



Telemetric tracking of scatterhoarding and seed fate in a Central African forest

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ABSTRACT

In seed predation studies, removal of a seed is only the first step of a dynamic process that may result in dispersal rather than seed death. This process, termed seed fate, has received little attention in African forests, particularly in Central Africa. We experimentally assessed the initial steps of seed fate for two tree species—the large-seeded *Pentaclethra macrophylla* and the relatively small-seeded *Gambeya lacourtiana*—in northeastern Gabon. Specifically, we evaluated whether seed size and seed consumer identity are important determinants of seed fate. We established experimental stations under conspecific fruiting trees, each comprising three seeds fitted with telemetric thread tags to facilitate their recovery, and a motion-sensitive camera to identify visiting mammals. In total, animals removed 76 tagged seeds from experimental stations. Small Murid rats and mice primarily removed small *Gambeya* seeds, whereas large-bodied rodents and mandrills primarily removed large *Pentaclethra* seeds. *Gambeya* seeds were carried shorter distances than *Pentaclethra* seeds and were less likely to be cached. The two large-bodied rodents handled seeds differently: *Cricetomys emini* larderhoarded nearly all ($N = 15$ of 16) encountered *Pentaclethra* seeds deep in burrows, while *Atherurus africanus* cached all ($N = 5$ of 5) encountered *Pentaclethra* seeds singly under 1–3 cm of leaf litter and soil, at an average distance of 24.2 m and a maximum distance of 46.3 m from experimental stations. This study supports the hypothesis that seed fate varies based on seed size and seed consumer identity, and represents the first telemetric experimental evidence of larderhoarding and scatterhoarding in the region.

Abstract in French is available with online material.

Key words: Africa; *Atherurus africanus*; *Cricetomys emini*; Gabon; larderhoarding; secondary seed dispersal; seed predation; telemetric thread tag

MUCH SEED PREDATION RESEARCH HAS EQUATED THE REMOVAL OF A SEED FROM AN EXPERIMENTAL PLOT with the seed's death. However, seed predators vary in their handling of seeds, with a diversity of consumption and hoarding behaviors (Janzen 1971, Vander Wall 1990, Hulme 1998, Forget *et al.* 2005, Vander Wall *et al.* 2005a, b). Methodological advances in studying these processes—ranging from simple seed thread tags to radioisotopes to telemetric tracking (Forget & Wenny 2005)—have prompted the realization that seed predation is a dynamic process, comprising multiple steps, complex mechanisms, and varied outcomes (Vander Wall *et al.* 2005a, b). The study of these pathways, collectively known as seed fate, follows seeds to either death or, in few cases, successful establishment as seedlings by way of various biotic and abiotic actors.

In tropical forests, seed fate has been examined most prominently in studies of acouchies, agoutis, and spiny rats, Neotropical seed-consuming rodents that can double as effective dispersers via the process of scatterhoarding (Morris 1962, Smythe 1978, Forget 1990, Adler & Kestell 1998, Brewer & Rejmánek 1999, Jansen *et al.* 2012). Though relatively well-studied in the Neotropics and in several temperate forests, scatterhoarding and seed fate have received very little attention in other tropical forest regions, particularly in Central Africa. For African forests as a whole, only a few studies have examined seed fate and the role of rodents in

seed dispersal (Doucet 2003, Nyiramana *et al.* 2011, Moupela *et al.* 2013, Aliyu *et al.* 2014, Dutton *et al.* 2014).

This research gap merits attention, as rodent seed predators are ubiquitous in tropical forests and can strongly influence plant population dynamics and patterns of tree recruitment (Janzen 1971, Fleming 1975, Asquith *et al.* 1997, Paine & Beck 2007). In Central African forests, large rodents—including Emin's giant pouched rat (*Cricetomys emini*) and the African brush-tailed porcupine (*Atherurus africanus*)—are common seed consumers, though very little is known about the fate of seeds they handle. A single captive study (Ewer 1968) noted caching behavior in *A. africanus*, though this has never been explicitly assessed in the wild. As both species are heavily hunted for meat (Fa *et al.* 2005), developing an understanding of their ecological roles may also impact forest management decisions.

In this study, we experimentally assess the initial steps of seed fate for two tree species, *Gambeya lacourtiana* and *Pentaclethra macrophylla*, in northeastern Gabon. Specifically, we evaluate whether seed size and the identity of the seed predator are important determinants of seed fate.

