



Contents lists available at ScienceDirect

## Animal Behaviour

journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)

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

Dumas Gálvez<sup>a,d,1</sup>, Bart Kranstauber<sup>a,b,1</sup>, Roland W. Kays<sup>c,d,2</sup>, Patrick A. Jansen<sup>a,d,e,\*</sup><sup>a</sup> Center for Ecological and Evolutionary Studies, University of Groningen<sup>b</sup> Migration and Immuno-ecology, Max Planck Institute for Ornithology, Radolfzell<sup>c</sup> New York State Museum<sup>d</sup> Smithsonian Tropical Research Institute<sup>e</sup> Centre for Ecosystem Studies, Wageningen University

## ARTICLE INFO

## Article history:

Received 15 April 2009

Initial acceptance 22 June 2009

Final acceptance 19 August 2009

Available online 3 October 2009

MS. number: 09-00247R

## Keywords:

cache pilferage

camera trapping

Central American agouti

*Dasyprocta punctata*

food availability

optimal cache spacing

scatter hoarding

seed dispersal

tropical forest

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 than 100-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

\* Correspondence: P. A. Jansen, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA, Haren, The Netherlands.

E-mail address: [p.a.jansen@rug.nl](mailto:p.a.jansen@rug.nl) (P.A. Jansen).

<sup>1</sup> D. Gálvez and B. Kranstauber are at the Center for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

<sup>2</sup> R. W. Kays is at the New York State Museum, CEC 3140, Albany, NY 12230, U.S.A. and the Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panamá, República de Panamá.

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

densities of animals. We used two motion-triggered camera traps (Reconyx RC55 Rapid Fire IR, Reconyx, Inc., Holmen, WI, U.S.A.) within each plot, and moved them to a new random location every 8 days. This produced data for a total of 104 trap-days per plot across eight random locations within each plot. The scale of our camera sampling (eight points within 1 ha) is large enough relative to agouti home range size to avoid local-level differences in animal movement (e.g. congregating around one fruit tree) from biasing our abundance estimate (Aliaga-Rossel et al. 2008). Agouti abundance was quantified as the capture rate, the number of agouti visits per day, which gave a relative measure of agouti foraging across the study plots. Note that a relatively high capture rate may arise from a site being used by more individuals, from individuals using a site more intensely, and from local individuals being more active. All are assumed to elevate feeding pressure on the locally available seeds. The relative availability of seeds to agoutis was then calculated as the number of seeds within the 1 ha plot divided by the average capture rate of agoutis per plot.

#### Cache Pilferage Experiments

The effect of food abundance on cache pilferage (hypothesis 1) was assessed in an experiment in which we mimicked agouti caches by burying *Astrocaryum* seeds ourselves and then monitoring cache pilferage. We created three 5 × 5 grids in each plot during 14–20 May with 2.5, 5 and 10 m interspacing, corresponding to cache densities of 0.16, 0.04 and 0.016/m<sup>2</sup>. These densities are similar to those used in pilferage experiments by Stapanian & Smith (1978, 1984). At each position, we cached one palm seed that was thread-tagged by drilling a 1 mm hole to the distal end of the seeds and tying a 100 cm green nylon thread to the seed, attached the free end of the thread to the nearest sapling or tree, and marked that tree at eye level with a numbered tag. Thus, it was unlikely that cache pilferers could tune in on place markers. We checked the caches at 1, 7, 11, 14, 24, 29, 43 and 56 days after placement, recorded seed disappearance, and calculated the rate of removal by pilferers (as in Vander Wall & Jenkins 2003).

#### Cache-spacing Experiments

The effect of local food abundance on cache spacing (hypothesis 2) was measured in a seed-tracking experiment. We collected intact *Astrocaryum* fruits outside of the plots, either from the ground or from fruit traps consisting of 5 m<sup>2</sup> pieces of shade cloth that we suspended below fruiting palms. We manually removed the exocarp from the seeds, soaked them for approximately 2 days, removed the rest of the pulp with a pocket knife, and air-dried the seeds on paper towel for 2 days. Then, we haphazardly assembled batches of 25 seeds of dissimilar sizes, to get a range of different masses within each batch, and weighed each seed. Mean seed mass per batch ± SD was 9.13 ± 0.71 g; the overall seed mass range was 7–15 g. All seeds were then individually tagged by attaching a 65 cm nylon thread to the seed (as above), attaching a 2.5 × 15 cm piece of brightly coloured flagging tape to the end of the thread, and writing a unique identity number on the tape with a permanent marker.

