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# Seed Removal by the Red-Rumped Agouti, *Dasyprocta leporina*, on a Caribbean Island

Benton Taylor

Clemson University, bentonneiltaylor@clemson.edu

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SEED REMOVAL BY THE RED-RUMPED AGOUTI, *Dasyprocta leporina*, ON A  
CARIBBEAN ISLAND

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A Thesis

Presented to

The Graduate School of

Clemson University

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In Partial Fulfillment

of the Requirement for the Degree

MASTER OF SCIENCE

Biological Sciences

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By

Benton Taylor

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Dr. Saara J. DeWalt, Committee Chair

Dr. Kalan Ickes

Dr. Michael Childress

Dr. Pat Gerard

## ABSTRACT

Agoutis are important seed dispersers as well as predators of numerous plant species in Neotropical continental rainforests, but little is known about their role as seed removers (dispersers and predators) on islands. We investigated seed removal of seven rain forest species on the island of Dominica in the Lesser Antilles by the entire seed remover community and specifically by the Red-rumped Agouti, *Dasyprocta leporina*, a scatterhoarding rodent introduced to the island approximately 2500 years ago. We recorded removal rates from 168 experimentally placed seed groups containing a total of 1356 seeds of six canopy tree species and one liana species. Seed groups were either accessible to the entire seed remover community or placed within exclosures designed to exclude agoutis. We found that 47 percent of the seeds were removed after 13 days, with 26 percent of removed seeds being taken by agoutis. Species with smaller seeds were preferentially taken by seed removers other than agoutis, whereas agoutis were responsible for the majority of the removal of the seeds of larger-seeded species. This introduced scatterhoarder clearly plays an important role in determining the movement and fate of seeds in Dominican rain forests, particularly for the largest seeded species that much of the rest of the animal community does not disperse or consume.

## DEDICATION

This thesis is dedicated to Thomas W. and Janet K. Taylor, whose tireless teachings and love of the natural world and its investigation led me to become the scientist that I am today.

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## CHAPTER ONE: LITERATURE REVIEW

### THE INTERACTIONS OF PLANTS AND ANIMALS

Within any ecosystem there exist numerous species occupying various habitats and trophic levels, and inevitably interacting with one another in a variety of different ways. For some species these interactions provide a source of food, for others a source of mortality, but for all species these interactions with the surrounding biota serve as a means of dividing up the resources found within the surrounding ecosystem.

One of the most common and most studied set of species interactions is those that exist between plants and animals. As primary producers of ecosystems, plants often serve as food sources for animals by transforming light energy into useable forms of carbon-based sugars. Thus plants serve as the base point of all useable energy within an ecosystem, and the availability of these plants often drives the type and number of animal species that can thrive in a particular location. Conversely, as animals consume plant material for the sugars it contains, they damage or kill the plants that they eat, which often controls the distributions of these plants and opens up potential space and resources for other competing plant species. In this way, plants and animals largely contribute to each others' success and distributions through the process of herbivory.

Interactions between plants and animals became vastly more diverse with the rise of angiosperms. Angiosperms, the flowering plants, arose early in the Cretaceous period, and diversified within 30 million years to the point that they dominated the species composition of ecosystems across the globe (Feild and Arens 2005). Angiosperms are

unique in that they depend on animals for assistance with a number of life cycle processes. Previous to angiosperm-dominated floras, the majority of interactions between plants and animals consisted of herbivory. With the rise of angiosperms, a new set of interactions between plants and animals was introduced including pollination and seed dispersal. These interactions are thought to be the major cause of the rapid evolution documented during the Eocene of both angiosperms (Herrera 1989) and the animals that interacted with them (Sussman 1991).

The diversification of angiosperms likewise diversified the ways that animals used these plants as resources and the ways that plants use animals to accomplish various life cycle processes. Animals can now use angiosperms as a source of nutrition by consuming leaf and stem pulp, flower material, fruit pulp, and seed material. Fruit and seeds are often richer in high energy sugars and lipids than the leaf and stem pulp, which was the only source of plant material available to animals previous to the emergence of angiosperms. The result of this coevolution of plants and the animals that interact with them is a wide variety of interactions between the two groups including herbivory, granivory, frugivory, nectivory, pollination, and seed dispersal. These interactions are not confined to one animal group but are represented in the natural histories of everything from insects to mammals.

## THE INTERACTIONS OF PLANTS AND MAMMALS

Relationships between mammals and plants have been shown to shape the composition and distribution of both groups in ecosystems worldwide (Coley and Barone

1996, Asquith et al. 1997, Cowan and Tyndale-Biscoe 1997, Ickes et al. 2003, Bergvall and Leimar 2005). Although herbivory is the most common interaction between mammals and the surrounding plant species, mammals also serve as important pollinators (Nassar et al. 1997, Zusi and Hamas 2001, Tschapka et al. 2008), dispersers (Fleming and Heithaus 1981, Forget and Milleron 1991, Williams et al. 2000, DeMattia et al. 2004), and habitat modifiers (Hobbs 1996, Miller *et al.* 2000, Pringle 2008). Given the high diversity of both groups, it is necessary to view any interactions between plants and mammals on an individual basis and in the context of the local community.

In ecosystems from the sub-arctic to the tropics, mammals serve as important herbivores, often controlling the recruitment patterns of the local plant communities (Hobbs 1996, Asquith *et al.* 1997, Forget *et al.* 2000). Because mammals are such a diverse taxonomic group covering a wide range of size classes and natural histories, the relationship between the mammals and plants of a local community can be drastically different depending on which specific species of each group are present. Large herbivorous mammals, such as many ungulates, have been shown to significantly alter the abundance and distribution of plant species in a number of habitats due to both the volume of plant material consumed and their large range sizes (Hobbs 1996). In the temperate and sub-arctic climates of North America, moose (Danell *et al.* 1994) and deer (Cote *et al.* 2004) can drastically change the relative abundances and distributions of local plant species by selectively browsing for the preferred broad-leaved, deciduous species thereby favoring species that are smaller, narrow-leaved, and less palatable. Often though, mammals impact plant community composition not because of their large

individual diets and ranges, but because of high local mammal abundances. Because of their high fecundity, rodents can often reach high population densities and have major effects on the distribution of plant species on the forest floor. Rodents are the main herbivorous mammals throughout the Neotropics. In a long-term study investigating the effects of rodent population densities on the local plant communities, it was shown that in predator-free environments rodents could reach densities 10-100 times greater than normal and have significant effects on seedling and sapling growth and survival (Terborgh *et al.* 2001). Thus, across a wide range of mammal densities and dietary needs, plant species can be profoundly affected by mammalian herbivory.

While herbivory negatively impacts the plant species with which the mammal community interacts, there are a number of plant-mammal relationships that prove beneficial to the plants involved including seed dispersal, habitat modification, and pollination. Bat species throughout the tropics are well known to feed on the nectar and secondarily transfer the pollen of many flowering plants (Heithaus *et al.* 1974, Sazima and Sazima 1978, Nassar *et al.* 1997). Many species of flowering plants depend on bats as their primary pollinators, and entire bat families have anatomical developments indicative of nectar feeding. Although bats are the most well known mammalian pollinators, there are numerous other nonflying mammals that have been shown to serve important roles as pollinators. Arid regions of South Africa are home to a set of plants in the genus *Colchicum* that rely heavily on ground-dwelling rodents for their pollination (Kleizen *et al.* 2008). Also in Africa, large monkeys have been observed pollinating a species of legume, thereby replacing extirpated Lepidoptera as the species' primary

pollinator (Gautierhion and Maisels 1994). Throughout Australia, studies have shown that both nonflying rodents of the Muridae (Cunningham 1991, Goldingay et al. 1991, Carthew and Goldingay 1997) and the typically carnivorous group of Dasyurid marsupials (Goldingay 2000) are significant pollinators of several local tree species. These studies all showed significant decreases in fruit formation in response to the removal of these mammalian pollinators, thus demonstrating that even nonflying mammals can have significant impacts on the pollination and reproduction of plants.

In addition to the positive effects that mammals have on plants as seed dispersers and pollinators, many mammal species serve as habitat engineers, significantly altering the environment in a way that can often facilitate the growth of many plant species. Burrowing rodents across the globe have been cited as substantially altering soil properties resulting in significant changes in plant composition on burrow soil (Ceballos *et al.* 1999, Wesche *et al.* 2007). Even carnivorous mammals can alter plant community structure as it has been shown that soil chemistry and nutrient levels can be significantly altered by the excrement of mammals. The effect of this nutrient deposition can change drastically with the changing diet of the mammal (Crait and Ben-David 2007). Additionally, mammals can modify the environment to facilitate plant growth through the pollination and dispersal of ectomycorrhizal fungi, which facilitate the roots of vascular plants in water and nutrient uptake (Claridge *et al.* 1992, Johnson 1996).

The positive effects of mammals as pollinators and habitat modifiers have been well demonstrated, yet the most common and well studied of the positive interactions between mammals and plants is undoubtedly seed dispersal. Whether through ingestion

and later defecation of eaten seeds or discarding the seeds of eaten fruit, mammals serve as major sources of long-distance seed dispersal for many plant species (Nunez-Iturri and Howe 2007, Stoner et al. 2007). In some cases, plants employ a single mammal species as the only means of seed dispersal, and in such cases the mammal species almost completely determines the success and distribution of the plant that it eats and disperses (Shanahan *et al.* 2001).

Mammalian seed dispersal is most often associated with frugivory as mammals consume all or part of a fruit and the contained seeds and then defecate the viable seeds in another location. More often than not, this passage of seeds through the guts of mammals actually enhances the germination of the seed, and in some cases is requisite (Traveset 1998).

## SCATTERHOARDING

Not all mammalian seed dispersal is based on fruit consumption, but in some cases the seed itself is the source of nutrition for the disperser. One of the most common yet complicated forms of vertebrate seed dispersal is the scatterhoarding behavior exhibited by many species of rodents (Theimer 2005) and some bird species (Fleck and Woolfenden 1997, Vander Wall 2001). Scatterhoarding of seeds by rodents is the burial of seeds in small holes, called caches, for later retrieval and consumption (Vander Wall 1990). Unrecovered seeds are effectively dispersed by these scatterhoarding rodents, and this form of seed dispersal serves as a major source of dispersal for many plant species across the globe, especially in areas of high rodent abundance. The purpose of this

caching behavior from the mammal's perspective is thought to be the protected storage of the seed until the animal returns to consume the seed, but there is an inevitable percentage of these cached seeds that are not recovered from caches, and it is thought that the burial of these seeds may provide a distinct advantage over seeds left open on the forest floor (Vander Wall 1990). Because of the dichotomy of final effects on the seed, scatterhoarders are considered to be simultaneous predators and dispersers of seeds.

Within the Neotropics, rodents are the primary scatterhoarders, and in many cases are the main dispersers of many of the canopy trees (Forget and Milleron 1991). In fact, they are the only known seed dispersers of some canopy species (Hallwachs 1986, Forget 1993, Asquith *et al.* 1999). This relationship between scatterhoarders and seed dispersal/predation is not confined to the tropics. Squirrels are important dispersal agents in temperate Asia (Hayashida 1989), North America (Vanderwall 1993, Steele *et al.* 2005), and Europe (Hulme and Borelli 1999) and Vander Wall (2001) suggests that the continental distribution of nut-bearing seeds following glacial retreat is the result of rodent seed dispersal.

The proportion of seeds that go unrecovered by scatterhoarders is dependent on the ratio of seeds to scatterhoarders. Theimer (2005) suggested that as the food source for these scatterhoarding mammals becomes increasingly scarce, scatterhoarders cache fewer seeds and thereby act as seed predators instead of seed dispersers. This scenario was exhibited by high rodent populations (creating low seed to rodent ratios) on predator-free islands in Gatun Lake, Panama, where seed predation was found to be significantly

higher than on islands where rodent populations were decreased due to predation (Asquith *et al.* 1997).

