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Roads as barriers to seed dispersal by small mammals in a neotropical forest

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Abstract: We sought to answer the question of whether tropical forest roads act as barriers to seed dispersal by small mammals. Ten paired seed stations were placed 100 m apart along the first 2 km of Pipeline Road in Soberanía National Park, Panamá, with each station containing 5 *Astrocaryum standleyanum* and 5 *Attalea butyracea* fruits with intact seeds. An industrial sewing bobbin was attached to each seed to allow movement to be tracked. We observed 154 seed movements; maximum distance moved was 20 m, with a mean of 5.75 m (SD = 5.19). More *A. butyracea* (131) were moved than *A. standleyanum* (23), and removal rates varied among the 10 stations. Although some seeds were moved sufficiently far to have crossed the road, none were, indicating that roads do act as barriers to seed dispersal in neotropical forests and that continued expansion of road networks into tropical forests may threaten biodiversity.

Resumen: Nosotros tratamos de responder a la pregunta de si los caminos en los bosques tropicales actúancomo barreras para la dispersión de semillas por mamíferos pequeños. Se colocaron 10 estaciones pareadas a intervalos de 100 m alo largo de los dos primeros kilómetros del Camino del Oleoducto en el Parque Nacional Soberanía, Panamá.Cada estación contenía cinco frutos de *Astrocaryum standleyanum* y cinco de *Attalea butyracea* con las semillas intactas. Se fijó una bobina de costura industrial a cada semillas para permitir rastrear su movimiento. Observamos 154 movimientos de semillas; la distancia máxima de movimiento fue 20 m, con una media de 5.75 m (DE = 5.19). Hubo más movimientos de *A. butyracea* (131) que de *A. standleyanum* (23) y las tasas de remoción variaron entre las 10 estaciones. Aunque algunas semillas fueron movidas a una distancia suficientemente grande como para poderhaber cruzado el camino, ninguna lo hizo. Esto indica que los caminos sí actúan como barreras para la dispersión de semillas en los bosques neotropicales y que la expansión continua de redes de caminos hacia el interior de los bosques tropicales pueden ser una amenaza para la biodiversidad.

Resumo: Procurou-se responder à questão de saber se as estradas florestais tropicais atuam como barreiras para a dispersão de sementes por pequenos mamíferos. Dez estações pareadas de colheita de sementes foram colocados a uma distância de 100 m ao longo dos primeiros 2 km daestrada Pipeline no Parque Nacional Soberania no Panamá, com cada estação contendo frutos com sementes intactas: 5 de *Astrocaryum standleyanum* e 5 de Attalea *butyracea.* Uma bobina industrial de linha de costura foi presa a cada semente para permitir que o seu movimento pudesse ser rastreado. Observou-se 154 movimentos de sementes sendo a

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distância máxima dos mesmos de 20 m, com uma média de 5,75 m (SD = 5,19). Mais sementes de *A. butyracea* (131) foram movimentadas do que para a *A. standleyanum* (23), e as taxas de remoção variaram entre as 10 estações. Embora algumas sementes tivessem sido transferidas suficientemente longe para ter atravessado a estrada, nenhuma indicou que as estradas tenham agido como barreiras à dispersão de sementes em florestas Neotropicais e que a contínua expansão das redes de estradas em florestas neotropicais possa ameaçar a biodiversidade.

Key words: Central Panama, forest regeneration, *Proechimys semispinosus*, roads, small mammals, seed dispersal.

Introduction

Tropical forests contain the greatest biodiversity on Earth but are also among the most threatened and least understood ecosystems. Sound conservation and management practices of such forests must be based on a thorough understanding of the ecological system (Leigh & Rubinoff 2005), but the general lack of such knowledge has long hindered conservation efforts. Of particular importance is an understanding of the origin and maintenance of tree diversity. While numerous factors are certainly involved in driving and maintaining tropical diversity, recent experimental studies have highlighted the importance of negative feedback imposed by species-specific pathogens in structuring forest communities (Comita *et al.* 2010; Mangan *et al.* 2010). Such studies highlight the importance of seed dispersal in maintaining the high levels of biodiversity in tropical forests (sensu Connell 1971; Janzen 1970).

