original cache sites for less than 3 days when cached by squirrels and for less than 5 days when experimentally placed in the ground by observers (M. A. Steele, personal observations). This observation suggests that pilfering rates are as high as those reported for other systems (Vander Wall & Jenkins 2003) and that they have probably shaped the behaviour of tree squirrels.

Pilferage by tree squirrels can occur long after food items are cached, usually by means of area-restricted olfactory searches by naïve conspecifics (Stapanian & Smith 1978, 1984; Vander Wall 1990). However, pilferage is also likely to be common at the time of caching if squirrel densities are high and conspecific encounters are as frequent as they are in our study areas and other similar urban sites (Vander Wall 1990; Steele & Koprowski 2001). Indeed, we have observed pilferage of caches by conspecifics immediately following cache placement and, on rare occasions, have observed potential pilferers searching empty cache sites immediately following a display of deceptive caching behaviour (M. A. Steele, personal observation).

Although tree squirrels, like other rodents, have a keen sense of smell, they are also noted among mammals for their acute vision (Steele & Koprowski 2001 and references therein). Recent studies also indicate that tree squirrels rely on spatial information (rather than nonspatial information such as olfactory cues) to remember cache locations (Lavenex et al. 1998) and that grey squirrels show an audience effect while caching such that individuals face away from nearby conspecifics while caching food items (Leaver et al. 2006). Thus, visual cues could be particularly important to pilferers at the time of caching, and deceptive caching behaviour could be a critical strategy for preventing cache losses at this time.

Deceptive caching behaviour, as described in this study, meets the formal criteria of behavioural deception, a false signal registered by a receiver that benefits the sender at some cost to the receiver (Semple & McComb 1996). Costs to the receiver are easily inferred from this and previous studies at our PA site. In those cases in which squirrels are successfully deceived by conspecifics, costs to the receiver are simply the wasted time and energy involved in searching for a food item in a covered but empty site. Although we have observed such events on occasion, we do not know the frequency with which they occur.

Our results further suggest that deceptive caching is a stable evolutionary strategy for three reasons: (1) the minimal cost to the receiver (i.e. failure to successfully

pilfer) is likely to result in only weak selective pressure for the ability of the receiver to falsify deceptive signals of the sender; (2) tree squirrels are not territorial, and encounters with other individuals are unpredictable and brief, allowing little opportunity for receivers to recognize or habituate to the deceptive behaviour of neighbours (Steele & Koprowski 2001); and (3) deceptive behaviour occurs at frequencies comparable to those theoretically predicted necessary to prevent invasion by any detection strategy by the receiver (Semple & McComb 1996), especially given the brief nature of associations between individual squirrels.

Our observations indicate that deceptive caching behaviour of grey squirrels also meets one of the definitions of tactical deception: a false signal consisting of 'acts from the normal repertoire of an individual' that are also used in 'honest' contexts (Byrne & Whiten 1985). However, without a more complete understanding of the previous experience and learning history of our study animals, we suggest that it is premature to suggest that the behaviour is cognitively tactical in nature (Whiten & Byrne 1988).

We submit that deceptive caching by grey squirrels qualifies as behavioural deception, and that covering empty sites functions to mislead observers about the location of cached food. We observed deceptive caching behaviour being performed intermittently, as one component of a suite of different types of pilferage-averting behaviour. Ceasing to take nuts may be another adaptive response to cache robbery as squirrels learn of their cache losses (Balda 1980). For example, we excluded three runs of the experiment from analysis because of limited data during attempted pilferage; in each of these, squirrels simply ceased taking nuts from the experimenters after pilfering was attempted for one to three cached nuts.

Different individuals in our study also performed deceptive caching in different ways, some by covering excavated empty cache sites before burying food, some by covering unexcavated sites after caching an item, and still others by performing a combination of techniques. Thus, we argue that deceptive caching and other pilferage-averting behaviour is not a preprogrammed, hardwired response (fixed or modal action pattern) to the risk of pilfering, nor a functionally irrelevant displacement behaviour. Instead, this is a higher-order set of adaptive behavioural responses that function to avert pilfering primarily at the time of caching when visual detection by potential pilferers may be likely. This suggests a sensitivity to the social context in which caches are made (i.e. a sensitivity to the presence and behaviour of potential cache pilferers; Emery et al. 2004; Preston & Jacobs 2005).

Our results, coupled with those of recent studies on corvids, indicate that these food-hoarding species may use a range of advanced cognitive skills in preventing cache pilferage (Heinrich 1999; Emery & Clayton 2001, 2004; Bugnyar & Kotrschal 2002, 2004; Emery et al. 2004; Bugnyar & Heinrich 2005; Dally et al. 2005, 2006b), including behavioural deception described here. More detailed studies, under more controlled conditions, however, are needed to understand what factors trigger deceptive behaviour and other pilferage-averting behaviour in tree squirrels.

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Supplementary Material

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