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The Role of Mammals in Creating and Modifying Seedshadows in Tropical Forests and Some Possible Consequences of Their Elimination

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ABSTRACT

Mammal populations are increasingly hunted, yet the consequences of their disappearance from tropical forests have only recently been explored. Here, we summarize current research on the role of mammals in seed dispersal and postdispersal processes, such as seed predation and secondary dispersal, in different tropical regions. We evaluate how mammal features influence seedshadows and ultimately forest regeneration. Finally, we discuss the potential effect of changes in seedshadows caused by the elimination of many medium- and large-sized mammals. The complex role that mammals play in creating and modifying seedshadows in tropical forests cannot be easily quantified, and in this review we emphasize the variation that exists both within and among mammal taxa and across continents. To bridge this gap in information, we suggest that more studies should evaluate the relative importance of the disappearance of both seed dispersers and seed predators for particular plant species so that we may begin to understand the balance between these two influences. We also suggest that future studies identify ecological redundancy in nonhunted vertebrates within any particular community to evaluate compensatory behavior that may help ameliorate some of the negative effects of hunting of large and medium mammals.

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Key words: conservation; frugivory; hunting; Neotropics; Paleotropics; seed dispersal; seed predation.

THE ROLE OF MAMMALS IN FOREST DYNAMICS has been a topic of interest since the first studies documenting the effects of mammals on temperate (Munns 1924, Beckwith 1954) and tropical (Phillips 1931) forest regeneration. Until the early 1980s, the overwhelming majority of studies on the effect of mammals on seed dispersal in tropical areas simply documented primary seed dispersal or fruit removal (Wang & Smith 2002), largely ignoring other effects of treatment of fruits/seeds by mammals on seed dispersal. As succinctly explained by Wang and Smith (2002), primary seed dispersal is only one step in the *seed dispersal cycle*, which functions as a "demographic bridge" linking the end of the adult plant reproductive cycle with the establishment of their offspring. In the last two decades, several new areas of research have evaluated other ways in which mammals may affect seed dispersal and ultimately the likelihood of seedling establishment from dispersed seeds. These include effects on seed deposition (*e.g.*, distance from conspecifics, microsite, and deposition density), seed predation, effects of secondary (and tertiary, quaternary, *etc.*) dispersal on seedling establishment, the effect of gut passage on seed germination, and effects of foraging movement and behavior on seedshadows (see Forget *et al.* 2005 for a comprehensive review).

An estimated 51 to 98 percent of canopy and subcanopy trees in Neotropical forests are vertebrate-dispersed; a similar estimate is found for the Paleotropics, with estimates ranging from 46 to 80 percent (Howe & Smallwood 1982). Mammals and birds are the most important vertebrate groups responsible for seed dispersal in tropical regions (Corlett 1998, Jordano 2001). Bats (Heithaus *et al.* 1975, Fleming 1988, Mickleburgh & Carroll, 1994, Lobova *et al.* 2003, Passos *et al.* 2003) and primates (Corlett 1998; Poulsen *et al.*, 2002; Lambert & Chapman 2005; McConkey 2005a,b) contain the most frugivorous species among mammals and are recognized as key taxonomic groups for seed dispersal in tropical forests. Other mammal taxa in the Americas, African, and Indomalayan regions that are documented to be primary dispersers as well include species from Carnivora, Rodentia, Proboscoidea, Perissodactyla and Artiodactyla (Table 1).

Mammals are increasingly hunted each day within tropical ecosystems (Peres & Lake 2003, Robinson & Bennet 2004, Fa *et al.* 2005, Corlett 2007, Peres & Palacios 2007); moreover, mammals

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TABLE 1. *Ecological roles in seed dispersal (listed in order of importance) and their vulnerability to human exploitation (*i.e., *hunting or trade) for the most important frugivorous mammalian taxa in three major geographical tropical forest regions. SD: primary seed dispersal, SSD: secondary seed dispersal, PDSP: predispersal seed predation, PosDSP: postdispersal seed predation. ND: No data were found for the taxonomic group in the region. Taxonomy follows Wilson and Reeder (2005).*