METHODS

We conducted this study in the forest surrounding the Ipassa Research Station, in the Ogooué-Ivindo region of northeastern Gabon. This region is dominated by lowland forest, and receives approximately 1700 mm of rain annually, with two rainy seasons

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(September–December and March–June). Despite its protected status as part of Ivindo National Park, the Ipassa forest is occasionally hunted. A few species of game animals, including bay duikers (*Cephalophus dorsalis*) and red river hogs (*Potamochoerus porcus*), have been reduced in abundance as a result (Okouyi *et al.* 2001, van Vliet *et al.* 2007). Nonetheless, the forest boasts high mammal diversity (Okouyi *et al.* 2002, Koerner *et al.* 2016) and an apparently intact rodent community (Markham 2015).

We selected the seeds of two tree species, *Gambeya lacourtiana* (Sapotaceae; basionym: *Chrysophyllum lacourtianum* De Wild.) and *Pentaclethra macrophylla* (Fabaceae; Fig. 1), because they were: (1) locally abundant, (2) divergent in size but both large enough for telemetric thread tagging, and (3) known to be commonly preyed upon. *Gambeya lacourtiana* (hereafter *Gambeya*) is a large tree, reaching over 50 m tall, with large succulent globose fruits (mean mass = 320 g) that are widely consumed by small, medium, and large-bodied mammals. *Gambeya* seeds, of which there are 4–5 per fruit, are relatively small in size (mean mass = 2.8 g) with a flattened ellipsoid shape (mean length = 29 mm, mean width = 14 mm). They have a prominent seed scar and a shiny brown seed coat that is hard but thin, and easily penetrated by mammalian seed predators. *Pentaclethra macrophylla* (hereafter *Pentaclethra*) is a medium to large tree, 20–30 m tall, with large woody seed pods (approximately 50 cm × 10 cm × 2 cm). Each pod contains 5–8 seeds, and dehisces explosively at maturity, scattering seeds up to 20 m from the tree (Archinewhu 1996). *Pentaclethra* seeds are very large (mean mass = 29.4 g), with a flat elliptical shape (mean length = 64 mm, mean width = 39 mm) and a shiny brown seed coat that is medium-hard, but is also easily penetrated by most seed predators.

We collected whole *Gambeya* fruits (July–August) and *Pentaclethra* seeds (September–October) from the ground beneath at least five fruiting individuals of each species, during their close but non-overlapping fruiting seasons. We extracted *Gambeya* seeds from their fruits, cleaned them of flesh, and dried them for 1–2 h in the sun to prevent fungal growth. We assessed all seeds for damage, discarding seeds with fungus, arthropod exit holes, and any seeds that floated in water. We conducted the experiment for both species during the same period, from September 22, 2014 to November 2, 2014, which required us to store cleaned *Gambeya* seeds indoors under ambient air conditions for a period

of approximately 45–60 days. Results from other experiments using these seeds indicate that this brief storage period did not affect seed removal or germination rates.

Immediately prior to experimental placement, we fitted seeds with telemetric thread tags (Hirsch *et al.* 2012) by attaching a 7 mm screw eye and threading it with 30 cm of black nylon-coated stainless steel leader wire. We also tied on a small piece of pink flagging labeled with an identification code unique to its experimental placement. Each cylindrical radiotransmitter (Advanced Telemetry Systems, Isanti, MN) weighed 4.10 g, including a 20 cm long wire antenna, and featured a magnet-operated on-off switch (Hirsch *et al.* 2012). Prior experimental tests have shown that seeds with telemetric thread tags are removed at equal rates to untagged seeds (Hirsch *et al.* 2012). We tested this for our study by scattering three tagged and three untagged seeds in a clump (1 m² in area), and monitoring their fate for 14 days. We repeated the procedure four times in different locations for each species.

We intended to pair the telemetric thread tag method with more traditional thread tags (Forget 1990), using 60-cm lengths of brightly-colored line threaded to each seed, with a flagging tape label at the distal end. Initial use of these simple thread tags was unsuccessful, as the cotton thread frequently caught on understory vegetation and was difficult to re-locate visually. Nylon thread, fine metal wire, or plastic fishing line might have been suitable alternatives, but were unavailable for our study.

