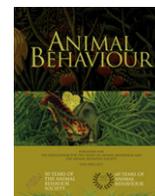


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## Evidence for cache surveillance by a scatter-hoarding rodent

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The mechanisms by which food-hoarding animals are capable of remembering the locations of numerous cached food items over long time spans has been the focus of intensive research. The ‘memory enhancement hypothesis’ states that hoarders reinforce spatial memory of their caches by repeatedly revisiting cache sites, yet no study has documented this behaviour in wild animals. We investigated whether scatter-hoarding Central American agoutis, *Dasyprocta punctata*, actively survey their seed caches. We placed remote cameras at sites where seeds were buried by known individuals and at nearby random locations to compare the behaviour and visiting rates between owners and naïve individuals. We found that cache owners were almost four times more likely to walk near their cache than to walk past random locations. Moreover, cache owners that passed in front of a cache camera were more than twice as likely to approach their caches than were naïve individuals but half as likely to excavate the seed when interacting with the cache. We conclude that agoutis remember the location of cached seeds, are aware of their ownership and actively survey their caches. Surveillance could serve to monitor cache theft and food quality as well as enhance spatial memory of cache locations; thus, this behaviour could have important fitness benefits and may be exhibited by other scatter-hoarding animals.

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Many bird and rodent species scatter-hoard seeds, especially in ecosystems with seasonal peaks and shortages in food abundance (Andersson & Krebs 1978; Vander Wall 1990; Brodin 2005). At times of high seed abundance, scatter hoarders hide seeds in hundreds to thousands of widely scattered caches, each containing one or few seeds (Vander Wall 1990; Wauters & Casale 1996). These cached seeds function as food reserves for times of food shortage and are thus typically retrieved several months after their initial placement (Vander Wall 1990; Balda & Kamil 1992). This phenomenon has led to the compelling question of whether and how animals are able to remember the locations of so many caches over long periods.

Long-term spatial memory of caches has been well documented in some corvid species (Balda & Kamil 1992; Bednekoff et al. 1997) and in captive black-capped chickadees, *Poecile atricapillus* (Roth et al. 2012). In other avian species, this ability is still debated (Pravosudov & Smulders 2010), despite observations that wild birds

successfully recover caches several months after being placed (Brodin & Ekman 1994; Brodin 2005). Indeed, most experiments with captive parids showed that individuals were not able to remember the location of caches after 1 month (Hitchcock & Sherry 1990; Healy & Suhonen 1995; Brodin & Kunz 1997; Male & Smulders 2007; but see Roth et al. 2012). In mammals, it is still largely unknown whether scatter hoarders have the ability to remember seed locations over long periods. Only grey squirrels, *Sciurus carolinensis*, and red squirrels, *Sciurus vulgaris*, have demonstrated the ability to remember and retrieve cached seeds over both short periods (12 and 20 days: Jacobs & Liman 1991; MacDonald 1997), and possibly as long as 62 days (MacDonald 1997). Several authors have observed seasonal patterns of cache production and retrieval in wild mammals that are consistent with long-term spatial memory, but it remains unknown whether individuals recover their own cached seeds, or exploit seed caches that they find accidentally and regardless of who made them (Smythe 1978; Wauters et al. 1995; Steele et al. 2001).

For animals that do remember the location of their caches, there remains the question of how they manage such a cognitively challenging task. One possible behavioural mechanism that could allow animals to reduce the rate of memory deterioration over

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time, and therefore remember cache locations over many months, is to repeatedly revisit cache sites to reinforce spatial memory (Huston & Oitzl 1989; Smulders et al. 2010; Roth et al. 2012), henceforth the ‘memory enhancement hypothesis’. Roth et al. (2012) speculated that the failure of prior studies to detect long-term memory abilities in parids was due to the one-trial nature of the studies. Roth et al. (2012) experimentally demonstrated that black-capped chickadees, which were found to only remember cache locations for up to 1 month in prior studies (Hitchcock & Sherry 1990), were in fact able to remember cache locations over long timescales ( $\geq 6$  months) when given the opportunity to revisit cache sites and enhance their memories.

