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A telemetric thread tag for tracking seed dispersal by scatter-hoarding rodents

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Abstract The seeds of many tree species are dispersed more than once, and this secondary seed dispersal is believed to enhance seedling recruitment. However, the effectiveness of secondary seed dispersal has rarely been assessed because it is difficult to track seeds until they die or germinate. We describe a new technique that uses thread tags attached to radio transmitters (telemetric thread tags) to track long-distance multistep seed dispersal by scatter-hoarding rodents. These telemetric thread tags can be turned off with a magnet and are reactivated when the seed moves. This method allows for seed tracking with minimal cache disturbance or distance bias, over long time spans, multiple seed movements, and with few effects on animal behavior. We used telemetric thread tags to track seed dispersal of the palm tree *Astrocaryum standleyanum* in a Neotropical forest, and achieved near-complete recovery of dispersed seeds tracked over distances as far as 241 m. We were also able to record the recovery time and fate of cached seeds without disturbing caches. Neither the removal rate nor the dispersal distance differed between seeds with telemetric thread tags and thread-tagged seeds. We conclude that telemetric thread tags can be used to document secondary seed dispersal by scatter-hoarding animals with unprecedented efficacy and precision. Given the size of these tags relative to the size of seeds and their dispersers, this method is applicable to the majority of tree species that are secondarily dispersed by scatter-hoarding mammals.

Keywords Radio telemetry · Seed tag · Animal dispersed seeds · *Astrocaryum* · Agouti

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Introduction

The dispersal of plant seeds is a critically important ecological process that remains poorly understood because following a seed from its source to the point of germination or death is notoriously difficult

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(Chambers and MacMahon 1994; Wang and Smith 2002; Bullock et al. 2006). In particular, secondary seed dispersal and ultimate seed fate remain insufficiently documented because existing tracking methods are biased against longer dispersal distances and higher-order movements. Many plant seeds are dispersed in a sequence of two phases that involve different dispersal agents, a phenomenon known as 'diplochory' or 'two-stage seed dispersal'(Wenny 1999; Vander Wall and Longland 2004; Vander Wall et al. 2005). During the first phase, primary dispersal, seeds are moved away from the parent by animals, wind, or gravity. During the following phase, secondary dispersal, these seeds are moved to new locations by animals or abiotic mechanisms (wind and water). For example, when vertebrates ingest and defecate fruit, viable seeds can be removed from feces by insects, birds, or mammals and dispersed again (Estrada and Coates-Estrada 1991; Forget and Milleron 1991; Levey and Byrne 1993; Wenny 1999). Scatter-hoarding rodents that bury seeds in the topsoil for use as food reserves are a particularly important source of secondary dispersal (Brodin 1993; Burnell and Tomback 1985). If cached seeds are not recovered and eaten, scatter-hoarding can yield effective dispersal (Jansen and Forget 2001). Vander Wall and Longland (2004) have argued that the combination of two dispersal mechanisms is often more beneficial to seeds than single means of dispersal.

Despite the importance of secondary dispersal by scatter-hoarding rodents, the degree to which rodents are effective seed dispersers has rarely been measured due to methodological limitations (Galvez et al. 2009; Galetti et al. 2010). Most published studies of seed dispersal focus on the initial dispersal of seeds from the source plant and do not record additional (aka secondary) dispersal (Vander Wall et al. 2005, Emmerson et al. 2010). In studies where seed caches have been monitored, it has often been assumed that seeds that were removed from the soil were eaten, but few studies have actually determined the location and fate of those missing seeds (Vander Wall et al. 2005). In this article, we describe a method to follow seeds during secondary dispersal, which allows one to determine the exact fate of these missing seeds.

The current standard method for tracking seed dispersal by scatter-hoarding mammals is to affix thread tags (with or without numbered flagging tape at the distal end) to seeds and retrieve dispersed seeds by visually searching for the tags in a radius around the point of release (Forget and Wenny 2005). Alternative tagging methods for tracking seed dispersal by animals include radioisotopes (Carlo et al. 2009; Vander Wall 2002a, b; Winn 1989), fluorescent dye (Lemke et al. 2009; Longland and Clements 1995), and metal or magnets (Den Ouden et al. 2005). A limitation of the above methods is that seeds dispersed over longer distances are less likely to be retrieved because search effort increases exponentially with search radius. Most studies omit non-retrieved seeds from the dataset, leading to an underestimation of the true seed dispersal distance (Hirsch et al. 2012; Vander Wall et al. 2005). Given the ecological importance of long-distance dispersal, there is a need for methods that allow for tracking seeds without bias against long distances (Cain et al. 2000; Nathan 2008; Portnoy and Willson 1993).

