ECOLOGY LETTERS

Ecology Letters, (2012) doi: 10.1111/ele.12000

LETTER

Directed seed dispersal towards areas with low conspecific tree density by a scatter-hoarding rodent

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Abstract

Scatter-hoarding animals spread out cached seeds to reduce density-dependent theft of their food reserves. This behaviour could lead to directed dispersal into areas with lower densities of conspecific trees, where seed and seedling survival are higher, and could profoundly affect the spatial structure of plant communities. We tested this hypothesis with Central American agoutis and *Astrocaryum standleyanum* palm seeds on Barro Colorado Island, Panama. We radio-tracked seeds as they were cached and re-cached by agoutis, calculated the density of adult *Astrocaryum* trees surrounding each cache, and tested whether the observed number of trees around seed caches declined more than expected under random dispersal. Seedling establishment success was negatively dependent on seed density, and agoutis carried seeds towards locations with lower conspecific tree densities, thus facilitating the escape of seeds from natural enemies. This behaviour may be a widespread mechanism leading to highly effective seed dispersal by scatter-hoarding animals.

Keywords

Astrocaryum, agouti, Barro Colorado Island, directed dispersal, density dependence, *Dasyprocta punctata*, secondary seed dispersal.

Ecology Letters (2012)

INTRODUCTION

Seeds and seedlings that are located in the vicinity of conspecific adults are more likely to be attacked by distance- or density-responsive pests and pathogens (Janzen 1970; Connell 1971; Peters 2003; Mangan *et al.* 2010; Terborgh 2012). Escaping the immediate vicinity of the parent plant is therefore one of the key benefits of seed dispersal (Nathan & Muller-Landau 2000). However, even after dispersal, seeds may still land near conspecific plants other than the parent, and this probability increases as conspecifics are more abundant (Janzen 1970). Because a high density of adult conspecifics leads to decreased seed and seedling survival (Schupp *et al.* 2002), the most effective strategy to achieve successful dispersal would be to have seeds move away from *all* conspecifics, not just parents. This may be possible if dispersal is in some way 'directed' via animals or other mechanisms. Directed dispersal, the disproportionate movement of seeds to favourable sites, is one of the hypothesised advantages of seed dispersal by vertebrates (Howe & Smallwood 1982; Howe 1986; Wenny 2001). Nonetheless, controversy still surrounds the hypothesis that vertebrates commonly provide directed dispersal in general, and directed dispersal away from conspecifics in particular (Russo & Augspurger 2004; Kwit *et al.* 2007; Spiegel & Nathan 2010). In fact, many animals move seeds to unfavourable locations, such as underneath fruit trees or sleep sites (e.g. Schupp *et al.* 2002; Kwit *et al.* 2007; Vander Wall & Beck 2011). Such seed dispersal may result in highly clumped aggregations of seeds and lower recruitment due to negatively density-dependent mortality (Kwit *et al.* 2007).

We investigated the possibility that the innate behavioural responses of scatter-hoarding rodents to food competition result in directed dispersal of seeds into areas with low conspecific density (Muñoz & Bonal 2011). Scatter-hoarding rodents tend to hide seeds in widely spaced caches in the soil surface as food reserves to be retrieved and eaten later (Vander Wall 1990; Jansen & Forget 2001). Optimal cache spacing theory (OCST) predicts that scatter-hoarding animals should hide stored food (i.e. seeds) in low densities to make it more difficult for competitors to discover and steal the food (Stapanian & Smith 1984). Many studies have demonstrated that cache robbery is indeed density dependent (e.g. Stapanian & Smith 1978, 1984; Waite 1988; Daly *et al.* 1992; Male & Smulders 2007). Theoretically, scatter hoarders could avoid high cache densities by selectively moving seeds into areas that have fewer food trees, and therefore fewer cached seeds (Muñoz & Bonal 2011). A predicted consequence of such a behavioural response to food theft is that these animals disperse seeds to areas where seeds and seedlings are less susceptible to natural enemies (Terborgh 2012). Several previous studies have documented scatter-hoarding animals moving seeds into different habitats to reduce cache pilferage, and consequentially away from conspecific adult trees (e.g. Stapanian & Smith 1986; Gomez 2003; Abe *et al.* 2006; Muñoz & Bonal 2011). However, it is not known whether animals within a continuous habitat change their caching strategies based on differences in local plant density.

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To date, no study has shown that scatter-hoarding animals directionally disperse seeds to areas with lower densities of adult conspecifics within the same habitat.

We tested the hypothesis that scatter-hoarding agoutis (*Dasyprocta punctata*) directionally disperse palm (*Astrocaryum standleyanum*) seeds towards locations that have lower background densities of palm trees. Recent studies have documented that agoutis disperse *Astrocaryum* seeds in multiple steps because they routinely steal seeds from caches made by conspecifics and re-cache the seeds at different locations (Jansen *et al.* 2012). Because of this stepwise dispersal, small levels of directed dispersal by agoutis could potentially add up to substantial reductions in surrounding conspecific density. We used telemetric thread tags to follow individual seeds from their initial placement through multiple cache locations (Hirsch *et al.* 2012). We then evaluated changes in conspecific density of the seed throughout its trajectory to test the predictions of the OCST and more importantly, to test if this behaviour results in seeds being directionally dispersed into areas with low adult palm densities, and thereby enhance the escape of seeds and seedlings from competition and natural enemies. We find that these scatter-hoarding rodents direct seed dispersal towards areas of relatively low conspecific tree density. This demonstrates that a behavioural mechanism to reduce food theft also plays an ecologically important role via the mitigation of Janzen–Connell effects.