Scatterhoarder populations are often controlled by food availability rather than predation. In such cases, as the density of conspecific scatterhoarders increases, so does the distance that scatterhoarders disperse seeds before caching them (Lahti *et al.* 1998). This type of experimental evidence has been used to support the hypothesis discussed later in this paper (see Jansen *et al.* 2004, page 16) that super-annual synchronous fruiting (mast fruiting) is a phenological adaptation of trees to satiate seed predator populations and increase the proportion of seeds cached rather than immediately consumed by increasing the seed to scatterhoarder ratio. Jansen (2004) tested this hypothesis with various masting tree species in French Guiana. This study showed that on a per capita basis, seed survival was four and a half times higher during periods of seed abundance as compared to seed poor years (Jansen *et al.* 2004). During years of seed abundance, seed predation was higher, but seeds were cached more often, which more than outweighed the increase in predation. Moore and Swihart (2008) used exclosures and seed tracking over both seed-rich and seed-poor years and showed that seed mortality rates varied from site to site and increased as seed crops decreased - a response they attributed to resource limitation of the scatterhoarders. Thus, the rates at which seeds are cached by scatterhoarders are not only variable from site to site but also are highly variable under different conditions at the same site.

Knowledge of caching rates by scatterhoarders must be complimented with a thorough understanding of the overall benefit that caching provides a seed. A seed may

benefit from caching in two ways: dispersal and protection. Because of the relative high mobility of most scatterhoarding animals, this can be a very effective means of seed dispersal. The distance a seed is carried before being cached is thought to be a tradeoff between the benefit gained by decreasing the chances of other scatterhoarders pilfering the cache and the cost of energy spent dispersing and caching the seed. As a result, caching behavior is influenced by the social aspect of multiple scatterhoarders feeding on seeds under the same tree. In such a scenario, Moore *et al.* (2007) found that dispersal distances doubled from ~10 m to ~20 m and caches were more evenly spread. However, it was also shown that in seed-rich years when scatterhoarders were found in groups, dispersal distances were shorter due to the abundant food supply available, and that under all scenarios larger seeds were dispersed farther distances, presumably because the greater source of nutrition was worth the extra energy invested (Moore *et al.* 2007). It is clear that while many plant-mammal relationships have negative effects on the plant species involved, there are also a variety of interactions between mammals and plants that increase plant fitness, and many of these relationships are critical to the survival of both species involved.

In addition to the many benefits of seed dispersal discussed later in this document, scatterhoarding provides a somewhat unique benefit to the plant of burying the dispersed seed - thereby protecting it from other types of seed predators as well as from pathogens. While the burial of a seed provides protection from other conspecific scatterhoarders (Brewer and Webb 2001), it hides the seed from non-scatterhoarding seed predators as well (Forget *et al.* 1994, Steele *et al.* 2005, Theimer 2005). In many environments,

insects are the main source of seed mortality for many tree species. Both temperate and tropical studies have shown greater than 73% predation of seeds by insects, suggesting that many species may be recruitment-limited by insect seed predation (Greig 1993, Xiao *et al.* 2007). In environments with such high seed mortality due to insect seed predation, protection of seeds from this source of mortality may greatly alter the recruitment patterns of target tree species. In addition to arthropod seed predators, fungal infection can be an important source of seed mortality but below-ground burial of a seed may drastically affect its contact with fungal spores. Finally, it has been suggested that by being cached, a seed is not only provided protection from other seed predators, but by being placed below the soil, is often in a more suitable environment for germination (Vander Wall 1990). Overall it is believed that these benefits to the survival of the seed derived from being cached can often more than make up for the proportion of seeds that scatterhoarders consume, thus creating an overall mutualistic relationship between scatterhoarders and the trees whose seeds they disperse.

## THE COEVOLUTION OF PLANTS AND MAMMALS

Because of these varied and critical interactions between mammals and plants, members of these two taxonomic groups have been co-evolving for millions of years. It is widely accepted that many fleshy-fruited plants have evolved such traits to attract mammalian seed dispersers, and that often mammals develop traits that aid in the consumption of fruits and dispersal of seeds. These relationships are thought to have started in the Tertiary and served as a basis for evolutionary diversification of both plants

and mammals (Tiffney 2004, Eriksson 2008). The products of this co-evolution of plants and mammals can be seen in adaptations ranging from chemical and physical plant defenses (Coley 1983, Coley and Barone 1996) to opposable thumbs in primates (Sussman 1991). It is thought that many of the adaptations exhibited in both groups, such as seed and fruit size in plants and physical dexterities and behavioral characteristics in mammals, evolved simultaneously rather than one after the other (Eriksson 2008). The ability of primates to collect fruits at the end of small branches because of their opposable thumbs (Sussman 1991), the elongated snout and tongue of nectivorous bats (Tschapka *et al.* 2008), and the preferential consumption of large seed sizes by ground rodents (Jansen *et al.* 2004) are all examples of adaptations found in mammals that are believed to be caused by co-evolution with plants. On the other side of the relationship, plants often develop intricate responses to predation from mammals. It is hypothesized that many species of plants that exhibit mast fruiting (super-annual synchronous fruiting of a single species or group of species) do so as a response to seed predation in order to satiate mammalian predators (Jansen *et al.* 2004).

Of all of these varied traits of plants and mammals that have co-evolved, seed size of angiosperms in response to vertebrate, and in large part mammalian, seed dispersal is one of the most widely discussed (Eriksson 2008). Fossil records show that seed size dramatically increased in the early Tertiary period coinciding with an increase in mammalian and avian seed dispersers (Tiffney 2004). These coinciding events, along with the continued correlation of seed size and animal dispersal throughout the fossil

record, provide substantial evidence for the co-evolution of seed size and mammalian seed dispersal.

## FRUIT TYPES AND DISPERSAL IMPLICATIONS

The divergence of seed sizes and increased biotic dispersal during the Tertiary has resulted in two distinct fruit types, fleshy and dry. These two fruit types serve the same purpose - to aid in seed dispersal - but in quite different ways. Dry fruits, typically holding smaller seeds, are mainly adapted for ballistic, wind, or water dispersal. Wind and ballistically dispersed seeds are often smaller in size, facilitating travel of the seed through the air. The most common of these dispersal methods, wind dispersal, relies on large numbers of seeds dispersing relatively long distances to compensate for a high rate of seed mortality due to little protection and nutritional reserves in the seeds. The high seed mortality for these small, dry seeds is counterbalanced by the higher number of seeds produced by each individual plant. Although some dry fruits adhere to the fur of mammals and feathers of birds, biotic seed dispersal is more typical of fleshy fruits.

Fleshy fruits have evolved characteristics to facilitate dispersal by entirely different means than dry fruits. Instead of expending energy producing large numbers of small seeds, fleshy fruited species typically produce a small number of large, well-protected seeds. A large amount of energy is also spent producing fleshy, carbohydrate-rich fruit designed to attract dispersers to either ingest or carry the fruit away before depositing the seed. Thick seed coats and large endosperm are characteristics that allow these large seeds to survive the transportation by biotic dispersers and provide nutrition

for germination, thereby lowering mortality rates for these species. Studies show that large seeds have a significantly higher germination rate than smaller seeds when sustaining greater than 50 percent seed damage from handling by seed predators (Mack 1998), which is an important characteristic for seeds being handled in the mouths or being passed through the digestive tracts of dispersers. After germination, it has been shown that larger initial seed size ( $> 5\text{g}$ ) also allows seedlings to regenerate and produce new leaves after suffering complete herbivory damage (Harms and Dalling 1997). Although there are many advantages of large, biotically dispersed seeds, large-seeded species are largely dependent on this relationship for spread of propagules. This implies that the distribution of large-seeded plant species is often determined by the distribution of their dispersers.

#### CONSEQUENCES OF SEED DISPERSAL

A wide variety of dispersal methods have been documented, each coinciding with specific plant physiological traits, but the reason for seed dispersal is an ecological question that continues to receive debate. Angiosperm seed dispersal is generally thought to take place along two axes: space and time. Spatial dispersal allows seeds to minimize intraspecific competition and for species to spread and colonize new sites. Temporal dispersal allows seeds to lay dormant in soil, often for many years, to wait for optimal conditions for germination.

At the most basic level, the spatial dispersal of seeds serves to move the propagule away from the parent plant. This can serve a number of different purposes

including: (1) reducing competition with both the parent plant and sibling plants, (2) increasing genetic variation at the population level by decreasing the likelihood of pollinating with individuals from the same parent plant once reproductively active, (3) increasing the probability of propagules being dispersed to a micro-site that is favorable for germination and plant growth (Howe and Smallwood 1982), and (4) reducing the negative effects of conspecific density-dependent mortality from host-specific herbivores and pathogens.

The latter of these benefits of spatial seed dispersal was largely popularized as the Janzen-Connell hypothesis, which states that host-specific sources of mortality will have the greatest effect on plants that are either clumped close to the parent plant or clumped close to other sibling plants. The hypothesis terms these as distance-dependent and density-dependent mortality, and suggests that farther seed dispersal can reduce the risk of both of these types of mortality for a juvenile plant (Janzen 1970, Connell 1971). Gilbert *et al.* (1994) provided evidence of the effects of density-dependent stem cankers on a common species of tree on Barro Colorado Island, showing that the distribution of this species favored farther seed dispersal due to the increased rate of infection of individuals in dense conspecific stands. Furthermore, this recruitment and survival based on density-dependent mortality has been shown to increase floral diversity within a community (Harms *et al.* 2000).

As previously noted, spatial dispersal is only one of the two means of angiosperm dispersal, the other being dispersal in time. The presence of a hard seed coat surrounding the seeds of angiosperms allows these seeds to lie dormant in the soil, in what is often

referred to as a seed bank, often for many years. In many species, seed dormancy serves as a strategy by which the seed waits for favorable environmental conditions for germination. This dormancy may enable a species to recover following large-scale environmental changes or catastrophes that reduce or eliminate much of the adult population of the species (Kalisz and McPeck 1993).

The combined effects of spatial and temporal seed dispersal can result in increased genetic variability within a population for a number of reasons. Not only does spatial dispersal potentially decrease inbreeding of a population, but it can also increase genetic variability by increasing gene flow between populations (Young 1996). Seed dispersal is the only means by which plants, as sessile organisms, can spread their genetic material to new sites for cross pollination with other genetically distinct individuals of the same species. Additionally, the seed bank created by temporal dispersal can serve as a valuable store of genetic variability, which may be needed for the species to respond and adapt to future environmental changes (Levin 1990, Vavrek et al. 1991).

## SEED DISPERSAL IN THE TROPICS

Seed dispersal has been shown to be especially important in tropical regions, and much of our evidence for distance- and density-dependent seed and seedling mortality comes from tropical regions (Janzen 1970, Connell 1971). However, some of the most common seed dispersal mechanisms in temperate regions, such as wind dispersal, are

much less common in most tropical forests. This results in the increase of many other forms of seed dispersal, namely animal dispersal, with increasing proximity to the equator.

It has long been noted that there is a general trend towards larger seeds with decreasing latitude, and a number of studies have recently quantified this at a global scale. Moles and Westoby (2003) used global data in a meta-analysis showing that average seed mass drops by an order of magnitude for every increase in 23 degrees of latitude. This relationship was later refined by Moles *et al.* (2007) when it was shown that this relationship between latitude and seed mass is not a linear one, but exhibits a sharp seven-fold drop in mean seed mass just outside the tropics.

Many reasons for this trend towards larger seeds in tropical regions have been proposed, and the literature on the subject has reached little consensus. Major factors driving seed mass are proposed to be growth form, precipitation, specific leaf area, and seedling metabolic requirements, among others. Numerous studies have shown that much of the increase in average seed mass at the tropics is due to the fact that there is a much higher percentage of woody plants in this region of the globe (Moles *et al.* 2005a, Moles *et al.* 2007), with the idea that woody plant species are more likely to produce larger seeds (Moles *et al.* 2005b). However, Lord *et al.* (1997) showed that the increase in mean seed mass with proximity to the tropics exists regardless of growth habit and proposed that this phenomenon is likely developed in response to the high metabolic requirements of seedlings in the dark understories of tropical forests. An analysis of seedling survival across latitudinal gradients and its relationship to seed mass concluded

that there is no correlation between seed mass and the ability of a species to gain a particular level of seedling survivorship (Moles *et al.* 2004).

Whatever the mechanism for creating the abundance of large seeds in tropical regions, the result is that a high percentage of tropical plant species employ vertebrates as a means of seed dispersal. Indeed it has been shown that throughout the tropics larger seeds are most often dispersed by vertebrates, namely mammals and birds (Hammond and Brown 1995). In fact, on a regional scale Almeida-Neto (2008) showed that fruit and seed size corresponded positively to the relative importance of vertebrates as seed dispersers. Howe & Smallwood (1981) went as far as to state that the majority of woody plants in tropical regions use vertebrates as their primary means of seed dispersal.