We studied seed caching and cache revisiting in the Central American agouti, *Dasyprocta punctata*. Specifically, we tested for the presence of cache surveillance, which is a key condition of the cache memory enhancement hypothesis. We monitored agouti-made caches with remote cameras. A portion of the agoutis were captured and marked for individual identification, allowing us to determine the ‘owner’ of a particular seed cache, and compare the behaviour of owners versus naive individuals at seed cache locations. We also deployed a series of cameras at random locations. If owners regularly revisit caches for the purpose of memory enhancement, they should be photographed at these cache sites more frequently than at other randomly chosen locations in their home range.

## METHODS

### Study Site and Species

We studied seed-caching and cache-visiting behaviour by agoutis on Barro Colorado Island (BCI), Panama (9°10'N, 79°51'W), a 1560 ha island covered with tropical moist forest, located in the Gatun Lake section of the Panama Canal. Our study area consisted of 25 ha of late-secondary forest in the central part of the island.

Agoutis are 2–4 kg caviomorph rodents that scatter-hoard seeds as food reserves for periods of food scarcity (Smythe 1978, 1989; Jansen et al. 2010). Agouti home ranges on the island average 2.71 ha and overlap widely with the home ranges of other agoutis (Emsens et al. 2013). Although agoutis are often observed chasing and acting aggressively, individual agoutis cannot maintain an exclusive territory on BCI (Aliaga-Rossel et al. 2008). Agoutis use multiple refuges (Emsens et al. 2013), but do not appear to preferentially cache seeds around these refuges (cf. Daly et al. 1992; Spritzer & Brazeau 2003). Agoutis have been observed to preferentially cache their seeds in areas with low densities of conspecific plants, presumably to avoid cache theft (Hirsch et al. 2012a). The agouti's diet generally consists of fruit pulp and seeds, supplemented by leaves and animal matter (Smythe 1978; Henry 1999). One of the most important food sources for agoutis on BCI are the fruits and seeds of *Astrocaryum standleyanum*, a Neotropical arborescent palm occurring from Costa Rica to Ecuador (Smythe 1989; Galvez et al. 2009). The local fruiting period for *Astrocaryum* occurs during March–early July (De Steven et al. 1987), and agoutis store these seeds for the high-rainy season of October–December, when plant fruit production declines precipitously (Leigh 1999). *Astrocaryum* seeds generally require at least 1 year to germinate (Potvin et al. 2003).

### Seed Tracking

We collected ripe *Astrocaryum* fruits using seed traps suspended below haphazardly selected fruiting trees. Seeds were defleshed using a knife to resemble natural defleshing by rodents (Jansen et al. 2010), air dried and given a 55 cm long ‘telemetric thread

tag’ (Hirsch et al. 2012b). Affixing thread tags to seeds is the widely accepted standard method for tracking seed dispersal by rodents because rodents will bury the seed but leave the thread above ground, allowing researchers to locate the seed (Forget & Wenny 2005). Telemetric thread tags consisted of a 30 cm black nylon-coated stainless-steel leader wire tied to a 4.1 g cylindrical VHF transmitter (Advanced Telemetry Systems Inc., Isanti, MN, U.S.A.) with a 20 cm antenna (Hirsch et al. 2012b). When seeds were buried, the transmitters affixed to the ends of the wire remained above ground, thus allowing us to place the transmitters on top of magnets that deactivated the transmitter and saved battery life. When the seed was moved by an agouti or other animal, the transmitter was activated, allowing us to find the new location of the seed with hand-held radiotelemetry equipment (for full details see: Hirsch et al. 2012b; Jansen et al. 2012). We covered the transmitter and flagging tape with loose leaf litter to reduce possible visual cues.

During May–July 2010, we placed a total of 589 seeds at 52 stations scattered across our study site and monitored seed removal with motion-triggered camera traps (RC55 or PC800, Reconyx, Holmen, WI, U.S.A.). We recorded the animal species and the exact time of seed removal for each seed (as in Jansen et al. 2002, 2004; Jansen & den Ouden 2005), and identified the individual if possible. Each seed plot was checked daily and removed seeds were located by sight or with hand-held radiotelemetry equipment (Yaesu-VR500, Cypress, CA, U.S.A.) to determine dispersal distance and seed fate. Individual seeds were frequently removed and recached by agoutis, resulting in stepwise dispersal for most seeds in our study (median number of caches per seed = 8, range 1–36; Jansen et al. 2012).