We established experimental seed stations under conspecific fruiting trees (5–10 m from the tree bole) for each species. Stations consisted of three telemetric thread tagged seeds, arranged 0.75 m apart in a triangle on soil cleared of leaf litter. We mounted a motion-sensitive trail camera (Bushnell Trophy Cam HD, set to 60-second video mode) on a nearby tree to identify visiting mammals and record their behavior (Fig. 2). Each seed station was located at a different tree and spaced a minimum of 250 m from any other station. Due to the cost of telemetric thread tags, we were limited to running four seed station experiments at any one time.

We checked seed stations three days after seed placement and again seven days after placement if seeds remained after the first check. To recover removed seeds, we first visually scanned the immediate area, and then used a handheld radio receiver with telemetry antenna, locating tagged seeds by their specific transmitter frequency. At each recovery location, we took the following data: movement distance (measured with a measuring tape), compass direction, and seed condition (intact, consumed, in burrow, or cached under soil or leaf litter).

If all seeds remained untouched after seven days, we closed the station and established a new experimental site. If some or all seeds were removed, we recovered the telemetric thread tags and attached them to new seeds, and we established a new station on the opposite side of the same tree (10–20 m away), or at an entirely new location if two experimental sites had already been used there. In one instance, we repositioned a trail camera to continue monitoring a tagged seed that had been removed and cached nearby. Equipment and field limitations prevented us



FIGURE 1. The seeds of two tree species, *Pentaclethra macrophylla* (on left) and *Gambeya lacourtiana* (on right), used in the study.



FIGURE 2. The major terrestrial mammalian seed predators of the Ipassa Reserve, 'caught' removing seeds from experimental stations. Clockwise from top left: African brush-tailed porcupine (*Atherurus africanus*), Emin's giant pouched rat (*Cricetomys emini*), small Murid rodent (Family: Muridae; circled), and mandrill (*Mandrillus sphinx*). Still images were taken from motion-sensitive trail camera videos.

from following seeds over time in all other cases; our data are limited to the first movement of seeds and their initial fate.

RESULTS

Tagged and untagged seeds were removed at equal rates in the pilot experiment, with no difference in time to removal or quantity removed; all seeds of both treatments were removed ($N = 42$ seeds across four stations) except at one station, where none of the seeds of either treatment were removed ($N = 6$ seeds). This supports previous experimental tests indicating that the telemetric thread tag does not affect seed removal (Hirsch *et al.* 2012). It is impossible to determine whether the telemetric thread tag affects eventual seed fate, as untagged seeds cannot be monitored.

In total, 76 telemetric thread tagged seeds were removed from experimental stations for the two species (*Gambeya* = 36 seeds, *Pentaclethra* = 40 seeds). Seeds for which the fate could not be determined (due to failure of the trail camera to capture the seed predator [$N = 6$], the thread tag being tangled on vegetation [$N = 5$], or transmitter failure [$N = 1$]) were excluded from analysis, as were the data from the pilot study.

Small Murid rats and mice removed greater proportions of small *Gambeya* seeds, whereas large-bodied rodents and mandrills (*Mandrillus sphinx*) removed greater proportions of large

Pentaclethra seeds (Table 1). For *Gambeya* seeds, the dominant seed predators were small-bodied Murid rats and mice, which removed 63% ($N = 20$) of all seeds, followed by large-bodied rodents, *C. emini* (34%, $N = 11$) and *A. africanus* (3%, $N = 1$). For *Pentaclethra* seeds, the dominant seed predator was *C. emini*, which removed 56% ($N = 18$) of all seeds, followed by *M. sphinx* (28%, $N = 9$) and *A. africanus* (16%, $N = 5$). No *Pentaclethra* seeds were removed by small-bodied Murid rodents.