METHODS

Site and species

This study was conducted on Barro Colorado Island (BCI), Panama (9°10′ N, 79°51′ W), a 1560-ha island covered with tropical moist forest, protected and administered by the Smithsonian Tropical Research Institute (Leigh 1999). The climate is seasonal, with a distinct 4-month dry season (January to April) and 2600-mm average annual rainfall. Our study area consisted of 25 ha of late-secondary forest (estimated at 100–120 year old) in the central portion of BCI.

The Central American agouti is a 2–4 kg caviomorph rodent that occurs throughout Central American tropical forests. Agoutis scatter hoard large seeds as food reserves for periods of food scarcity. On BCI, *Astrocaryum* seeds are a particularly important food resource because they remain dormant and edible for a year or more (Smythe 1978, 1989; Jansen *et al.* 2010). Agoutis are known to disperse *Astrocaryum* seeds further in areas of low food abundance, resulting in greater spacing between seeds in areas with low adult densities (Galvez *et al.* 2009). Agoutis on BCI have overlapping home ranges varying in size from 1 to 4 ha (Smythe 1978), where agoutis inhabiting areas with relatively fewer *Astrocaryum* trees tend to have larger home ranges (Emsens *et al.* 2012).

The arborescent palm *A. Standleyanum* (Arecacae) is distributed from Costa Rica to Ecuador and is among the ten most abundant tree species in central Panama (Pyke *et al.* 2001). Adult palms produce up to eight pendulous infructescences, each up to 150 cm long with up to 500 brightly coloured, sweet-fleshy fruits (Jansen *et al.* 2010). Each fruit contains a c. 9.6-g stone consisting of a large seed enclosed in woody endocarp (henceforth 'seed'; Jansen *et al.* 2010). Ripe *Astrocaryum* fruits are normally available from April to June (Jansen *et al.* 2008). After falling to the ground, seeds are typically dispersed by agoutis (Smythe 1989; Jansen *et al.* 2012).

Study design

Our study design involved radio tracking of agouti-dispersed seeds, measuring the density of *Astrocaryum* trees around each location at which a seed was cached, and determining whether these densities were lower than those that would result from random movements. Ripe *Astrocaryum* fruits were collected using 2 × 4-m shade cloth seed traps suspended below haphazardly selected fruiting trees. Seeds were defleshed by hand using a small knife to mimic natural defleshing by rodents and other frugivores (cf. Jansen *et al.* 2010), air dried and given a telemetric thread tag (Hirsch *et al.* 2012). Any seed that was significantly larger or smaller than average (± 2 g) was excluded from the experiments. Telemetric thread tags comprise a 30-cm black nylon-coated stainless steel leader wire (Surflon 1 × 7 black coating, American Fishing Wire, Coatesville, PA, USA) attached to a 7-mm screw eye inserted into the basal tip of the seed, and a 3.8-g cylindrical VHF transmitter attached to the end of the wire (Advanced Telemetry Systems Inc., Isanti, MN, USA) (Hirsch *et al.* 2012). Affixing thread tags to seeds is a widely accepted method for tracking seed dispersal by scatter-hoarding rodents because rodents will bury the seed, but leave the thread above the ground allowing researchers to locate the seed (Forget & Wenny 2005). When cached seeds were located, we placed the transmitter on top of an 8 × 22-mm magnet taped to the head of a 10-cm nail that was pushed into the soil approximately 25 cm from the seed. This turned off the transmitter and conserved battery life. If the seed was removed, the transmitter was pulled off the magnet and activated (Hirsch *et al.* 2012).

A total of 589 seeds were placed at 52 stations in the 25-ha study area during May to July 2010. Each seed station was monitored using a motion-sensitive camera trap pointed at the tagged seeds (RC55 or PC800, Reconyx Inc., Holmen, WI, USA). Five seeds were placed at each station for a maximum of 8 days. If seeds remained after 8 days, the seeds were replaced with fresh seeds, or the entire station was cancelled. Each seed plot was checked daily and removed seeds were located by sight or with hand-held radio-telemetry equipment (Yaesu-VR500, Cypress, CA, USA) to determine dispersal distance and seed fate. If the seed was found < 20 m from the seed plot, the dispersal distance was measured with measuring tape, and the direction of movement was recorded using a precision compass (Sunto KB-14, Suunto Oy, Vantaa, Finland). If the seed was moved > 20 m, the location of the seed was recorded using a GPS receiver (Garmin 60CSx, Garmin Intl., Olathe, KS, USA). To increase GPS accuracy, we averaged at least 50 waypoints per seed location. If the seed was cached, we turned off the transmitter by placing it on a magnet, and continued to monitor the seed. Of the initial 589 seeds, a total of 224 cached seeds were continuously followed for up to 1 year. Many seeds were moved and cached multiple times, and information related to higher order seed movements (seeds moved more than once) were recorded in the same manner described above (Jansen *et al.* 2012).

