

Thieving rodents as substitute dispersers of megafaunal seeds

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Edited* by John W. Terborgh, Duke University, Durham, NC, and approved June 14, 2012 (received for review April 3, 2012)

The Neotropics have many plant species that seem to be adapted for seed dispersal by megafauna that went extinct in the late Pleistocene. Given the crucial importance of seed dispersal for plant persistence, it remains a mystery how these plants have survived more than 10,000 y without their mutualist dispersers. Here we present support for the hypothesis that secondary seed dispersal by scatter-hoarding rodents has facilitated the persistence of these large-seeded species. We used miniature radio transmitters to track the dispersal of reputedly megafaunal seeds by Central American agoutis, which scatter-hoard seeds in shallow caches in the soil throughout the forest. We found that seeds were initially cached at mostly short distances and then quickly dug up again. However, rather than eating the recovered seeds, agoutis continued to move and recache the seeds, up to 36 times. Agoutis dispersed an estimated 35% of seeds for >100 m. An estimated 14% of the cached seeds survived to the next year, when a new fruit crop became available to the rodents. Serial video-monitoring of cached seeds revealed that the stepwise dispersal was caused by agoutis repeatedly stealing and recaching each other's buried seeds. Although previous studies suggest that rodents are poor dispersers, we demonstrate that communities of rodents can in fact provide highly effective long-distance seed dispersal. Our findings suggest that thieving scatter-hoarding rodents could substitute for extinct megafaunal seed dispersers of tropical large-seeded trees.

Pleistocene extinctions | seed predation | cache pilferage | telemetry

The Neotropics are rich in woody plant species with large-seeded fruits that are structurally similar to fruits of trees dispersed by megafauna (mammals >1,000 kg) in the Paleotropics (1, 2). Guimarães et al. (2) operationally defined these “megafaunal” fruits as oversized (4–10 cm in diameter) fleshy fruits that contain one to five extremely large seeds. Because such fruits and seeds are typically too large to be swallowed by extant wildlife (1, 2), Janzen and Martin (1) argued that these plants are in fact adapted to seed dispersal by Pleistocene megafauna, which ingested entire fruits and defecated the seeds intact away from the source. This dispersal mutualism would have been disrupted at the end of the Pleistocene, when nearly all megafauna of the Neotropics became extinct (3). Whether these plants are really “megafaunal” is controversial, partly because it is unclear how these species could have persisted >10,000 y without their dispersal mutualists (4–7). Seed dispersal is a critical requirement for plants to persist in the face of predators and pests that attack offspring (8–10). Additionally, plants need long-distance seed dispersal to maintain gene flow between populations, colonize new sites, and move their range as climate changes (10, 11). Plant species that fail to disperse are predicted to be outcompeted by others and ultimately to go extinct. The question remains as to how megafaunal species can still be widespread, and often locally common, throughout the Neotropics.

One hypothesized mechanism by which any megafaunal tree species may have persisted is substitute seed dispersal by scatter-hoarding rodents (2, 12–14). These rodents bury seeds as food reserves in shallow caches, each containing one or a few seeds. The buried seeds are protected against invertebrates and sit in ideal conditions to germinate and establish into seedlings if the animals fail to recover them (15). Scatter-hoarding rodents are already known to disperse seeds that they collect from dung piles (12, 16, 17). These rodents could have then become primary dispersers of megafaunal plant species after Pleistocene megafauna disappeared (1), an example of “evolutionary partner switching” by the plant (18).

The substitution hypothesis has met skepticism because rodents generally are not considered effective seed dispersers. First, they are believed to move seeds only over small areas. Documented seed dispersal distances produced by scatter-hoarding rodents are usually small (<25 m) (15), which may be inadequate to help seeds escape the intense competition and pest pressure near parent trees. The maximum distance at which a rodent might disperse seeds would be within an individual's small home range; therefore, seeds would never travel far enough to colonize new sites. Second, scatter-hoarding rodents are believed to depredate most of the seeds they cache; documented survivorship of seed caches is extremely low, and primary caches almost never persist until a seedling has established (19). Thus, available data would suggest that rodents cannot be substitutes for megafaunal seed dispersers.