Order Family (Common name)	Americas	Africa	Indomalayan	Susceptibility^{1,2,3}	References (Americas; Africa; Indomalayan)
Primates					
Callitrichidae (marmosets and tamarins)	SD	Absent	Absent	Low	Garber 1986, Lambert & Garber 1998
Cebidae (New World monkeys)	SD, PDSP	Absent	Absent	High	Garber 1986; Kinzey & Norconk 1990, 1993; Peres 1991; Kinzey 1992; Lambert & Garber 1998; Norconk *et al*. 1998; Link & Di Fiore 2006
Cercopithecidae (Old World monkeys)	Absent	SD, PDSP	SD, PDSP	High	Gautier-Hion *et al.* 1985, 1993; Corlett & Lucas 1990; Davies 1991; Corlett 1998, 2007; Kaplin & Moermond 1998; Lambert & Garber 1998; Kitamura *et al.* 2002
Pongidae (great apes)	Absent	SD	SD	High	Tutin *et al.* 1991; Corlett 1998; Lambert & Garber 1998; Rogers *et al.* 1998; McConkey 2005a
Hylobatidae (gibbons)	Absent	Absent	SD, PDSP	High	Corlett 1998, 2007; Kitamura *et al.* 2002; McConkey 2005b
Chiroptera					
Phyllostomidae (Leaf-nosed bats)	SD	Absent	Absent	Low	August 1981, Fleming & Heithaus 1981, Galindo-González *et al.* 2000, Korine *et al.* 2000
Pteropodidae (flying foxes)	Absent	SD	SD	High	Corlett 1998, 2007; Duncan & Chapman 1999; Banack & Grant 2002; Nyhagen *et al.* 2005; Stier & Mildenestein 2005
Carnivora					
Canidae (coyotes, jackals and foxes)	SD	SD	SD	Low	Campos & Ojeda 1997; Corlett 1998; Dalponente & De Souza 1999; Atkinson *et al.* 2002; Kaunda & Skinner 2003
Mustelidae (badgers, weasels, skunks, otters)	SD	No data	SD	Low	Corlett 1998; Quadros & Monteiro-Filho 2000
Procyonidae (racoons, coatmundis, olingos and kinkajous)	SD	Absent	Absent	High	Kays 1999, Alves Costa *et al.* 2004
Viverridae (civets, genets)	Absent	SD	SD	High	Corlett 1998, 2007; Ray & Sunquist 2001; Kitamura *et al.* 2002
Rodentia					
Agoutidae (pacas)	No data	Absent	Absent	High	
Dasyproctidae (agoutis, acouchis)	PDSP, SSD	Absent	Absent	High	Forget 1990, 1993; Forget *et al.* 1998; Wenny 1999; Jansen & Forget 2001; Forget & Jansen 2007
Echimyidae (spiny rats)	PosDSP, SSD	Absent	Absent	Low	Adler & Kestell 1998; Beck & Terborgh 2002; Feer & Forget 2002; Russo 2005
Heteromyidae (kangaroo rats and pocket mice)	PosDSP, SSD PDSP	Absent	Absent	Low	Brewer & Rejmánek 1999; DeMattia *et al.* 2004
Hystricidae (Old World porcupines)	Absent	PDSP	PosDSP	High	Gautier-Hion *et al.* 1985; Corlett 1998, 2007; Kitamura *et al.* 2004

Continued

TABLE 1. *Continued.*

Order Family (Common name)	Americas	Africa	Indomalayan	Susceptibility[1,2,3]	References (Americas; Africa; Indomalayan)
Muridae (mice, rats)	PDSP, PosDSP, SSD	PDSP	PDSP, PosDSP, SSD	Low[4]	Gautier-Hion *et al.* 1985; Blate *et al.* 1998; Yasuda *et al.* 2000; Viera *et al.* 2003; DeMattia *et al.* 2004; Kitamura *et al.* 2004; Wells & Bagchi 2005
Sciuridae (squirrels)	PDSP, SSD	No data	PDSP, SD	Low	Glanz *et al.* 1990; Corlett 1998; Gathua 2000; Clark *et al.* 2001; Kitamura *et al.* 2002, 2004
Proboscidea					
Elephantidae (elephants)	Absent	SD	SD	High	Chapman *et al.* 1992; Corlett 1998, 2007; Dudley 1999; Hawthorne & Parren 2000; Kitamura *et al.* 2002
Perissodactyla					
Rhinocerotidae (rhinoceros)	Absent	No data	SD	High	Corlett 1998, 2007
Tapiridae	SD, PDSD, SSD	Absent	SD	High-Americas Low-Indomalayan	Janzen 1981; Fragoso 1997; Corlett 1998, 2007; Fragoso & Huffman 2000; Henry *et al.* 2000; Galleti *et al.* 2001; Foerster & Vaughan 2002; Holden *et al.* 2003
Artiodactyla					
Bovidae (antelopes)	Absent	PDSP, SD		High	Gautier-Hion *et al.* 1985, Feer 1995, Miller 1996, Or & Ward 2003, Shiponeni & Milton 2006
Cervidae (deer)	PDSP, SD	SD	PDSP, SD	High	Corlett 1998, 2007; Gayot *et al.* 2004, 2006; Prassad *et al.* 2006
Suidae (wild pigs)	Absent	No data	PDSP, SD	High	Corlett 1998, 2007; Curran & Webb 2000
Tayassuidae (peccaries)	PosDSP, SD	Absent	Absent	High	Bodmer 1991; Dirzo & Miranda 1991; Miller 1996; Vellend *et al.* 2003; Gayot *et al.* 2004; Beck 2005
Tragulidae (mouse-deer)	Absent	PDSP, SD	SD	High	Gautier-Hion *et al.* 1985; Corlett 1998, 2007; Kitamura *et al.* 2002

[1] Americas: Roldán & Simonetti 2001, Peres 2000, Lopes & Ferrari 2000, Wright *et al.* 2000.