### Animal Tagging

We marked a total of 16 agoutis with overlapping home ranges so that they were individually recognizable in photographs. Agoutis were captured with live traps (Tomahawk Live Trap co., WI, U.S.A.) baited with bananas and were checked twice daily (cf. Emsens et al. 2013). Adults ( $N = 12$ ,  $> 2.3$  kg; Smythe 1978) were fitted with a VHF radiotransmitter, which had a unique pattern of reflective tape affixed to the collar. Subadults ( $N = 4$ ) were individually marked with small freeze brands on their sides (Hadow 1972). These tags allowed us to determine the identity of these agoutis in black-and-white photographs from our remote cameras. All trapping and marking procedures were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (STRI IACUC number 2007-20-12-15-07) and conducted under research permits authorized by the Barro Colorado Nature Monument.

### Video Surveillance of Agouti Behaviour

We used remote cameras to monitor a total of 87 caches for which we knew the identity of the agouti cache owner. These caches were made by nine of the 16 tagged agoutis. As soon as we found the location of the cached seed, we mounted a camera onto a nearby tree or a U-shaped metal rebar pushed into the ground at  $\sim 1.5$  m distance from the cache (Hirsch et al. 2012b). To scale the scene, we then placed two pieces of rope (5 m long), marked with tape every 20 cm, in a cross formation on top of the cache location, took a picture with the camera and removed the rope. This calibration allowed us to determine the distance between cache locations and passing animals directly from the photographs. We were careful not to disturb the cache location, as digging into the soil or moving leaves near the cache site can provide a cue for rodents to find the buried seed (Vander Wall et al. 2003; Guimarães et al.

2005). After the rope was removed, the motion-triggered camera took photos whenever animals passed in front, and agoutis generally trigger the camera from an average distance of 2.54 m (Rowcliffe et al. 2010). The cameras were set to take approximately one photo per second, essentially recording a video clip that allowed us to verify the identity and behaviour of the agoutis. To obtain a control for comparison with the cache cameras, we deployed cameras at 140 points spaced 100 m apart in a grid across our study area. Each control camera was active for 8–10 days, during the same season when our cache-monitoring cameras were in use (August–October 2010).

For both the cache and control deployments, we recorded the rate of visits and the total number of times that agoutis (both the cache owner and any naïve individuals) passed in front of the camera. For each of the camera-monitored seed caches, we also recorded whether the agouti (1) passed directly over the cached seed (the head passed within 20 cm of the seed), (2) 'investigated' the cache and (3) removed the seed. If an agouti bent its head down and appeared to smell the area above the cache, or stuck its nose in the leaf litter above the cache location, we classified this as investigative behaviour.

### Statistical Analyses

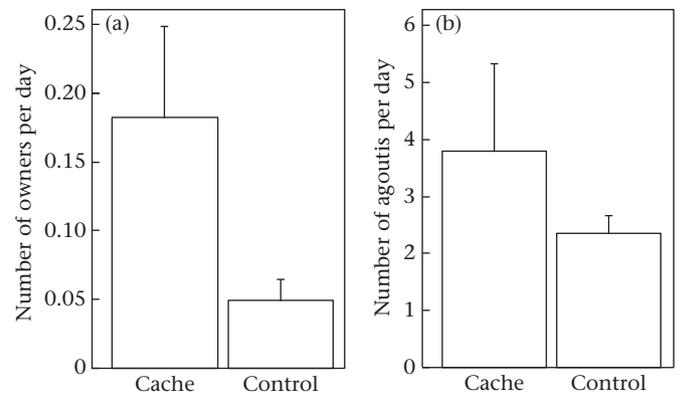
We used linear mixed models (LMM) to determine whether caches were more frequently visited by agoutis than control locations, and in particular, whether cache owners visited caches more frequently. We used generalized linear mixed models (GLMM) to determine whether owners were proportionally more abundant at caches (Pinheiro & Bates 2000). We paired each cache with the nearest control point (mean distance between control and cache = 20.8 m, range 6–59 m). If the nearest control location fell outside the home range of the cache owner, we chose the closest camera within the home range of the agouti cache owner (home ranges were determined in a concurrent study; Emsens et al. 2013). Agouti identity was included as random effect, as were pairs of cameras (cache and control), nested within agouti identity. Whether agoutis and owners visited caches more often than control points was tested by fitting an LMM on the visit rates recorded. Whether owners were proportionally more abundant at caches than at control points was tested by fitting a GLMM with binomial errors on the weighted proportions.