However, it is conceivable that the effectiveness of seed dispersal by scatter-hoarding rodents has been underestimated because reliably tracking seed movements and seed fate is notoriously difficult (20). Most seed tracking studies use traditional passive tags that are practical only for tracking seeds over short distances. The inability to track far-dispersed seeds and the categorization of those seeds as “missing” results in a heavy bias against longer dispersal distances (21). That rodents are capable of dispersal over longer distances is demonstrated by the occasional observance of seeds dispersed >100 m (e.g., refs. 22–24). Additionally, although most studies of seed dispersal only consider “primary” movement, the initial

Author contributions: P.A.J., B.T.H., V.Z.-G., M.W., and R.K. designed research; P.A.J., B.T.H., W.-J.E., V.Z.-G., and R.K. performed research; P.A.J., B.T.H., W.-J.E., V.Z.-G., and R.K. analyzed data; and P.A.J., B.T.H., W.-J.E., V.Z.-G., M.W., and R.K. wrote the paper.

The authors declare no conflict of interest.

Data deposition: The data reported in this paper has been deposited in the Movebank database, www.movebank.org (doi: 10.5441/001/1.9t0m888q).

*This Direct Submission article had a prearranged editor.

Freely available online through the PNAS open access option.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1205184109/-DCSupplemental.

movement of seeds from the parent tree, some have shown that seeds recovered from caches are sometimes recached rather than eaten and that sequences of multiple secondary movements occur (23–27). These limitations suggest that the dispersal effectiveness of scatter-hoarding rodents may have been underestimated owing to methodological limitations.

Here we investigated seed dispersal of a reportedly megafaunal tree species by one of the Dasyproctidae, scatter-hoarding rodents that occur throughout the Neotropics. Our study species was *Astrocaryum standleyanum* (Arecaceae), a cocosoid palm that produces hard stony endocarps with large seeds, enclosed in brightly colored, sweet fruits that typify the megafaunal syndrome of oversized fleshy fruits with one or few extremely large seeds (2). It has been hypothesized that such fruits evolved to attract megafaunal seed dispersers that are now extinct, such as elephant-like gomphotheres (1, 2), which would have ingested the fruits without cracking the hard stones and defecated the seeds intact, as is still seen today in African elephants (28). Today, *A. standleyanum* palm is primarily dispersed by Central American agoutis (*Dasyprocta punctata*) that scatter-hoard the seeds across their 2- to 3-ha home ranges as food reserves for the low-fruit season (29). Janzen and Martin (1) suggested that the agouti was “once a trivial dispersal agent [that] figured primarily as seed predator” of seeds that it removed from the megafaunal dung piles, but then took the role as the principal seed disperser after the extinction of the Pleistocene megafauna.

Our goal was to obtain unbiased estimates of seed dispersal distance and survivorship produced by scatter-hoarding rodents to determine how effective they are as seed dispersers. To overcome the problem of bias against long-distance dispersal we affixed motion-sensitive telemetric thread tags (30) to seeds and used manual and automated telemetry (31) to continuously track their movement. We tracked the seeds regardless of how far and how often they were moved, until they were finally eaten or left to germinate. We also assessed the mechanism causing cache dynamics and multistep movement, distinguishing between cache theft and cache recovery by “owners.” For this aspect of our study, we tagged agoutis for individual identification and monitored cached seeds with camera traps.