Although tropical trees employ a wide variety of dispersal mechanisms, a high proportion of them are reliant on animal dispersers (Howe & Smallwood 1982), including small granivorous and frugivorous rodents. These animals may play crucial roles in forest regeneration through their actions as seed dispersers and predators (Adler 1995; Adler & Kestell 1998; Asquith *et al.* 1997; Hoch & Adler 1997; Lambert *et al.* 2005; Struhsaker 1997; Terborgh *et al.* 2001). In fact, studies in both the Old and New World tropics have documented completely-suppressed forest regeneration after disturbance, an effect at least partially attributable to increased small mammal abundance and consequent seed predation (Struhsaker 1997; Terborgh *et al.* 2001). Numerous studies have documented the effects of large-scale disturbance, such as fragmentation and logging, on small mammal communities and seed dispersal (Lambert *et al.* 2003; Lambert *et al.* 2005; Struhsaker 1997; Terborgh *et al.* 2001). However, to date no studies have examined the impacts of smaller-scale disturbances such as road construction in tropical forests. Given the continuing expansion of road networks in many tropical regions, such studies are urgently needed (Laurance 2006; Skole & Tucker 1993).

Studies conducted in temperate forests indicate that even unimproved roads can greatly impact ecosystems by fragmenting habitat, providing sources of mortality, and acting as barriers to animal movement (Arima *et al.* 2005; Forman & Alexander 1998; Spellerberg 1998; Swihart & Slade 1984). Roads that disrupt animal movement can influence density and home range size (Clevenger *et al.* 2003; Marsh *et al.* 2005; McDonald & St. Clair 2004; McGregor *et al.* 2008). Furthermore, roads create edge habitat, which can profoundly affect animal communities (Lovejoy *et al.* 1986).

If tropical small mammals respond to roads in manners similar to their temperate counterparts, then the expansion of road networks in the tropics could disrupt seed dispersal patterns by either changing the movement patterns of small mammals or affecting how and where mammals disperse and cache seeds. Such disruption may limit the ability of seeds to gain access to suitable areas in which to germinate, which in turn may hinder forest regeneration, thereby ultimately affecting biodiversity. In this study, we sought to answer the question of whether tropical forest roads act as barriers to seed dispersal by small mammals.

Materials and methods

The study was conducted along Pipeline Road in Soberanía National Park (9°10´N, 79°45´W), a 22,000-ha tract of tropical moist forest in central Panamá. Pipeline Road runs from southeast to northwest and provides access to second-growth forest that is in various stages of regeneration and patches of old-growth forest. The pipeline and its associated road were constructed during World War II. The road was formerly asphalt but has since degraded to mostly dirt and gravel. Currently, the single lane road (~3m wide) receives periodic maintenance, including grading, and light vehicle and foot traffic (TDL pers obs.). Our study was conducted along the first 2 km of Pipeline Road, at the southern terminus. Forest in this area is mostly early successional (ca. 60 - 100 years old), with canopy heights ranging from ca. 5 - 20 m. This area was selected because younger forests often harbor higher-density small mammal populations than older forests, which would increase the number of seed removal events we could expect (Lambert & Adler 2000) and because such forests are actively regenerating from past widespread disturbances (e.g., logging and pasturage).