We also used GLMM with binomial errors to test for differences in behaviour between owners and naïve animals that were photographed at the caches. Here, cache identity was included as random factor. For caches that were excavated during the monitoring (65), observations of agoutis after excavation were excluded. Coefficients from the fitted models were used to calculate the likelihood ratio between owners and naïve individuals for each behaviour.

Finally, we fitted a Cox proportional hazards model with a Wald test to compare the rate at which caches were depleted by owners versus naïve animals. Cache excavation by owners and naïve individuals were treated as competing risks (i.e. excavation by an owner at a certain time implied censoring of the observation for naïve individuals at that same time and vice versa). All analyses were conducted in R version 2.12.2 (R Development Core Team 2011) with the libraries nlme (Pinheiro et al. 2011), MASS (Venables & Ripley 2002) and survival (Therneau & Lumley 2011).

## RESULTS

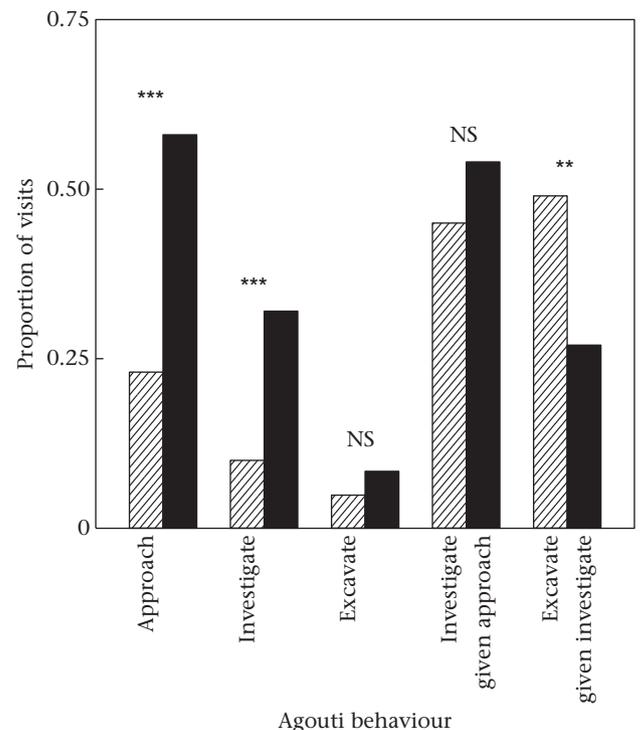
The rate at which agoutis passed in front of the cameras did not differ significantly between cache and control locations (3.7/day versus 2.3/day; LMM with cache–control pair nested within home range as a random factor:  $t_{86} = 0.92$ ,  $P = 0.36$ ; Fig. 1). However,



**Figure 1.** Mean  $\pm$  SE number of times per day that agoutis were photographed by camera traps at cache and control locations: (a) cache owners; (b) all agoutis.

caches were visited by owners 3.7 times more often than were the nearby control points (0.18/day versus 0.05/day;  $\beta = 0.13$ ,  $t_{86} = 2.27$ ,  $P = 0.026$ ). Owners' proportion of visits to caches was 4.2 times (model estimated) greater than that to control points (7.5% versus 2.0%; GLMM with binomial errors:  $\beta = 1.50$ ,  $t_{82} = 4.81$ ,  $P < 0.001$ ).