Radio transmitters offer a long-distance tracking solution, because they are detectable over many hundreds or thousands of meters and have recently been miniaturized to the extent that they can be attached to seeds. Radio transmitters mounted onto or inside seeds have been successfully used to track dispersal of acorns by mice in Spain (Pons and Pausas 2007) and Japan (Sone et al. 2002), and of walnuts by squirrels and mice in Japan (Tamura et al. 2002). A major shortcoming of these small transmitters is that they have short-lived batteries, and therefore a limited window of time to track seed movement. So far, this has made transmitters unsuitable for the long-term monitoring (>2–3 months) needed to determine ultimate seed fate. Other complications include attaching the transmitter to the seed and designing a transmitter with an antenna sufficiently long and exposed to improve detection range.

Here, we describe the use of thread tags with integrated motion-sensitive miniature transmitters (i.e. telemetric thread tags) for tracking seed dispersal by scatter-hoarding rodents. The telemetric thread tagging technique was designed to meet four criteria:

(1) There should be little or no bias against long-distance dispersal.
(2) Monitoring should be possible over a time span long enough to track seeds until they germinate and establish into seedlings.
(3) Identification of cached seeds should be possible without disturbing the cache. Opening caches to visually identify seeds could strongly affect seed fate since rodents are known to use soil

disturbance as a cue for finding seeds (Vander Wall et al. 2003).

(4) There should be little or no effect of the tag on disperser behavior, either negative or positive.

We report details of the method along with successful and failed field trials with the rodent-dispersed palm species *Astrocaryum standleyanum* in a Neotropical forest. We describe advantages and disadvantages of the method, general guidelines as to when the method can be used, and reasons why we believe telemetric seed monitoring has the potential to substantially increase our understanding of plant dispersal and forest ecology.

Methods

Telemetric thread tracking

The telemetric thread tag consists of a small cylindrical radio transmitter with a 20-cm wire antenna (Fig. 1). The transmitter is pulled behind the seed in the same manner as traditional thread tags, which are the current standard for tracking rodent-dispersed seeds (Forget and Wenny 2005). A general advantage of thread tags is that it is possible to identify buried seeds without disturbing the cache, as soil disturbance potentially affects subsequent cache and seed fate (Guimaraes et al. 2005; Murie 1977). Having the transmitter separated from the seed by a thread makes it possible to manually turn off the transmitter when a seed is buried, thus greatly extending battery life, and making it possible to follow multiple movements of the same seed over periods of >1 year. All previous studies that radio-tracked seeds put transmitters directly onto or inside the seed, and could only track seeds over short time spans (Pons and Pausas 2007; Sone et al. 2002; Tamura et al. 2002).

A key aspect of our method is that the transmitters consume power only when dispersal events happen, and not during the long time spans during which seeds remain motionless. We developed two designs for turning off transmitters when not moving (in collaboration with Advanced Telemetry Systems, Isanti, MN). In the first design, transmitters contained an internal tip switch that was designed to turn on the transmitter when the seed was moved. Beta testing of these first generation transmitters in 2006 showed them to be too sensitive; they often turned on during heavy rains or from subtle movements of the leaf litter. These switches were sensitive to high humidity and many got stuck over time, thus we do not recommend this method for future studies.

The second- and third-generation transmitters used a magnet operated switch inside the transmitter to turn off radio transmitters until they are ready to be used (Kenward 2001). These tags were deactivated by placing 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 ~25 cm from the seed (Fig. 1). When a seed was moved, the transmitter was pulled off the magnet, reactivating the radio signal. A small piece of wire inserted into the second-generation transmitters provided enough magnetic attraction to the magnet to ensure that the transmitter did not easily slip off the magnet during rain storms, but provided little resistance when an animal pulled the transmitter