We measured the density of conspecifics adult trees, which should be the variable most strongly related to distance-dependent effects (Terborgh 2012). The density of *Astrocaryum* trees is also highly correlated to the total number of seeds produced within a given area ($R^2 = 0.88$, Emsens *et al.* 2012), which is related to density-dependent effects (Terborgh 2012). All *Astrocaryum* trees within the study area were mapped by surveying the study area on foot. Trees were labelled and their locations were recorded using a GPS receiver. All locations were surveyed twice to ensure that no trees were overlooked. We estimated the neighbourhood density of *Astrocaryum* by using the buffer tool in ArcGIS 9.3 (ESRI, Inc. Redlands, CA, USA) to count the number of *Astrocaryum* trees within 25 m of each seed location. This radius represents a biologically realistic spatial scale at which agoutis could respond to food abundance, and is not overly sensitive to GPS error. To ascertain that our choice of radius did not influence the results, we repeated these analyses using 10 m and 50-m buffers.

To determine the presence of density-dependent effects on the survivorship of seeds and seedlings, we surveyed seeds and seedlings at 143 points spaced 100 m apart in a grid of sampling sites throughout our mapped study area. At each point, we counted all adult *Astrocaryum* trees within 25 m as described above, counted all seedlings with maximum leaf length $\leq$ 1 m within 3 m of the sampling point, and counted all *Astrocaryum* seeds in a 1-m^2 area on the soil surface and in the soil up to a depth of 15 cm (cf. Wright *et al.* 2000). We then compared the log–log relationship between seed and seedling density. If survival of seeds to seedlings is independent of seed density (i.e. a fixed proportion of seeds survive to the seedling stage), then the slope of the log–log relationship should be approximately one (cf. Harms *et al.* 2000).

Analyses

We tested whether rodents carried seeds to areas with lower *Astrocaryum* tree densities by comparing the observed neighbourhood densities with densities resulting from simulated random movements. All spatial analyses were performed in ArcGIS 9.3. First, each observed seed movement was paired with 100 random seed movements generated using the observed start position, a random direction, and a distance randomly drawn from the overall probability distribution of observed movement distances. For example, if one seed was moved four times (e.g. Fig. 1), 100 random movements were simulated for each of the four observed seed movements by combining the observed cache location with a random distance and direction. We used a generalised mixed model (GLMM) to test whether the observed movements produced a greater decrease in neighbourhood density than did random movements (all GLMM's were run in STATISTICA 6.1, StatSoft Inc. Tulsa, OK, USA). The dependent variable was the change in *Astrocaryum* tree density from the starting location of the seed to the next location. As most seeds were moved multiple times, we included seed ID as a random effect to assure statistical independence. The density of *Astrocaryum* trees within 25 m at the beginning of a seed movement was included as a fixed effect. Second, we tested whether the final locations of seeds (i.e. the last observed location of the seed) had lower *Astrocaryum* tree densities than the starting locations. For this analysis, we calculated the total Euclidian distance that each seed was displaced from the initial placement location to the final location. We then simulated random movements for each of the 224 seeds using a random direction and a distance drawn from the distribution of these total Euclidian distances.

We repeated both analyses using different modelling criteria. First, we used 10 m or 50-m radii for calculating *Astrocaryum* neighbourhood density, instead of 25 m. Second, we repeated both analyses with random seed movements simulated differently, by combining random directions with observed dispersal distances, instead of drawing random distances from the overall distribution of observed distances (Appendix S1).

RESULTS

Camera monitoring indicated that agoutis took 83% of seeds that were removed from the seed stations (n = 423) and took 94% of the caches (n = 134), confirming that *Astrocaryum* seed dispersal was primarily by agoutis (Jansen *et al.* 2012). The 224 seeds that were followed throughout the study period were moved 5.5 times on