In each plot, we placed two batches of 25 tagged seeds below an adult palm, in a grid with 5.5 cm distance between seeds. We monitored one of the two grids with a camera trap (Reconyx RC55 Rapid Fire IR) that recorded video clips whenever triggered by the motion of a warm-blooded animal in front of the lens. From the video, we determined the species of the animal that removed the seeds, as well as the order and time of seed removal per individual seed. After most of the seeds had been removed, we searched the surrounding area up to a distance of 40 m for thread tags

protruding from the ground, which showed the location of a cache (agoutis bury the seeds but not the threads). Caches were mapped using tape measures, an ultrasonic rangefinder (Haglöf DME 201, Haglöf, Inc., Madison, WI, U.S.A.) and a precision compass (Suunto KB-14, Suunto Oy, Vantaa, Finland).

We used two point pattern analysis techniques to quantify cache density. First, we determined the minimum spanning tree (MST): the set of lines with the smallest total distance that connects all points (cached seeds) into a single structure without cycles (Dale 1999). MST yields a set of nearest-neighbour distances (NND) that can be compared between plots. Smaller distances imply a higher density. Second, we calculated the minimum convex polygon (MCP) encompassing all mapped caches using the library spatstat (function convexhull.xy) in the statistical software package R version 2.7.1 (R Development Core Team 2008). Here, cache density was expressed as the number of caches divided by the area enclosed by the MCP. The MCP has previously been used to estimate caching areas (Vander Wall 1995; Pons & Pausas 2007).

#### Data Analyses

All analyses were done in R 2.7.1 (R Development Core Team 2008) and SPSS 14.0 (SPSS Inc., Chicago, IL, U.S.A.). We used Cox proportional hazards modelling to test whether cache pilferage rates decreased with food availability and increased with cache density (hypothesis 1). Here, we treated the time until pilferage of a cached seed as time-to-event, assuming right censoring, and censored the times for caches still present at the end of the monitoring period at 56 days. Cache density was included as a covariate. We used the cluster option to account for dependence of observations within density plots. Under hypothesis 1, we expected a significant decrease in the pilferage rate with food availability.

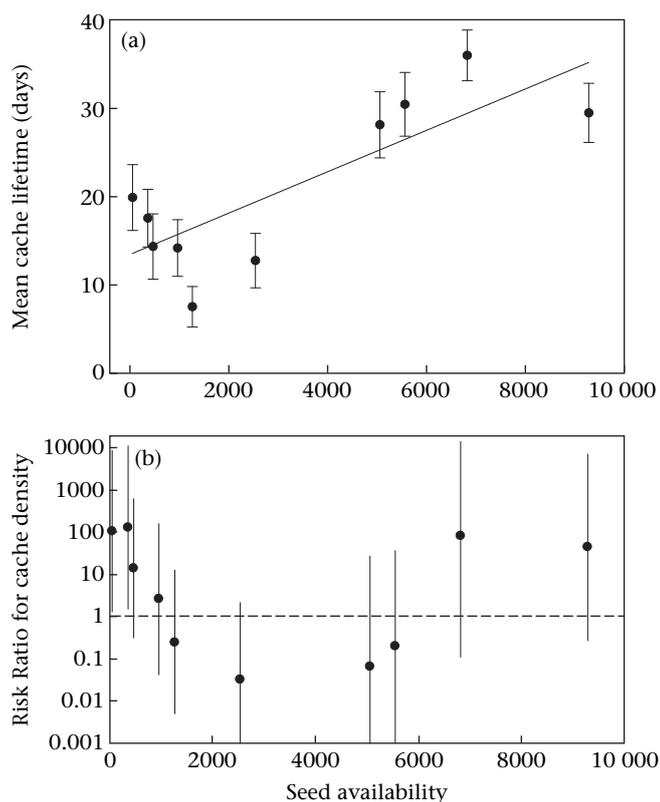
We used a linear mixed model (LMM) to test whether cache density increased with food availability (hypothesis 2). Here, we regressed distance, NND and density against food availability, with fresh seed mass as covariate. The 1 ha plots were included as a random (grouping) factor to account for dependence of observations within plots. Under hypothesis 2, we expected a significantly negative relationship of distance or NND with food availability, or a significantly positive relationship of density with food availability.

