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Primate Seed Dispersal
Linking Behavioral Ecology with Forest Community Structure

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INTRODUCTION

The role of animals in seed dispersal is well recognized. As many as 75% of tropical tree species produce fruits presumably adapted for animal dispersal (Frankie et al. 1974, Howe and Smallwood 1982), and animals are estimated to move more than 95% of tropical seeds (Terborgh et al. 2002). Some vertebrate groups may be particularly important seed dispersers. Primates, for example, comprise between 25% and 40% of the frugivore biomass in tropical forests (Chapman 1995), eat large quantities of fruit, and defecate or spit large numbers of viable seeds (Lambert 1999). Primate frugivory and seed dispersal have been quantified by studies in South America (Garber 1986, Julliot 1996, Stevenson 2000, Dew 2001, Vulinec 2002), Central America (Estrada and Coates-Estrada 1984, 1986; Chapman 1989a), Africa (Gautier-Hion 1984; Gautier-Hion et al. 1985; Wrangham et al. 1994; Chapman and Chapman 1996; Kaplin and Moermond 1998; Lambert 1999; Voysey et al. 1999a,b), and Asia (Corlett and Lucas 1990, Davies 1991, Leighton 1993, Lucas and Corlett 1998, McConkey 2000). This research has illustrated that primates disperse significant numbers of seeds. For example, on Borneo, a single gibbon group (*Hylobates mulleri* × *agilis*) dispersed a minimum of 16,400 seeds · km^{-2} · year^{-1} of 160 species; and since the survival rate of seeds to 1 year was 8%, a group of gibbons effectively dispersed 13 seedlings · ha^{-1} · year^{-1} (McConkey 2000).

Although it is clear that primates play an important role in dispersing many seeds throughout tropical forests, the ecological and evolutionary significance of these activities is not well understood. The objective of this chapter is to review the role that primate seed dispersal plays in shaping the ecology of tropical forests and to shed light on inconsistencies in the literature in order to point to new directions for research. We first evaluate how variation among primate species in traits such as digestive anatomy, body size, social structure, movement patterns, and diet influences the spatial distribution of dispersed seeds (the *seed shadow*, App. 31.1) and thereby produces a diversity of seed shadows. We then consider how traits of fruiting species, including patch characteristics and fruit and seed traits, influence the seed shadow that different primates generate. Few studies have

quantified primate-generated seed shadows. However, to understand their effect on plants, it is important to consider primate seed shadows in light of plant population and community ecological theory. To this end, we next review current theories and concepts and evaluate the role that primate seed dispersal plays in plant ecological processes. This analysis of variation in seed shadows points to two critical areas in which our understanding of primates' roles is currently lacking: the significance of primates dispersing seeds in clumped versus scattered patterns and the consequences of primate seed dispersal to different distances away from the parent tree. We conclude by discussing potential conservation implications related to changes in the nature of primate–plant interactions.

VARIATION IN SEED SHADOWS GENERATED BY PRIMATES

Dispersal of seeds by primates results in a seed shadow (App. 31.1). The shape of the seed shadow is defined by the dispersal processes that produce it, namely, what proportion of seeds are dispersed from parent tree crowns, which depends on the visitation rate and the number of seeds dispersed per visit of a dispersal agent, how far those seeds are moved from the parent (*seed dispersal distance*, App. 31.1), and the locations and densities at which seeds are deposited (*dispersal sites* and *seed density*, App. 31.1). The interaction between traits of primates and of the fruit-producing plant species that they feed upon influences these dispersal processes, thereby shaping the seed shadow. The shape of the seed shadow is important because it influences the survival of seeds to the seedling stage (Janzen 1970, McCanny 1985), which is a critical demographic process in the life cycle of a plant, and may ultimately influence the spatial distribution of plants in later life stages (Nathan and Muller-Landau 2000, Wang and Smith 2002).

Traits of Primates

As seed dispersal agents, frugivorous primates have high functional diversity in traits influencing dispersal processes,

such as digestive anatomy, body size, social structure, movement patterns, and diet, all of which generate heterogeneity in seed shadows. Few studies have quantified how variation in these factors affects seed deposition patterns. However, data are becoming available that identify trends in these relationships, which should be further evaluated in future studies.