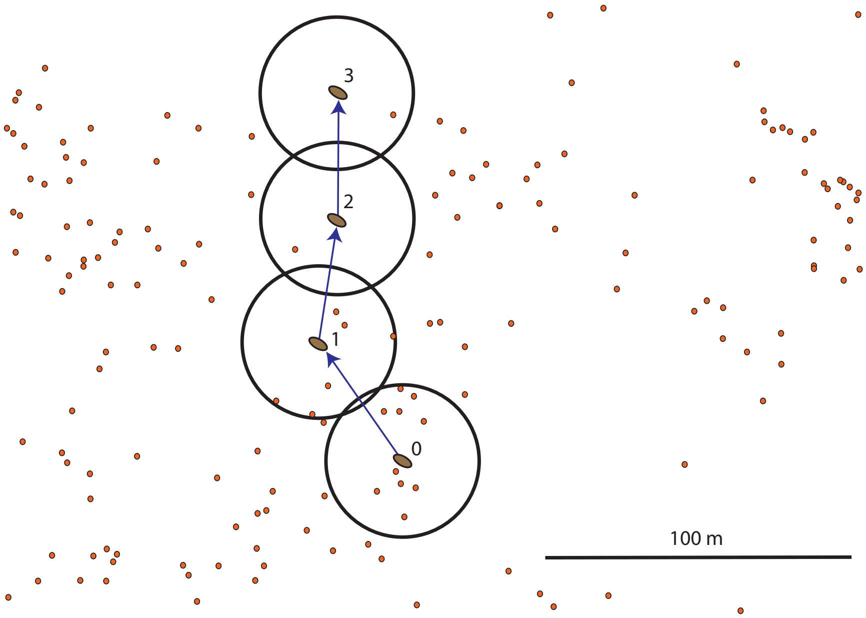

Figure 1 Observed movement path (blue arrows) of one *Astrocaryum standleyanum* seed in relation to the distribution of adult trees (orange dots) on Barro Colorado Island, Panama. The location at which the tagged seed was released is represented by a 0, whereas a three indicates the final location. Each location is surrounded by a 25-m radius across which the tree density was calculated.

Table 1 GLMM testing factors that influence changes in neighbourhood density of conspecific adults for *Astrocaryum* seeds as they are moved by scatter-hoarding agoutis. Model includes all seed movements, including multiple movements of the same seed

Variable		DF	F	*P*
Seed ID	Random	224	47.87	<0.001
Observed vs. random movements	Fixed	1	27.84	<0.001
Initial seed density	Fixed	1	10910.70	<0.001

average (range 1–36 times; Jansen *et al.* 2012). Seeds were dispersed over an average distance of 18.1 m per movement (range 0–241 m ± 21.53 SD, *n* = 1425). The observed total distance travelled by seeds averaged 54.9 m (range 1–280 m ± 48.26 SD, *n* = 224).

Considering each movement step individually, seeds were moved to areas with disproportionally lower *Astrocaryum* tree densities (predicted number of trees within 25 m = 3.24 trees < 25 m, ± 3.75 SD, observed = 2.93 ± 3.45 SD, $F_{1,143924}$, $P < 0.001$, Table 1). These differences accumulated along the trajectory of the seeds,