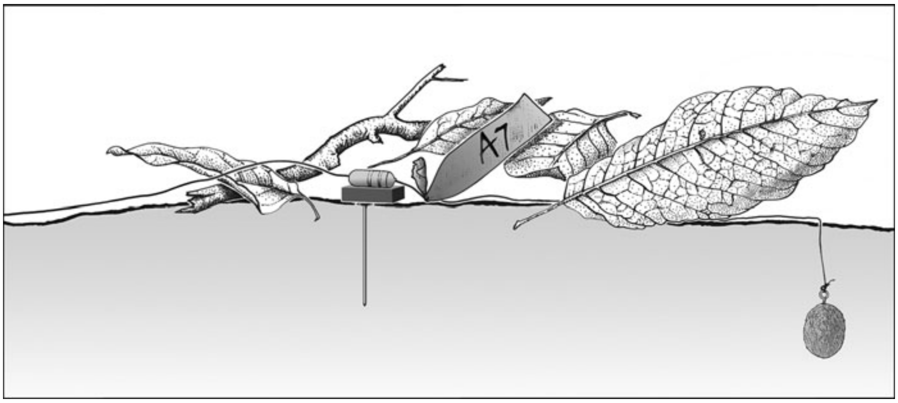

Fig. 1 Diagram showing the telemetric seed tag (*center*) connected by wire to a buried seed (*bottom right*). The telemetric seed tag is laid on top of a magnet which has been staked into the ground with a nail. Drawing by Patricia Kernan

off the magnet. The second-generation transmitters weighed 4.10 g, including a 20-cm long wire antenna.

We experimented with two power sources. The first- and second-generation transmitters had one cylindrical 3-V lithium pin battery (25 mAh, 4.2 × 25.9 mm, 0.55 g; National BR425, New York, NY). These transmitters experienced high rates of battery failure (>60 % of transmitters of second generation failed during a 6-month period). A third generation of transmitters used two 1.55 V silver oxide button cells (80 mAh, 5.4 × 7.9 mm, 1.5 g; Renata 393, Itingen, Switzerland) and had a low failure rate (2 %) over a 6-month period. The third generation transmitters attached to magnets without an inserted metal wire in the transmitter housing, resulting in a lighter transmitter (3.80 g). The approximate lifespan of a radio transmitter was 6–8 weeks of continuous transmission. Because the transmitters were generally turned off within 24 h of moving they worked in the field much longer (>10 months). As seeds were eaten or censored during the course of the study, we were able to reuse the transmitters on different seeds, thus the long lifespan of the transmitter allowed us to follow more seeds than we initially had telemetric tags for. These transmitters cost the same as standard radio collars (~$200 per unit, or less with bulk discount), thus reusing tags allowed us to obtain more data without increasing the cost of the study.

Field application

We used telemetric thread tags to track seed dispersal of the palm *A. standleyanum* on Barro Colorado Island, Panama (9°10′N, 79°51′W), a 1,560 ha island covered with tropical moist forest. Each *Astrocaryum* tree produces up to 1,500 fruits per year. Each fruit contains a ca. 9.6 g stone consisting of a large seed enclosed in woody endocarp (Wright et al. 2010). The seeds are typically dispersed by the Central American agouti, *Dasyprocta punctata*, a 2–4 kg caviomorph rodent that scatter hoards the stones as food reserves for periods of food scarcity (Smythe 1978, 1989; Jansen et al. 2010). Astrocaryum seeds generally germinate during the wet season, one or more years after being dispersed (Smyth 1989; Potvin et al. 2003).

Telemetric tags were attached to *A. standleyanum* stones (henceforth "seeds") with 30 cm of black nylon-coated stainless-steel leader wire (American fishing wire: Surflon 1 × 7 black coating) tied to a 7-mm screw eye inserted halfway into the basal tip of the seed. Screws were inserted opposite to the embryo, thus the endosperm was hardly penetrated and not exposed to water or microbes which could have affected germination. The wire tied to the screw was difficult to visually detect, and the wire and screw were relatively difficult for rodents to cut in comparison to traditional thread tags. To facilitate visual retrieval and individual recognition, we attached a 7 cm piece of pink flagging tape to the wire near the transmitter.

We tracked the fate of tagged seeds with traditional manual telemetry in combination with an Automated Radio Telemetry System (ARTS, Kays et al. 2011). Most seed tracking was conducted with manual telemetry, while the ARTS provided a backup for determining if transmitters were still turned on in the field. Whereas transmitters in a typical study would each have a unique radio frequency, seed transmitters in our study were tuned to one of four frequencies in the 150–152 MHz range, which reduced the number of frequencies that needed to be monitored with ARTS. A drawback to using multiple transmitters with the same frequency was that locating the transmitters was more difficult. In some cases, we could hear 20 or more seed transmitters of the same frequency from one location, resulting in a chorus of beeping transmitters. We were still able to manually locate transmitters by walking toward the strongest signal, which was typically the closest seed, turning this transmitter off and then continuing toward the next strongest signal. We strongly recommend using unique frequencies for each seed in future studies.