This high reliance on vertebrates for seed dispersal in tropical regions makes studies investigating the distributions, densities, and dispersal capabilities of tropical vertebrates especially important. If higher rates of seed and seedling mortality in the tropics do, in fact, create a great need for seed dispersal in this region as above-mentioned studies suggest, and the majority of seed dispersal in this region occurs via vertebrates, clearly the interaction between these two groups is an important topic. High diversity of both woody plants and animals in tropical rainforests creates a system with a variety of dispersers utilizing many different dispersal techniques to disperse a wide variety of fruit types. This makes it important to investigate each pairing of plant and disperser to fully understand the role that seed dispersal has on the distributions of both groups.

## BIOGEOGRAPHY OF TROPICAL ISLANDS

It is widely known that tropical rainforests are some of the most diverse ecosystems on the planet, but it is important to note that not all tropical rainforests are created equal. Mechanisms such as high speciation rates (Jablonski *et al.* 2006) and increased growing season (Wiens *et al.* 2006), among others, have been proposed to affect diversity in tropical regions. However, at the most basic level, the number of species present at any given location is a product of immigration, speciation, and extinction, and these factors can vary widely from one location to another within the tropics.

The biogeography (the positioning of living things) of islands has received much attention dating back to the writings of Darwin (1889) and Wallace (Wallace 1906). However much of our current ideas regarding the presence and absence of species on islands stems from a book written in the middle part of the twentieth century, MacArthur and Wilson's The Theory of Island Biogeography (1967). This book theorizes the major factors determining the number of species present on an island and the turnover rate of species on the island to be the opposing rates of immigration and extinction. The authors go on to suggest that these rates of immigration and extinction are largely determined by the size of the island and the proximity of the island to a (mainland) population source. Thus, the proximity of the island to the mainland (and to a lesser degree, island size) determines how easily species can immigrate to the island, and the size of the island determines the rate of extinction on the island. MacArthur and Wilson go on to propose

that the number of species present on an island is the point of equilibrium between these opposing forces of immigration and extinction.

As the size and isolation of an island are the major factors determining extinction and immigration rates on the island, they are thus the major factors controlling the number of species present on the island. The farther an island is from a mainland population source, the harder it will be for species to immigrate to the island from that mainland source. Indeed it has been suggested in the literature that for plants, long distance seed dispersal is one of the most crucial and understudied factors in determining the colonization of islands (Cain *et al.* 2000). While MacArthur and Wilson's theory assumes that all species have equal dispersal abilities and thus an equal chance of immigrating to an island, in practice this is of course not the case. For plants with seeds dispersed by various vectors, a species' ability to immigrate to an island relies heavily if not completely on the ability of the dispersal vector to successfully transfer the seed from the source population to the island. For animals, often only species with the ability to traverse large amounts of water, such as migratory birds and semi-aquatic species, are found on very isolated islands. Thus for a plant that is typically vertebrate dispersed, it is likely reliant on a small number of potential dispersers that are capable of reaching isolated islands for its long-distance dispersal to the island. Additionally, once established on the island, plant dispersal vectors may be limited to the number of vertebrate species that have been able to successfully immigrate to the island as well.

The number of species present on an island is the product of a number of factors as outlined above, and the type of species present on an island is an even more complex

issue. Factors such as resource availability on the island, prevailing wind patterns, and source population diversity also likely affect the number and type of species that can colonize an island. While it has been shown that immigration rates are actually lower to tropical islands than islands in temperate regions, overall diversity of species in source populations in tropical regions is sufficiently greater than source populations in temperate regions to result in a higher number of species immigrating to tropical islands (Diamond 1971).

#### ISLANDS OF THE LESSER ANTILLEAN ARCHIPELAGO

The Lesser Antilles is a string of volcanic islands stretching from Puerto Rico southward toward the eastern coast of Venezuela forming the partition between the Caribbean Sea and the Atlantic Ocean. This archipelago is made up of thousands of islands, reefs, and keys, most of which are of volcanic formation resulting from the subduction of the North American tectonic plate under the Caribbean tectonic plate. Volcanic activity forming the string of islands is thought to have begun approximately 40 million years ago (Morris *et al.* 1990). It is important to note that the volcanic formation of the islands means that these landmasses began void of terrestrial life and all of the species present today had to immigrate to the island. This differs from continental islands that detach from the mainland and thus start their insular existence with a preexisting suite of species.

The Caribbean region is prone to large-scale disturbances, often in the form of violent hurricanes. Significant hurricanes pass through the Lesser Antilles on an annual

to biannual basis (Elsner *et al.* 1999). These hurricanes have been shown to have significant impacts on both the flora (Tanner *et al.* 1991, Wen *et al.* 2008) and fauna (Willig and Camilo 1991, Vilella and Fogarty 2005, Tossas 2006) of the islands that they encounter with the effects often lasting decades. Frequent hurricane activity in the region potentially affects both the rates of extinction on these islands from large-scale damage as well as immigration rates as high winds may aid in long-distance dispersal to Lesser Antillean islands. Thus this type of frequent large scale disturbance is thought to have significant effects on the number and type of species that inhabit the islands of this region (Tanner *et al.* 1991).

This effect of regular hurricane activity combined with the fact that the Lesser Antilles creates a string of islands that form somewhat of a chain from the coast of South America creates a unique scenario of semi-connected, yet relatively isolated oceanic islands with experiencing heavy disturbance activity. All of these factors together shape the biotic communities present on these islands.

#### DOMINICA, WEST INDIES

Dominica (15°25'N, 61°20'W) is approximately 724 km<sup>2</sup> in area, with a population of approximately 72,000 people, most of whom are descendents of African slaves and Amerindian natives. Created by volcanic activity resulting from the subduction of the North American plate under the Caribbean plate (Lindsay *et al.* 2003), the island of Dominica has had a violent geologic past, which has played a significant role in the biota present on the island. Not only have species present on Dominica

successfully disperse to an oceanic island, but they also have survived the somewhat frequent large scale geologic disturbances that mark Dominica's history such as volcanic eruptions, earthquakes, and flank collapses (Lindsay *et al.* 2003, Samper *et al.* 2008). Moreover, because of its geographic placement, the island experiences large catastrophic hurricane damage at a frequency of approximately every century.

Mammals native to the island are restricted to approximately 12 bat species (Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Vespertilionidae, Molossidae). Non-volant mammal species, including agouti (*Dasyprocta leporina*), opossum (*Didelphis marsupialis*), rats and mice (*Mus musculus*, *Rattus rattus*, *Rattus norvegicus*), and wild pigs (*Sus scrofa*) were introduced either intentionally or unintentionally at various times during the island's human inhabitation. The introduction of the Red-rumped Agouti (*D. leporina*) dates approximately 2500 years b.p. when the Kalinago people brought the species to the island primarily as a food source (Wing 2001). Stemming from its original reason for introduction, *D. leporina* has received constant hunting pressure from humans throughout its history on Dominica, but game hunting of agoutis is now seasonally regulated by the government. The only other predator of *D. leporina* on the island is the boa (*Boa constrictor nebulosus*), which is also hunted.

#### DASYPROCTA LEPORINA

Agoutis are a widespread group of medium-sized (5-12 kg) rodents of the genus *Dasyprocta*, which are found from Mexico to Argentina in a variety of habitat types (Emmons and Reid 2008). The common name of agouti is often confused with the genus

name for the Caviomorph rodent, *Agouti paca*, which is similar in look and ecological role, but which is smaller and stems from a different phylogenetic origin (Eisenberg and Redford 2000). Native to Brazil, much of northwestern South America, and parts of lower Central America, *D. leporina* is a common species throughout its native and introduced (many of the Lesser Antillean islands) ranges (Eisenberg and Redford 2000).

There is disagreement as to whether agoutis are nocturnal or diurnal, but consensus is growing that they are most active foragers at dawn and dusk (Silvius and Fragoso 2003). While occasionally seen in small groups of up to a dozen individuals, agoutis most often forage solitarily or with one mate (Dubost 1988) either in rainforest interior or along forest edge habitat. Estimates on the home-range sizes of *D. leporina* vary from 3 to 8.5 hectares, typically containing several stands of fruit trees and numerous suitable resting sites (Eisenberg and Redford 2000, Silvius and Fragoso 2003). These home ranges are often centered around particularly fecund trees (Aliaga-Rossel *et al.* 2008) and home range sizes decrease dramatically when large numbers of fruit trees are present in a particular area (Jorge and Peres 2005). While agoutis typically sleep in hollow logs and stumps, they do not often habituate to one specific home site, but are semi-nomadic throughout their home range (Aliaga-Rossel *et al.* 2008).

When foraging, *D. leporina* feeds primarily on fruit pulp and seed material, gaining supplementary nutrition from leaves, young stem fiber, and animal matter (Henry 1999). Plant families that agoutis primarily feed on include Fabaceae, Palmae, Sapotaceae, Chrysobalanaceae, Myristicaceae, and Meliaceae (Hallwachs 1986, Forget and Milleron 1991, Peres and Baider 1997, Brewer and Rejmanek 1999, Wenny 1999).

Agoutis are considered primarily to be scatterhoarding rodents, and much of the literature that exists on this genus involves testing their role as scatterhoarders, yet stomach analyses show that these rodents are primarily frugivorous (consuming fruit pulp) for much of the year when ripe fruit is abundant on the forest floor (Silvius and Fragoso 2003). However, the diet of *D. leporina* changes considerably across seasons and with changes in fruit availability (Dubost 1988, Henry 1999, Silvius and Fragoso 2003, Dubost and Henry 2006), with data showing a swing from 92 percent fruit consumption in the height of the wet season to 76 percent seed consumption during months of fruit scarcity (Henry 1999). As fruit becomes scarce, agoutis may often feed on insect larvae found inside the rotting endocarp of fruit on the forest floor (Silvius 2002), which provides further evidence that as ripe fruit and seeds become scarce during dry season months, agoutis often exploit a wide variety of supplemental nutrition (Henry 1999, Silvius and Fragoso 2003, Dubost and Henry 2006).

*Dasyprocta leporina* encounters significant competition with a wide variety of frugivorous and granivorous rodents and birds present throughout its native range. Natural predators consist mainly of predatory cats such as puma, jaguar, and ocelot, but agoutis have also been known to fall prey to large vipers and constrictors (Aliaga-Rossel *personal communication*). Local hunting of agoutis occurs throughout the Neotropics, and while this is not seen as a threat to the overall health of agouti populations, studies have shown that seedling recruitment can be significantly affected by the absence of ground-dwelling mammals such as agoutis in localized areas of intense hunting

(Beckman and Muller-Landau 2007, Forget and Jansen 2007, Stoner et al. 2007, Wright et al. 2007).

## FOCAL PLANT SPECIES

The research presented in chapter two of this document used the seeds of six rainforest tree species and one rainforest liana to investigate seed removal by agoutis and the rest of the seed-remover community present on the island of Dominica. Study species were selected based on local availability and seed size. Seeds had to be sufficiently large to be relocated numerous days after placement on the open forest floor and sufficiently abundant to provide seeds for the numerous replicate seed removal piles used in this study. Average seed masses ranged from 1.9 to 21.4 g, providing a large gradient of seed sizes, the smallest of which are easily within the handling capabilities of most of the vertebrate seed remover community while the largest of which likely exceed the handling capabilities of all but the largest seed removers on Dominica, such as agoutis.

*Connarus grandifolius*: A rainforest canopy liana in the Connaraceae family, *C. grandifolius* (Planch) is a Lesser Antillean endemic. This species is found somewhat commonly on the island of Dominica and is also represented in Guadeloupe, Martinique, and Saint Kitts. Vegetatively, *C. grandifolius* has compound, alternate leaves with relatively large leaflets and grows via twining. Single fruits are crescent shaped and maroon in color producing a single black seed with an average mass of 3.13 g. Fruits are dry and dehiscent with the seed being connected to the fruit via a fleshy aril attached to

one end of the seed. Aril flesh is bright orange in color and often detaches from the fruit upon maturity, dropping the seed and aril together.