Results

Camera-trap monitoring of 589 radio-tagged seeds placed at 52 experimental stations across Barro Colorado Island (BCI) showed that seeds were quickly removed (Fig. S1A). Seeds were almost exclusively removed by scatter-hoarding rodents, and mostly by agoutis (83% of 423 removed seeds). Radio-tracking allowed us to retrieve nearly all (97%) of the removed seeds and record their fate, regardless of how far they traveled. The majority (85%) of the 409 seeds that we retrieved were buried in caches, and only 3% were eaten. Agoutis cached 88% of the seeds they removed. The median initial dispersal distance of seeds removed from the stations was just 8.75 m, which is similar to prior studies of seed dispersal by rodents, yet the tail of the distribution ranged as far as 159 m (Fig. 1A). Studies using traditional tagging methods such as thread tags would typically have missed the one fifth of the seeds that were carried >25 m (21).

The survivorship of 224 first-order agouti-made caches that we monitored was short. Most seeds (57%) were recovered by an animal within 1 wk after caching, and 99% of the caches were ultimately recovered (Fig. 1B). However, only 13% of the seeds removed from the primary seed cache were actually eaten; the majority were recached. Moreover, most seeds were dug up and recached multiple times (median eight times; Fig. S1B), sometimes twice in a single day. This repeated recaching produced stepwise movement along paths of up to 892 m long [median 131 m (confidence interval [CI] 100–188 m)]; Fig. S1C) and gradually dispersed seeds farther away from the point of release [median 68 m (CI 51–86); Figs. 1A and 2 and Movie S1]. One seed was cached as

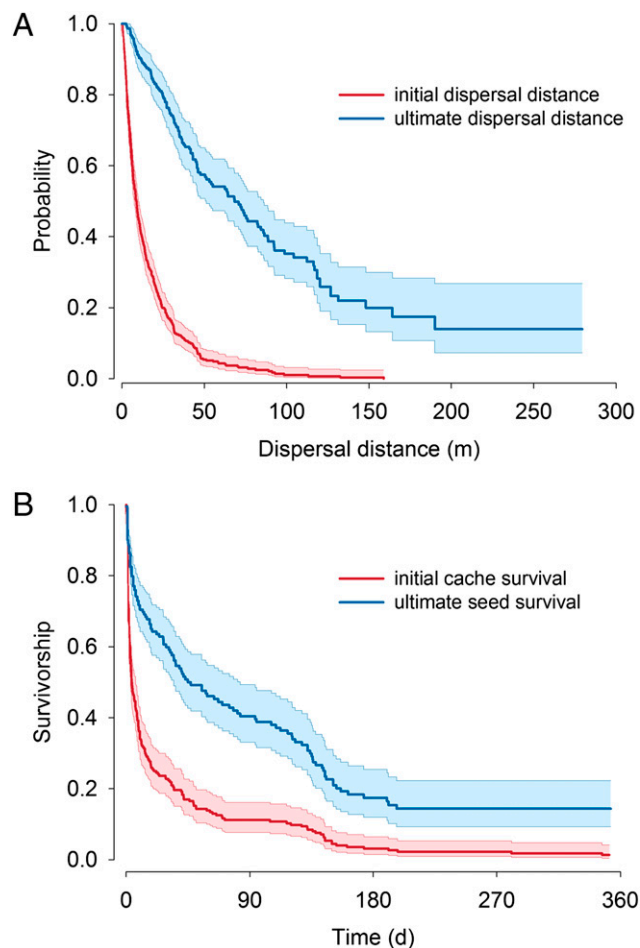


Fig. 1. Dispersal distance and survival of *Astrocaryum standleyanum* palm seeds handled by scatter-hoarding rodents on BCI, Panama. Curves shown are Kaplan-Meier survivorship estimates (colored lines), with 95% confidence envelopes. (A) Probability of seed dispersal up to a given distance, for the initial movement (red, lower graph) and for the ultimate movement after multiple instances of recaching (blue, upper graph). Initial seed dispersal was generally limited, with just 18% of the seeds moving >25 m away from the parent tree. However, ultimate dispersal distance, after up to 36 secondary movements, included 35% long-distance dispersal (>100 m). (B) Survivorship of first-order rodent-made caches (red, lower graph) and for the seeds that those caches contained (blue, upper graph). Most caches were recovered within 1 wk, but recovered seeds were usually recached rather than eaten, and ultimate survival was nevertheless high, with an estimated 14% survival to 1 y.