[2] Africa: Refisch & Kone 2005, Hedges *et al.* 2005, Heinen & Srikosamatara 1996, Barnes 2002, Waltert *et al.* 2002, Fa *et al.* 2002, Juste *et al.* 1995.

[3] Indomalayan: Corlett 1998, 2007; Lee *et al.* 2005; Semiadi & Meijaard 2006; Riley 2002; Marshall *et al.* 2006.

[4] In some areas of Africa, Giant Pouched Rats (*Cricetomys gambianus and C. emini*) are threatened by hunting and capture to be sold for pets (Juste *et al.* 1995).

represent the vertebrate group most important to hunters world wide (Robinson & Bennett 2000). How the elimination of mammals and other large vertebrates may affect tropical forest dynamics is the theme of this Special Section.

The first goal of this review is to synthesize our understanding of the role of mammals in primary seed dispersal, as well as their role in postdispersal processes such as seed predation and secondary dispersal. The second goal is to make cross-continental comparisons of seed dispersal by mammalian taxa to identify patterns across continents or mammal groups. The final goal of this review is to discuss the potential effects of hunting of medium- and large-sized mammalian seed dispersers on forest regeneration. Our review concentrates on examples and comparisons among frugivorous mammalian taxa that are either frequently hunted (medium- and large-sized), or rarely hunted (small-sized). The ubiquity of small mammals in tropical forests makes them important components of the seed dispersal cycle, especially in the absence of medium- and large-sized mammals.

SEEDSHADOWS CREATED BY MAMMALS IN TROPICAL FORESTS

A primary constraint in evaluating the impact of mammals on forest regeneration is determining parental origin of dispersed seeds. Few studies have been successful in determining the actual seedshadow and dispersal curves produced by frugivorous mammals (Wang & Smith 2002). Nevertheless, novel tracking techniques using genetic information promise new insights into the knowledge of this phenomenon (Godoy & Jordano 2001, Grivet *et al*. 2005, Wang *et al*. 2007). Below, we review and compare what is currently known about seedshadows produced by some mammalian taxa in the tropics and discuss how some specific mammal features (*e.g*., body size, digestive strategies, ranging behavior, and defecation patterns) affect them. Seedshadows created by mammals are largely determined by initial handling of seeds. Seeds may be swallowed, spat out, dropped directly below the parent tree, or masticated and destroyed.

SWALLOWED SEEDS.—Many primates (Lambert & Garber 1998, Lambert & Chapman 2005) and bats (Fleming & Heithaus 1981, Shilton *et al*. 1999, Stier & Mildenstein 2005), both in the Neotropics and Paleotropics, swallow seeds whole, without destroying them in the process of extracting pulp from fruit. In addition to bats and primates, many large mammals, including members of Proboscoidea, Perissodactyla, Carnivora, and some Artiodactyla swallow seeds whole and hence contribute to the seedshadows of particular plant species in tropical regions (Table 1).

Once seeds are swallowed, several mammal features, including body size, digestive strategies, ranging behavior, and defecation patterns, influence seedshadows. Comparisons among primates illustrate how mammal body size affects seed fate. Small primates can swallow small seeds, spit medium seeds, and rarely exploit large seeds (Garber 1986). Medium primates swallow small and many medium seeds and spit large seeds. The largest primates in Africa and S-E Asia can swallow most seeds (Lambert 1998, 1999).

The time required for seeds to pass through the digestive tract affects the fate of swallowed seeds; seeds that spend more time in the digestive tract are generally deposited at greater distances from the mother plant. For example, Old World flying foxes (Pteropodidae) swallow fruits with small seeds and may retain viable seeds in their guts for up to 12 h moving considerable distances (Shilton *et al*. 1999). In contrast, New World leaf-nosed bats (Microchiroptera: Phyllostomidae) have relatively short gut retention times (20–45 min; Utzurrum & Heidman 1991) and usually create mixed species seedshadows from feces that are concentrated around fruiting trees, under night roosts, and in day roosts (Fleming & Heithaus 1981). In general, ungulates have long gut retention times that enhance their ability to disperse seeds long distances. Neotropical forest deer (*Mazama* spp.) have gut retention times of between 13 and 20 h (Domingues de Oliveira & Barbanti Duarte 2006) whereas some small Old World deer have even longer retention times (Asian mouse deer: 49 h, pudu: 30 h, Maxwell's duikier, 42 h; Van Soest *et al*. 1995). Some seeds actually need to be swallowed by ungulates in order to germinate (Rohner & Ward 1999, Or & Ward 2003). Nevertheless, some ungulates exhibit fermentation chambers that destroy seeds (Gardener *et al*. 1993). Given these digestive characteristics, ungulates can serve as both seed dispersers and predators (Dinerstein 1989, Fragoso *et al*. 2003).

