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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 (≥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 ~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.

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