many as 36 times, traveled more than 749 m, and ended 280 m from its starting point, when it was dug up and eaten by an agouti 209 d after initial dispersal. This recaching behavior resulted in an estimated 87% of seeds moving past the immediate vicinity of the parent tree (<15 m), the primary zone of Janzen-Connell effects. An estimated 35% of seeds attained a net dispersal distance >100 m, which is often used as a threshold for long-distance seed dispersal (32–34). Many seed movements extended well beyond the size of the typical agouti home range, suggesting the involvement of other individuals besides the initial cache owner.

Remote cameras placed at a subset of the agouti-made caches revealed that most cache recovery was by conspecifics [94%, vs. 4% by spiny rat (*Proechimys semispinosus*), 1% by squirrel (*Sciurus granatensis*), and 1% by land crab *Potamocarcinus richmondii*; $n = 134$]. For 116 agouti-made caches, we were able to distinguish whether agoutis recovering the seed were the owner or a thief, because 16 agoutis in the study area were individually

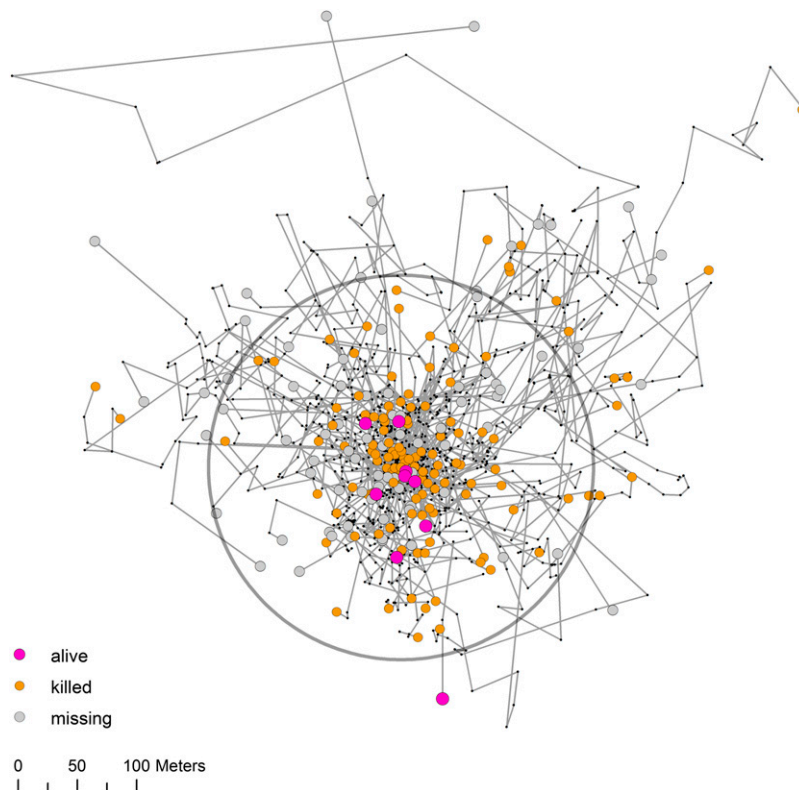


Fig. 2. Relative movement paths (gray lines) of 224 radio-tagged *A. standleyanum* palm seeds handled by rodents on BCI, Panama. Colored dots mark locations at which 129 seeds were found killed (i.e., eaten; orange), 86 seeds were last seen before they lost their tags (gray), and 9 seeds (pink) that were still alive, cached, and being monitored after 1 y. We estimated that another 22 (CI 11–40) of the censored seeds (gray) survived to 1 y. All start locations were standardized to point (0,0), and this figure combines data from all 52 seed stations, which were actually scattered throughout our study site. Seed movement beyond the gray circle with a radius of 100 m represents long-distance dispersal. [Movie S1](#) shows an animation of the movements.