Animals moved *Gambeya* seeds shorter distances (mean = 3.2 m, max = 13.5 m) than *Pentaclethra* seeds (mean = 15.9 m, max = 46.3 m), and consumed a higher proportion of *Gambeya* seeds on the spot, within 0.5 m of experimental placement (31% [$N = 11$] for *Gambeya* versus 18% [$N = 7$] for *Pentaclethra*; Fig. 3). A single *Gambeya* seed was cached (in a Murid rodent burrow), while 20 *Pentaclethra* seeds were cached (five seeds cached under 2–3 cm of soil and leaf litter by *A. africanus*, 15 seeds cached in burrows by *C. emini*). Of the five seeds cached by *A. africanus*, one was subsequently found and removed by a *C. emini* individual, and the remaining four were still cached at the conclusion of the study, approximately two weeks after deposition. To assess the fate of seeds cached in *C. emini* burrows, we dug up one burrow, which had two entrances, a total length of 7.4 m, and a depth of 1.2 m at the center, where seeds were cached. A total of 104 seeds of four species (*Pentaclethra*, along

TABLE 1. Removal percentages (by seed consumer) and movement distances of telemetric thread tagged seeds.

Species of seed	% removed by:				Movement Distance (m)	
	Murid rodents	<i>Cricetomys emini</i>	<i>Atherurus africanus</i>	<i>Mandrillus sphinx</i>	Mean	Max
<i>Gambeya</i> ($N = 36$)	63	34	3	0	3.2	13.5
<i>Pentaclethra</i> ($N = 40$)	0	56	16	28	15.9	46.3

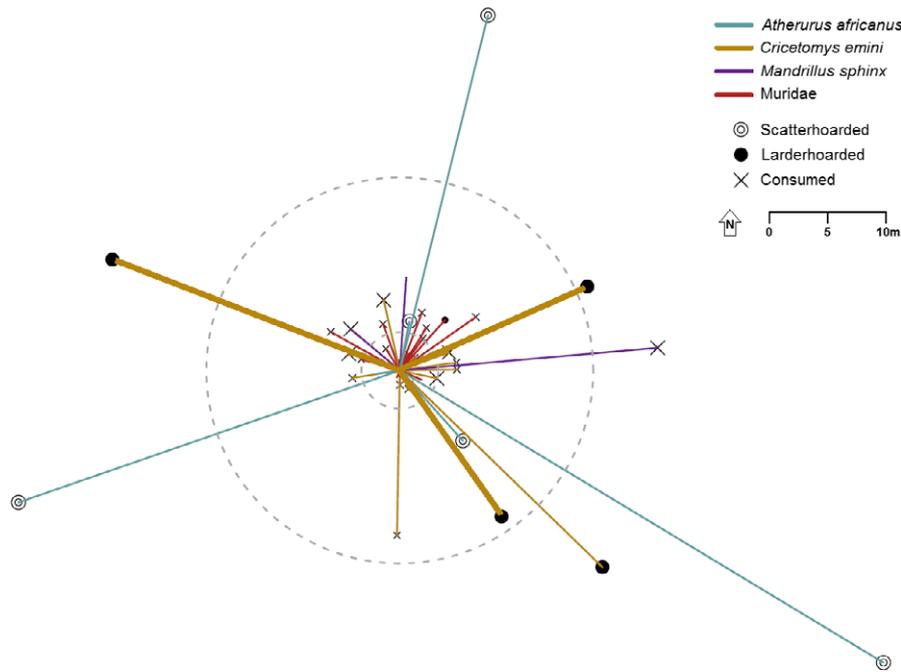


FIGURE 3. Movement and fate of telemetric thread tagged seeds. Line color represents the identity of the seed predator, symbol type represents the fate of the seed, and symbol size represents seed size (small symbols for small-seeded *Gambeya*, large symbols for large-seeded *Pentaclethra*). The location of each point represents a given seed's movement direction and distance (in meters) from its experimental plot, with all plots combined into one figure. The gray dashed lines indicate mean dispersal distance for *Gambeya* (small circle, radius = 3.2 m) and *Pentaclethra* (large circle, radius = 15.9 m). Seeds for which movement distance was <0.5 m ($N = 17$) were excluded from the figure, and seeds recovered intact on the leaf litter are represented by a line with no end symbol. In cases where multiple seeds were moved to the same location by the same seed predator (i.e., *Cricetomys emini* taking multiple tagged seeds from a single station back to its burrow), the data are represented by thicker lines.

with *Coula edulis*, *Pentaclethra eetveldeana*, and *Scorodophloeus zenkeri*) were recovered from this single burrow cache, of which 78 were *Pentaclethra*, with a total seed mass of 2.47 kg, approximately twice the average body mass of the rodent.