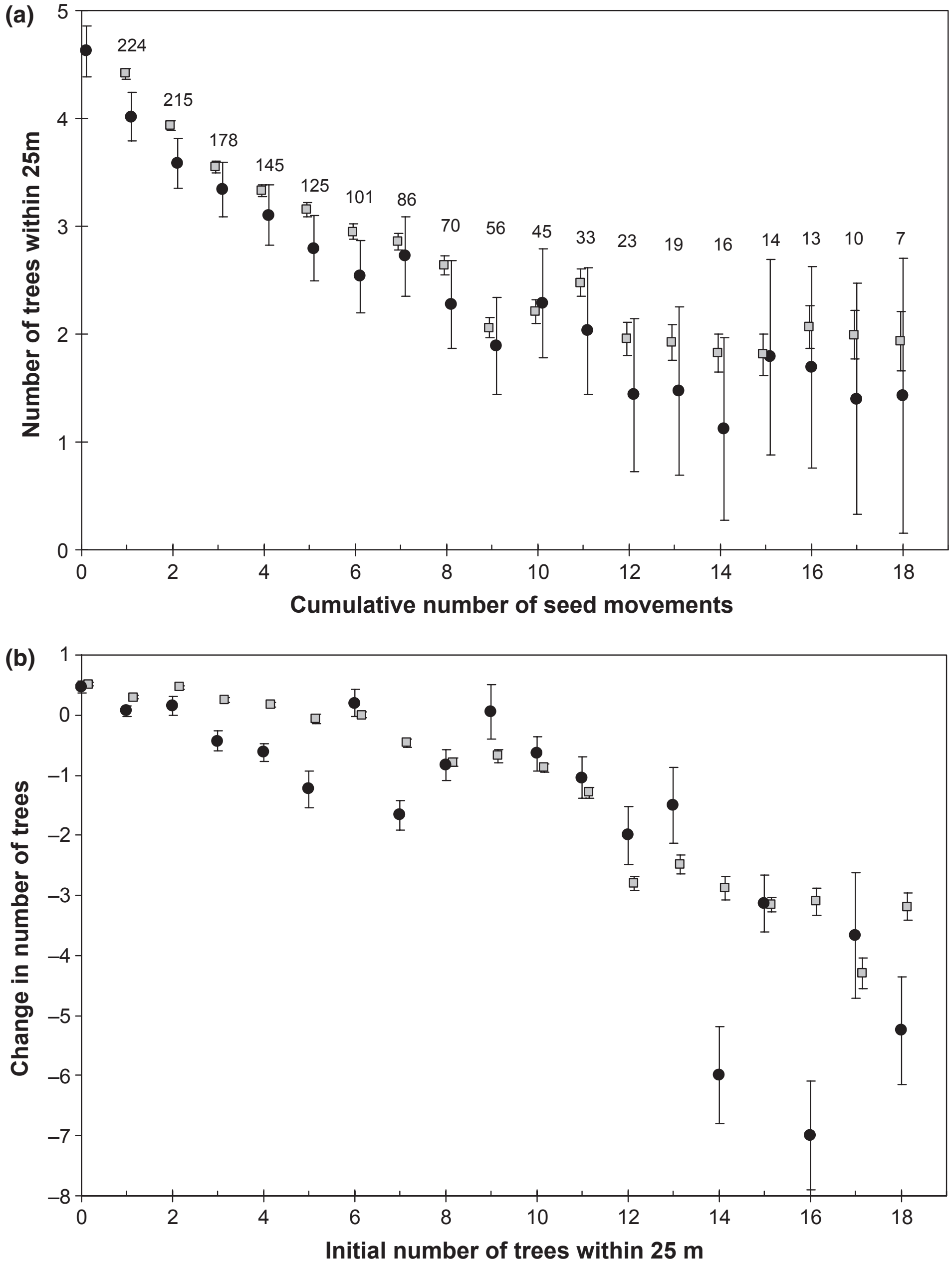

Figure 2 Directed dispersal of *Astrocaryum standleyanum* seeds by scatter-hoarding agoutis. (a) Decline in neighbourhood density of adult *Astrocaryum* (number of trees within 25 m) for seeds over a sequence of repeated caching (*n* = 224 seeds). (b) Net change in neighbourhood density of adult *Astrocaryum* after dispersal as a function of the density at the original location. Dots represent observed changes in density with standard errors. Squares indicate predicted density change with 95% quantiles, based on simulated random movements. Dispersed seeds were moved into areas with lower densities of adult *Astrocaryum* more than expected under random dispersal, particularly in areas with higher adult density. Seeds movements greater than 18 (*n* = 6 seeds) are not shown in Fig. 2a.

with *Astrocaryum* tree density declining progressively as seeds were moved more often (Fig. 2). The areas that seeds ultimately reached had 36% lower *Astrocaryum* tree densities than their initial placement locations (mean tree density at initial location = 4.45 ± 4.26 SD, range = 0–21, final location = 2.85 ± 3.22 SD, range 0–17; Paired *t*-test: $t = -6.19$, df = 223, $P < 0.001$). These densities were significantly lower than those predicted by simulated random movements (predicted number of trees within 25 m = 3.94 ± 0.03, observed = 2.95 ± 0.25, $F_{1,22623} = 10.0$, $P = 0.002$). The change in *Astrocaryum* tree density was negatively related to the starting density of the seed ($P < 0.001$, Table 1), that is, seeds that were originally located in high-density areas experienced a greater reduction in density over than did seeds that started in lower density areas (Fig. 2). Similar results were found when using random seed movements that were generated differently (Table S1) and when 10 m and 50-m radii were used to calculate neighbourhood density (Tables S2 & S3).

We found that the slope of the log–log relationship of seedling density with seed density ($\beta = 0.053$) was significantly smaller than one ($F_{1,143} = 110$, $P < 0.001$), indicating negative density dependence of the seed-to-seedling transition (Fig. 3). Moreover, the slope did not differ significantly from zero ($F_{1,143} = 0.36$, $P = 0.55$), that is, seedling density was entirely independent of the seed density. Thus, the average ratio of seeds to seedlings declined steeply, from 10 : 1 at a seed density of 1 m^{-2} to 1000 : 1 at 100 seeds m^{-2}.

DISCUSSION

We documented that scatter-hoarding agoutis directionally moved seeds to locations with a lower background density of conspecific adult trees within the same habitat. This process is critically important to trees, which have no way to direct the movement of their seeds. The behavioural strategies of scatter-hoarding agoutis to reduce pilferage resulted in seeds being carried into areas of low adult tree density and thus low background seed density. This dispersal pattern should result not only in cached seeds having a lower probability of being stolen by competing rodents but also seeds and nascent seedlings should be less likely to encounter natural enemies. Distance- and density-dependent mortality of seeds and seedlings have been found in numerous plant species in both tropical and temperate ecosystems (reviewed in: Carson *et al.* 2008), and we provide evidence that *A. standleyanum* responds similarly. By carrying seeds to areas with a 36% lower density of conspecific trees, agoutis in our study system directed seed dispersal to areas that should have significant benefits for seed and seedling survival.

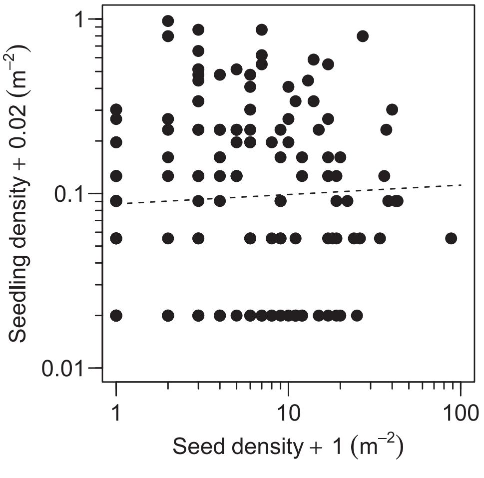

Figure 3 Relationship between seed and seedling density for *Astrocaryum standleyanum*. The slope of the fitted log–log relationship is less than one ($\beta = 0.053$), indicating that the seed-to-seedling transition is negatively density dependent.