The effect of telemetric thread tags on seed removal rates and dispersal distance was evaluated by comparing fate between seeds with first-generation telemetric thread tags, seeds with traditional thread tags, and untagged seeds. During 2006, we placed ten seed stations across BCI that each contained five seeds of each treatment (150 seeds in total). We monitored seed removal with a motion-triggered camera trap (Silent Image, Reconyx, Holmen, WI) and then compared time-to-removal between the three types. We located as many dispersed seeds as we could and compared dispersal distance between radio-tagged and thread-tagged seeds (untagged seeds could not be retrieved). During 2009 and 2010, we only used telemetric thread tags (second and third generation tags).

The overall field performance of the third generation telemetric tags was evaluated for 589 seeds with telemetric thread tags in 2010. We placed five tagged seeds at a time in 52 stations scattered across BCI, and monitored removal with a motion-triggered camera trap (RC55 or PC800, Reconyx, Holmen, WI) (Fig. 2). We recorded the animal species and time of seed removal for each seed (as in Jansen et al. 2002, 2004, Jansen and den Ouden 2005, Yasuda et al. 2000, 2005). Seed stations were placed in the field for a maximum of 8 days. If seeds remained at the end of 8 days, the seeds were replaced with fresh seeds, or the entire station was canceled. Seeds were removed by rodents from 32 of 52 stations. Each seed plot was checked daily and removed seeds were located by sight or with hand-held radio-telemetry equipment (Yaesu-VR500, Cypress, CA) to determine dispersal distance and seed fate. If the seed was found <20 m of 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). If the seed was moved >20 m, the location of the seed was recorded using a GPS receiver (Garmin 60CSx). 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. Higher-order seed movements (seed removed from caches) were treated in the same way. Seeds moved frequently after being first set out, in some cases more than once per day. After 3–4 months, many seeds were eaten and the remaining seeds were moved less frequently. We gradually decreased the amount of manual seed checks after four months of daily checks, and used the ARTS to determine if any seeds had moved before manually checking seeds.

Possible effects of telemetric tags on cache fate were evaluated by following the fate of caches for a subset of 46 seeds in 2010 with camera traps to determine whether rodents used the telemetric seed tags as cues for finding caches. A camera was mounted onto a nearby tree or onto a U-shaped metal rebar pushed into the ground 1.5 m from the seed cache (Fig. 2), and set to continuously take photos when animals passed in front. We closely investigated the series of photos taken when a cache was removed to check for cueing behavior. If agoutis or other rodents are able to use the telemetric seed tags as a cue to the location of buried seeds, we expected that we would be able to observe this behavior from the photos. In addition, we verified whether the cameras themselves influenced the likelihood of a cache being removed by comparing removal rates between caches with and without cameras.

Fig. 2 Motion-sensitive camera trap mounted on a U-shaped concrete-reinforcement bar, used to monitor removal of seeds from an experimental station or from a cache

Results

Telemetric seed tag efficacy

The telemetric tags did not affect seed removal. The 2006 tests yielded no significant difference in the proportion of seeds removed between seeds without tag (92.0 %), with a traditional thread tag (86.7 %), and with a telemetric thread tag (94.0 %; Chi-square test $\chi^2_{2,145}$, $p = 0.440$), nor was there a significant difference in time-to-removal (Fig. 3a; Kaplan–Meier survival analysis with log-rank test on lumped data: $n = 145$, $\chi^2_2 = 1.3$, $p = 0.516$). Also, dispersal distance did not differ between thread-tagged seeds and radio-tagged seeds (Fig. 3b; $n = 72$, $\chi^2_1 = 0.5$, $p = 0.482$). We cannot evaluate, however, whether dispersal distance differed between tagged and untagged seeds, because there was no way to retrieve untagged seeds.