DISCUSSION

In this first telemetric examination of seed fate in Central Africa, we found that the fate of *Gambeya* and *Pentaclethra* seeds differed due to two related factors: the size of the seed and the identity of the seed predator. The 10-fold difference in seed size probably resulted in divergent rates of consumption by different animal species; small Murid rats and mice removed greater proportions of small *Gambeya* seeds, whereas large-bodied rodents and mandrills removed greater proportions of large *Pentaclethra* seeds. *Gambeya* seeds were also more likely to be eaten on the spot rather than carried away, particularly among larger-bodied rodents.

When removed, small *Gambeya* seeds were carried shorter distances than large *Pentaclethra* seeds, and were less likely to be cached. This result supports the conclusion of several studies that large seeds are more likely to be carried farther and to be cached than small seeds (Hallwachs 1994, Forget *et al.* 1998, Jansen *et al.* 2004). Differential treatment of seeds along a seed size axis may allow seed-eating rodents to minimize exposure to predators, by

consuming small seeds that are quick to process and carrying large seeds that are time-intensive to process to a safe space such as a burrow (Smith & Reichman 1984, Vander Wall 1990). Hoarding few large seeds is also energetically favorable and makes better use of limited caching sites than hoarding many small seeds (Stapanian & Smith 1978, Jansen *et al.* 2002). In our study, the weight of the transmitter and difficulty in dragging the tag may have inhibited small Murid rodents from caching *Gambeya* seeds, as the additional 4.1 g increased total seed mass by almost 250 percent. Thus, small rodents may cache small untagged seeds more often than observed. The transmitter-to-body mass ratio for the two large rodents was much lower (33.5 g [transmitter+*Pentaclethra* seed] vs. 1200 g [*C. emini* mass] or 2750 g [*A. africanus* mass]), so the added transmitter weight was unlikely to alter their removal or caching behavior.

The two large-bodied rodents – *Cricetomys emini* and *Atherurus africanus* – consistently handled seeds differently from each other. *C. emini*, a large-bodied cheek-pouched burrowing rat, was responsible for the most seed removal (45% of 76 seeds overall), particularly for large seeds (56% of 36 seeds), and carried nearly all ($N = 15$ of 16) encountered *Pentaclethra* seeds to their burrows to be larderhoarded (see Results for a description of one burrow and its recovered seeds). At a depth of 1 m underground, even seeds that germinate will be unable to establish as seedlings, thus

the fate of seeds removed by *C. emini* is death. This result supports the assertion that *Cricetomys spp.* rodents are primarily seed predators, not dispersers (Guedje *et al.* 2003, Kankam & Oduro 2009, Seufert *et al.* 2009). However, two recent studies have implicated *Cricetomys spp.* rodents as scatterhoarders of large seeds. Nyiramana *et al.* (2011) studied the fate of threaded *Carapa grandiflora* seeds in a montane forest in Rwanda, recovering several cached seeds and finding seedling cotyledon evidence that indicated scatterhoarding by seed-dispersing rodents. Aliyu *et al.* (2014) documented scatterhoarding of numerous threaded seeds in a fragmented montane forest in Nigeria, attributing this dispersal to *Cricetomys sp.* rodents, as they were the most commonly observed seed consuming animal visiting the seed plots. Though these studies have large seed sample sizes, neither study linked visual camera observations with specific seed movements, and neither used methods that allow for the recovery of seeds moved long distances or deposited deep in burrows. It is possible that the scatterhoarding observed in these studies has been incorrectly attributed to *Cricetomys spp.* rodents, as the anatomical and behavioral traits of this rodent taxon, along with the results presented here, suggest that it transports multiple seeds in its cheek pouches and hoards them in large burrow larders rather than small scattered caches. It is also possible, though perhaps less likely, that the differences among the several *Cricetomys* species and the habitats in which they live are sufficient to drive divergent seed handling behaviors. More research will be necessary to evaluate the degree to which these behaviors are consistent across different forest types and with respect to variables such as rodent densities, fruiting phenology, and resource availability (P.-M. Forget, personal communication).