Primates largely disperse seeds by *endozoochory* (App. 31.1), but once an animal has located and acquired fruit, there remains the challenge of what to do with the seeds. Protective seed coats are typically difficult to digest, and seeds themselves can also account for more than half of the weight of fruits consumed by primates (van Roosmalen 1984, Waterman and Kool 1994). Swallowed seeds can thus represent a significant cost in that they not only increase an animal's body mass but may also displace more readily processed, nutritious digesta from the gut. Given these constraints, it is somewhat surprising that seed swallowing is by far the most common means of primate seed dispersal in the Neotropics (Estrada and Coates-Estrada 1984, Chapman 1989a, Andresen 1999). In the Paleotropics, many primates also swallow seeds (Lieberman et al. 1979, Corlett and Lucas 1990, Wrangham et al. 1994, Lambert 1999, Kaplin and Lambert 2002); however, seed spitting is common in African and Asian cheek-pouched monkeys (Cercopithecinae, Gautier-Hion 1980; Rowell and Mitchell 1991; Kaplin and Moermond 1998; Lambert 1999, 2000). Cheek pouches of cercopithecines have nearly the same capacity as their stomachs (Fleagle 1999) and allow these monkeys to store multiple fruits and extract the pulp without incurring the costs of ingested seeds (Lambert 1999). They may process the fruits and spit out seeds at or away from parent trees.

Other primates consistently prey upon seeds (App. 31.1) as ingested seeds do not appear in feces or are fragmented. These include black and white colobus (*Colobus guereza*, Poulsen et al. 2001), saki monkeys (*Pithecia pithecia* and *Chiropotes satanas*, Kinzey and Norconk 1993), and red leaf monkeys (*Presbytis rubicunda*, Davies 1991). The extent to which primates act as seed predators is likely underreported since some authors lump seed predation with the ingestion of fruit. Primates' seed-handling strategies depend on the interactions between their digestive anatomy and the traits of the fruiting species (Norconk et al. 1998).

Variation in seed-handling strategies, social structure, and movement patterns shapes the seed shadows primates generate (Fig. 31.1). Some of these characters are predictably related to body size. Primates range in body mass from the 30 g pygmy mouse lemur (*Microcebus myoxinus*) to the 200 kg gorilla (*Gorilla gorilla*, Fleagle 1999). Larger primates typically have larger gut capacities, longer digesta passage times, and longer day ranges than smaller primates, although substantial variation in these relationships exists (Kay and Davies 1994, Lambert 1998, Nunn and Barton 2000). In particular, similarly sized species may have different ranging patterns due to different social systems. These characters, in turn, influence the quantity of seeds dispersed as well as their sizes, passage times, dispersal distances, and
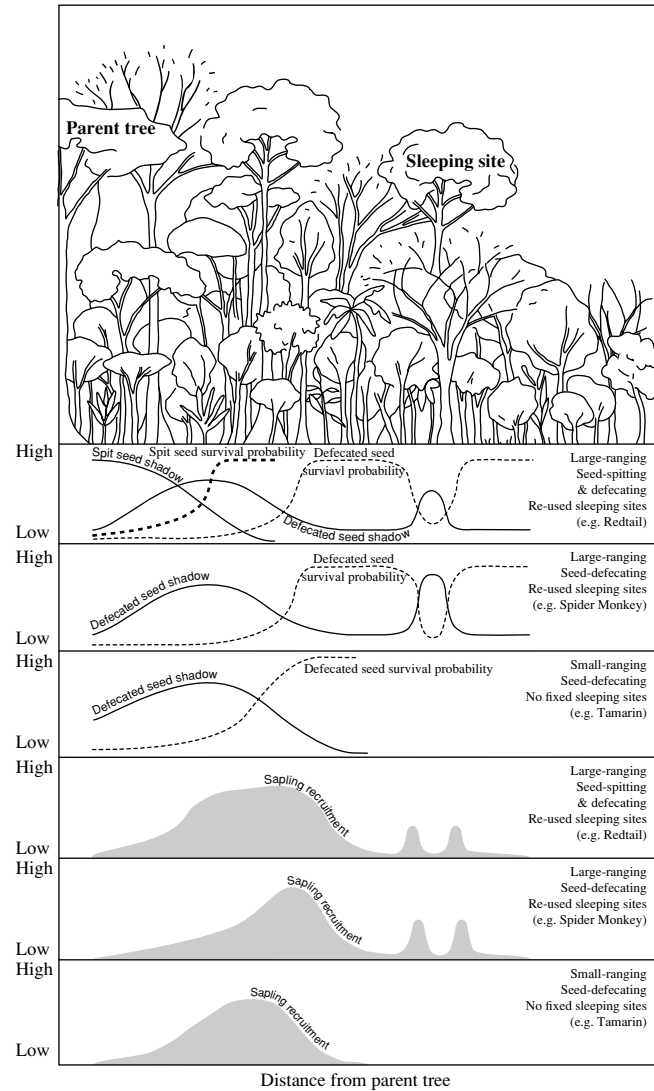