Rates of seed recovery after dispersal were extremely high. Of the 589 seeds placed during 2010, 424 (72 %) were removed by animals. Of these 424, we recovered 97 %. Of the 13 non-retrieved seeds, 11 were lost because rodents chewed through the wire attaching the transmitter to the tag, and two seed tags were never found, presumably because of transmitter failure. Assuming that tag cutting and radio failure are independent of dispersal distance, the method captured dispersal with minimal bias against long distances.

Turning off transmitters during inactive periods allowed us to monitor seeds over long time spans. We tracked higher-order movements for a subset of the 424 seeds removed during 2010. We followed 224 cached seeds across multiple seasons, until these either were eaten or had survived to 1 year. When a seed had been eaten or a tag cut, we would reuse the transmitter, thus we were able to monitor far more than 100 seeds. During 2010, only 2 out of the 100 third generation transmitters were lost over a span of 6 months. It was not known whether these transmitters had internal malfunctions, premature battery failure, were damaged by animals (we observed chew marks of rats on some transmitters), or were taken so far that we were unable to detect the radio signal. It is unlikely that seeds dispersed too far to be detected since signals were typically detected >400 m from the ground, and 1,000 m from the ARTS towers.

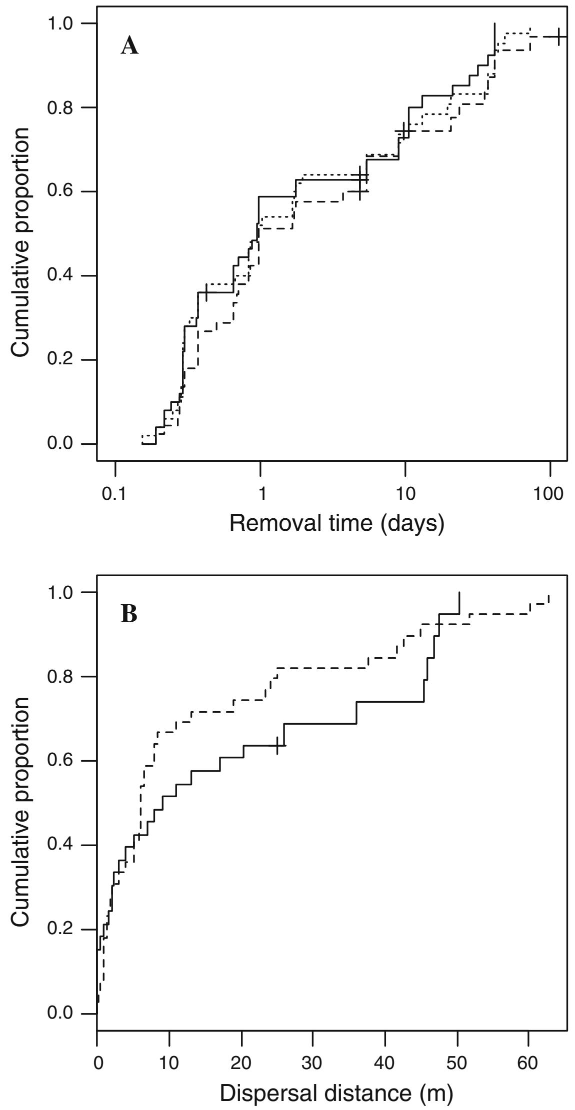

Fig. 3 Time-to-removal (**a**) and dispersal distance (**b**) by rodents for *Astrocaryum standleyanum* seeds with telemetric thread tags (*dashed line*), with traditional thread tags (*solid lines*), and without any tag (*dotted line*), on Barro Colorado Island, Panama during 2006. Values shown are inverse Kaplan–Meier survivorship estimates. The differences were not significant

The rate of severed tags was low (2.5 % per movement), much lower than the proportions reported in studies with traditional thread tags. However, the probability of a transmitter being cut off increased over time, as the same seeds could be handled multiple times. Ultimately, 60 (26.7 %) of the 224 seeds had the wire portion of their seed tags cut off, and this remained a major source of seed loss.

Dispersal distance

We recorded a total of 1,582 first- and higher-order seed movements during 2010. The mean movement distance was 16.8 m (range 0.1–241.3 m), which is within the normal search radius for seed dispersal studies using thread tags. However, 280 movements (17.7 %) exceeded 30 m, and would normally have resulted in loss of the seed in studies using other tagging methods (Howe 1990, de Steven 1994).