## RESULTS

The 10 study plots covered a wide gradient of palm abundance, as intended. Seed density varied between plots by more than two orders of magnitude and increased significantly with palm abundance ( $F_{1,8} = 461$ ,  $R^2 = 98.3$ ,  $P < 0.001$ ). The agouti capture rate on the camera traps increased significantly with seed abundance, but was far from proportional (capture rate =  $0.49 \times [\text{seed density}]^{0.16}$ ,  $R^2 = 0.65$ ); agouti numbers varied between plots just threefold. Thus, relative seed availability, that is, the ratio seed-to-agouti, varied among plots 170-fold.

#### Cache Pilferage

The survival rate of experimental caches increased significantly with seed availability (Cox regression with clustering of observations per density plot:  $RR = 0.85 \times 10^{-3}$ ,  $Wald_1 = 22.8$ ,  $P < 0.001$ ). Also, Kaplan–Meier estimates of mean cache survival increased significantly with seed availability (linear regression:  $F_{1,8} = 14.9$ ,  $R^2 = 0.65$ ,  $P < 0.005$ ; Fig. 1a). These results are in agreement with hypothesis 1 that food availability affects cache pilferage. The cache density treatment, however, did not have a consistent effect. Although on average low-density caches had longer half-lives



**Figure 1.** Pilferage of experimental caches of *Astrocarylum standleyanum* seeds across a gradient of food availability at Barro Colorado Island, Panama. (a) Overall cache survivorship expressed as the Kaplan–Meier estimate of mean survival time  $\pm$  SE. (b) Effect of cache density on cache pilferage expressed as the Risk Ratio, estimated by plotwise Cox regression. Food availability of experimental plots was expressed by the seed-to-agouti ratio, calculated as the number of *Astrocarylum* seeds/ha divided by the average number of agouti appearances on camera traps/day.

(18 days) than medium-density (13) and high-density caches (10 days), in agreement with the prediction, these differences were not significant even when the data were pooled (Kaplan–Meier survival analysis, log-rank test:  $\chi^2_2 = 2.58$ ,  $P = 0.28$ ). This lack of effect reflected the finding that the mean survival times (estimated with Kaplan–Meier survival analysis) decreased across the three cache densities in just four of 10 plots (Table 1). Similarly, the Risk Ratio for cache density, which represents the estimated increase in pilferage risk per unit increase in density, differed significantly from zero only in the two lowest-density plots (Cox regression for each of the 10 plots separately), and decreased with seed availability only up to half the range of seed availability (Fig. 1b).

### Cache Spacing

Agoutis removed all tagged seeds with video evidence in just four of the 10 experiments. These were in plots that all had a relatively low seed availability, but still ranged in seed availability 50-fold. In these plots, we located 83 caches out of 100. Heavier seeds were cached further from the source (LMM with plots as random factor:  $F_{1,77} = 8.34$ ,  $P = 0.005$ ) and more so as plots had lower seed availability (interaction term:  $F_{1,77} = 5.29$ ,  $P = 0.024$ ). Thus, agoutis cached seeds further away from the source when the seeds were scarcer (Fig. 2a) and when seeds had a greater nutritional value, which is in agreement with hypothesis 2.