recognizable by tags or marks. We found that just 16% of the seeds were recovered by their owner; the majority (84%) were stolen by other agoutis. Theft was strongly reciprocal: individuals that were robbed also stole cached seeds from others (Fig. 3). Thus, the stepwise dispersal of seeds across home range boundaries was driven by reciprocal theft.

Because seeds recovered from caches were usually recached rather than eaten, seeds ultimately survived more than 10 times longer than caches, on average [half-life, 45 d (CI 35–83 d) vs. 3.9 d; Fig. 1*B*]. Although the majority of seeds (58%) were found eaten or moved into tree cavities, an estimated 14% survived buried underground to the next year (CI 9–22%). This estimation is based on 4% of the seeds surviving, accounting for 38% censored observations due to severed tags (72) or failing transmitters (14), the ultimate fate of which remained unknown. By that time, a next generation of fresh seed crops had ripened, drawing the attention of the rodents away from the older caches and potentially allowing the seeds to germinate and establish into seedlings.

Discussion

Our results indicate that rodents may disperse seeds over much longer distances than was ever anticipated, and with much higher seed survivorship. Although initial dispersal distances were mostly short, repeated movements resulted in seeds being dispersed outside the immediate vicinity of the parent, the primary zone of Janzen-Connell effects (35). One third of the seeds attained a net dispersal distance >100 m, the often-used threshold for long-distance seed dispersal (32–34), which is far enough to colonize new habitats and shift ranges over generations in the tropics, where climatic shifts are much smaller than in the temperate zone. Finally, one seventh of the seeds survived to the next year.

The extremely fast recovery of caches found in this study is typical for rodent-mediated dispersal (19). Similar low cache survivorship in previous studies has fueled the argument that scatter-hoarding rodents are essentially seed predators rather than seed dispersers (36). Our study, however, demonstrates that low cache survivorship is not equivalent to seed survivorship. In fact, most seeds dug up by animals from caches were recached, usually at further dispersal distances, and potentially in more suitable environments. Although previous studies had found high proportions of recaching (23–27), no study had been able to estimate ultimate survivorship because traditional tracking methods were biased against seeds that moved more often or traveled longer distances. Our improved tracking method makes our estimate of 14% survival of cached seeds to the next year robust, regardless of the extent of movements.

The multistep dispersal and massive reciprocal cache robbery we discovered resulted in scatter-hoarding agoutis moving seeds much farther than expected. Home range sizes of agoutis are small relative to that of many other vertebrate seed dispersers (37), but robbing agoutis gradually moved seeds across home range boundaries. The ultimate dispersal distances were far enough for most seeds to escape Janzen-Connell effects around parent trees and colonize new sites. Previous studies that tracked secondary seed movement also found multiple movements of individual seeds (23–27), but the maximum number of movements per seed in these studies (five movements) pales in comparison with the median of eight movements per seed in our study (range, 1–36). Some seeds in our study were moved more than once per day. Such detail would have gone unseen if we had censused caches only at regular time intervals, as is typical in seed-tracking studies.