Cueing

Seed caches monitored with remote cameras were removed more slowly than normal seeds (average time-to-removal for non-camera caches = 7.8 days, camera caches = 19.7 days, Kruskal–Wallis $\chi^2 = 52.14$, $p = <0.001$). We were able to determine the species of animal that recovered the seed from 92.5 % of caches. In 12.5 % of these cases, the photo sequences of cache retrieval suggested that agoutis sometimes cued on the flagging tape for finding cached seeds. In these cases, agoutis approached the flagging tape, and either followed the attached wire toward the location of the cached seed ($n = 10$), or started digging in soil nearby the flagging tape ($n = 7$). This behavior was very distinct from the typical seed discovery seen in the other cases where animals tune in on the seed or digging traces; in those cases the animal typically walked straight toward the cached seed, and dug immediately above the location of the seed.

Discussion

How effective are telemetric seed tags for tracking seed dispersal?

Traditional seed dispersal studies are limited because dispersing seeds are notoriously difficult to track, resulting in bias against long-distance dispersal and secondary seed movements (Wang and Smith 2002). In this article, we have described seed tracking with telemetric thread tags as a method for studying seed dispersal by scatter-hoarding rodents without these biases. Field tests in Panama indicated that the method fulfilled all four of our performance criteria: (1) the transmitters allowed near-complete retrieval of dispersed seeds with minimal bias against longer distances, (2) the thread design allowed continued monitoring of cached seeds without disturbance of the caches, 3) a simple motion-sensitive triggering mechanism allowed the monitoring of seeds over long time spans, and (4) tag effects on seed fate were minor and all related to the optional flagging.

The telemetric thread tags allowed us to quickly and accurately find seeds regardless of dispersal distance, including seeds that had been dispersed >200 m, which would have been nearly impossible to retrieve with traditional tagging methods. Retrieval with minimal distance bias is a major advantage of telemetric tags compared to other tags. Studies using non-telemetric tags invariably involve searching the area around the location of seed dispersal up to a certain radius, typically <30 m, as search effort increases exponentially with distance (Howe 1990, de Stevens 1994). The inherent bias against dispersal distances exceeding this radius is a major problem that is poorly dealt with (Hirsch et al. 2012). In our trials, 17.7 % of the dispersal events exceeded 30 m, and would normally have resulted in loss of the seed in studies using traditional tagging methods. One potential limitation of these telemetric seed tags is that our hand-held radio-tracking equipment had a maximum detection range of ~400 m. In our case, even the seeds that were dispersed the furthest (almost 250 m) still remained within this detection range. If an extreme long-distance dispersal event occurred (Higgins et al. 2003), we may not have been able to discover the seed with hand-held equipment (although we almost certainly would have detected the seed through the ARTS system). For this reason, researchers using telemetric thread tags may need to use caution in interpreting results when seeds disappear from the system.

Our final transmitter design was robust, with a maximum 2 % failure rate over 6 months, similar to previous seed-tracking studies that used telemetry (0–4.5 %; Pons and Pausas 2007; Sone et al. 2002; Tamura et al. 2002). The most common source of seed loss was due to animals cutting the wire attaching the transmitter to the seed. Even with wire cutting, the rate of seed loss was much lower than studies using traditional non-telemetric seed tags (up to 100 % Forget and Wenny 2005), yet wire cutting remains a significant problem for tracking seeds that are handled by rodents multiple times. We saw no evidence of any pattern or bias in seeds with cut wires, thus we do not expect cutting to bias dispersal distance estimates. However, we are unable to conclusively eliminate the possibility that agoutis preferentially cut seeds they intended to disperse particularly far.

All previous telemetric studies of seed movement used transmitters directly mounted onto, or inside, the seed or nut (Pons and Pausas 2007; Sone et al. 2002; Tamura et al. 2002). Our integration of the transmitter into a thread tag has several advantages to direct mounting. Because the transmitter was not buried during seed caching, we could determine the identity of the seed without disturbing the cache, avoiding soil disturbance that rodents use as cue for cache finding (Guimaraes et al. 2005; Murie 1977). It also allowed us to turn the transmitter off when seeds were not moving, which saved battery power. Frequent deactivation allowed us to use small, lightweight tags for monitoring seeds over many months to determine their ultimate fate; germination or death. We checked seeds once per day during the initial 4 months of our study, but different study systems may require more or less frequent seed monitoring, depending on the number of seeds being tracked and their rate of movement.