Ranging behavior also is an important component determining the seedshadows produced by mammalian taxa. In general, mammals that travel widely in a day will deposit seeds over a greater area than mammals that intensively exploit a smaller day range moving shorter distances (Portnoy & Willson 1993, Willson & Traveset 2000, Muller-Landau *et al*. 2003). Howler monkeys (*Alouatta* spp.) spend from 28.5 to 50 percent of their feeding time consuming fruit, and are reported to disperse the seeds of several plant species (Estrada & Coates-Estrada 1984, Stoner 1996). They spend many hours in the same feeding tree and range less than 600 meters in a day (Bravo & Sallenave 2003). In French Guiana, 60 percent of *Alouatta seniculus* defecations were beneath sleeping trees, which in many cases were feeding trees; seeds that were dispersed away from the sleeping tree were moved on average 255 ± 129 m from sleeping trees (Julliot 1996). In contrast to this scenario, spider monkeys (*Ateles* spp.) feed in several different trees in 1 d (Link & Di Fiore 2006). Furthermore, unlike howler monkeys, spider monkeys range widely in a day—up to 5 km (Nunes 1998). The ranging patterns of spider monkeys result in many seeds being widely dispersed throughout the forest (Russo & Augspurger 2004).

Ranging behavior of many ungulates affect the patterns of seedshadows produced by them. For example, Neotropical tapirs have home ranges of several thousand hectares and therefore contribute to long-distance seed dispersal (Fragoso 1997). Neotropical deer also are considered to be important vectors in the long-distance dispersal of forest understory herbs in tropical forests (Dirzo & Miranda 1991). Although peccaries are principally seed predators, they do participate in seed dispersal through endozoochory of small seeds (Beck 2005). Since they may move considerable distances in 1 d (up to 10 km) and have a gut retention time of up to 3 d, they are important long-distance dispersers of several small-seeded fruits (Beck 2005). In the Paleotropics, impalas, giraffes, and kudus also have been recognized as important long-distance seed dispersers because of their ranging behavior (Miller 1996).

Mammalian defecation patterns influence seedshadows produced. Defecated seeds may be deposited in high-density clumps, singly, or in low-density clumps (Howe 1989). For example, tapirs defecate in latrines, resulting in clumped seed deposition. Certain palm seeds eaten by tapirs exhibit a highly clumped distribution across landscape scales and this distribution is consistent with the use of latrines by these mammals (Fragoso *et al*. 2003). Some primates also defecate in particular areas (Feer & Forget 2002, Russo & Augspurger 2004). For example, clumped defecations at sleeping sites of spider monkeys results in lower per capita seed-to-seedling survival for the tree *Virola calophylla* compared to defecations that occurred at diurnal dispersal sites away from sleeping trees (Russo & Augspurger 2004).

SPIT AND DROPPED SEEDS.—Spit and dropped seeds are more likely to be deposited in close proximity to the parent tree than seeds that are swallowed (Dominy & Duncan 2005), which are more likely to be dispersed some distance away from the parental trees and often long distances (Nunes 1998). Spit and dropped seeds are also more likely to be deposited in dense clumps rather than in a scattered pattern (Dominy & Duncan 2005).

Swallowing seeds can be costly to frugivores because they increase an animal's body mass and also displace incoming nutritious digesta (food) from the gastrointestinal tract (Corlett & Lucas 1990, Lambert 1999). For these reasons, seed spitting is most common in frugivores with long gut retention times; good examples are some primate species that perform seed-spitting as a primary seed-handling behavior. The Paleotropical subfamily Cercopithecinae has the longest (both absolutely and relatively) gut transit times across the Primate order (Lambert 1998, 2002). Seed spitting is thus important for these monkey species because, if large-seeded fruit were swallowed whole to remove pulp, then the energetic cost of indigestible seed ballast would be incurred for an absolutely and relatively long time. Moreover, it could severely limit space for incoming food. African and Asian hominoids, on the other hand, are larger mammals, exhibiting the more typical emphasis of fast (relative to body size) digestive processing common to frugivores (Milton & Demment 1987, Lambert 1998). Some flying foxes (Pteropodidae) avoid ballast by only removing the juice of fruits and discarding remaining fiber and seeds from large-seeded fruits (Phua & Corlett 1989). Spit seeds are generally deposited in a clumped form and due to density dependent effects may have negative implications for seed germination and ultimately seedling survival (Phua & Corlett 1989, Corlett & Lucas 1990, Dominy & Duncan 2005).

Spit and dropped seeds may be exploited by other mammalian seed dispersers such as rodents, deer, peccaries, and tapirs (Forget 1990, Miura *et al.* 1997, Fragoso & Huffman 2000, Chen *et al.* 2001, Beck 2005), which may then serve either as primary dispersal agents (dropped fruits), secondary dispersal agents (spit seeds), or seed predators (Vander Wall *et al.* 2005). Rodents also may secondarily remove seeds from feces or regurgitate (Forget & Milleron 1991, Wenny 1999, Feer & Forget 2002). Recently, it has been suggested that some rodents may play a particularly important role in diplochory by scatterhoarding seeds. Secondary dispersal by rodents offers several advantages to the seeds including: (1) burial avoids escape from fungal attacks and terrestrial predation by other animals; (2) burial in a variety of different cache sites results in less sibling competition; and (3) burial in a new, more favorable microhabitat favors germination and seedling success (Vander Wall & Longland 2004). The distance to which mammals remove seeds relative to deposition site (secondary dispersal) or parental trees (primary dispersal) varies significantly among species. For example, peccaries and tapirs perform long-distance seed movement (up to 10 km and 20 km, respectively; Fragoso *et al.* 2003, Beck 2005), while small-bodied mammals such as rodents move seeds much shorter distances (5–100 m; Jansen & Forget 2001).