*Dussia martinicensis*: This is one of two species in this study in the family Fabaceae. *Dussia martinicensis* (Krug & Urban) is found in Dominica, Guadeloupe, Martinique, Saint Vincent, and Saint Lucia in the Lesser Antilles, and in continental rainforests of northwest South America and Central America. This is a large canopy tree with compound, alternate leaves. *D. martinicensis* produces purple flowers which mature into large, dull orange dehiscent fruits containing one to two large seeds. Seeds are green in color and average 21.4 g in mass. A bright orange fleshy aril completely encases each seed individually and falls to the ground with the seed upon fruit maturation.

*Sterculia caribaea*: *Sterculia caribaea* (R. Br.) is extremely common in Dominican rainforests, and is a Lesser Antillean endemic found on Guadeloupe, Martinique, Montserrat, Saint Lucia, and Saint Vincent. This is one of the largest canopy trees in Dominican rainforests producing simple, alternate leaves, which are typically large and palmately lobed. Flowers are small and white, fruits are large, dry, and dehiscent. Fruits are radially arranged on infructescences typically containing three to eight fruits. Each fruit is a follicle made up of a thick wall that splits at maturation dropping three to ten black seeds averaging 2.7 g in mass. No aril is produced by *Sterculia caribaea* but the inside of each fruit is lined with small, clear urticating hairs which easily dislodge when touched, but which are not present on the seeds themselves.

*Swartzia caribaea*: This endemic of the Lesser Antilles is locally common in the lower montane rainforests of Dominica, Guadeloupe, and Saint Lucia. A member of the

family Fabaceae, *Swartzia caribaea* (Grisebach) reaches a much smaller maximum height than most of the other tree species in this study. Leaves of this species are compound and alternate, and flowers are white. Its dehiscent fruits are bright orange and exhibit a smooth, waxy coating. Fruits typically hold one to two seeds (although when a fruit is double-seeded, each seed is half the size of a normal seed) weighing an average of 11.1 g. Each black seed is attached to the fruit via a white, fleshy aril at one end of the seed, which typically detaches from the fruit upon maturity and falls to the ground along with the seed.

*Tovomita plumieri*: A common tree of the rainforests of Dominica, Guadeloupe, Martinique, and Saint Lucia, this species' elevational range extends beyond many of those used in this study to encompass upper montane and cloud forests habitats. A Lesser Antillean endemic, *T. plumieri* (Grisebach) is a member of the Clusiaceae. This species has large, simple, opposite leaves and is easily identifiable by its stilt roots and its bright yellow sap. The fruits of *T. plumieri* are dark maroon in color and separated into five sections, each of which rolls backwards when dehiscing to reveal one to five seeds weighing 4.9 g each. Each individual light brown seed is covered in a bright orange aril, much like that of *D. martinicensis*. This aril does not connect the seed to the fruit, but rather completely surrounds the rather oblong seed, falling intact to the ground.

*Trichilia septentrionalis*: Of all of the species used in this study, *T. septentrionalis* (C. Dc.) has one of the largest geographical distributions, which covers most of Northern South America, Central America, and many islands in the Caribbean including Dominica, Guadeloupe, Martinique, and Saint Vincent. Notably, it is absent from Saint Lucia,

which typically shares a large number of species with Dominica. A member of the family Meliaceae, *T. septentrionalis* is a rainforest canopy tree with compound, alternate leaves with large leaflets. The fruits of this species are single, dry, dehiscent fruits, which are dull brown in color and separate into three sections when dehiscing. Interior to the fruit is a single seed weighing 1.94 g, which is covered in a relatively thick, fleshy, bright-maroon aril. This aril material completely surrounds the seed and is attached to the seed coat quite well. Once the ripe fruit has completely dehisced, the seed and aril material fall to the ground intact.

*Turpinia occidentalis*: This member of the Staphyleaceae family also has a relatively wide geographical distribution being found from the northern parts of South America, throughout Central America, and all the way into Mexico. In the Caribbean, *T. occidentalis* (Sw. Don.) is found on Dominica, Grenada, Guadeloupe, Martinique, Saint Lucia, and Saint Vincent, but is locally rare on many of these islands, including Dominica. Local common names include bois lat, bois pilor, and bwa pilowi, of which the first is suggestive that the species was once used as material for roofs. This species is a rainforest tree with compound, opposite leaves and fruits that are born in clusters at the end of branches. *T. occidentalis* produces round green fruits containing one to three seeds which lack aril material and are released upon ripening.

## CHAPTER TWO: RESEARCH MANUSCRIPT

### INTRODUCTION

The relationship between plants and animals that disperse their seeds is often a dynamic one, with animals driving plant abundances and spatial distributions via dispersal patterns (Crawley 2000, Nathan and Muller-Landau 2000) and plants contributing to disperser distribution and abundance via local food availability (Jorge and Peres 2005). For most tropical plants, vertebrates are the primary seed dispersers (Howe and Smallwood 1981), and in many cases are thought to largely determine the distributions of the species they disperse (Morales and Carlo 2006). Within the Neotropics, an important group of vertebrate dispersers is the ground-dwelling caviomorph rodents, including the *Dasyproctidae*, of which acouchies, pacas, and agoutis are members (Mckenna and Bell 1997). In continental Neotropical rainforests, agoutis (*Dasyprocta* spp.) are the main dispersers of numerous plant species (Forget 1992, Peres *et al.* 1997, Guimaraes *et al.* 2005, Galetti *et al.* 2006) and are the only known dispersers of many larger-seeded species (Hallwachs 1986, Asquith *et al.* 1999). However, their importance as dispersal agents in rainforests of volcanic islands is unknown.

Agoutis are secondary seed dispersers – moving seeds from the forest floor where they are deposited following primary dispersal (Chambers and Macmahon 1994). They eat some seeds on site but, through a process called scatterhoarding, move other seeds to shallow burial sites, called caches, for storage until later consumption. In part because the time to germination is short for most seeds in the tropics (Farnsworth 2000), a portion of cached seeds will inevitably go unrecovered. Removal of a seed from a spot on the

forest floor by an agouti can therefore indicate that the seed was predated or dispersed. Scatterhoarding can be an effective means of seed dispersal because agoutis are highly mobile and disperse many seeds well away from the maternal plant and seed burial provides some protection from other seed predators and pathogens, leading to higher germination of cached vs. uncached seeds (Asquith *et al.* 1997, Hallwachs 1986, Vander Wall 1990).

Beginning several thousand years ago, several species that disperse or consume seeds (henceforth: seed removers) were introduced to Dominica, a small volcanic island in the center of the Lesser Antilles in the Caribbean Sea. The Red-rumped Agouti (*Dasyprocta leporina*), opossum (*Didelphis marsupialis*), rats and mice (*Mus musculus*, *Rattus rattus*, *Rattus norvegicus*), and wild pig (*Sus scrofa*) were added to a small suite of native seed removers. Only several small bird species, one species of large pigeon (*Columba squamosa*), a land crab (*Guinotia dentate*), and four species of frugivorous bats (*Brachyphylla cavernarum*, *Ardops nichollsi*, *Artibeus jamaicensis*, *Sturnira lilium*) are seed dispersers native to Dominica. All of the introduced species are secondary dispersers, but only land crabs are native secondary dispersers.

Preferences for particular species of seeds by seed removers and the proportion of seeds that are predated versus dispersed are driven by several factors including size and density of the seed remover as well as size and availability of the seeds. A seed remover's size and the maximum size of seed they commonly remove are positively correlated (Munoz and Bonal 2008), although even large-seed removers will remove small seeds resulting in smaller-seeded species being dispersed by a more diverse set of

dispersers (Wheelwright 1985, Tamura and Hayashi 2008). Scatterhoarders tend to prefer caching large seeds (Jansen *et al.* 2004, Vander Wall 2010) because the energy gain of caching a few large seeds is higher than that of caching many small seeds (Stapanian and Smith 1978). Thus, larger scatterhoarders are more likely to be dispersers of large seeds. Scatterhoarder densities have been shown to differ significantly between forest interiors and forest edges with lower abundance of smaller scatterhoarding species on forest edges than interiors (Jorge 2008). Scatterhoarder densities can affect both the number of seeds removed (Li and Zhang 2007) and the percentage of seeds dispersed versus predated (Jorge and Howe 2009). For most types of seed removers, seed removal is highest when seed abundance is high (Blendinger *et al.* 2008, Pizo and Almeida-Neto 2009); however, there is little consensus for the effect of seed availability on removal for scatterhoarders (Theimer 2005), with studies showing both increased (Carvajal and Adler 2008) and decreased (Li and Zhang 2007) seed removal in response to high seed availability. There is a general agreement in the literature, however, that high seed abundance generally increases scatterhoarders' tendency to act as dispersers rather than seed predators (Vander Wall 2002, Jansen *et al.* 2004, Li and Zhang 2007, Zhang *et al.* 2008, Vander Wall 2010).

We investigated seed removal (predation and dispersal) in rainforests of Dominica for seven rainforest species ranging in seed mass between 1.9 and 21.4 g. In particular, we were interested in the extent of seed removal by agoutis, which are known to be important seed removers of continental rainforest species, relative to other seed removers. We placed seeds on the forest floor at forest edge and interior sites in agouti exclosures or

open areas to address the following questions: 1) what proportion of seeds lying on the forest floor is removed by the seed remover community? 2) how much of the removal can be attributed to agoutis? 3) do agoutis and the rest of the seed remover community preferentially remove seeds of particular plant species? 4) if so, are the preferences related to seed size or seed availability, as inferred by conspecific adult density? and 5) is the proportion of seeds removed different on the forest edge where agoutis and other seed removers may be at different densities than in the forest interior?

It is important to note that this study was designed to examine the removal of seeds from the forest floor, not the final fates of these seeds once removed. Final seed fates would allow us to determine the proportion of seeds dispersed vs. predated (Forget and Wenny 2005), but distinguishing between these two fates was beyond the scope of this study. There is a growing consensus that agoutis have a positive net effect on the recruitment of large-seeded plants (Vander Wall 1990, Brewer and Rejmanek 1999, Vander Wall 2001, Jansen et al. 2004, Tuck Haugaasen et al. 2010); therefore, we expect that seed removal attributed to agoutis on Dominica indicates a positive, but currently unquantifiable, effect on plant species.

## METHODS

STUDY SITE.—The island of Dominica (15°25'N, 61°20'W) encompasses 724 km<sup>2</sup> and lies at the center of the Lesser Antillean archipelago, 560 km north of the coast of Venezuela (Fig. 1). The volcanic activity that created the island is thought to have begun 5-15 mya (Maury *et al.* 1990). Since its formation, Dominica has experienced numerous

large-scale volcanic eruptions (Sigurdsson and Carey 1981) as well as a regular regime of hurricane damage (Tanner *et al.* 1991), both of which have undoubtedly influenced the biota present on the island. Dominican forests have low tree diversity compared to continental Neotropical rainforests; Fisher's  $\alpha$  diversity of trees  $\geq 10$  cm in diameter is 9.8 for Dominican rainforests (K. Ickes and S. J. DeWalt, unpublished data) as compared to 41.9 at La Selva, Costa Rica (Lieberman and Milton 1987), 37.7 on Barro Colorado Island, Panama (Leigh 1999), and 89.5 at Cocha Cashu, Peru (Gentry 1988).

DASYPROCTA LEPORINA. — *Dasyprocta leporina*, the Red-rumped or Brazilian Agouti, is common throughout its native range, which includes Brazil, much of northwestern South America, and parts of lower Central America. This species is an important seed disperser and predator across its range (Eisenberg and Redford 2000). *Dasyprocta leporina* is thought to have been introduced to Dominica by the Kalinago people approximately 2500 ybp from northwestern South America (Wing 2001). *Dasyprocta leporina* has an average body size of 4.45 kg and home-range size of 3 to 8.5 ha in continental rainforests (Eisenberg and Redford 2000, Silvius and Fragoso 2003), but the home-range size can vary dramatically depending on local food availability (Jorge and Peres 2005). Agoutis are a common food source for predatory cats, such as ocelots (*Leopardus pardalis*) and puma (*Puma concolor*), in continental rainforests, where more than 50 percent of agouti mortality may be attributed to these predators (Aliaga-Rossel *et al.* 2006). The only predators of agoutis in Dominica are humans and the native boa constrictor (*Boa constrictor nebulosus*; E. Aliaga-Rossel, personal communication).