In contrast to *C. emini*, *A. africanus*, a rat-like porcupine that relies on natural-shelter burrows (Emmons 1983, Kingdon 2012), deposited all ($N = 5$ of 5) encountered *Pentaclethra* seeds in shallow caches, at an average distance of 24.2 m and a maximum distance of 46.3 m from the experimental stations (Fig. 3). In each case, seeds were cached singly under 1–3 cm of soil and leaf litter – an ideal microsite for germination and establishment. Due to equipment limitations, we were unable to continue monitoring seeds after their initial movement (e.g. Jansen *et al.* 2012), therefore it is impossible to quantify the proportion of scatterhoarded seeds that established as seedlings. Jansen *et al.* (2012) determined that most *Astrocaryum standleyanum* seeds hoarded by agoutis at one site in Panama were quickly recovered and eaten, but an estimated 14 percent of cached seeds survived to 1 year, with seeds being re-cached up to 35 times. Though the caching behavior of the two species is undoubtedly different, it is possible that a similar proportion of seeds scatterhoarded by *A. africanus* can survive to germinate and establish. However, *A. africanus* is frequently hunted (Fa *et al.* 2005) and occurs at lower densities than the other rodent species in our study (pers. obs. from trail camera footage), and it is likely that only a small minority of seeds removed by rodents in this region can survive to germination. Therefore, while scatterhoarding of seeds can promote tree recruitment (Jansen & Forget 2001), this mechanism of dispersal may be of secondary importance to widespread endozoochory by

abundant medium- and large-bodied mammals of African forests. The strongest benefit of scatterhoarding by rodents in the region may be to decrease clumping of previously dispersed seeds and to increase dispersal distances of seeds dispersed abiotically, both of which can reduce seed mortality due to distance- and density-responsive natural enemies (Janzen 1971, Hammond & Brown 1998, Terborgh 2012).

Our study supports the notion that telemetric thread tags can provide unique information on seed movement and fate beyond traditional tagging methods (Hirsch *et al.* 2012). Seeds removed and larderhoarded by *C. emini* would have been difficult or impossible to recover using traditional thread tags, due to the length and depth of their burrows. In these cases, the entirety of a traditional thread tag (typically ~ 60 cm long) would be dragged underground. Additionally, the long distance movements of seeds scatterhoarded by *A. africanus* (three of which were moved ≥ 30 m from experimental stations) would have precluded the recovery of these seeds by a visual search alone. Though other methods of seed tracking can provide greater quantities of data with less expense in both research costs and time, many of the seed movements observed in our study might have been missed. Ideally, telemetric tagging could be paired with the use of traditional thread tags to maximize both the quality and quantity of observations.

This study represents the first use of telemetric thread tags to assess seed fate in Central Africa, an important step in determining potential seed fate pathways and the influence of factors such as seed size and seed predator identity. We also present the first telemetric experimental evidence of larderhoarding and scatterhoarding by large-bodied rodents of the region. However, this study was limited to observing only the first steps of the seed fate process and represents a relatively small sample for two tree species. Our results support the conclusion that seed removal is often just the beginning of a process with many possible outcomes (Hulme 1998, Forget *et al.* 2005, Vander Wall *et al.* 2005a, b, Jansen *et al.* 2012). Future research in the region and elsewhere should focus on longer term monitoring of removed seeds to examine the full seed-to-seedling transition and quantitatively evaluate the role of seed predators in both predation and dispersal. Understanding the role these animals play in both intact and ecologically eroded (*sensu* Poulsen *et al.* 2013) tropical forests will be particularly important in establishing baselines for ecosystem function and integrity, and protecting critical ecological processes in forests under threat.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: <http://dx.doi.org/10.5061/dryad.91g52> (Rosin & Poulsen 2016)