MASTICATED AND DESTROYED SEEDS.—Many seeds are first masticated and thereby killed before swallowing. Several factors influence seed predation, including seed or fruit density, seed hardness, and seed size. Mammal groups that most frequently consume tropical seeds include primates, rodents, and ungulates; moreover, taxa that are primarily seed dispersers (*e.g.*, cercopithecine monkeys) can also masticate and destroy a certain percentage of seeds from fruits they consume (Kaplin & Moermond 1998).

Although primates are generally thought to be principally seed dispersers, several species are seed predators. Indeed, some primates exhibit anatomical specializations that are argued to have evolved specifically for seed predation (Kinzey & Norconk 1990, 1992; Kinzey 1992). Members of the subfamily Pithecinae, for example, exhibit a derived anterior dentition, including large, laterally splayed canines and anteriorly inclined upper and lower incisors. Primate taxa other than pitheciines also prey on seeds. In lowland Brazil, brown capuchins (*Cebus apella)* overcome seed protection mechanisms with their manipulative skills and strong jaw, and have a significant predatory impact on several plant species (Peres 1991). In Borneo, leaf monkeys (*Presbytis rubicunda*) chisel fruit pulp off seeds, drop the pulp to the forest floor, and then break the seed coat and swallow seeds (Davies 1991). Gautier-Hion *et al.* (1993) found that in Zaire, Wolf's guenon (*Cercopithecus wolfi*) were seed eaters when fleshy fruit were unavailable.

After primates, rodents are perhaps the second largest group of mammalian seed predators in tropical regions. Rodents can be characterized as seed predators, seed cachers, or seed hoarders. Families that are principally composed of seed predators include most species of Muridae (rats and mice), Sciuridae (squirrels), and Hystricidae (Old World porcupines; Table 1). Although rodents that practice seed-caching and seed-hoarding principally consume seeds, distinctions between those taxa that cache seeds for further use and those that do not are important to eventual seed fate. Two main foraging behaviors employed by many rodents, scatterhoarding and larder-hoarding (Vander Wall 1990), produce different seedshadows and ultimately have different effects on seed survival. In larder-hoarding, seeds are usually buried more deeply and in fewer locations, while in scatterhoarding, seeds are buried less deeply and in several locations. Scatterhoarding may contribute to seed survival when one of the following occurs: (1) the rodent forgets the location of a cache, (2) the rodent has a superabundance of seeds in several caches, and thus does not return to all of them, or (3) the rodent suffers mortality and fails to return to a cache (Jansen *et al.* 2004). The depth of larder-hoarded seeds results in a low probability of germination; therefore rodents that principally larder-hoard are mostly seed predators (Hulme 2002). Many rodents that consume seeds practice some scatterhoarding, and therefore contribute to some seed dispersal (Vander Wall & Longland 2005).

Many ungulates regularly consume and destroy seeds and thus may be particularly important in affecting seedshadows in tropical forests. Peccaries, for example, bite off seeds and are the main source of mortality to the buriti palm (*Mauritia flexuosa)* in Amazonian forests where they occur (Antonik 2005). Wild (*S. scrofa*) and bearded pigs (*S. barbatus*) are two of the most important predators of fallen fruits and seeds in Southeast Asia and are particularly important predators of mast fruiting species in this region (Curran & Leighton 2000, Curran & Webb 2000).

In sum, regardless of which fruit processing behavior is employed, the way a mammal initially handles the fruit/seed will directly influence both the distance of dispersal and the density of seeds dispersed. Both of these characteristics directly influence the success of germination and establishment of the seeds handled by mammals. Body size, digestive strategies, ranging behavior, and defecation patterns are all important characteristics that influence seedshadows created by mammals.

CAN WE IDENTIFY ECOLOGICAL EQUIVALENCY OF MAMMALS IN SEED DISPERSAL BETWEEN CONTINENTS?

Few studies have been designed to conduct cross-continental comparisons for any attributes of tropical forests, including the ecological equivalence of mammals in seed dispersal (Corlett & Primack 2006). Nevertheless, a comparison of the ecological role in seed dispersal of mammalian taxa in different tropical regions may provide some insights into our understanding of the potential effects of their removal. Comparing seven orders of frugivorous mammals (Table 1), Primates and Chiroptera play similar roles in an inter-continental comparison; these orders mostly remove seeds, performing primary seed dispersal. Nevertheless, both primate and chiroptera frugivory are quite variable across continents.