Our result that agoutis preferentially cache seeds in areas of lower tree density is fully consistent with predictions from optimal cache spacing theory (OCTS; Stapanian & Smith 1978; Clarkson *et al.* 1986; Dally *et al.* 2006; Galvez *et al.* 2009). Directed seed dispersal was particularly important in our study system because of the complicated movement paths of individual seeds that are moved and cached multiple times, which results in progressively longer dispersal distances (Jansen *et al.* 2012). This frequent removal of cached seeds by kleptoparasitic conspecifics should exert considerable pressure on agoutis to choose locations that have lower risk of cache theft. As seeds were repeatedly moved and re-cached, this behaviour was amplified, and the stepwise dispersal progressively moved seeds into sites with lower densities of palm trees. Stepwise dispersal due to re-caching has already been documented in a variety of species (e.g. Vander Wall 1995; Vander Wall & Joyner 1998), and appears to be a general phenomenon in scatter-hoarding rodents in conditions with high pilferage rates. It is likely that a variety of scatter-hoarding birds and rodents provide directed seed dispersal into areas with low conspecific tree densities in other ecosystems where food trees have heterogeneous distributions. We posit that this behaviour is most likely to be found in systems where seed and scatter-hoarder densities vary across the landscape and where competition for seeds is high, thus providing the basis for a behavioural response consistent with OCTS.

Previous studies have documented directed dispersal by seed-caching rodents towards microsites that are beneficial for seed survival, germination and seedling establishment (e.g. Vander Wall 1993, 1997; Vander Wall & Joyner 1998; Hoshizak *et al.* 1999; Pearson & Theimer 2003; Briggs *et al.* 2009). Pearson & Theimer (2003), for example, found that *Peromyscus* mice in Arizona cached *Pinus edulis* seeds disproportionally in small-particle soils near rocks, where seed survival appeared higher. Likewise, Vander Wall (1993) and Briggs *et al.* (2009) found that *Tamias* chipmunks in Nevada cached *Pinus jeffreyi* seeds disproportionally at depths and at microsites favourable for seedling establishment. Wenny (2001) argued that the burial of seeds by scatter-hoarding rodents is a second form of directed dispersal towards a favourable microhabitat.

In this study, we demonstrate a third form of directed dispersal by scatter-hoarding rodents, towards areas with low densities of conspecific adult trees. This is exactly opposite to the general trend in which directed dispersal tends to result in seeds being taken to locations with elevated seed density (Kwit *et al.* 2007; Spiegel & Nathan 2010). Our findings add to previous studies in which scatter-hoarding animals moved seeds away from conspecific adult trees and into different habitats, presumably to reduce pilferage. For example, scatter-hoarding European jays moved *Quercus* seeds from oak woodlands into adjacent pine stands (Gomez 2003), Fox squirrels moved *Juglans nigra* seeds from forests into adjacent prairies (Stapanian & Smith 1978), wood mice dispersed *Camellia japonica* seeds from old-growth forest into adjacent bamboo thickets (Abe *et al.* 2006) and mice dispersed *Quercus ilex* seeds away from parent trees into open areas (Muñoz & Bonal 2011). Although these behaviours could also facilitate the escape of seeds from natural enemies, they also moved seeds outside the native habitat, and not necessarily into favourable growth conditions. In contrast, the rodents in this study moved seeds away from conspecific trees *within* the native habitat, thus facilitating the escape of seeds from Janzen–Connell effects which should lead to increased seed survival and seedling establishment. This form of directed seed dispersal may be particularly effective and indicates that scatter-hoarding rodents may play a much more important ecological role in ecosystems than previously believed.

Our results show that agoutis respond to the distribution of food trees in their home ranges when hoarding seeds. The question of how they do so remains. One possibility is that agoutis directly avoid fruiting trees, which they recognise as concentrations of seeds and competitor activity. Behavioural responses could also work indirectly, via densities of cached seeds. For example, Vander Wall (1995) found that scatter-hoarding Yellow pine chipmunks (*Tamias amoenus*) chose cache locations based on their knowledge of previously cached seeds. A third possibility is that agoutis respond to a variation in rates at which food competitors are encountered. The rate at which agoutis are photographed on camera traps across Barro Colorado Island is positively related to the abundance of *Astrocaryum* trees (Ben T Hirsch, Roland Kays, Patrick A Jansen, unpubl. data), thus moving seeds into areas with relatively low densities of adult trees should simultaneously reduce encounters with conspecifics, that is, potential cache thieves. As discussed above, the behaviour of jays and squirrels carrying seeds out of forests and into open fields has also been explained as a strategy to avoid cache thieves, which are more abundant in the forest (Stapanian & Smith 1978).

In conclusion, we found that the behaviour of agoutis results in directed dispersal towards areas with low conspecific tree densities. As the same ecological pressures that lead to directed seed dispersal by agoutis are likely present for other scatter-hoarding animals, we expect that the patterns observed here are a widespread phenomenon in habitats in which food trees are unevenly distributed. Scatter-hoarding animals can generate seed dispersal patterns that are fundamentally different from patterns produced by other dispersal types (e.g. frugivores, wind or water), and may be far more effective seed dispersers than previously assumed. Given that seed dispersal patterns generate the template for post-dispersal processes (Jordano & Herrera 1995; Schupp & Fuentes 1995; Wang & Smith 2002), directed seed dispersal as observed in this study should have a profound effect on the spatial structure of plant communities.