Greater dispersal distance translated into wider cache spacing. Nearest-neighbour distance of caches increased with cache

distance from the source (LMM with plots as random factor:  $F_{1,77} = 124$ ,  $P < 0.001$ ) and this increase was stronger when seed abundance was lower (interaction term:  $F_{1,77} = 15.2$ ,  $P < 0.001$ ). As a result, cache spacing decreased with increasing seed availability, both in terms of nearest-neighbour distance between caches (linear regression on means:  $F_{1,2} = 18.4$ ,  $R^2 = 0.90$ ,  $P = 0.05$ ; Fig. 2b) and cache density ( $F_{1,2} = 31.53$ ,  $R^2 = 0.94$ ,  $P = 0.03$ ; Fig. 2c). Thus, agoutis spaced out their caches more widely when less food was available to them, which is also in agreement with hypothesis 2.

Camera monitoring yielded complete sequences of seed removal from the feeding stations for 58 seeds in three plots. Short intervals between successive removal events and similarity of the photographed individuals suggested that subsequent caches were made by one individual agouti per plot. The order of seed removal correlated significantly with the distance the seed was moved so that those removed later were cached further away (LMM with plots as random factor:  $F_{1,54} = 13.5$ ,  $P < 0.001$ ).

### DISCUSSION

A key prediction of optimal cache spacing theory (OCST, Stapanian & Smith 1978; Clarkson et al. 1986) is that cache spacing increases with food value. Our study is among the first (but see Hopewell et al. 2008) to test this prediction in terms of economic value, that is, value-of-exchange, by comparing cache pilferage and cache spacing across a spatial gradient of ambient food availability, which we quantified as the number of seeds over relative agouti abundance (cf. Theimer 2005). Moreover, this study is the first to test OCST in a tropical environment.

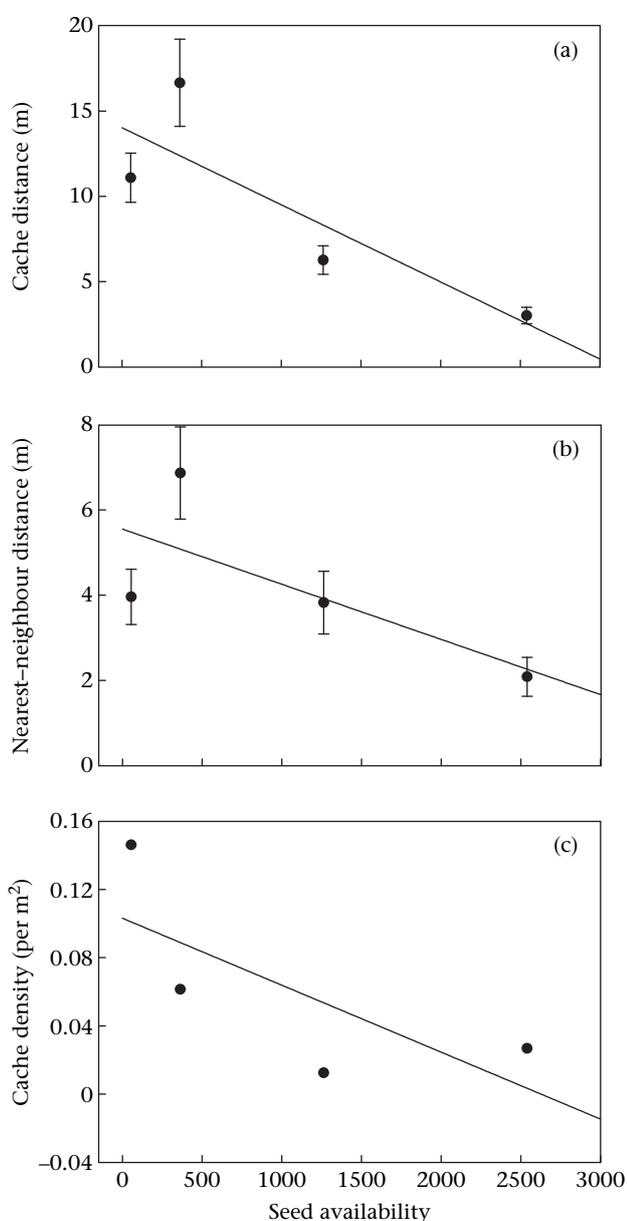
We found that pilferage rates of experimentally cached *Astrocarylum* palm seeds, a principal food resource of agoutis, decreased with ambient seed availability, presumably because of satiation of the agoutis. Thus, hoarding seeds in low-food areas, everything else being equal, came with a higher risk of cache loss to food competitors. This implies that food scarcity requires greater investments of scatter hoarders in strategies to minimize pilferage risk (Dally et al. 2006). Second, we found that agoutis cached *Astrocarylum* palm seeds further away and into lower densities where ambient food availability was lower and hence cache pilferage risk higher. That agoutis spaced out caches further under lower food abundance is fully consistent with OCST, and with Hopewell et al. (2008), who found that cache distance in semi-habituated grey squirrels, *Sciurus carolinensis*, increased with manipulated food abundance. Together, these findings suggest that food scarcity increases the pressure of food competitors on caches, which in turn stimulates agoutis to put more effort into caching seeds to create lower cache densities. These results are strong evidence for the dependence of spatial patterns of cache pilferage and scatter hoarding on the economic value of food (Jansen et al. 2004). They add to previous studies which showed that scatter hoarders varied their caching strategy in response to the presence of food competitors (reviewed in Dally et al. 2006; Hopewell et al. 2008).