PERCENT SEED REMOVAL. —We measured proportion of seed removal from the forest floor for the island's entire disperser community and specifically agoutis for six rainforest tree and one liana species (Table 1). All seeds were collected from the forest floor or from ripe fruit on live branches, and arils were removed to standardize the presentation of seeds. To determine average seed mass and size per species, at least 30 seeds of each species were individually weighed and measured for length and width.

Transects were established across three regions of Dominica: northeast (NE), northwest (NW), and southwest (SW; Fig. 1). The three regions are somewhat geographically and environmentally distinct from one another (K. Ickes and S. J. DeWalt, unpublished data), so we accounted for the influence that regional differences might have on seed removal patterns by distributing our transects across these regions. We investigated whether seed removal differed between forest edge and interior by comparing removal between transects placed in the forest interior (three in each study region) and transects adjacent and parallel to the forest edge (one each in the NE and SW and two in the NW). Interior transects were oriented on a random trajectory, excluding orientations prohibited by terrain, away from the forest edge to ensure that all stations on interior transects were > 250 m from the forest edge.

Each transect measured 250 m in length and comprised six stations spaced 50 m apart. Each station included one control seed group randomly placed 5 m to the left or right of the transect on the open forest floor and one treatment seed group placed 5 m to the other side of the transect within an agouti enclosure. This 10 m separation of seed

groups at each station doubles the conservative estimate of olfactory detection of seeds by agoutis made by Aliaga-Rossel *et al.* (2008). Seeds were placed into groups on the forest floor within 10 cm x 10 cm areas. Each group of seeds consisted of nine seeds: one of each of the species listed in Table 1 with the exception of *Trichilia septentrionalis*, for which there were three seeds per group due to the abundance of seeds collected for this species. The results of a pilot study conducted in the summer of 2008 investigating possible behavioral effects of our experimental methods showed that seed removal was 35 percent higher from areas cleared of leaf litter than from the undisturbed forest floor (B. Taylor, unpublished data). To mimic conditions of natural seed removal, leaf litter was therefore not removed from sites of seed placement in this study. Seeds were checked 3, 6, and 13 days after placement. On day 13, each remaining seed was visually examined for damage due to fungi or insects and for rotting.

Exclosures were designed to exclude *D. leporina*, which does not substantially jump, climb, or burrow. Exclosures were constructed of galvanized wire mesh set up in a 1 m x 1 m fence measuring 80-cm tall with an open top and a 7-cm space between the bottom of the mesh and the ground. Similar design and dimensions were used to exclude agoutis in a seed predation study in Peru (Paine and Beck 2007). The open top allowed access to avian, arboreal, and climbing seed removers, and the space between the bottom of the exclosure and the ground allowed access to small, ground-dwelling seed removers, such as crabs, mice, and rats. Opossums are similar in size to agoutis and may have been prevented from entering under the mesh, but opossums could have gained access to seeds in the exclosures by climbing. In addition, they do not normally consume seeds; seed

dispersal by opossums is a by-product of fruit consumption (Caceres & Monteiro-Filho 2001). Thus, it is unlikely that opossums were significant removers of our study species, which all have dry, dehiscent fruits that would not be consumed by them. The only other species that might have been excluded by the agouti exclosures was *Sus scrofa*.

Although pigs are present on the island, neither pigs nor pig activity was seen near our study sites, suggesting that the seed removal of rainforest species by them is negligible.

We considered the possibility that seed removers that had access to seeds within exclosures were deterred from visiting them simply because of the presence of the exclosure fencing. To test for this possible deterrence, an exclosure was erected 1.5 m above one control group of seeds in each transect. This height was sufficient to allow all possible seed removers full access to the seeds while still presenting the exclosure as a possible deterrent. A least squares means contrast showed no significant difference in removal between the types of control treatments ( $F_{5,521} = 0.93$ ,  $P = 0.33$ ), suggesting that the presence of the fencing around exclosures did not significantly deter seed removers other than *D. leporina* from removing seeds.

To determine whether adult plant density was related to seed removal, we estimated the density of adults of each species for each of the three study regions of the island using 17 0.25-ha permanent vegetation plots in which all trees  $\geq 1$  cm and lianas  $\geq 0.5$  cm diameter have been measured, tagged, and identified (K. Ickes and S.J. DeWalt, unpublished data). Six permanent plots are located in the NE, four in the NW, and seven in the SW. We calculated the density of trees  $\geq 10$  cm and lianas  $\geq 2$  cm diameter at

breast height, as only individuals above these size thresholds are likely to be reproductive.

ANALYSES. —All statistical analyses were performed using the GLIMMIX procedure in SAS v.9.2 (SAS Institute Inc., Cary, NC), specifying a binomial error distribution and logit link. A model was used to test whether the probability of seed removal depended on the main fixed effects of treatment (control or enclosure), species of seed, and position (forest edge or interior) and interaction effects of treatment\*position and treatment\*species. The analysis also accounted for the random effects of region and transect. We tested for the effect of treatment for each species using the SLICE option in the LSMEANS statement of PROC GLIMMIX. A second model was used to test the effect of adult tree density on the probability of seed removal. Adult tree density was defined as the density (individuals/ha) of conspecific adults for each species in each region. This model used the fixed effects of treatment and adult density within a region as well as the interaction between the two, and also used region and transect as random effects. A third model was used to determine the relationship between seed mass and the probability of seed removal, and how this relationship may differ between agoutis and the rest of the seed remover community. This model used fixed effects of treatment and seed mass (average mass for each species) and random effects of region and transect. Denominator degrees of freedom for all tests were calculated using the Kenward-Rogers adjustment, which is recommended for unbalanced data and inclusion of between-site

random effects (Littell et al. 2006). This method resulted in non-integer denominator degrees of freedom in many cases.

## RESULTS

Of the 1356 individual seeds used in this study, 510 seeds were removed. Over half of the removed seeds were taken within 3 days of placement. The majority of seeds remaining on day 13 had germinated, were damaged, or were rotting. We found no significant difference in probabilities of seed removal for seeds placed in the forest interior compared with those placed adjacent to the forest edge ( $F_{1,7.9} = 0.00$ ,  $P = 0.99$ ). There was also no difference in the effect of treatment on the forest edge vs. interior ( $F_{1,1006} = 1.47$ ,  $P = 0.23$ ).

The probability of a seed being removed was significantly higher for seeds placed in control groups than for seeds placed within agouti exclosures ( $F_{1,1006} = 50.89$ ,  $P < 0.001$ ). The total percentage of seeds removed from control treatments, representing the overall natural seed removal on the island, was 47 percent. In contrast, only 21 percent of seeds were removed from the exclosure groups, suggesting that agoutis were responsible for 26 percent of seeds removed from control groups.

Seed removal of the seven plant species differed significantly, indicating that the seed remover community preferred some species over others ( $F_{6,1006} = 15.39$ ,  $P < 0.001$ ). In particular, *Sterculia caribaea* and *Trichilia septentrionalis* were removed more often, whereas *Tovomita plumieri* and *Swartzia caribaea* were removed less often. Agoutis significantly increased the probability of seed removal of all but two of the study species

(*Sterculia caribaea* and *Tovomita plumieri*; Fig. 2A), and their seed species preferences differed from those of the rest of the seed remover community (*i.e.*, significant treatment\*species interaction;  $F_{6,1006} = 3.30$ ,  $P < 0.01$ ).

Overall, larger-seeded species were removed less often than smaller-seeded species, but larger seeds were taken more often when agoutis were allowed access (control) than when agoutis were excluded (exclosure; seed mass\*treatment interaction:  $F_{1,1040} = 9.17$ ,  $P < 0.01$ ; Fig. 2B). Thus, agoutis were responsible for more of the removal of larger-seeded species than smaller-seeded species.

The probability of a seed being removed was significantly related to the regional density of adult trees of that species ( $F_{1,1040} = 29.23$ ,  $P < 0.001$ ; Fig 3). This correlation was positive, indicating that a seed was more likely to be removed when regional adult tree density of the same species was greater.

Of the 846 seeds remaining after 13 days, only 8.0 percent were found to be damaged by insects (2.1%) or fungus (5.9%). Both insect damage and fungal infestation seemed to be somewhat host-specific, with 83 percent of the insect damage occurring on *Sterculia caribaea* and 70 percent of the fungal infestations occurring on *Trichilia septentrionalis*.

## DISCUSSION

In Dominica, removal of seeds from one spot on the rainforest floor and presumed predation or secondary dispersal of these seeds was related to seed size and conspecific adult density but did not differ between forest edge and interior sites. Overall, however,

seed removal rates appeared low. Sixty-two percent of seeds were left untouched after approximately 2 weeks, suggesting that many of the seeds of these seven species are left to germinate where they land. Of the seeds removed, agoutis were responsible for the majority of the removal of larger seeds.

The impact that the introduction of agoutis to Dominica has had on large-seeded rainforest species is likely much greater than the impact on small-seeded species. Not only can agoutis handle larger seeds than the rest of the seed remover community on Dominica, but evidence from other studies suggests that scatterhoarders such as agoutis remove large seeds more often (Hallwachs 1994, Forget *et al.* 1998, Jansen *et al.* 2004) and disperse them farther (Hallwachs 1994, Jansen *et al.* 2002) than smaller seeds. Jansen *et al.* (2004) showed that large seed size is an important factor stimulating scatterhoarders to act primarily as seed dispersers rather than seed predators. Thus, both the *ability* and *preference* of agoutis to disperse large seeds suggests that the introduction of agoutis to the island of Dominica has increased the amount, and possibly distance, of secondary dispersal of the island's largest-seeded rainforest species.

It has been shown elsewhere that forest fragmentation has a positive effect on agouti densities (Jorge 2008), and numerous studies have reported that forest fragmentation alters the predation and dispersal of scatterhoarded seeds (e.g., Dennis *et al.* 2005, Fleury and Galetti 2006). Forest edges, caused by forest fragmentation, often experience high incidence of human activity. We therefore expected altered agouti densities, and in turn seed removal, on the edge than interior of the forest. No significant differences were found in the probability that a seed would be removed from the forest

interior versus along the forest edge, regardless of seed species or treatment. Therefore, seed remover densities may not be affected by proximity to forest edge in Dominica.

The greater removal of seeds of locally common species suggests that more abundant seeds are preferred by all seed removers in rainforests of Dominica. The local availability of seeds has been shown to significantly increase the scatterhoarding and secondary dispersal of large-seeded species in continental rainforests (Forget 1992, Jansen *et al.* 2004). Increasing the local availability of a species' seeds increases the likelihood that scatterhoarders will cache seeds rather than predate them. In Dominican rainforests, this suggests that in regions of high seed availability, a species' seeds may not only be removed but also dispersed more often.

The species used for this study produce dehiscent fruits with relatively large seeds (median seed mass = 3.94 g), many of which are likely too large for secondary seed dispersers and predators other than agoutis to move. Previous to the introduction of agoutis, dispersal agents of our largest study species were likely limited to a few species of frugivorous bats and possibly the Scaly-naped Pigeon (*Columba squamosa*). This pigeon is known to feed on ripe fruits in the branches of fruiting trees (Cruz 1980) and either passes or regurgitates seeds intact. Judging from its size and the reported gape widths of congeneric pigeons (Wheelwright *et al.* 1984), however, the seeds of our largest study species exceed the maximum seed size that *C. squamosa* could disperse.

The four species of frugivorous bats that are known to inhabit Dominica are the most likely native primary dispersers of the large seeds. Of these bats, the largest species is the Jamaican fruit-eating bat (*Artibeus jamaicensis*), which has an average body mass

of 36 – 48 g (Ortega and Castro-Arellano 2001), making it capable of carrying even our largest study species at least short distances. Although no literature exists reporting that *A. jamaicensis* consumes any of our study species, Janzen *et al.* (1976) reported that this species removes whole legume fruits, consuming at least part of the fleshy aril and dropping the seed intact below feeding roosts. That study combined with reports of *A. jamaicensis* carrying seeds much larger than any of our study species (Gardner 1977) suggest that this bat species has the ability to disperse even our largest study species, two of which are legumes. Indeed, fruit bats are well known as dispersers for other large-seeded species on Dominica, such as *Terminalia catappa* (A. James, *personal communication*). Nevertheless, bats do not remove fruits from the ground, and therefore their activities would be limited to primary seed dispersal.