LITERATURE CITED

- ADLER, G., AND D. KESTELL. 1998. Fates of Neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica* 30: 677–681.
- ALIYU, B., H. ADAMU, E. MOLTCHANOVA, P. M. FORGET, AND H. CHAPMAN. 2014. The interplay of habitat and seed type on scatterhoarding behavior in a fragmented afro-montane forest landscape. *Biotropica* 46: 264–267.
- ARCHINEWHU, S. 1996. The African Oil Bean (*Pentaclethra macrophylla* Benth.). In E. Nwokolo, and J. Smartt (Eds.). Food and feed from legumes and oilseeds, pp. 130–139. Chapman & Hall, London.
- ASQUITH, N. M., S. J. WRIGHT, AND M. J. CLAUS. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama *Ecology* 78: 941–946.
- BREWER, S. W., AND M. REJMÁNEK. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *J. Veg. Sci.* 10: 165–174.
- DOUCET, J.-L. 2003. L'alliance délicate de la gestion forestière et de la biodiversité dans les forêts du centre du Gabon. Dr. Diss.
- DUTTON, P. E., H. M. CHAPMAN, AND E. MOLTCHANOVA. 2014. Secondary removal of seeds dispersed by chimpanzees in a Nigerian montane forest. *Afr. J. Ecol.* 52: 438–447.
- EMMONS, L. 1983. A field study of the African brush-tailed porcupine, *Atherurus africanus*, by radiotelemetry. *Mammalia* 47: 183–194.
- EWER, R. 1968. The ethology of mammals. Plenum Press, New York.
- FA, J. E., S. F. RYAN, AND D. J. BELL. 2005. Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in Afrotropical forests. *Biol. Conserv.* 121: 167–176.
- FLEMING, T. 1975. The role of small mammals in tropical ecosystems. In F. Golley, K. Petruszewicz, and L. Ryszkowski (Eds.). Small mammals: their productivity & population dynamics, pp. 268–198. Cambridge University Press, Cambridge, UK.
- FORGET, P. 1990. Seed-dispersal of *Vouacaponia americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *J. Trop. Ecol.* 6: 459–468.
- FORGET, P.-M., J. Lambert, P. Hulme, and S. Vander Wall (Eds.). 2005. Seed fate: predation, dispersal and seedling establishment. CABI Publishing, New York, NY.
- FORGET, P.-M., T. MILLERON, AND F. FEER. 1998. Patterns in post-dispersal seed removal by neotropical rodents and seed fate in relation to seed size. In D. Newbery, H. Prins, and N. Brown (Eds.). Dynamics of tropical communities, pp. 25–50. Blackwell Science, Oxford, UK.
- FORGET, P.-M., AND D. WENNY. 2005. How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal. In P.-M. Forget, J. Lambert, P. Hulme, and S. Vander Wall (Eds.). Seed fate: predation, dispersal and seedling establishment, pp. 379–394. CABI Publishing, Cambridge, MA.
- GUEDJE, N. M., J. LEJOLY, B. A. NKONGMENECK, AND W. B. J. JONKERS. 2003. Population dynamics of *Garinia lucida* (Clusiaceae) in Cameroonian Atlantic forests. *For. Ecol. Manage.* 177: 231–241.
- HALLWACHS, W. 1994. The clumsy dance between agoutis and plants: scatterhoarding by Costa Rican dru forest agoutis (*Dasyprocta punctata*: Dasyproctidae: Rodentia). Cornell University, Ithaca NY.
- HAMMOND, D. S. D., AND V. BROWN. 1998. Disturbance, phenology and life-history characteristics: factors influencing distance/density-dependent attack on tropical seeds and seedlings. In D. Newbery, H. Prins, and N. Brown (Eds.). Dynamics of tropical communities. Blackwell Science, Inc, Malden, MA. Available at: <http://www.cabdirect.org/abstracts/19980612339.html> [Accessed October 8, 2013].
- HIRSCH, B., R. KAYS, AND P. JANSEN. 2012. A telemetric thread tag for tracking seed dispersal by scatter-hoarding rodents. *Plant Ecol.* 93: 3–943.
- HULME, P. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. *Perspect. Plant Ecol. Evol. Syst.* 1: 32–46.
- JANSEN, P., M. BARTHOLOMEUS, F. BONGERS, J. ELZINGA, J. Den OUDEN, AND S. Van WIERREN. 2002. The role of seed size in dispersal by a scatterhoarding rodent. In D. Levey, W. Silva, and M. Galetti (Eds.). Seed dispersal and frugivory: ecology, evolution and conservation, pp. 209–226. CABI Publishing, New York.
- JANSEN, P., F. BONGERS, AND L. HEMERIK. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecol. Monogr.* 74: 569–589.
- JANSEN, P. A., AND P.-M. FORGET. 2001. Scatterhoarding rodents and tree regeneration. In F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Thery (Eds.). Nouragues: dynamics and plant-animal interactions in a neotropical rainforest, pp. 275–288. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- JANSEN, P. A., B. HIRSCH, W.-J. ESENS, V. ZAMORA-GUTIERREZ, M. WIKELSKI, AND R. KAYS. 2012. Thieving rodents as substitute dispersers of megafaunal seeds. *Proc. Natl Acad. Sci. USA* 109: 12610–12615.
- JANZEN, D. H. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465–492.
- KANKAM, B. O., AND W. ODURO. 2009. Frugivores and fruit removal of *Antiaris toxicaria* (Moraceae) at Bia Biosphere Reserve, Ghana. *J. Trop. Ecol.* 25: 201.
- KINGDON, J. 2012. The kingdon field guide to African mammals. Bloomsbury Publishing, London.
- KOERNER, S. E., J. R. POULSEN, E. BLANCHARD, J. OKOUI, AND C. J. CLARK. 2016. Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *Journal of Applied Ecology*. In Press.
- MARKHAM, I. 2015. Of Mice and Men in Gabon: Changes in Rodent Communities Associated with Logging and Hunting. Master's Thesis, Duke University. Available at: <http://dukespace.lib.duke.edu/dspace/handle/10161/9607>.
- MORRIS, D. 1962. The behaviour of the green acouchi (*Myoprocta pratti*) with special reference to scatter hoarding. *Proc. Zool. Soc. London* 139: 701–732.
- MOUPELA, C., J.-L. DOUCET, K. DAINOU, N. TAGG, N. BOURLAND, AND C. VERMEULEN. 2013. Dispersal and predation of diaspores of *Coula edulis* Baill. in an evergreen forest of Gabon. *Afr. J. Ecol.* 52: 88–96.
- NYIRAMANA, A., I. MENDOZA, B. KAPLIN, AND P. FORGET. 2011. Evidence for seed dispersal by rodents in tropical montane forest in Africa. *Biotropica* 43: 654–657.
- OKOUI, J., P. POSSO, A. LEPETRE, AND P. SCAPS. 2002. Estimations des densités de populations de macro-mammifères de la Reserve d'Ipassa Makokou (Gabon). *Bull. la Soc. Zool. Fr.* 127: 121–135.
- OKOUI, J., P. POSSO, AND P. SCAPS. 2001. La reserve d'Ipassa: constat d'une surexploitation de la faune. *Canopee* 21: 8–10.
- PAINE, C. E. T., AND H. BECK. 2007. Seed predation by Neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology* 88: 3076–3087.
- POULSEN, J. R., C. J. CLARK, AND T. PALMER. 2013. Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biol. Conserv.* 163: 122–130.
- ROSIN, C., AND J. R. POULSEN (2016). Data from: Telemetric tracking of scatterhoarding and seed fate in a Central African forest. Dryad Digital Repository. doi:10.5061/dryad.91 g52

