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Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory

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Optimal cache spacing theory predicts that scatter-hoarding animals store food at a density that balances the gains of reducing cache robbery against the costs of spacing out caches further. We tested the key prediction that cache robbery and cache spacing increase with the economic value of food: the ratio of food to consumer abundance. We quantified cache pilferage and cache spacing by the Central American agouti, *Dasyprocta punctata*, in the tropical forest of Barro Colorado Island, Panama, across 10 1 ha plots that encompassed a more than100-fold range in the availability of *Astrocaryum* palm seeds, the agouti's principal food. We found that caches were pilfered at higher rates in plots with lower seed availability, and that agoutis cached seeds further away and into lower densities where seed availability was lower. Food scarcity apparently increased the pressure of food competitors on caches, stimulating agoutis to put more effort into caching seeds to create lower cache densities, fully consistent with theory. We conclude that the optimal cache density depends not only on the nutritional value of food but also on the economic value, which may vary in space as well as time.

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Food hoarding is an important strategy for animals to overcome periodic variation in food availability (Vander Wall 1990; Tsurim & Abramsky 2004). Typically, hoarders store food during periods of high availability and retrieve and consume this food during periods of relative scarcity. An important problem for hoarders is the risk of cache robbery by food competitors, which can imperil the animal's reserves and thereby lower its survival and future reproductive capacity (Wauters et al. 1995). So-called scatter hoarders deal with this risk by spreading their reserves over numerous caches that are spaced out into such a low density that they cannot be efficiently exploited by cache robbers (Dally et al. 2006). Several studies have shown that cache robbery is indeed density dependent (e.g. Stapanian & Smith 1978, 1984; Waite 1988; Daly et al. 1992; Tamura et al. 1999; Male & Smulders 2007a; but see Kraus 1983; Jensen 1985; Henry 1986; Van Horik & Burns 2007).

Stapanian & Smith (1984) proposed that scatter-hoarding animals must space out their caches to a degree that optimally balances the benefits of reducing cache robbery risk and the costs of carrying food items to caches: 'optimal cache spacing' (Stapanian & Smith 1978; Clarkson et al. 1986; Dally et al. 2006). Empirical tests of optimal cache spacing theory (henceforth, OCST) have yielded mixed results; whether cache robbery is indeed density dependent and whether scatter hoarders actually cache seeds in an optimal density have remained controversial. Key predictions of OCST are that the risk of cache robbery and the spacing of caches both increase with food value. Food items of high value should therefore be cached into lower densities than food items of lower value. As far as food value is determined by nutritional value, empirical support for the above prediction is strong. Several studies have found that scatter-hoarding rodents and birds tend to cache large, more nutritious seeds further away (and thus at lower densities) than

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small seeds (e.g. Bossema 1979; Hurly & Robertson 1987; Forget et al. 1998; Jansen & Forget 2001; Jansen et al. 2002, 2004; Vander Wall 2003; Leaver 2004; but see Brewer 2001).

Jansen et al. (2004) argued that the value of food to hoarders is determined not only by the nutritional content (i.e. the energetic value, or the 'value-of-use') but also by the overall availability of food (i.e. the economic value, or the 'value-of-exchange'). Thus, under OCST, cache spacing and cache robbery should both respond not only to (1) variation in the nutritional value of food items, but also to (2) temporal and (3) spatial variation in food availability. Empirical support for response of cache spacing with temporal variation in food availability comes from studies that have found that the distance at which scatter hoarders cache seeds is greater in seed-poor years than in seed-rich years (Jansen et al. 2004 and references therein; Moore et al. 2007). Just one study has addressed how cache spacing is affected by spatial variation in food availability (Hopewell et al. 2008). Moreover, few studies (Hurly & Robertson 1987; Leaver 2004; Jansen et al. 2004) have actually demonstrated responses to food value in terms of cache density besides measures of cache distance from the food source, which may not be related to cache density depending on the local distribution of other food sources.

In the case of animals that scatter-hoard seeds, perhaps the most common and best-studied form of scatter hoarding, cache-spacing behaviour has important consequences for the population dynamics of their food plants. Further and more scattered caching results in further seed dispersal for the food plant, which, if caches for some reason are never retrieved, generally results in increased plant reproductive success. If scatter hoarding is more extensive where food is scarce, as predicted by OCST, then food plants may achieve better seed dispersal where they occur in isolation than where they occur amid conspecifics. In other words, seed dispersal by scatter hoarders would be negatively density dependent (cf. Janzen 1970).