Agouti behaviour was recorded at 86 caches with known owners (naïve individuals at 82, cache owners at 50) on 1600 occasions until cache excavation. Among passing individuals, passing owners ( $N = 143$ ) were 2.3 times more likely than naïve individuals ( $N = 1457$ ) to approach the exact location of the focal cache (58% versus 23%; GLMM with binomial errors and cache as random factor:  $\beta = 1.76$ ,  $t_{45} = 8.99$ ,  $P < 0.001$ ; Fig. 2), which implies either the use of memory or the location of caches along frequently used paths, or both. Overall, owners were 2.5 times more likely than



**Figure 2.** Behaviour of agoutis at seed caches on Barro Colorado Island, Panama, recorded with camera traps pointed at caches of known owners. ■: cache owners; ▨: naïve individuals. Significance levels: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

naïve animals to investigate or excavate the cache when in view of the camera (32% versus 10%;  $\beta = 1.29$ ,  $t_{45} = 5.5$ ,  $P < 0.001$ ), but equally likely to excavate the seed from the cache (8.4% versus 4.9%;  $\beta = 0.58$ ,  $t_{45} = 0.97$ ,  $P = 0.34$ ).

Among agoutis that approached the exact location of a focal cache, owners ( $N = 83$ ) and naïve animals ( $N = 332$ ) were equally likely to investigate or excavate the cache (54% versus 45%;  $\beta = 0.15$ ,  $t_{35} = 0.58$ ,  $P = 0.57$ ). Among individuals that investigated a cache, owners ( $N = 45$ ) were half as likely as naïve animals ( $N = 148$ ) to excavate the seed from the cache (27% versus 49%;  $\beta = -1.33$ ,  $t_{19} = 3.67$ ,  $P = 0.0016$ ), suggesting that owners purposely retained the cache, and implying a sense of ownership as well as memory. Cameras recorded the excavation of seeds by agoutis at 83 of the 87 caches. Just 12 seeds (14.5%) were excavated by owners, between zero and 120 days after burial ( $N = 12$ , mean  $\pm$  SE =  $25.37 \pm 44.54$ /day). The remaining 71 seeds were removed by cache thieves. The temporal rate of cache excavation by naïve individuals was 5.9 times faster than the rate of excavation by cache owners (Cox regression:  $\beta = 1.78$ , Wald<sub>1</sub> = 32,  $P < 0.001$ ; Fig. 3).

## DISCUSSION

Cache revisiting is a hypothesized mechanism by which scatter-hoarding animals enhance their memory to remember locations over long periods (DeGange et al. 1989; Brodin 1992; Grubb & Pravosudov 1994; Roth et al. 2012). We found that Central American agoutis in Panama regularly inspected their caches, which supports a key assumption of the memory enhancement hypothesis. Cache owners typically visited their cache locations almost once every 5 days, which is nearly four times as often as random locations within their home range. Moreover, owners passing the cache cameras were more likely to sniff the ground or walk directly above their caches than were naïve individuals, yet cache owners did not remove seeds at higher rates than did naïve individuals. The observation that cache owners were less likely to remove seeds after inspection is consistent with the hypothesis that cache owners frequently save their cached seeds for later, while naïve

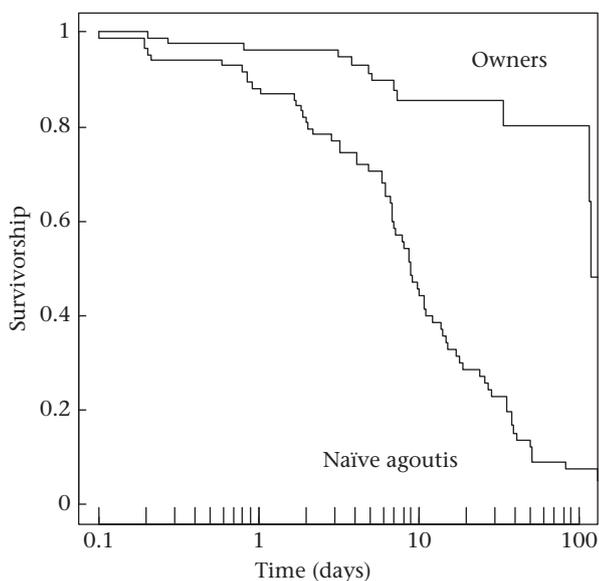
agoutis often remove newly discovered seeds immediately (Fig. 3). These observations demonstrate that cache owners have knowledge of their buried seeds and actively survey their caches.