Elevation along the road ranges from ca. 40 - 200 m (Karr 1990), and the annual rainfall ranges from a mean of 2188 mm at the southern terminus of the road, where the study was conducted, to 2685 mm at the northern terminus (Windsor 1990). The area is highly seasonal and experiences a pronounced four-month dry season from January through April, during which <10 % of the annual precipitation occurs. The seasonal patterns in rainfall produce distinct patterns in fruit and seed availability (Adler & Lambert 2008; Adler *et al.* 1998). The project was conducted at the start of the rainy season (June & July) in 2009 (55 nights) and 2010 (45 nights), utilizing two species of large-seeded palms (*Astrocaryum standleyanum* (L. H. Bailey) and *Attalea butyracea* (Mutis ex L.f.) Wess. Boer)). *Astrocaryum standleyanum* fruits range in length between 2.5 - 6 cm and 3 - 4.5 cm in diameter, whereas *A. butyracea* fruits are least 4.5 - 8.5 cm long and 3 - 4.5 cm in diameter (Henderson *et al.* 1995). Both species typically fruit when the study was conducted, with *A. standleyanum* fruit production generally peaking slightly earlier than that of *A. butyracea* (Adler & Lambert 2008).

From the beginning of Pipeline Road, we placed two seed-removal stations on either side of the road at ca. 100-m intervals, for a total of ten stations. Stations were placed within the forest approximately 3 m from the edge of the road. Ten fresh ripe fruits (5 *A. standleyanum* and 5 *A. butyracea*) with seeds intact were placed at each station. To each seed, we attached an industrial sewing bobbin by drilling a small hole in one end of the seed, passing a short piece of 22-gauge wire through the seed, and attaching the other end to the bobbin. The loose end of the thread was secured to vegetation. Bobbins contained ca. 200 m of tightly-wound thread that unraveled as the seed was moved, thereby allowing us to view the path of removed seeds in three dimensions (Kilgore *et al.* 2010). Three species of seed-dispersing mammals were common in the study area: the terrestrial rodent *Proechimys semispinosus* (Tomes 1860) (Central American spiny rat), the arboreal/scansorial *Sciurus granatensis* (Humboldt 1811) (red-tailed squirrel) and the terrestrial *Dasyprocta punctata* (Gray 1842) (Central American agouti). On a 5-day cycle, the sites were alternately exclosed using semi-permeable wire exclosures and then exposed. The exclosures allowed access to seeds by smaller mammals (spiny rats and squirrels), while excluding larger mammals (e.g., agoutis). The combination of alternating exclosures and the three-dimensional tracking capabilities of the bobbins allowed us to examine the relative importance of the three main seed-dispersing mammals at the study site.

Seed stations were examined daily, and all overly-ripe, moldy, or removed fruits were replaced. For each removed fruit or seed, we recorded the distance moved, the seed's final location, and the seed's fate (fruit eaten in situ and seed intact, fruit eaten and seed cached in the ground, fruit eaten and seed dropped to the ground, and seed eaten). Seeds that were either cached or dropped were further monitored for tertiary dispersal or predation events.

Statistical analysis was conducted using a full three-way ANOVA. We accounted for species, presence of exclosures, and site, including all interaction terms. Insignificant interactions ($P > 0.05$) were removed, and the analysis was repeated. All analysis was conducted using SAS.

Results and discussion

During the course of the study, fruits were presented for 55 nights in 2009 (six 5-day trials exclosed; five 5-day trials exposed) and 45 nights in 2010 (four 5-day trials exclosed; five 5-day trials exposed) for a total of 10,000 fruit nights (5,000 for *A. standleyanum* and 5,000 *A. butyracea*) where one fruit presented for one night equals 1 fruit night. A total of 154 seeds were moved (23 *A. standleyanum* and 131 *A. butyracea*). None of these seeds were moved across Pipeline Road. Of the 154 removed seeds, 33 were taken into

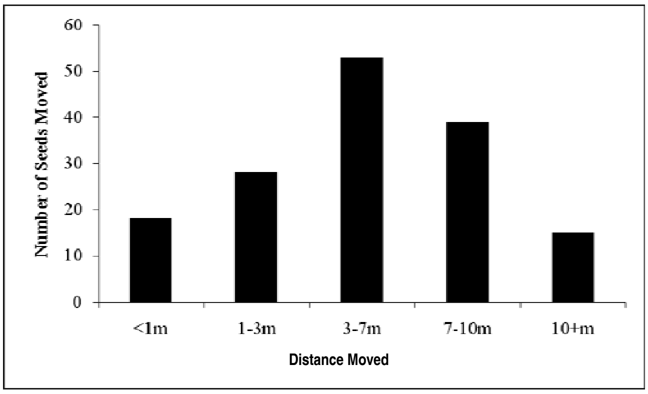

Fig. 1. Number of seeds moved < 1 m, ≤ 1-3 m, ≤ 3-7 m, ≤ 7-10 m and distances greater than 10 m. As stations were set a maximum of 3 m from the edge of the road and the road was approximately 3 m wide, seeds moved 3 m would be able to reach the edge of the road, and those moved ≤ 6 could have crossed the road.