ACKNOWLEDGEMENTS

We thank Willem-Jan Emsens, Jose-Alejandro Ramirez, Sumana Serchan and Brian Watts for field assistance; Martin Wikelski, Daniel Obando, and Alejandro Ortega for ARTS help; Walter Carson, Scott Mangan, Marco Visser, Rob Klinger, and two anonymous referees for comments on early versions of the manuscript; STRI for facilities and administrative support; the National Science Foundation (NSF-DEB-0717071 to RK), the Netherlands Foundation for Scientific Research (NWO-WOTRO W85-239 and NWO-ALW 863-07-008 to PAJ), the Smithsonian Tropical Research Institute and the Frank Levinson Family Foundation for financial support.

AUTHORSHIP

BTH, RK, VP and PAJ designed the study. BTH and VP carried out the fieldwork. BTH, RK and PAJ analysed the results and wrote the manuscript.

REFERENCES

Abe, H., Matsuki, R., Ueno, S., Nashimoto, M. & Hasegawa, M. (2006). Dispersal of *Camellia japonica* seeds by *Apodemus speciosus* revealed by maternity analysis of plants and behavioral observations of animal vectors. *Ecol. Res.*, 21, 732–740.

Briggs, J.S., Vander Wall, S.B. & Jenkins, S.H. (2009). Forest rodents provide directed dispersal of Jefferey pine seeds. *Ecology*, 90, 675–687.

Carson, W.P., Anderson, J., Leigh, E. & Schnitzer, S.A. (2008). Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique. In: *Tropical Forest Community Ecology* (eds Carson, W.P. & Schnitzer, S.A.). Blackwell Publishing, Oxford, pp. 211–241.

Clarkson, K., Eden, S.F., Sutherland, W.J. & Houston, A.I. (1986). Density dependence and magpie food hoarding. *J. Anim. Ecol.*, 55, 111–121.

Connell, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. In: *Dynamics of Populations* (eds Den Boer, P.J. & Gradwell, G.). PUDOC, Wageningen, pp. 298–312.

Dally, J.M., Clayton, N.S. & Emery, N.J. (2006). The behaviour and evolution of cache protection and pilferage. *Anim. Behav.*, 72, 13–23.

Daly, M., Jacobs, L.F., Wilson, M.I. & Behrends, P.R. (1992). Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. *Behav. Ecol.*, 3, 102–111.

Emsens, W.-J., Suselbeek, L., Hirsch, B.T., Kays, R., Winkelhagen, A.J.S. & Jansen, P.A. (2012). Effects of food abundance on space and refuge use in the Central American agouti (*Dasyprocta punctata*). *Biotropica*, DOI: 10.1111/j.1744-7429.2012.00888.x.

Forget, P.-M. & Wenny, D.G. (2005). A review of methods used to study seed removal and secondary seed dispersal. In: *Seed Fate: Predation, Secondary Dispersal, and Seedling Establishment* (eds Forget, P.-M., Lambert, J.E., Hulme, P. E. & Vander Wall, S.B.). CAB International, Wallingford, pp. 379–394.

Galvez, D., Kranstauber, B., Kays, R.W. & Jansen, P.A. (2009). Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory. *Anim. Behav.*, 78, 1327–1333.

Gomez, J.M. (2003). Spatial patterns in long-distance dispersal of quercus ilex acorns in a heterogeneous landscape. *Ecography*, 26, 573–584.

Harms, K.E., Wright, J.S., Calderon, O., Hernandez, A. & Herre, E.A. (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.

Hirsch, B.T., Jansen, P.A. & Kays, R. (2012). A telemetric thread tag technique for tracking seed dispersal by scatter hoarding animals. *Plant Ecol.*, 213, 933–943.

Hoshizak, K., Suzuki, W. & Nakashizuka, T. (1999). Evaluation of secondary dispersal in a large-seeded tree Aesculus turbinate: a test of directed dispersal. *Plant Ecol.*, 144, 167–176.

Howe, H.F. (1986). Seed dispersal by fruit-eating birds and mammals. In: *Seed Dispersal* (ed Murray, D.R.). Academic Press, Sydney, pp. 123–189.

Howe, H.F. & Smallwood, P.D. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.*, 13, 201–228.

Jansen, P.A. & Forget, P.M. (2001). Scatterhoarding rodents and tree regeneration in French Guiana. In: *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest* (eds Bongers, F., Charles-Dominique, P., Forget, P.M. & Théry, M.). Kluwer Academic Publishers, Dordrecht, pp. 275–288.

Jansen, P.A., Bohlman, S.A., Garzon-Lopez, C.X., Olff, H., Muller-Landau, H.-C. & Wright, S.J. (2008). Large-scale spatial variation in palm fruit abundance across a tropical moist forest estimated from high-resolution aerial photographs. *Ecography*, 30, 33–42.