Various other potential dispersers, both extant and extinct, are known for the Caribbean region, such as rice rats, hutias, primates, and ground sloths, but it is likely that none ever inhabited Dominica. A brief study recently conducted on Dominica found no evidence of rice rats having ever inhabited the island (A. James, *personal communication*). Hutias, which are highly endangered even in their native range, are believed to have been restricted to the Greater Antillean islands (Clough 1976, Berovides-Alvarez and Comas-Gonzalez 1991). A review of mammalian biogeography in the Caribbean by Davalos (2004) showed no evidence of primates or sloths ever having inhabited the Lesser Antillean islands. Thus, agoutis, an introduced species on Dominica, represent the only secondary disperser of many of the largest-seeded species on Dominica.

The reduction of dispersal and ultimately distributions of large-seeded plants following the removal of medium- to large-sized mammalian seed dispersers from a forest has been documented throughout the tropics (e.g., Wright 2000, Meehan et al. 2002, Beckman and Muller-Landau 2007, Forget and Jansen 2007, Stoner et al. 2007). It follows similar logic that the introduction of a new disperser sufficiently large to remove larger seeds than the rest of the secondary disperser community on Dominica may be increasing both distributions and abundances of large-seeded species. Studies in the Mediterranean have reported disruption of native plant-disperser interactions in response to the introduction of non-native frugivores to island systems (Garcia 2002, Lopez-Darias and Nogales 2008). However, our study in Dominica is the first to our knowledge that demonstrates potential novel positive impacts of an introduced secondary seed disperser. Non-native seed dispersers and predators have been introduced to island rainforests throughout the tropics, likely having different impacts for each island. The islands of the Caribbean make up one the 25 global biodiversity hotspots (Brooks *et al.* 2002), and islands are known to house a variety of endemic species of plants, making it crucial to better understand how altered secondary dispersal patterns affect species distributions in island systems.

#### ACKNOWLEDGMENTS

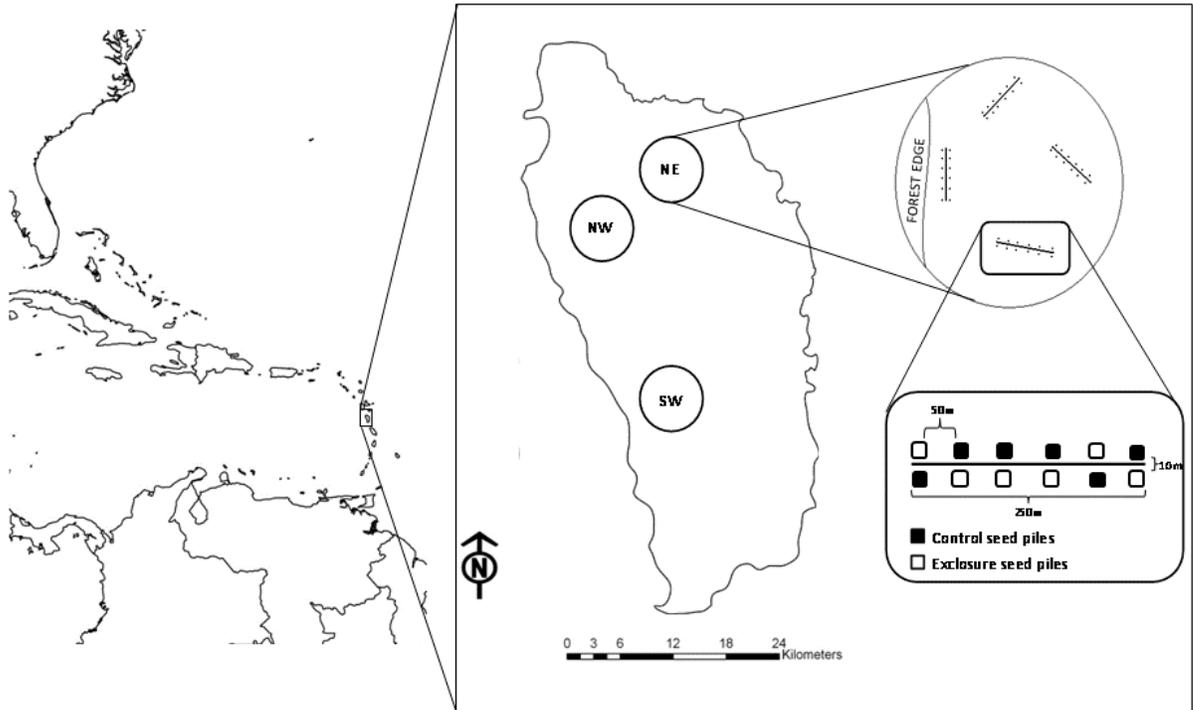
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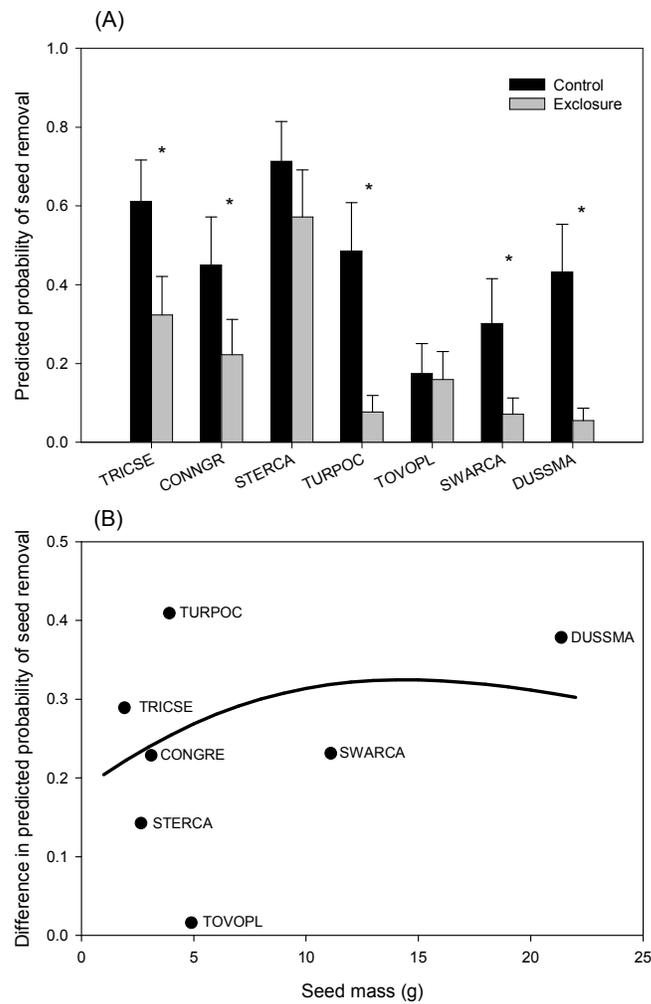
**Table 1.** Seed mass, length, width, and the average adult densities in each study region (individuals/ha) of each study species. Adult densities were estimated from 0.25-ha tree plots found in each region (6 in the NE, 4 in the NW, and 7 in the SE).

Species	Family	Growth habit	Species code	Seed mass (g)	Seed length (mm)	Seed width (mm)	Adult density		
							NE	NW	SW
<i>Connarus grandifolius</i>	Connaraceae	Liana	CONNGR	3.13	2.93	1.56	26.7	0.0	13.1
<i>Dussia martinicensis</i>	Fabaceae	Tree	DUSSMA	21.38	5.41	2.99	0.0	1.0	0.6
<i>Sterculia caribaea</i>	Malvaceae	Tree	STERCA	2.68	2.43	1.51	54.7	49.0	74.3
<i>Swartzia caribaea</i>	Fabaceae	Tree	SWARCA	11.13	3.41	2.56	4.7	6.0	24.6
<i>Tovomita plumieri</i>	Clusiaceae	Tree	TOVOPL	4.92	3.98	1.57	6.7	4.0	0.6
<i>Trichilia septentrionalis</i>	Meliaceae	Tree	TRICSE	1.94	2.56	1.21	2.0	3.0	7.4
<i>Turpinia occidentalis</i>	Staphyleaceae	Tree	TURPOC	3.94	2.18	2.13	0.0	0.0	0.0

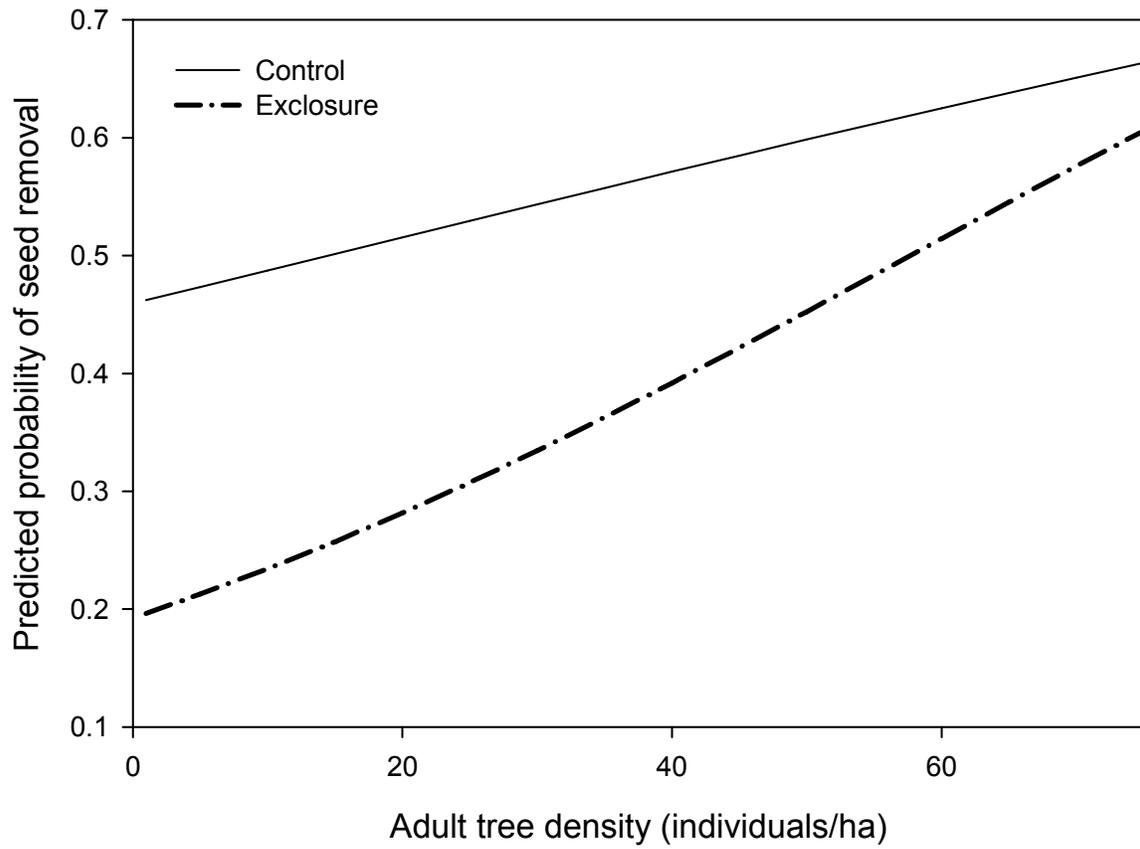
**Figure 1.** Diagram of the three study regions on the island of Dominica, the placement of transects within each region (NE, NW, SW), and the placement of seed groups along each transect.



**Figure 2.** (A) Predicted probability of seed removal (+ 1 SE) for each study species in control treatments (all seed removers allowed) and exclosure treatments (agoutis excluded). Species are arranged in order of increasing seed mass. Asterisks indicate species for which the probability of a seed being removed differed significantly between control and exclosure treatments. (B) Difference in predicted probability of seed removal (curve) between control and exclosure treatments as a function of seed mass. The difference between control and exclosure treatments is the amount of seed removal attributed to agoutis. Average seed mass (points) for each study species is plotted against the probability of seed removal of that species by agoutis for reference. Species codes correspond to those presented in Table 1.



**Figure 3.** Predicted probability of seed removal in control and exclosure treatments as a function of regional conspecific adult seed density.