subterranean burrows where germination would not be successful; the remainder of the removed seeds were cached under leaf litter where they could presumably regenerate. The maximum distance moved was 20 m, with a mean distance of 5.75 m (SD = 5.19). More seeds (89 total; 3 *A. stand-leyanum* and 86 *A. butyracea*) were moved in 2010 than in 2009 (65 total, 20 *A. standleyanum* and 45 *A. butyracea*). In addition to the seeds that were moved, 37 total seeds (18 *A. standleyanum* and 19 *A. butyracea*) had their fruit consumed without the seed being removed from its original location. The presence of the exclosures did not affect removal rates (F = 0.30, d.f. = 8, P = 0.11), *A. butyracea* had higher removal rates than *A. standleyanum* (F = 8.71, d.f. = 8, P = 0.0043) and seed removal rates differed among the 10 sites (F = 3.42, d.f. = 8, P = 0.0016). All removed seeds followed paths along the ground, with none being transported into the canopy or subcanopy.

Despite recording 154 total seed movements, including 54 seeds that moved ≥ 7 m farther than the distance across Pipeline Road (Fig. 1), no seeds were moved across the road. These observations are in contrast to our concurrent observations of the key seed-dispersing rodents in the study area. Not only did we frequently observe agoutis crossing the road during the day, but trapping and tracking studies (J. Dittel unpublished data) revealed that *P. semispinosus* also crossed the road at night. These observations indicate that even unimproved, infrequently-travelled roads may act as barriers to seed dispersal and thus may hinder forest regeneration and ultimately pose a threat to biodiversity. The ability of roads to limit seed dispersal could be especially problematic in areas where road expansion leads to habitat degradation and fragmentation through logging, over hunting, and agriculture. In these areas, seeds produced in the few remaining tracts of intact forest may not cross even small barriers to colonize degraded habitat, leading to a gradual but continual loss of biodiversity from the landscape.

The observation that the key seed-dispersing rodents often crossed the road but never carried seeds with them is consistent with road effects in temperate areas, where roads disrupt home ranges, with the road often acting as one boundary of an individual's home range (Clevenger *et al.* 2003; Marsh *et al.* 2005; McDonald & St. Clair 2004; McGregor *et al.* 2008). Because the rodents are moving seeds, often to cache them for later consumption, it follows that they would deposit such seeds within their home ranges. Although the road likely represents habitat that would be inhospitable to seed caching, studies employing similar methods (Kilgore *et al.* 2010) found cache locations to be non-random. Therefore, within the forest seeds are often carried through habitat unsuitable for caching. Furthermore, the lack of cover on the roads represents areas of high predation risk for the seed-dispersing rodents. Thus, while the rodents may be willing to cross the road, they are less likely to do so while burdened with seeds. Indeed, we tracked numerous seeds that moved toward the road, but all of those were dropped by the removal agent at the road's edge, perhaps indicating that the rodent crossed the road after dropping the seed.