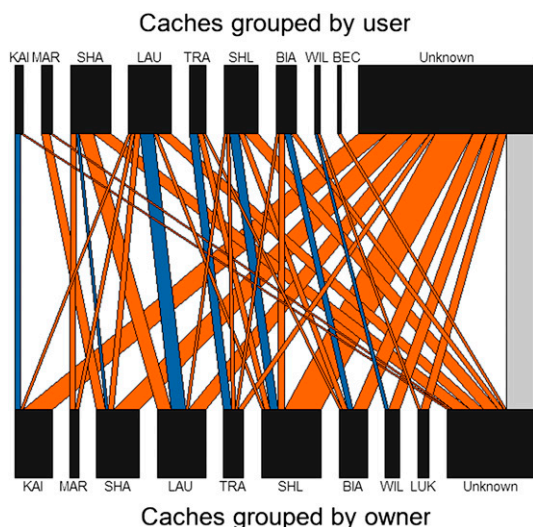


Fig. 3. Interaction network showing reciprocal theft of cached *A. standleyanum* seeds by agoutis on BCI, Panama. Connections represent transfer of seeds from the “owners” that cached them (bottom row) to the “users” (top row) that subsequently dug them up. Bars are proportional to the number of seeds cached or recovered by an individual. Three-letter abbreviations refer to individual agoutis, “unknown” refers to agoutis of unknown identity. Owners were responsible for cache recovery in few cases (blue connections). The far majority of recovery (84%) was theft (orange). For the gray connections, owner and user could not be distinguished.

The fact that seeds were frequently moved beyond the typical home-range size of agoutis suggested that multiple individuals were involved. Our unique combination of radio tracking of seeds, individual tagging of agoutis, and camera monitoring of caches revealed that the stepwise dispersal of seeds was driven by reciprocal theft. All monitored agoutis engaged in stealing also lost caches to conspecific theft. The resulting theft rates were high: less than one out of six caches were recovered by the owner. Reciprocity has been put forward as an explanation for the evolutionary persistence of scatter-hoarding behavior in the face of high theft (19). However, never before had reciprocal pilferage been demonstrated so convincingly in wild populations.

Multistep seed dispersal as observed in this study is driven by competition for food among conspecifics. Rates of cache pilferage, as well as distances over which scatter-hoarding rodents move seeds, are both known to increase with seed scarcity, which can be calculated as the ratio of rodents to seeds (23, 38, 39). Although our study was conducted during a year of average fruit abundance, the extent of multistep seed dispersal observed could have been influenced by the high density of agoutis on BCI. In years of high fruit abundance or in locations with low agouti abundance due to hunting, pilferage rates and dispersal distances are predicted to be smaller. This relationship with abundance implies that hunting may affect seed dispersal by agoutis even more than believed (40), as seeds are predicted to be moved less often and over shorter distances.

Dispersing seeds are notoriously difficult to track (20), and the low estimates of seed dispersal distances and survivorship that dominate the literature on seed dispersal by rodents are likely an artifact of using tagging systems that cannot reliably record the fate of seeds that are moved multiple times and over longer distances. We overcame these limitations by tracking seeds with telemetric thread tags (30). Radio tags have previously been used to track primary dispersal of *Quercus* acorns by jays in Spain (41) and by mice in Japan (42), and dispersal of *Juglans* walnuts by squirrels and mice in Japan (43, 44), yielding dispersal distances up to 168 m (squirrels) and 550 m (for jays). However, these studies relied on prescheduled physical censuses for monitoring

seed location and fate and had limited duration due to battery constraints. We introduced motion triggering, so that tags started transmitting only when the seeds were moved, (30) and an automated radio telemetry system (31) to continuously listen for transmitter signals of any seeds that moved. This combination of techniques allowed us to record seed fate pathways in great detail and for a full year, despite the battery limitations inherent to miniature transmitters.