Previous studies of scatter hoarding have demonstrated that cache spacing responds to temporal fluctuations in seed production, for example between masting and nonmasting years (reviewed in Jansen et al. 2004). Also, many studies have found a positive relationship between dispersal distance and seed size (e.g. Hurly & Robertson 1987; Forget et al. 1998; Jansen & Forget 2001; Jansen et al. 2002, 2004; Vander Wall 2003; this study). The above responses all make sense in terms of economy: seed scarcity in time or space increases the 'value-of-exchange' of seeds while seed size increases the 'value-of-use', which together determine the economic value of seeds. As food competitors increase their foraging effort with the economic value, scatter hoarders are left

**Table 1**  
Variation in survival of experimentally cached *Astrocaryum* palm seeds with cache density class across 10 forest plots with different food abundance

Plot	Food abundance (seed:agouti ratio)	Survival time (days) per class (mean±SD)			Difference in survival*		
		High	Medium	Low	L>M	M>H	L>M>H
1	9284	26.4±3.1	27.0±3.2	35.1±2.5	Y	Y	Y
2	6822	33.4±2.9	35.0±3.1	39.6±1.6	Y	Y	Y
3	5562	30.0±3.4	34.0±3.1	27.4±3.2	N	Y	N
4	5058	29.8±3.3	22.2±2.2	25.8±3.5	Y	N	N
5	2540	19.1±3.4	8.8±1.6	10.4±2.4	Y	N	N
6	1263	14.3±1.9	15.4±3.4	12.9±3.0	N	Y	N
7	964	9.4±1.9	11.7±2.8	17.4±3.5	Y	Y	Y
8	469	4.1±0.6	7.6±1.6	10.9±2.9	Y	Y	Y
9	363	10.1±2.1	30.5±2.7	12.1±1.8	N	Y	N
10	55	15.6±3.4	14.9±2.9	29.2±2.8	Y	N	N

\* Difference in mean survival time between density treatments as predicted (Y) or not (N).



**Figure 2.** Cache spacing by agoutis across a range of relative food availability at Barro Colorado Island, Panama. (a) Mean cache distance ± SE, (b) mean nearest-neighbour distance ± SE and (c) cache density estimated as the number of caches over the area delimited by the Minimum Convex Polygon.

with no other choice than to invest more in hiding seeds or lose them to cache thieves.

#### Density Dependence of Cache Pilferage

Density dependence of cache pilferage has been demonstrated in many studies, which typically, like our study, added experimental caches to the environment (Stapanian & Smith 1984; Clarkson et al. 1986; Daly et al. 1992; Vander Wall 1995). Moore et al. (2007) argued that, under OCST, the density dependence of cache pilferage should increase with the risk of pilferage. Thus, lowering cache density would be more effective in reducing pilferage under low food abundance, where adding caches may considerably increase the absolute density of caches and thereby increase the foraging efficiency of pilferers (Kraus 1983), than under high food abundance, where variation in the density of added caches will be nullified against the background of the numerous existing caches, and where adding caches hardly affects the absolute density of caches and the foraging efficiency of pilferers (Moore et al. 2007).