Our observation that cache and control locations had similar rates of overall agouti activity shows that the disproportionate visiting of caches by cache owners was not an artefact of differences in habitat use or suitability between caches and control points. It is possible that the seed caches were placed at locations that their owners frequented relatively often. For example, caches may have been placed along trails that a particular individual used to patrol its home range. However, the fact that cache owners in our study actively interacted with their caches in a way that was distinctly different from naïve individuals demonstrates that the higher visiting rates were not simply an artefact of relatively high use of the locations in which caches were placed. These differences also cannot be explained by possible cueing of the animals on the tags that were attached to the cached seeds, as such responses should be similar for owners and naïve individuals.

While the patterns that we observed could serve to enforce spatial memory, as the memory enhancement hypothesis assumes, cache revisiting and inspection behaviours could also have at least two additional, nonmutually exclusive, functions. First, agoutis might revisit seed caches to monitor rates of seed theft. Previous studies have shown that seed-caching birds and rodents respond to an increase in cache theft rates by increasing their rate of food caching (Vander Wall & Jenkins 2003; Dally et al. 2006; Huang et al. 2011; but see Dally et al. 2006 for alternate responses to cache theft), suggesting that this information is important to hoarders. It is possible that the agoutis in our study surveyed their caches to assess theft risk, which would allow them to recover caches and move them to safer places if necessary (Hirsch et al. 2012a, b; Jansen et al. 2012), but whether these activities are a response to perceived theft risk is not known.

A second possible function of cache surveillance is to monitor the quality or germination state of cached seeds (Jansen & Forget 2001). For example, acouchies in French Guiana appear to survey caches for seed germination. When encountering a sprout that emerges from a cache, they dig up the seed, cut the sprout and root, and recache the seed, presumably to preserve the food stores (Jansen et al. 2006). Likewise, Wrzen & Wrzen (1982) noted that 'chipmunks nip off sprouts as they appear (Elliott 1978) and so show some degree of cache surveillance'. While agoutis have not been directly observed engaging in this behaviour, seedlings emerging from caches on BCI are often severed, apparently by rodents (P. A. Jansen, unpublished data). We cannot rule out the possibility that agoutis in our study revisited caches in order to monitor the quantity and quality of food stores and respond appropriately by adjusting consumption or modifying seeds.

An important factor that influences behaviour in seed-caching animals is the presence of cache thieves (Dally et al. 2006). Unlike larder hoarders, scatter-hoarding animals are not able to effectively guard their cached seeds (Vander Wall & Jenkins 2003). To reduce the likelihood of theft, scatter hoarders have been shown to space caches out in a manner that reduces theft (Galvez et al. 2009), take seeds to areas of lower seed density (Hirsch et al. 2012b), make false caches in the presence of potential thieves (Steele et al. 2008) and deposit caches out of view of potential robbers (Dally et al. 2005a). It is possible that the cache surveillance behaviours reported here could tip-off potential cache thieves to the location of caches, thus increasing theft rates (Dally et al. 2005a, b, 2006; Steele et al. 2008; Pravosudov 2008; Pravosudov et al. 2010). On one occasion, our cameras observed a cache owner usurped by another agouti while in the process of retrieving a cache (Supplementary Video S1). After the cache owner was chased away, the competitor proceeded to steal the cache. Such aggressive kleptoparasitism may have been



**Figure 3.** Cache excavation by the Central American agouti on Barro Colorado Island, Panama, over time, for cache owners versus naïve individuals (thieves) as revealed by camera traps pointed at caches of known owners. Lines are Kaplan–Meier survivorship curves for excavation of 87 caches, with owners and thieves as competing risks. Note log scale of time axis.

facilitated by behavioural eavesdropping on cache surveillance by the aggressor. Eavesdropping thieves may represent a real cost of cache surveillance in this system.

The cache revisiting and inspection behaviours observed in this study are fully consistent with the predictions of the memory enhancement hypothesis (DeGange et al. 1989; Brodin 1992; Grubb & Pravosudov 1994; Roth et al. 2010), yet they do not conclusively demonstrate that cache surveillance actually serves to strengthen spatial memory. Experimental confirmation is needed to determine whether agouti cache surveillance increases long-term spatial memory and is a mechanism facilitating the ability of agoutis to remember cache locations 120 days after burial. For example, using a similar experimental protocol as Roth et al. (2012) would allow one to test whether frequent cache revisiting in agoutis lengthens spatial memory in this species.

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### Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2013.04.005>.

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