PRIMATES.—African monkeys consume more species with medium-sized fruits (>1 to < 3 cm) while Neotropical monkeys consume more species with larger fruits (>3 cm) (Lambert & Garber 1998). In addition, Old World frugivorous primates show a preference for more greenish fruits (Dominy & Lucas 2001), while Neotropical frugivorous species such as spider monkeys (*Ateles geoffroyi*) prefer reddish fruits (Stoner *et al.* 2005). As a consequence of having cheek pouches, high-crowned bilophodont molars, and very long digestive retention times, seed-spitting among Asian and African monkeys (Cercopithecinae) is much more common than it is in the Neotropics (Corlett & Lucas 1990; Lambert 1999, 2001). Primates also play an important role in predispersal seed predation; however, their role as predispersal seed predators is restricted to particular primate species within each region. Predispersal seed predation has been reported for *Cercopithecus ascanius* and *Cercocebus albigena* in Africa (Lambert & Garber 1998), *Pithecia pithecia*, *Chiropotes satanas* (Kinzey & Norconk, 1990, 1993; Kinzey 1992; Norconk *et al*. 1998) and brown capuchins *Cebus apella* (Peres 2001) in the Neotropics, and leaf monkeys (*P. rubicunda*) (Davies 1991) and proboscis monkeys *Nasalis narvatus* in the Indomalyan region (Yeager 1989).

CHIROPTERA.—The importance of New World leaf-nosed bats (Phyllostomidae: Microchiroptera) and Old World fruit bats (Pteropodidae: Megachiroptera) in seed dispersal is similar based on the number of species they disperse; nevertheless, seedshadows produced by these groups are different because of their respective food processing techniques and foraging distances. Approximately 400 plant species have been identified as bat-dispersed in the Neotropics (Lobova & Mori 2004) and approximately 300 plant species are consumed, and presumably dispersed by bats in the Paleotropics (Shilton *et al.* 1999). In the Krakatau Islands of Indonesia, Megachiropterean bats are important for seed dispersal for primary succession where they are the principal dispersers of approximately 14 plant species (Whittaker & Jones 1994). Frugivorous Pteropodidae may fly up to 20 km in one night foraging (Banack & Grant 2002), while the greatest distance documented for a frugivorous Phyllostomid is 8 km (Morrison 1978). Gut passage increases percent germination in four of seven species of seeds carried by Phyllostomids, while gut passage increases percent germination in only three of 15 species of seeds carried by Pteropodids (Traveset 1998). In general, Neotropical bats consume more small-seeded fruits (< 2.5 mm) than large-seeded fruits (> 2.5 mm), compared to Paleotropical bats (Richards 1990, Shilton *et al.* 1999, Passos *et al.* 2003). This difference may be largely due to the overall smaller size of Neotropical bats (< 100 g) compared to the large frugivores (up to 1.2 kg) found in the Pteropodiade family of the Paleotropics, since larger bat species can remove larger fruits (Dumont 2003). In Indomalyan areas, large pteropodid bats can carry fruits as big as 200 g and play a particularly important role in the dispersal of large-seeded species in this region (Corlett 1998). Bats play an important role in primary dispersal of fig species in both Paleotropical and Neotropical areas (August 1981, Shilton *et al.* 1999, Korine *et al*. 2000, Shanahan *et al.* 2001, Stier & Mildenstein 2005).

CARNIVORA.—The Carnivora also represent an important group of seed dispersers in one of the three tropical areas compared. Their impact is greatest in the Indomalayan region where they represent the third largest group of importance among frugivorous mammals (Kitamura *et al.* 2002). Civets (Viverridae) are the most important family within this group, which includes the genera *Paguma, Paradoxurus, Arctictis*, and *Viverricula*. Several other families play an important role in fruit removal in the Indomalayan regions as well, including Ursidae, Mustelidae, Ailuridae, Canidae, Herpestidae, and Felidae (Corlett 1998). Seed dispersal is less common by carnivores in Africa but has been documented in side-striped jackals (*Canis adustus*) and African civets (*Civettictis civetta;* Ray & Sunquist 2001, Atkinson *et al*. 2002, Kaunda & Skinner 2003). Similarly, in Neotropical areas, few families of carnivores are frugivorous. Two genera within the Procyonidae (*Potos* spp. and *Nasua* spp.) represent the most frugivorous of Neotropical carnivores (Kays 1999). Other groups within the Carnivora such as river otters (Mustelidae: *Lutra* spp., Quadros & Monteiro-Filho 2000), tayras (Mustelidae: *Eira barbara*; Konecny 1989), and some canids in South America (*Cerdocyon thous, Lycalopex vetulus, Chrysocyon brachyurus*) also play a minor role in seed dispersal in the Neotropics (Dalponente & De Souza 1999, Pizo 2002).