In this study, we empirically tested whether patterns of seed cache spacing by a scatter-hoarder rodent, measured in terms of both distance and density, correlated with spatial variation in ambient food abundance in manner consistent with OCST. We tested two hypotheses: (1) rates of cache pilferage decrease with ambient seed availability and (2) cache distance and density decrease with ambient seed availability. We included cache density as a covariate in our test of hypothesis 1, and considered seed size as a covariate in our test of hypothesis 2. We studied cache pilferage by the mammal community and cache spacing by the Central American agouti, *Dasyprocta punctata*, in the Neotropical forest of Barro Colorado Island, Panama. The food items were seeds of the Neotropical palm *Astrocaryum standleyanum*, which are the principal food source for agoutis, which scatter-hoard the palm seeds into shallow soil-surface caches, and heavily rely on these cached seeds after the fruiting season (Smythe 1989). Cached *Astrocaryum* seeds are also heavily searched for by a variety of terrestrial vertebrate species including conspecifics that pilfer caches (Smythe et al. 1982).

METHODS

Study Site

Fieldwork was conducted from 5 April to 30 June 2008 at Barro Colorado Island (BCI, 9°10′N, 79°51′W). This 1560 ha protected island, administrated by the Smithsonian Tropical Research Institute, was isolated from the mainland with the formation of Lake Gatun and the Panama Canal around 1912. It is covered with moist and semideciduous forest in different successional stages. We worked in late-secondary forest of about 100 years old. Annual rainfall averages 2600 mm, with a marked dry period between December and April (Leigh et al. 1982). Standardized censuses have shown that densities of mammalian herbivores on BCI are comparable with those at much more remote sites, with the exception of the absence of white-lipped peccaries, *Tayassu pecari* (Wright et al. 1994). Detailed descriptions of BCI can be found in Leigh et al. (1982).

Study Species

Agoutis are medium-sized caviomorph rodents (2–4 kg) that inhabit tropical forests from Central America and the West Indies to northern South America (Woods & Kilpatrick 2005). They are mainly diurnal, are almost monogamous, and breed throughout the year. Agoutis occupy territories of approximately 1–4 ha. Males have larger territories than females, which they defend aggressively against conspecific intruders (Smythe 1978; Aliaga-Rossel et al. 2008). Agoutis scatter-hoard seeds of several large-seeded plant species during the period of highest fruit abundance, and retrieve them during the scarcity period, which includes the dry season. Because some of the cached seeds are never recovered, agoutis function as seed dispersers of their food plants (Smythe et al. 1982; Smythe 1983).

Astrocaryum standleyanum is a Neotropical arborescent palm occurring from Costa Rica to Ecuador. Trees annually produce three to six pendulous infructescences with 300–800 ovoid fruits each (De Steven et al. 1987). Fruits are composed of a 2 × 3 cm seed enclosed in a tough endocarp (1.5–3 mm), 4–5 mm of fleshy mesocarp and a thin (<1 mm) pericarp (Smythe 1989). The fruiting period is from March to the beginning of July (De Steven et al. 1987). The fruit pulp (mesocarp) is consumed by a variety of mammal species. The seeds are considered one of the most important food sources for agoutis on BCI (Smythe et al. 1982). In turn, *A. standleyanum* is believed to depend strongly on scatter hoarding by agoutis, as the cleaning, dispersal and burial of seeds significantly increase the chances of survival and germination (Smythe 1989). Cached seeds are mainly retrieved for consumption during the late wet season and the dry season, from September to March (Smythe 1978; Smythe et al. 1982).

Experimental Design

We compared cache spacing and cache pilferage between 10 1 ha forest plots that ranged widely in the abundance of *A. standleyanum*. Plot selection was based on high-resolution aerial photographs of BCI from which canopy-statured individuals of *Astrocaryum* were mapped across the entire island (C.X. Garzon-Lopez unpublished data). Individuals with sun-exposed crowns account for the majority of the seeds produced; hence crown densities on aerial photos are a good proxy for relative seed abundance (Jansen et al. 2008). We selected five locations that had a relatively high density of *Astrocaryum* crowns and five that had a relatively low density.

We quantified food availability in each plot as the ratio of seeds per agouti, following Theimer (2005). We estimated *Astrocaryum* seed abundance by counting the infructescences on each tree, estimating the number of fruits per infructescence (as in Jansen et al. 2008) and summing these totals. This was a fair estimate of food abundance for agoutis, because *Astrocaryum* was the only large-seeded species fruiting during the study period. Agouti abundance was estimated within each plot with camera trapping. Because we could not recognize individual agoutis in the photographs, we followed the principles outlined in Rowcliffe et al. (2008); we placed cameras in randomized locations and presumed that the difference in photo rates reflects differences in the

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