## Literature Cited

- Aliaga-Rossel, E., R. W. Kays, and J. M. V. Fragoso. 2008. Home-range use by the Central American agouti (*Dasyprocta punctata*) on Barro Colorado Island, Panama. *Journal of Tropical Ecology* **24**:367-374.
- Aliaga-Rossel, E., R. S. Moreno, R. W. Kays, and J. Giacalone. 2006. Ocelot (*Leopardus pardalis*) predation on agouti (*Dasyprocta punctata*). *Biotropica* **38**:691-694.
- Almeida-Neto, M., F. Campassi, M. Galetti, P. Jordano, and A. Oliveira. 2008. Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography* **17**:503-513.
- Asquith, N. M., J. Terborgh, A. E. Arnold, and C. M. Riveros. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. *Journal of Tropical Ecology* **15**:229-235.
- Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. *Ecology* **78**:941-946.
- Beckman, N. G. and H. C. Muller-Landau. 2007. Differential effects of hunting on pre-dispersal seed predation and primary and secondary seed removal of two neotropical tree species. *Biotropica* **39**:328-339.
- Bergvall, U. A. and O. Leimar. 2005. Plant secondary compounds and the frequency of food types affect food choice by mammalian herbivores. *Ecology* **86**:2450-2460.

- Berovides-Alvarez, V. and A. Comas-Gonzalez. 1991. The critical condition of hutias in Cuba. *Oryx* **25**:206-208.
- Blendinger, P. G., B. A. Loiselle, and J. G. Blake. 2008. Crop size, plant aggregation, and microhabitat type affect fruit removal by birds from individual melastome plants in the Upper Amazon. *Oecologia* **158**:273-283.
- Brewer, S. W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* **92**:245-255.
- Brewer, S. W. and M. Rejmanek. 1999. Small rodents as significant dispersers of tree seeds in a Neotropical forest. *Journal of Vegetation Science* **10**:165-174.
- Brewer, S. W. and M. A. H. Webb. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. *Oikos* **93**:32-41.
- Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**:909-923.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* **87**:1217-1227.
- Carthew, S. M. and R. L. Goldingay. 1997. Non-flying mammals as pollinators. *Trends in Ecology & Evolution* **12**:104-108.
- Carvajal, A. and G. H. Adler. 2008. Seed dispersal and predation by *Proechimys semispinosus* and *Sciurus granatensis* in gaps and understorey in central Panama. *Journal of Tropical Ecology* **24**:485-492.

- Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Pages 161-172.
- Chambers, J. C. and J. A. Macmahon. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics **25**:263-292.
- Claridge, A. W., M. T. Tanton, J. H. Seebeck, S. J. Cork, and R. B. Cunningham. 1992. Establishment of ectomycorrhizae on the roots of 2 species of eucalyptus from fungal spores contained in the feces of the long nosed potoroo (*Potorous tridactylus*). Australian Journal of Ecology **17**:207-217.
- Clough, G. C. 1976. Current status of two endangered Caribbean rodents. Biological Conservation **10**:43-47.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs **53**:209-233.
- Coley, P. D. and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics **27**:305-335.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298-312 in Advanced Study Institute on Dynamics of Numbers in Populations. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

- Cote, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology Evolution and Systematics* **35**:113-147.
- Cowan, P. E. and C. H. TyndaleBiscoe. 1997. Australian and New Zealand mammal species considered to be pests or problems. Pages 27-36.
- Crait, J. R. and M. Ben-David. 2007. Effects of river otter activity on terrestrial plants in trophically altered Yellowstone Lake. *Ecology* **88**:1040-1052.
- Crawley, M. 2000. Seed predators and plant population dynamics. *in* M. Fenner, editor. *Seeds: The ecology of regeneration in plant communities*. CABI, New York, NY.
- Cruz, A. 1980. Avian feeding assemblages in Puerto Rico. *Caribbean Journal of Science* **15**:21-28.
- Cunningham, S. A. 1991. Experimental evidence for pollination of *Banksia spp* by nonflying mammals. *Oecologia* **87**:86-90.
- Danell, K., R. Bergstrom, and L. Iedenius. 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Journal of Mammalogy* **75**:833-844.
- Darwin, C. 1889. *Journal of Researches into the Natural History and Geology of the Countries Visited During the Voyage of H.M.S. "Beagle" Round the World*. Fifth edition. Ward, Lock and Co., London, England.
- Davalos, L. M. 2004. Phylogeny and biogeography of Caribbean mammals. *Biological Journal of the Linnean Society* **81**:373-394.

- DeMattia, E. A., L. M. Curran, and B. J. Rathcke. 2004. Effects of small rodents and large mammals on Neotropical seeds. *Ecology* **85**:2161-2170.
- Dennis, A. J., G. J. Lipsett-Moore, G. N. Harrington, E. N. Collins, and D. A. Westcott. 2005. Seed predation, seed dispersal and habitat fragmentation: does context make a difference in tropical Australia? Pages 117-135 *in* P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. *Seed fate: predation, dispersal and seedling establishment*. CABI Publishing, Cambridge, MA.
- Diamond, J. M. 1971. Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. *Proceedings of the National Academy of Sciences* **68**:2742-2745.
- Dubost, G. 1988. Ecology and social life of the Red Acouchi, *Myoprocta exilis* - Comparison with the Orange-rumped Agouti, *Dasyprocta leporina*. *Journal of Zoology* **214**:107-123.
- Dubost, G. and O. Henry. 2006. Comparison of diets of the acouchy, agouti and paca, the three largest terrestrial rodents of French Guianan forests. *Journal of Tropical Ecology* **22**:641-651.
- Eisenberg, J. F. and K. H. Redford. 2000. *Mammals of Neotropics: Ecuador, Bolivia, Brazil*. University of Chicago Press, Chicago.
- Elsner, J. B., A. B. Kara, and M. A. Owens. 1999. Fluctuations in North Atlantic hurricane frequency. *Journal of Climate* **12**:427-437.
- Emmons, L. and F. Reid. 2008. IUCN Red list of threatened species. IUCN 2008, IUCN.

- Eriksson, O. 2008. Evolution of Seed Size and Biotic Seed Dispersal in Angiosperms: Paleocological and Neocological Evidence. *International Journal of Plant Sciences* **169**:863-870.
- Farnsworth, E. 2000. The ecology and physiology of viviparous and recalcitrant seeds. *Annual Review of Ecology and Systematics* **31**:107-138.
- Feild, T. S. and N. C. Arens. 2005. Form, function and environments of the early angiosperms: merging extant phylogeny and ecophysiology with fossils. *New Phytologist* **166**:383-408.
- Fleck, D. C. and G. E. Woolfenden. 1997. Can acorn tannin predict scrub-jay caching behavior? *Journal of Chemical Ecology* **23**:793-806.
- Fleming, T. H. and E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica* **12**:45-53.
- Fleury, M. and M. Galetti. 2006. Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation* **131**:1-13.
- Forget, P.-M. and P. A. Jansen. 2007. Hunting increases dispersal limitation in the tree *Carapa procera*, a nontimber forest product. *Conservation Biology* **21**:106-113.
- Forget, P.-M., E. Munoz, and E. G. Leigh, Jr. 1994. Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* **26**:420-426.
- Forget, P. M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* **24**:408-414.

- Forget, P. M. 1993. Post dispersal predation and scatterhoarding of *Dipterix panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* **94**:255-261.
- Forget, P. M. and T. Milleron. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* **87**:596-599.
- 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. Pages 25-47 in D. M. Newberry, N. Brown, and H. H. T. Prins, editors. *Dynamics of tropical communities*. Blackwell Science, Oxford, UK.
- Forget, P. M., T. Milleron, F. Feer, O. Henry, and G. Dubost. 2000. Effects of dispersal pattern and mammalian herbivores on seedling recruitment for *Virola michelii* (Myristicaceae) in French Guiana. *Biotropica* **32**:452-462.
- 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. Pages 379-393 in P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. *Seed fate: predation, dispersal and seedling establishment*. CABI Publishing, Cambridge, MA.
- Galetti, M., C. I. Donatti, A. S. Pires, P. R. Guimaraes, and P. Jordano. 2006. Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society* **151**:141-149.
- Garcia, J. D. D. 2002. Interaction between introduced rats and a frugivore bird-plant system in a relict island forest. *Journal of Natural History* **36**:1247-1258.

- Gardner, A. L. 1977. Feeding Habits. Pages 1-364 in R. J. Baker, J. K. J. Jr., and D. C. Carter, editors. Biology of the bats of the New World family Phyllostomatidae. Part II. Texas Tech University Press, College Station, TX.
- Gautierhion, A. and F. Maisels. 1994. Mutualism between a leguminous tree and large african monkeys as pollinators. Behavioral Ecology and Sociobiology **34**:203-210.
- Gentry, A. H. 1988. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences of the United States of America **85**:156-159.
- Goldingay, R. L. 2000. Small dasyurid marsupials are they effective pollinators? Australian Journal of Zoology **48**:597-606.
- Goldingay, R. L., S. M. Carthew, and R. J. Whelan. 1991. The importance of nonflying mammals in pollination. Oikos **61**:79-87.
- Greig, N. 1993. Predispersal seed predation on 5 piper species in tropical rain-forest. Oecologia **93**:412-420.
- Guimaraes, P. R., B. Z. Gomes, Y. J. Ahn, and M. Galetti. 2005. Cache pilferage in red-rumped agoutis (*Dasyprocta leporina*) (Rodentia). Mammalia **69**:431-434.
- Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pages 285-304 in A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr W Junk Publishers, The Hague.

- Hallwachs, W. 1994. The clumsy dance between agoutis and plants: scatterhoarding by Costa Rican dry forest agoutis (*Dasyprocta punctata*: Dasyproctidae: Rodentia). Dissertation. Cornell University, Ithaca, NY.
- Hammond, D. S. and V. K. Brown. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil types in wet Neotropical forests. *Ecology* **76**:2544-2561.
- Harms, K. E. and J. W. Dalling. 1997. Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology* **13**:617-621.
- Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493-495.
- Hayashida, M. 1989. Seed dispersal by red squirrels and subsequent establishment of Korean Pine. *Forest Ecology and Management* **28**:115-129.
- Heithaus, E. R., P. A. Opler, and H. G. Baker. 1974. Bat activity and pollination of *Bauhinia pauletia* - Plant pollinator coevolution. *Ecology* **55**:412-419.
- Henry, O. 1999. Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana. *Journal of Tropical Ecology* **15**:291-300.
- Herrera, C. M. 1989. Seed dispersal by animals: a role in angiosperm diversification? *American Naturalist* **133**:309-322.

- Hobbs, N. T. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* **60**:695-713.
- Howe, H. F. and J. Smallwood. 1981. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**:201-228.
- Howe, H. F. and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**:201-228.
- Hulme, P. E. and T. Borelli. 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* **145**:149-156.
- Ickes, K., S. J. DeWalt, and S. C. Thomas. 2003. Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. *Journal of Ecology* **91**:222-233.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**:102-106.
- Jansen, P. A., M. Bartholomeus, F. Bongers, J. A. Elzinga, J. Den Ouden, and S. E. Van Wieren. 2002. The role of seed size in dispersal by a scatterhoarding rodent. Pages 209-225 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, Wallingford, UK.
- Jansen, P. A., F. Bongers, and L. Hemerik. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. *Ecological Monographs* **74**:569-589.

- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501-528.
- Janzen, D. H., G. A. Miller, J. Hackforth-Jones, C. M. Pond, K. Hooper, and D. P. Janos. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology* **57**:1068-1075.
- Johnson, C. N. 1996. Interactions between mammals and ectomycorrhizal fungi. *Trends in Ecology & Evolution* **11**:503-507.
- Jorge, M. 2008. Effects of forest fragmentation on two sister genera of Amazonian rodents (*Myoprocta acouchy* and *Dasyprocta leporina*). *Biological Conservation* **141**:617-623.
- Jorge, M. and H. F. Howe. 2009. Can forest fragmentation disrupt a conditional mutualism? A case from central Amazon. *Oecologia* **161**:709-718.
- Jorge, M. S. P. and C. A. Peres. 2005. Population density and home range size of red-rumped agoutis (*Dasyprocta leporina*) within and outside a natural Brazil nut stand in southeastern Amazonia. *Biotropica* **37**:317-321.
- Kalish, S. and M. A. McPeck. 1993. Extinction dynamics, population growth and seed banks. *Oecologia* **95**:314-320.
- Kleizen, C., J. Midgley, and S. D. Johnson. 2008. Pollination systems of *Colchicum* (Colchicaceae) in Southern Africa: Evidence for rodent pollination. *Annals of Botany* **102**:747-755.