In central Panama, smaller spiny rats and squirrels and larger agoutis move and cache seeds (Adler & Kestell 1998; Carvajal & Adler 2008; Flagel *et al.* 2009; Forget & Milleron 1991; Hoch & Adler 1997). However, little is known concerning the relative importance of those two size classes of seed dispersers. We examined relative removal rates by the two size classes by alternating between having seeds under exclosures that excluded agoutis and exposed seeds that allowed access by all three species. Similar removal rates of the exclosed and exposed seeds indicate that spiny rats or squirrels were the primary seed removal agents and both apparently scatter-hoarded seeds. Thus, smaller seed dispersers must be considered in seed-dispersal models. However, it is likely that the relative importance of these species in seed dispersal varies across the landscape. Kilgore *et al.* (2010) used similar methods near our study site and found that *S. granatensis* would frequently remove seeds from the ground and carry them into the canopy or subcanopy. However, all of tracked seeds moved along the ground, with none being brought into the canopy or subcanopy, (Kilgore *et al.* 2010), indicating that in this study *P. semispinosus* was the primary dispersal agent. Carvajal & Adler (2008) found that seed removal by *S. granatensis* was higher in areas of intact forest than forest gaps; as all of our seed stations were in the forest edge along the road, it is possible *S. granatensis* avoided these areas. Removal rates in our study varied among the sites, further indicating that the local abundance of small mammals directly influenced removal rates. Together, these results indicate that the relative importance of various mammalian dispersal agents varies across the landscape.

We also observed higher removal rates for *A. butyracea* than for *A. standleyanum*. Previous studies (Flagel *et al.* 2009; Kilgore *et al.* 2010) also documented more removals for *A. butyracea*. However, those studies did not simultaneously present removal agents with both seeds. Therefore, previous studies suggested that the greater number of *A. butyracea* removals was the result of those fruits tending to be available later in the rainy season when other fruits were less abundant. By contrast, our results indicate that *A. butyracea* is in fact preferred by the small mammals, a result likely attributable to the higher nutritional value and larger size of *A. butyracea* (Henderson *et al.* 1995).

In summary, our results support the findings that small mammals play important roles in tropical systems, acting as seed dispersers and seed predators (Adler 1995; Adler & Kestell 1998; Asquith *et al.* 1997; Hoch & Adler 1997; Lambert *et al.* 2005; Struhsaker 1997; Terborgh *et al.* 2001). Furthermore, our findings suggest that at least in certain microhabitats, smaller rodents such as *P. semispinosus* may play a larger role in dispersal than larger rodents such as *D. punctata.* Most importantly, we found that roads do in fact act as barriers to seed movement because despite documenting 154 seed movements, we observed no seed being dispersed across the road. Thus, expanding road networks into tropical forests could limit seed dispersal and ultimately present a subtle yet potentially significant threat to the long-term maintenance of biodiversity in fragmented landscapes. This effect is particularly important given the patchy and over-dispersed spatial distribution of many species of neotropical trees (Hubbell 1979).

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References

Adler, G. H. 1995. Fruit and seed exploitation by Central American spiny rats, *Proechimys semispinosus*. *Studies on Neotropical Fauna and Environment* **30**: 237-244.

Adler, G. H. & D. W. Kestell. 1998. Fates of neotropical tree seeds influenced by spiny rats (*Proechimys semispinosus*). *Biotropica* **30**: 677-681.

Adler, G. H., S. A. Mangan & T. D. Lambert. 1998. Reproductive phenologies of *Cryosophila warscewiczii* in central Panamá. *Principes* **42**: 185-189.

Adler, G. H. & T. D. Lambert. 2008. Spatial and temporal variation in fruiting phenology of palms in isolated stands. *Plant Species Biology* **23**: 9-17.

Arima, E. Y., R. T. Walker, S. G. Perz & M. Caldas. 2005. Loggers and forest fragmentation: behavioral models of road building in the Amazon Basin. *Annals of the Association of American Geographers* **95**: 525-541.

Asquith, N., S. Wright & M. Clauss. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* **8**: 941-946.

Carvajal, A. & G. H. Adler. 2008. Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in central Panama. *Journal of Tropical Ecology*: **24**: 1-8.

Clevenger, A., B. Chruszcz & K. Gunson. 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biological Conservation* **109:** 15-26.

Comita, L. S., H. C. Muller-Landau, S. Aguilar & S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundance in a tropical tree community. *Science* **329:** 330-332.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. pp. 298-312. *In:* P. J. den Boer & G. R. Gradwell (eds.) *Dynamics of Populations*. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Flagel, D., G. H. Adler & T. D. Lambert. 2009. Influence of seed height on removal rates by rodents in Central Panama. *Mammalia* **72:** 55-56.