RODENTIA.—The Rodentia function as seed predators in all tropical areas (Table 1). Nevertheless, their role in secondary seed dispersal is particularly important in the Neotropics where some genera (*i.e.*, *Dasyprocta, Proechimys*, and *Heteromys*) act as important secondary seed dispersers by scatterhoarding seeds (Forget & Milleron 1991). This is particularly important as one tree species depends fully on caviomorph rodents to disperse its seeds (Forget 1992, 1993; Asquit *et al.* 1999). The role of rodents in secondary dispersal in the Paleotropics has only recently been explored. Yasuda *et al.* (2000)

showed that scatterhoarding is practiced by the long-tailed giant rat (Muridae: *Leopoldamys Sabanus*) and the three-striped ground squirrel (Sciuridae: *Lariscus insignis)* at Pasoh Forest Reserve, Peninsular Malaysia. In a recent review of scatterhoarding mammals, Forget and Vander Wall (2001) suggest that scatterhoarding behavior in Malaysia and Neotropical terrestrial rodents has evolved independently in these two tropical regions. Secondary seed dispersal by rodents in the African region has not been documented.

Squirrels play a significant role in predispersal seed predation in all tropical regions where they are present. In Neotropical areas, the red-tailed squirrel *Sciurus granatensis* can consume up to 58 seed species, generally destroying the seeds. This squirrel represents the principal predispersal seed predator of at least two species of palms (*Astrocaryum standleyanum* and *Scheelea zonensis*) and of the canopy tree *Dipteryx panamensis* on Barro Colorado Island, Panama (Glanz *et al*. 1990). In a coastal forest in Kenya, squirrels are the main seed predator of the canopy tree *Afzelia quanzensis* (Gathua 2000). Nevertheless, in Cameroon, Clark *et al.* (2001) suggest that squirrels also play an important role in seed dispersal, principally by dropping fruits and allowing them to escape other potential arboreal seed predators. Furthermore, Corlett (1998) suggest that squirrels have the potential to be important seed dispersers in Indomalayan regions.

PROBOSCIDEA, PERISSODACTYLA, AND ARTIODACTYLA.—In the Paleotropics, there are more species of large terrestrial ungulates, and several megaherbivores that are not present in the Neotropics (Dinerstein 1989). The social behavior of herbivores greatly influences their impact on vegetation and seeds. The largest herbivores in the Paleotropics, elephants, travel in social groups. In contrast, the largest herbivore in the Neotropics, the tapir, is generally solitary (Fragoso *et al.* 2003). Other large terrestrial herbivores in the Neotropics include peccaries and deer. Rain forest deer are solitary, whereas peccaries often travel in large herds (Kiltie & Terborgh 1983). In both the Paleotropics and Neotropics, herbivores moving in herds tend to destroy much vegetation, either through rooting for buried resources, trampling, or uprooting (Feer 1995, Fragoso 1998). These differences among regions may result in different patterns of seed dispersal by ungulates. For example, very large elephant-dispersed seeds in Uganda are dispersed for long distances and along created swaths (Chapman *et al.* 1992). In the Neotropics, herding behavior by peccaries results in long-distance seed dispersal and a clumped pattern of deposition (Fragoso 1998). Ungulates are missing from some tropical forests, such as New Guinea and Madagascar (Corlett & Primack 2006), but are hypothesized to fill a similar niche in African tropical rain forests as large rodents, such as paca (*Agouti paca*), do in South America (Dubost 1968).

Perissodactyla represent some of the largest terrestrial mammals that consume fruit in tropical areas. They specialize on consuming fallen fruits, resulting in seed dispersal a distance from the parent tree (Fragoso & Huffman 2000). Tapirs in the Indomalayan (Corlett 1998) and Neotropical (Foerster & Vaughan 2002, Galleti *et al.* 2001) regions, and rhinos in African and the Indomalayan regions (Corlett, 1998) are important seed dispersers of large-seeded fruits.

Artiodactyla also represent an important group that consumes fruits in tropical areas. Indomalayan and African regions possess the greatest diversity of this group compared to Neotropical regions. Artiodactyla are mostly seed predators (peccaries and wild pigs) but seed dispersal has been reported for several species (Asian mouse deer, brocket deer, and some antelope). Some species of Artiodactyla in the Indomalyan region can be important secondary seed dispersers, as they consume fruits that are defecated by arboreal frugivores such as orangutans (Corlett 1998). In the African region, it is likely that Artiodactyla more frequently act as seed predators than dispersers; however, at least 13 species of plants are dispersed by this group of ruminants (Gautier-Hion *et al.* 1985).

In summary, general taxonomical groups of frugivorous mammals appear to play similar roles in different tropical regions; however there are some distinct differences (Table 1). These differences depend on the original pool of mammals, the taxonomic structure of the fruit plants, and the evolution of particular mammal´s behavior within each tropical region (Fleming *et al.* 1987, Mack 1993).