- Lahti, K., K. Koivula, S. Rytönen, T. Mustonen, P. Welling, V. V. Pravosudov, and M. Orell. 1998. Social influences on food caching in willow tits: A field experiment. *Behavioral Ecology* **9**:122-129.
- Leigh, E. G., Jr. 1999. Tropical forest ecology: a view from Barro Colorado Island. Oxford University Press, New York, NY.
- Levin, D. A. 1990. The seed bank as a source of genetic novelty in plants. *American Naturalist* **135**:563-572.
- Li, H. J. and Z. B. Zhang. 2007. Effects of mast seeding and rodent abundance on seed predation and dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecology and Management* **242**:511-517.
- Lieberman, D. and L. Milton. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *Journal of Tropical Ecology* **3**:347-358.
- Lindsay, J. M., M. V. Stasiuk, and J. B. Shepherd. 2003. Geological history and potential hazards of the late-Pleistocene to Recent Plat Pays volcanic complex, Dominica, Lesser Antilles. *Bulletin of Volcanology* **65**:201-220.
- Lopez-Darias, M. and M. Nogales. 2008. Effects of the invasive Barbary ground squirrel (*Atlantoxerus getulus*) on seed dispersal systems of insular xeric environments. *Journal of Arid Environments* **72**:926-939.
- Lord, J., J. Egan, T. Clifford, E. Jurado, M. Leishman, D. Williams, and M. Westoby. 1997. Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography* **24**:205-211.

- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Mack, A. L. 1998. An advantage of large seed size: tolerating rather than succumbing to seed predators. *Biotropica* **30**:604-608.
- Maury, R. C., G. K. Westbrook, P. E. Baker, P. Bouysse, and D. Westercamp. 1990. Geology of the Lesser Antilles. Pages 141-166 in G. Dengo and J. E. Case, editors. The Geology of North America. . Geological Society of America, Boulder, CO.
- Mckenna, M. C. and S. K. Bell. 1997. Classification of mammals above the species level. Columbia University Press, New York, NY.
- Meehan, H. J., K. R. McConkey, and D. R. Drake. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *Journal of Biogeography* **29**:695-712.
- Miller, B., R. Reading, J. Hoogland, T. Clark, G. Ceballos, R. List, S. Forrest, L. Hanebury, P. Manzano, J. Pacheco, and D. Uresk. 2000. The role of prairie dogs as a keystone species: Response to Stapp. *Conservation Biology* **14**:318-321.
- Moles, A. T., D. D. Ackerly, J. C. Tweddle, J. B. Dickie, R. Smith, M. R. Leishman, M. M. Mayfield, A. Pitman, J. T. Wood, and M. Westoby. 2007. Global patterns in seed size. *Global Ecology and Biogeography* **16**:109-116.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, A. J. Pitman, and M. Westoby. 2005a. Factors that shape seed mass evolution. *Proceedings of the National Academy of Sciences* **102**:10540-10544.

- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005b. A brief history of seed size. *Science* **307**:576-580.
- Moles, A. T., D. I. Warton, R. D. Stevens, and M. Westoby. 2004. Does a latitudinal gradient in seedling survival favour larger seeds in the tropics? *Ecol Letters* **7**:911-914.
- Moles, A. T. and M. Westoby. 2003. Latitude, seed predation and seed mass. *Journal of Biogeography* **30**:105-128.
- Moore, J. E., A. B. McEuen, R. K. Swihart, T. A. Contreras, and M. A. Steele. 2007. Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. *Ecology* **88**:2529-2540.
- Moore, J. E. and R. K. Swihart. 2008. Factors affecting the relationship between seed removal and seed mortality. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **86**:378-385.
- Morales, J. M. and T. S. Carlo. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* **87**:1489-1496.
- Morris, A. E. L., I. Taner, H. A. Meyerhoff, and A. A. Meyerhoff. 1990. Tectonic evolution of the Caribbean region: alternative hypothesis. Pages 433-457 in G. Dengo and J. E. Case, editors. *The Geology of North America*. Geological Society of America, Boulder, CO.
- Munoz, A. and R. Bonal. 2008. Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour* **76**:709-715.

- Nassar, J. M., N. Ramirez, and O. Linares. 1997. Comparative pollination biology of Venezuelan columnar cacti and the role of nectar-feeding bats in their sexual reproduction. *American Journal of Botany* **84**:918-927.
- Nathan, R. and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* **15**:278-285.
- Nunez-Iturri, G. and H. F. Howe. 2007. Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in Western Amazonia. *Biotropica* **39**:348-354.
- Ortega, J. and I. n. Castro-Arellano. 2001. *Artibeus jamaicensis*. *Mammalian Species*:1-9.
- Paine, C. E. T. and H. Beck. 2007. Seed predation by neotropical rain forest mammals increases diversity in seedling recruitment. *Ecology* **88**:3076-3087.
- Peres, C. A. and C. Baider. 1997. Seed dispersal, spatial distribution and population structure of Brazilnut trees (*Bertholletia excelsa*) in southeastern Amazonia. *Journal of Tropical Ecology* **13**:595-616.
- Peres, C. A., L. C. Schiesari, and C. L. DiasLeme. 1997. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: A test of the escape hypothesis. *Journal of Tropical Ecology* **13**:69-79.
- Pizo, M. A. and M. Almeida-Neto. 2009. Determinants of fruit removal in *Geonoma pauciflora*, an understory palm of neotropical forests. *Ecological Research* **24**:1179-1186.

- Pringle, R. M. 2008. Elephants as agents of habitat creation for small vertebrates at the patch scale. *Ecology* **89**:26-33.
- Samper, A., X. Quidelleur, G. Boudon, A. Le Friant, and J. C. Komorowski. 2008. Radiometric dating of three large volume flank collapses in the Lesser Antilles Arc. *Journal of Volcanology and Geothermal Research* **176**:485-492.
- Sazima, M. and I. Sazima. 1978. Bat pollination of passion flower, *Passiflora mucronata*, in southeastern Brazil. *Biotropica* **10**:100-109.
- Shanahan, M., S. So, S. G. Compton, and R. Corlett. 2001. Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* **76**:529-572.
- Sigurdsson, H. and S. Carey. 1981. Marine tephrochronology and Quaternary explosive volcanism in the Lesser Antilles arc. Pages 255-280 *in* R. S. J. Sparks and S. Self, editors. *Tephra Studies*. Reidel, Holland.
- Silvius, K. M. 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or 'grubivory'? *Journal of Tropical Ecology* **18**:707-723.
- Silvius, K. M. and J. M. V. Fragoso. 2003. Red-rumped agouti (*Dasyprocta leporina*) home range use in an Amazonian forest: Implications for the aggregated distribution of forest trees. *Biotropica* **35**:74-83.
- Stapanian, M. A. and C. C. Smith. 1978. A model for seed scatterhoarding: Coevolution of Fox squirrels and Black walnuts. *Ecology* **59**:884-896.
- Steele, M., L. A. Wauters, and K. W. Larsen. 2005. Selection, predation and dispersal of seeds by tree squirrels in temperate and boreal forests: are tree squirrels keystone

- granivores? Pages 205-221 *in* P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. Seed fate: predation, dispersal and seedling establishment. CABI Publishing, Cambridge, MA.
- Stoner, K. E., P. Riba-Hernandez, K. Vulinec, and J. E. Lambert. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. *Biotropica* **39**:316-327.
- Sussman, R. W. 1991. Primate origins and the evolution of angiosperms. *American Journal of Primatology* **23**:209-223.
- Tamura, N. and F. Hayashi. 2008. Geographic variation in walnut seed size correlates with hoarding behaviour of two rodent species. *Ecological Research* **23**:607-614.
- Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. *Biotropica* **23**:513-521.
- Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923-1926.
- Theimer, T. C. 2005. Rodent scatterhoarders as conditional mutualists. Pages 283-295 *in* P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. Seed fate: predation, dispersal and seedling establishment. CABI Publishing, Cambridge, MA.
- Tiffney, B. H. 2004. Vertebrate dispersal of seed plants through time. *Annual Review of Ecology Evolution and Systematics* **35**:1-29.

- Tossas, A. G. 2006. Effects of Hurricane Georges on the resident avifauna of Maricao State Forest, Puerto Rico. *Caribbean Journal of Science* **42**:81-87.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* **1**:151-190.
- Tschapka, M., E. B. Sperr, L. A. Caballero-Martinez, and R. A. Medellin. 2008. Diet and cranial morphology of *Musonycteris harrisoni*, a highly specialized nectar-feeding bat in western Mexico. *Journal of Mammalogy* **89**:924-932.
- Tuck Haugeaasen, J. M., T. Haugeaasen, C. A. Peres, R. Gribel, and P. Wegge. 2010. Seed dispersal of the Brazil nut tree (*Bertholletia excelsa*) by scatter-hoarding rodents in a central Amazonian forest. *Journal of Tropical Ecology* **26**:251-262.
- Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, IL.
- Vander Wall, S. B. 1993. A model of caching depth - implications for scatter hoarders and plant dispersal. *American Naturalist* **141**:217-232.
- Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. *Botanical Review* **67**:74-117.
- Vander Wall, S. B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* **83**:3508-3516.
- Vander Wall, S. B. 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**:989-997.

- Vavrek, M. C., J. B. McCgraw, and C. C. Bennington. 1991. Ecological genetic variation in seed banks .3. Phenotypic and genetic differences between young and old seed populations of *Carex bigelowii*. *Journal of Ecology* **79**:645-662.
- Vilella, F. J. and J. H. Fogarty. 2005. Diversity and abundance of forest frogs (Anura : Leptodactylidae) before and after Hurricane Georges in the Cordillera Central of Puerto Rico. *Caribbean Journal of Science* **41**:157-162.
- Wallace, A. R. 1906. *The Malay Archipelago, the Land of the Orangutan and the Bird of Paradise*. MacMillan Co., New York, NY.
- Wen, S. Y., N. Fetcher, and J. K. Zimmerman. 2008. Acclimation of tropical tree species to hurricane disturbance: ontogenetic differences. *Tree Physiology* **28**:935-946.
- Wenny, D. G. 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *Journal of Tropical Ecology* **15**:481-496.
- Wesche, K., K. Nadrowski, and V. Retzer. 2007. Habitat engineering under dry conditions: The impact of pikas (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *Journal of Vegetation Science* **18**:665-674.
- Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* **66**:808-818.
- Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* **16**:173-192.

- Wiens, J. J., C. H. Graham, D. S. Moen, S. A. Smith, and T. W. Reeder. 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *American Naturalist* **168**:579-596.
- Williams, P. A., B. J. Karl, P. Bannister, and W. G. Lee. 2000. Small mammals as potential seed dispersers in New Zealand. *Austral Ecology* **25**:523-532.
- Willig, M. R. and G. R. Camilo. 1991. The effect of hurricane Hugo on 6 invertebrate species in the Luquillo experimental forest of Puerto Rico. *Biotropica* **23**:455-461.
- Wing, E. S. 2001. Native American Use of Animals in the Caribbean. Pages 481-518 *in* C. A. Woods and F. E. Sergile, editors. *Biogeography of the West Indies: Patterns and Perspectives*. CRC Press LLC.
- Wright, S. J. 2000. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology* **14**:227-239.
- Wright, S. J., K. E. Stoner, N. Beckman, R. T. Corlett, R. Dirzo, H. C. Muller-Landau, G. Nunez-Iturri, C. A. Peres, and B. C. Wang. 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* **39**:289-291.
- Xiao, Z. S., M. K. Harris, and Z. B. Zhang. 2007. Acorn defenses to herbivory from insects: Implications for the joint evolution of resistance, tolerance and escape. *Forest Ecology and Management* **238**:302-308.

- Young, H. J. 1996. Pollen and seed movement in populations of *Silene latifolia*: The probability and consequences of inbreeding. *Bulletin of the Ecological Society of America* **77**:497.
- Zhang, H. M., J. R. Cheng, Z. S. Xiao, and Z. B. Zhang. 2008. Effects of seed abundance on seed scatter-hoarding of Edward's rat (*Leopoldamys edwardsi* *Muridae*) at the individual level. *Oecologia* **158**:57-63.
- Zusi, R. L. and M. J. Hamas. 2001. Bats and birds as potential pollinators of three species of *Marcgravia* lianas on Dominica. *Caribbean Journal of Science* **37**:274-277.