Conclusion

Our findings demonstrate that scatter-hoarding rodents can be effective seed dispersers. Communities of stealing rodents can provide long-distance dispersal comparable to other vertebrates that are considered good seed dispersers (45, 46). Although this seed movement is not as far as provided by large-bodied frugivores, such as megafauna that can transport seeds over multiple kilometers (47, 48), the survival potential of scatter-hoarded seeds is likely superior to that of hundreds of seeds deposited together in megafauna dung piles (48–50). Our results make it conceivable that secondary seed dispersal by rodents can be sufficiently effective to substitute for primary dispersal of megafaunal seeds by large mammals. Because Dasyproctids, such as agoutis and the similarly behaving acouchis, are common throughout the Neotropics, this may explain how many Neotropical tree species that once relied on large megafaunal seed dispersers have persisted in the wake of the Pleistocene extinctions (1). However, the relationship between rodents and large nuts is much older than the Pleistocene, appearing as early as the Late Paleocene (>55 MyBP), which is the same period as when large terrestrial frugivores abounded (51). These plants may have a long history of seed dispersal by rodents, and perhaps never depended on megafauna in the first place.

Materials and Methods

We radio-tracked the movement of megafaunal palm seeds in tropical moist forest of Central Panama to determine the seed dispersal distances and survivorship that scatter-hoarding rodents produced. We individually tagged agoutis and monitored cached seeds with camera traps to assess the role of theft in cache dynamics.

Site and Species. Field work was carried out on BCI, Panama (9°10'N, 79°51'W), a 1,560-ha island covered with tropical moist forest, administered by the Smithsonian Tropical Research Institute (52). Our study area consisted of 50 ha of late-secondary forest in the central part of BCI. We tracked seeds of *A. standleyanum*, a large-fruited and large-seeded palm that is presumed to be adapted for seed dispersal by megafauna now extinct (1, 2). *A. standleyanum* trees produce 10-g stony endocarps with large seeds, enclosed in bright-orange, sweet-fleshy fruits (53). *Astrocaryum* on BCI has a seasonal fruiting peak during May–June, when each tree produces up to 1,500 fruits. This palm is now dispersed primarily by the Central American agouti (*D. punctata*), a 2- to 4-kg caviomorph rodent that scatter-hoards large seeds across its 2- to 3-ha home range as food reserves (29, 54). Agoutis feed almost exclusively on these reserves during times of fruit scarcity (54–56).

Radio-Tracking of Seeds. Ripe *Astrocaryum* fruits were collected using seed traps suspended below haphazardly selected fruiting trees. Seeds were defleshed using a knife to resemble natural defleshing by rodents (cf. 53), air dried, and given a 55-cm-long “telemetric thread tag” (30) consisting of a 30-cm black nylon-coated stainless steel leader wire (Surflon 1 × 7 black coating; American Fishing Wire) and a 4.1-g cylindrical very high frequency (VHF) transmitter (Advanced Telemetry Systems) with 20-cm antenna. Affixing thread tags to seeds is the widely accepted standard method for tracking seed dispersal by rodents (57), because rodents will bury the seed but leave the thread above ground, allowing researchers to locate the seed.

The telemetric thread tag was attached to the seed by tying the leader wire to a 7-mm screw eye that was inserted in the basal end of the stone (away from the embryo) via a 1.5- to 3-mm drilled hole. A 7-cm piece of pink flagging with a unique code was attached to the wire near the transmitter. Experimental tests indicated that agoutis do not discriminate between telemetric and standard thread tags (30). To prolong battery life, the transmitter was shut down during intervals without movement. We did this by placing the

transmitter on a small magnet taped to the head of a 10-cm nail that was pushed into the ground 25 cm away from the seed. The radio was reactivated when a seed was moved, thereby pulling the transmitter off the magnet (30).

A total of 589 radio-tagged seeds were placed at 52 seed stations scattered across the study area during May 16–July 16, 2010. Each seed station contained five seeds arrayed in a line with 3-cm interspacing. We checked each station daily. After 8 d, or when all seeds were removed from the station, we either replaced the seeds or discontinued placing seeds at that location. Stations received 5–25 seeds in total (mean \pm SD, 11.3 ± 5.9). Removed seeds were located by sight if possible, or otherwise with hand-held radio-telemetry equipment (Yaesu-VR500), to record their fate and movement distance. If the seed was found within 20 m of the seed station, the dispersal distance was measured with measuring tape, and the direction was recorded using a precision compass (Suunto KB-14). If the seed moved >20 m, the new location was recorded using a global positioning system receiver (Garmin 60CSx). Seed removal from all stations was also monitored with remote cameras (RC55 or PC800; Reconyx) that took a continuous series of photographs at 1 s^{-1} when animals triggered the motion sensor. These cameras allowed us to determine which species removed the seeds and the exact date and time of removal (cf. 58).