EFFECTS OF MAMMAL HUNTING ON SEEDSHADOWS

Mammal size is one of the most important characteristics determining both hunting pressure (Jerozolimski & Peres 2003, Peres & Palacios 2007) and seed manipulation. Indeed, large-seeded fruits are generally dispersed only by large vertebrates, which often are the taxa most vulnerable to hunting pressure in tropical regions (Table 1). Furthermore, many of the hunted large mammals also range widely; thus, hunting not only affects the size-class of seeds dispersed, but also the distance of dispersal. Long-distance seed dispersal is especially prominent in large herbivores such as elephants (Dudley 1999, Cristoffer & Peres 2003), tapirs (Galetti *et al*. 2001, Fragoso *et al*. 2003), and some deer (Bodmer 1991). Several species of primates, such as spider monkeys in the Neotropics (Russo & Augspurger 2004) and gibbons in the Paleotropics are also important for long-distance seed dispersal (McConkey 2005b) and are highly sought after as game species. It is likely that the elimination of this guild (large frugivorous mammal seed dispersers) will ultimately result in less recruitment of large-seeded species and eventually will have negative demographic effects on species that are principally dispersed by this guild. Direct observations of the large-seeded vertebrate dispersed canopy tree *Antrocaryon klaineanum (Anacardiacea)* in Cameroon indicate that seed removal is severely reduced in hunted areas (Wang *et al.* 2007). Furthermore, in this same study, genetic analysis shows that 2 percent of the seeds found below the canopy of 'mother' trees in hunted areas actually have a different genetic mother, while 42 percent of seeds found below 'mother' trees in protected areas represent dispersed seeds with different genetic mothers.

Hunting also targets the larger Neotropical seed hoarders, including agoutis and acouchis. A recent study by Forget and Jansen (2007) shows that hunting negatively affects the dispersal of *Carapa procera* seeds. They suggest that consistently lower rates of seed dispersal caused by hunting agoutis and acouchis will likely result in lower levels of seedling recruitment. As densities of these species continue to be reduced, smaller rodents that tend to be principally seed predators may become the dominant rodents affecting seeds in Neotropical forests (Wright et al. 2000, DeMattia *et al.* 2004, Dirzo *et al.* 2007). In addition, changes in rodent communities caused by hunting may influence plant distributions through differential treatment of nuts of various sizes by different sized rodents. For example, small nuts are often buried farther away and retrieved less often from site of deposition than large nuts (Brewer & Webb 2001). Geographic differences in the rodent guild are particularly important with these highly abundant mammals. Small seed predators are more common in Asian rain forests; predation rates in one study in Indonesia were higher for smaller seeds, a finding generally contradictory to what is found in the Neotropics (Blate *et al.* 1998).

The reduction in density of medium- and large-sized seed dispersers and predators will likely result in fewer large-seeded species being dispersed and a concomitant reduction in predispersal seed predation for large-seeded species. Indeed, this hypothesis is supported by the work of Beckman and Muller-Landau (2007)—a large-seeded species (only consumed by medium- and large-sized mammals) experienced a significant reduction in predispersal seed predation by mammals in areas with hunting, whereas a second smaller-seeded species showed little predispersal seed predation by mammals at hunted and protected sites.

Since so much variation exists in mammal features affecting seed dispersal, both within and between mammalian taxa, as well as between continents, the ultimate effect of the removal of these mammals from particular tropical forests will depend on the local composition of the mammal community. The extent to which compensatory changes may occur between hunted and not-hunted mammals will also vary among different mammal communities and undoubtedly will determine the ultimate effect that hunting has on any particular community (Wright 2003).

CONCLUDING REMARKS

The complex role that mammals play in seed dispersal and ultimately tropical forest regeneration cannot be easily quantified. This review emphasizes the variation in seed dispersal that exists both within and between mammal taxa and among continents. Nevertheless, the papers compiled within this Special Section show that we are beginning to understand and document the effects of the removal of mammals on tropical forest regeneration (Wright *et al.* 2007).

The removal of medium and large mammals through hunting not only directly affects their densities but also may affect the behavior of the remaining individuals. That trend may in turn have consequences for seed dispersal and ultimately affect the structure and composition of regenerating forests. For example, ungulates, including deer and peccaries, have been shown to change their habitat preference from drier areas to low-flooded forests in response to hunting pressure in Campeche, Mexico (Reyna-Hurtado & Tanner 2005). In Africa, megaherbivores such as elephants and rhinos avoid forest edges in areas where they are hunted (Kinnaird *et al.* 2003). Finally, the foraging behavior of flying foxes is directly dependent on population density; under conditions of high density aggressive interactions result in 58 percent seed dispersal, as opposed to less than 1 percent dispersal under a threshold level of low density (McConkey & Drake 2006). The long-term consequences of behavior modification due to hunting have not yet been evaluated, but are an important component that requires investigation.

We have presented information on seed dispersal from the Neotropics in more detail than the Paleotropics because of the lack of studies on seed dispersal for many mammal groups in the latter region. This dearth of information reveals an important gap in our knowledge and suggests avenues for future research. In addition, more studies should evaluate the relative importance of the disappearance of both seed dispersers and seed predators for particular plant species so that we may begin to understand the balance between these two forces. Finally, it is also important that future studies identify ecological redundancy in nonhunted vertebrates within any particular community to evaluate compensatory behavior that may help buffer some of the negative effects of hunting of large and medium mammals.

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