Camera-trap footage of cache recovery suggested that agoutis occasionally used flagging tape as a cue for finding cached seeds. The videos revealed that the animals cued on the pink-flagging tape rather than the black wire, transmitter, or transmitter antenna. After noticing the flagging, some agoutis appeared to use the wire thread to guide them to cached seed, even though the wire appeared difficult for rodents to see. If the visual cue provided by the flagging tape was eliminated, we expect that animals would not have found the seeds using only the wire. Although cueing on flagging had a minor effect on the results, we recommend that future studies should aim to eliminate the flag, thus minimizing this problem. Finding transmitters without flagging is more difficult for field workers, but still possible. A unique serial number written onto or inserted inside the transmitters along with unique transmitter frequencies can be used as to identify these seeds when no flagging is present. Our finding that some animals cue on flags to find seeds also suggests that thread tags may have influenced removal rates and survival times of caches in past studies.

We were also concerned that agoutis might have learned to associate the cameras with cached seeds. We found the opposite effect, and it appears that the cameras may have scared the agoutis away from the caches. This result is unexpected given the widespread use of remote cameras (with and without cached seeds) in the study area from 2008 through 2010. Despite this effect, we found that the cache cameras were an effective method to record the species which removed cached seeds, and the behavior of the animals when retrieving cached seeds.

Broader potential

Since most seeds are small, and can take many months to reach their ultimate fate, the size and lifespan of radio transmitters has limited their use in the tracking of seed movement. However, the size of radio tags continues to drop, with various companies now offering transmitters that weigh just 0.2 g, ushering in a new era of study of small animals, such as bees and dragonflies (Wikelski et al. 2006, 2010). We believe that the study of seed dispersal is also ripe for discovery with miniature tags. Seed size in the Plant Kingdom ranges from the 1-µg dust seeds of orchids to the 20-kg seeds of the double coconut *Lodoicea seychellarum* (Harper 1977). Based on our experiences with the telemetric thread tag, we argue that many more plant species can be radio tracked than is currently believed.

The accepted guideline for placing a radio transmitter on an animal is that the transmitter should not be >5–10 % of an animals' body weight (Murray and Fuller 2000, Kenward 2001), but there is no reason for applying this rule to the weight of seeds themselves, which are being voluntarily moved by animals much larger than themselves. Our telemetric thread tags added 40 % weight to the seeds of *A. standleyanum*, but only 0.1 % to the weight of the agoutis that carried the seeds, and this did not appear to affect their behavior.

To estimate how widespread this technology might be used for studying animal dispersed seeds, we linked the fruit species consumed by two common scatter-hoarding mammals in Central Panama; spiny rat (*Proechimys semispinosus*) and agouti (Adler 1995; Aliaga-Rossel et al. 2008) to the corresponding seed sizes (Wright et al. 2010). A majority of the plant species consumed by these animals have seeds $\geq$0.5 g, the mass of the smallest available radio transmitter (spiny rat = 50.1 %, agouti = 77.5 %). The maximum weight of seeds taken by these two species far exceeds that of our seed transmitters (spiny rat =13.3 g, agouti = 63.7 g). For mammals that carry relatively heavy seeds, adding additional weight to a seed should not noticeably change the animals' behavior. Indeed, Muñoz and Bonal (2008) found that rodents regularly moved seeds up to 70 % as heavy as their own body mass.

We experimented with several different methods for attaching the transmitters to seeds and conserving battery power. We recommend experimenting with threads, glues, and other techniques to find the right solution for a given seed-mammal combination. In the case of seeds ingested by frugivores, gut passage time and seed dispersal can be measured by placing seed-shaped transmitters inside fresh fruit (Mack and Druliner 2003). In each case, the key test will be how the animals handle the modified seeds relative to unmodified ones, a relatively simple test to make with modern camera traps.

Conclusion

The telemetric thread tag method can be used to track dispersing seeds at distances far greater than traditional techniques, identify cached seeds without disturbing the cache site, document secondary dispersal, and identify ultimate seed fate. Combining telemetric thread tags with remote cameras can be used to document the exact time of removal, and the species which removed the seed (Jansen and Den Ouden 2005). These techniques can be used in various combinations to investigate a wide variety of ecological questions in a large number of biological systems. Given the importance of studying secondary dispersal, we believe that our methods represent an important methodological step to help understand the dynamics of seed dispersal and forest regeneration (Vander Wall et al. 2005).

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