Forget, P. -M. & T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* **87**: 596-599.

Forman, R. & L. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology, Evolution and Systematics* **29:** 207-231.

Henderson, A., G. Galeano & R. Bernal. 1995. *Field Guide to the Palms of the Americas*. Princeton Univ. Press, Princeton, NJ.

Hoch, G. A. & G. H. Adler. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). *Journal of Tropical Ecology* **13**: 51-58.

Howe, H. F. & J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**: 201-228.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**: 1299-1309.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104:** 501-528.

Karr, J. R. 1990. The avifauna of Barro Colorado Island and pipeline road. pp. 183-198. *In* : A. H. Gentry (ed.) *Four Neotropical Forests*. Yale Univ. Press, New Haven, CT.

Kilgore, A., T. Lambert & G. H. Adler. 2010. Lianas influence seed and fruit use by rodents in a tropical forest. *Tropical Ecology* **51**: 265-271.

Lambert, T. D. & G. H. Adler. 2000. Microhabitat use by a tropical forest rodent, *Proechymis semispinosus*, in Central Panama. *Journal of Mammalogy* **81**: 70-76.

Lambert, T. D., G. H. Adler, C. M. Riveros, L. Lopez, R. Ascanio & J. Terborgh. 2003. Rodents on tropical land-bridge islands. *Journal of Zoology* **260**: 179-187.

Lambert, T. D., J. R. Malcolm & B. L. Zimmerman. 2005. Effects of mahogany (*Swietenia marcophylla*) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon basin, with implications for conservation. *Forest Ecology and Management* **206:** 381-398.

Laurance, S. G. W. 2006. Rainforest roads and the future of forest-dependent wildlife: A case study of understory birds. pp. 253-268. *In*: W. F. Laurance & C. A. Peres (eds.) *Emerging Threats to Tropical Forests*. The University of Chicago Press, Chicago, IL.

Leigh, E. G. Jr. & I. Rubinoff. 2005. Understanding and conserving tropical diversity: perspectives from Barro Colorado Island. pp. 223-250. *In:* E. Bermingham, C. W. Dick & C. Moritz. (eds.) *Tropical Rainforests: Past, Present and Future*. University of Chicago Press, Chicago IL.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, I. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart & M. B. Hay. 1986. Edge and other effects of isolation on Amazon forest fragments. pp. 257-285. *In*: M. E. Soule (ed.) *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, USA.

Mangan, S, S. Schnitzer, E. Herre, K. Mack, M. Valencia, E. Sanchez & J. Bever. 2010. Negative plant-soil feedback predicts tree species relative abundance in a tropical forest. *Nature* **466**: 752-756.

Marsh, D., G. Milam, N. Gorham & N. Beckman. 2005. Forest roads as partial barriers to terrestrial salamander movement. *Conservation Biology* **19:** 2004-2008.

McDonald, W. & C. St. Clair. 2004. The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. *Oikos* **105:** 397-407.

McGregor, R., D. Bender & L. Fahrig. 2008. Do small mammals avoid roads because of the traffic? *Journal of Applied Ecology* **45**: 117-123.

Skole, D. & C. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* **260**: 1905-1910.

Spellerberg, I. 1998. Ecological effects of road and traffic: a literature review. *Global Ecology and Biogeography Letters* **7**: 317-333.

Struhsaker, T. T. 1997. *Ecology of an African Rain Forest: Logging in Kabale and the Conflict Between Conservation and Exploitation*. University of Florida Press, Gainesville, FL, USA.

Swihart, L. & N. Slade. 1984. Road crossing in

Sigmodon hispidus and *Microtus ochrogaster*. *Journal of Mammalogy* **65**: 357-360.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert & L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294:** 1923-1926.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panama. *Smithsonian Contributions to the Earth Sciences* **29**: 1-145.

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