- SEUFERT, V., B. LINDEN, AND F. FISCHER. 2009. Revealing secondary seed removers: results from camera trapping. *Afr. J. Ecol.* 91: 4–922.
- SMITH, C. C., AND O. J. REICHMAN. 1984. The evolution of food caching by birds and mammals. *Annu. Rev. Ecol. Syst.* 15: 329–351.
- SMYTHE, N. 1978. The natural history of the Central American agouti (*Dasyprocta punctata*) Smithson. Contrib. Zool. 257: 1–52.
- STAPANIAN, M. A., AND C. C. SMITH. 1978. A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*. 59: 884–896.
- TERBORGH, J. 2012. Enemies maintain hyperdiverse tropical forests. *Am. Nat.* 179: 303–314.
- VANDER WALL, S. 1990. Food hoarding in animals. The University of Chicago Press, Chicago, IL.
- VANDER WALL, S., P.-M. FORGET, J. LAMBERT, AND P. HULME. 2005a. Seed Fate Pathways: Filling the Gap Between Parent and Offspring. In P.-M. Forget, J. Lambert, P. Hulme, and S. Vander Wall (Eds.). Seed fate: predation, dispersal and seedling establishment, pp. 1–8. CABI Publishing, New York, NY.
- VANDER WALL, S., K. KUHN, AND M. BECK. 2005b. Seed removal, seed predation, and secondary dispersal. *Ecology* 86: 801–806.
- van VLIET, N., R. NASI, L. EMMONS, F. FEER, P. MBAZZA, AND M. BOURGAREL. 2007. Evidence for the local depletion of bay duiker *Cephalophus dorsalis*, within the Ipassa Man and Biosphere Reserve, north-east Gabon. *Afr. J. Ecol.* 45: 440–443.