Our experiment with mimicked seed caches, however, yielded no consistent effect of seed density on pilferage. Pilferage rates increased with cache density in just four of 10 sites. Moreover, density dependence of pilferage did not clearly decrease with seed availability. Density dependence of cache pilferage was significantly positive only at the two sites with the lowest food availability, and was highly variable with density across the further range of food abundance. We offer two possible explanations for these anomalous results. First, unknown spatial variation in background density of existing caches may have caused random noise in our density treatment, introducing attenuation bias of our analyses. This would imply that our assumption of a single common background density across each experimental plot did not hold. Second, cache pilferage rates may vary across spatial scales much smaller than the 1 ha plots in our study, for example because of occupancy by individual cache-pilfering animals, while we assumed that pilferage pressure would be uniformly distributed across each 1 ha plot.

#### Correlates of Cache Spacing

Our results showed that the density of agouti-made caches declined with increasing cache distance, in agreement with the prediction of Clarkson et al. (1986), but not Stapanian & Smith (1978), who predicted that density should not be affected by distance. Several earlier studies have reported a similar negative relationship (Cowie et al. 1981; James & Verbeek 1985; Clarkson et al. 1986; Jansen et al. 2004). Jansen et al. (2004) argued that cache density in caviomorph rodents is simply a by-product of

dispersal distance; nondirectionally carrying seeds away from the food source automatically lowers cache densities. Our study, however, suggests that agoutis are able to manipulate cache density directly as we found that the relationship between cache density and distance was stronger under lower food availability than under high food availability.

Furthermore, the individual photo monitoring of seed removal allowed us to relate removal sequence to cache distance. We found that the distance at which agoutis cached seeds increased with the sequence of removal. This finding is in agreement with Clarkson et al. (1986), who, based on OCST, predicted that the first seeds should be cached closer to the food source and the subsequent seeds both near and far, but the correlation in our study was much lower ( $R^2 = 0.16$ ) than in Clarkson et al. ( $R^2 = 0.60$ ). With the exception of Clarkson et al. (1986), no other studies that considered successive cache distances have found support for this prediction (Stapanian & Smith 1978; Cowie et al. 1981; Vander Wall 1995). Thus, removal sequence seems a poor predictor of cache distance in general.

### Conclusions

This study revealed that cache spacing by scatter-hoarding rodents may vary with food abundance not only between subsequent years of contrasting food production at a single place (Jansen et al. 2004; Moore et al. 2007) but also between adjacent areas of contrasting food abundance at a single time (Hopewell et al. 2008). Agoutis scatter-hoarded seeds of *Astrocaryum* further away in areas where this palm was less abundant. Our findings may have important implications for the potential functioning of agoutis as seed dispersers of their food plants, many of which rely on incomplete recovery of caches for seedling recruitment. By favouring the dispersal and recruitment potential of seeds from trees isolated from conspecifics relative to trees in conspecific clumps, adaptive caching behaviour of agoutis may result in negative density dependence of seed dispersal and ultimately seedling recruitment.

### Acknowledgments

We gratefully acknowledge critical comments by Anders Brodin, Lisa Leaver and Ana Sendova-Franks, field assistance by Anthony Turner, Nadia Sitas, Anouk de Plaa, Carol Garzón-López, Liliana Ballesteros, Signe Brinkløv, Robert Horan, Erin Kurten and Katrin Petsch, logistical support by Belkys Jimenez, Oris Acevedo and the Smithsonian Tropical Research Institute, and financial support from the National Science Foundation (NSF-DEB 0717071 to R.W.K.), the Netherlands Foundation for Scientific Research (NWO-ALW 863-07-008 to P.A.J.) and the Marco Polo Fund (to D.G. and B.K.).

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