We monitored 224 radio-tagged cached seeds during 12 mo by checking for radio signals every day in the first 6 mo and at least once per month thereafter, which yielded a total of 1,453 movements. Ultimately, 129 seeds (58%) were found eaten. For 86 seeds (24%), movement paths and fates were censored because rodents cut off the tag (4.8% per movement) or because the radio failed to initiate (1.1% per movement). Tag cutting typically happens when agoutis carry out their routine of meticulously cleaning seeds before caching (53). Nine cached seeds were still alive and being monitored at the last census (May 2011).

Animal Tagging. In our study area, a total of 16 agoutis were individually recognizable. These agoutis were captured with live traps (Tomahawk Live Trap) that were baited with banana and checked twice daily. Adult individuals (>2.3 kg) (54) were fitted with a VHF radio transmitter that had a unique pattern of reflective tape affixed to the collar. Subadult animals were individually marked with freeze brands (59). The trapping and marking procedures were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute and conducted under research permits authorized by the Barro Colorado Nature Monument.

Video Surveillance of Cache Theft. To determine whether cached seeds were recovered by owners or thieves, we monitored 154 agouti-made caches (multiple caches for each of 59 seeds) with remote cameras. Footage allowed us to identify the species for 134 cached seeds that were retrieved on camera. For 116 of 126 caches retrieved by agoutis, we could determine whether seed removal was theft, because 16 agoutis were individually recognizable. Reciprocal theft of seeds among individual agoutis was visualized with the R package *BIPARTITE* (60).

Analyses. All analyses were conducted in R 2.12.2 (61). Seed removal and cache survival were analyzed as waiting times using Kaplan-Meier survival analysis with the R package *SURVIVAL* (62). Seeds that had not experienced the focal event (removal from the station or recovery from a cache) before monitoring ended were included as censored observations. Dispersal distance was also analyzed using Kaplan-Meier survival analysis, essentially treating distance as time (cf. 21, 23, 63). Here, seeds that could no longer be followed because their tag failed or was cut off from the seed were included as observations censored at the last recorded distance. Likewise, the number of movements per seed was analyzed using Kaplan-Meier survival analysis, whereby the number of movements per seed was treated as time, and seeds that could no longer be followed were included as censored observations. Reciprocal theft of seeds among individual agoutis was visualized with the R package *BIPARTITE* (60).

ACKNOWLEDGMENTS. We thank Tom Garin (Advanced Telemetry Systems), Daniel Obando, Alejandro Ortega, and Meg Crofoot for technical support; Lieneke Bakker, Reyna Bell, Chris Carson, Matt McElroy, Veronica Pereira, Torrey Rodgers, Sumana Serchan, Michiel Veldhuis, and Brian Watts for field assistance; Joe Wright for the original idea of automated radio-tracking of seeds; John Terborgh and two anonymous reviewers for comments; and the Smithsonian Tropical Research Institute for facilities and administrative support. Financial support was provided by National Science Foundation Grant NSF-DEB-0717071 (to R.K. and M.W.), Netherlands Foundation for Scientific Research Grants NWO-WOTRO W85-239 and NWO-ALW 863-07-008 (to P.A.J.), the Leiden University Fund, the Huygens Scholarship program, a Leiden University Lustra Scholarship, the "Fonds voor Onderzoek ten behoeve van het Natuurbehoud" (to V.Z.-G.), the Smithsonian Tropical Research Institute, and the Frank Levinson Family Foundation.

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