Jansen, P.A., Elschot, K., Verkerk, P.J. & Wright, S.J. (2010). Seed predation and defleshing in the agouti-dispersed palm *Astrocaryum standleyanum*. *J. Trop. Ecol.*, 26, 1–8.

Jansen, P.A., Hirsch, B.T., Emsens, W.-J., Gutierrez, V.Z., Wikelski, M. & Kays, R.W. (2012). Thieving rodent as substitute dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci. USA*., 31, 12610–12615.

Janzen, D.H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat*., 104, 501–528.

Jordano, P. & Herrer, C.M. (1995). Shuffling the offspring: Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *Ecoscience*, 2, 230–237.

Kwit, C., Levey, D.J., Turner, S.A., Clark, C.J. & Poulsen, J.R. (2007). Out of one shadow and into another: causes and consequences of spatially contagious seed dispersal by frugivores. In: *Seed Dispersal: Theory and Its Application in a Changing World* (eds Dennis, A.J., Schupp, E.W., Green, R.J. & Westcott, D.W.). CAB International, Wallingford, UK, pp. 427–444.

Leigh, E.G. Jr (1999). *Tropical Forest Ecology: A View From Barro Colorado Island*. Oxford University Press, New York, 245 pp.

Male, L.H. & Smulders, T.V. (2007). Hyperdispersed cache distributions reduce pilferage: a field study. *Anim. Behav*., 73, 717–726.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K., Valencia, M., Sanchez, E. *et al.* (2010). Negative plant-soil feedback predicts relative species abundance in a tropical forest. *Nature*, 466, 752–756.

Muñoz, A. & Bonal, R. (2011). Linking seed dispersal to cache protection strategies. *J. Ecol*., 99, 1016–1025.

Nathan, R. & Muller-Landau, H.C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol*., 15, 278–285.

Pearson, K.M. & Theimer, T.C. (2003). Seed-caching responses to substrate and rock cover by two *Peromyscus* species: implications for pinyon pine establishment. *Oecol*., 141, 76–83.

Peters, H.A. (2003). Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecol. Lett*., 6, 757–765.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001). Floristic composition across a climatic gradient in a neotropical lowland forest. *J. Veg. Sci*., 12, 533–566.

Russo, S.E. & Augspurger, C.K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecol. Lett*., 7, 1058–1067.

Schupp, E.W. & Fuentes, M. (1995). Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, 2, 267–275.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds Levey, D.J., Silva, W.R. & Galetti, M.). CABI International, Oxfordshire, UK, pp. 19–33.

Smythe, N. (1978). The natural history of the Central American agouti (*Dasyprocta punctata*). *Smithsonian Contrib. Zool*., 157, 1–52.

Smythe, N. (1989). Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica*, 21, 50–56.

Spiegel, O. & Nathan, R. (2010). Incorporating density dependence into the directed-dispersal hypothesis. *Ecology*, 91, 1538–1548.

Stapanian, M.A. & Smith, C.C. (1986). How fox squirrels influence the invasion of prairies by nut-bearing trees. *J. Mammal*., 67, 326–332.

Stapanian, M.A. & Smith, C.C. (1978). A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*, 59, 884–896.

Stapanian, M.A. & Smith, C.C. (1984). Density-dependent survival of scatterhoarded nuts: an experimental approach. *Ecology*, 65, 1387–1396.

Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *Am. Nat*., 179, 303–314.

Vander Wall, S.B. (1990). *Food Hoarding in Animals*. University Of Chicago Press, Chicago.

Vander Wall, S.B. (1993). A model of caching depth- implications for scatter-hoarders and plant dispersal. *Am. Nat*., 141, 217–232.

Vander Wall, S.B. (1995). Sequential patterns of scatter hoarding by yellow pine chipmunks (*Tamias amoenus*). *Am. Midl. Nat*., 133, 312–321.

Vander Wall, S.B. (1997). Dispersal of single leaf piñon pine (*Pinus monophylla*) by seed caching rodents. *J. Mammal*., 78, 181–191.

Vander Wall, S.B. & Beck, M.J. (2011). A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. *Bot. Rev*., 78, 10–31.

Vander Wall, S.B. & Joyner, J.W. (1998). Recaching Jeffrey pine (Pinus jeffreyi) seeds by yellow pine chipmunks (Tamias amoenus): potential effects on plant reproductive success. *Can. J. Zool*., 76, 154–162.

Waite, T.A. (1988). A field test of density dependent survival of simulated gray jay caches. *Condor*, 90, 247–249.

Wang, B.C. & Smith, T.B. (2002). Closing the seed dispersal loop. *Trends Ecol. Evol*., 17, 379–385.

Wenny, D.G. (2001). Advatanges of seed dispersal: a re-evaluation of directed dispersal. *Evol. Ecol. Res*., 3, 51–74.

Wright, S.J., Zeballos, H., Domínguez, I., Gallardo, M.M., Moreno, M.C. & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. *Cons. Biol*., 14, 227–239.

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Editor, Marcel Rejmanek
Manuscript received 20 June 2012
First decision made 18 July 2012
Manuscript accepted 9 August 2012