Figure 31.1 The predicted patterns of seed deposition, seed survival, and sapling recruitment for a hypothetical tree species dispersed by primates with different seed-handling strategies and ranging patterns. For many forest tree species, including the hypothetical one depicted here, some habitats may be more suitable for recruitment than others. Hence, the shape of the survival curve will depend on the plant species, but this source of variation is not depicted in the figure. Actual recruitment probabilities are entirely dependent on the actual seed densities relative to realized per-capita-survival probabilities, but in this schematic we show possible qualitative relationships. The relative difference in the height of the seed shadow curve and the survival curve will determine whether clumped seed deposition patterns remain clumped as individuals age. This will partly be determined by the strength of distance- and density-dependent mortality at the seed and seedling stages, as well as other sources of mortality that are nonrandom in space or time, relative to the spatial scale and strength of clumping of seed deposition.

spatial distribution (Table 31.1, App. 31.1). However, based on the limited available data (Table 31.1), we found no statistically significant relationship between either the mean or the maximum seed dispersal distance of primate species and body size (Spearman rank correlation $r = 0.009$, $p = 0.979$, $n = 11$, mean distance; $r = 0.108$, $p = 0.818$, $n = 7$, maximum distance).

Table 31.1   Estimates of the Straight-Line Distance (m) that Primate Species Disperse Seeds Away From the Parent Plant

SPECIES	WEIGHT[1] (KG)	SOCIAL STRUCTURE[2]	PASSAGE TIME[3] (HR)	DISTANCE (SD) (M)	MODE (M)	RANGE (M)	REFERENCE
Seeds swallowed							
Saguinus spp.	0.5	1	3.3	–	100–200	34–513	Garber (1986)
Cebus apella	2.5	3	3.5	390 (215)	–	–	Zhang and Wang (1995)
Cebus capucinus[4]	3.3	3	3.5	–	–	200–1,000	Rowell and Mitchell (1991)
Cebus capucinus[4]	3.3	3	3.5	208 (113)	–	20–844	Wehncke et al. (2003)
Alouatta palliata[4]	6.2	1	20.4	–	–	10–811	Estrada and Coates-Estrada (1984)
Alouatta seniculus	7.3	1	35.0	225 (129)	–	0–550	Julliot (1996)
Ateles paniscus	6.2	2	5.3	151 (241)	–	11–1,119	Russo (2003a)
Ateles paniscus	6.2	2	5.3	254 (145)	–	–	Zhang and Wang (1995)
Ateles belzebuth	6.0	2	–	245	–	50–500	Dew (2001)
Lagothrix lagotricha	6.3	2	6.8	300	–	0–390	Stevenson (2000)
Lagothrix lagotricha	6.3	2	6.8	354 (213)	300–400	0–989	Stevenson (2000)
Lagothrix lagotricha	6.3	2	6.8	245	–	50–500	Dew (2001)
Cercopithecus ascanius	3.6	3	20.2	1,178			Lambert (1997)
Hylobates mulleri × *agilis*	5.9	1	–	220 (215)	0–1,250		McConkey (2000)
Pan troglodytes	36.4	2	23.2	3,000			Lambert (1997)
Seeds spit out							
Cercopithecus ascanius	3.6	3	20.2	2	10	0–100	Lambert (1999)
Cercopithecus mitis	6.0	3	21.3	–	–	30–50	Rowell and Mitchell (1991)
Pan troglodytes	36.4	2	23.2	4	1	0–20	Lambert (1997, 1999)

[1] Average of male and female weight (from Harvey et al. 1987).
[2] Social structures are 1, cohesive; 2, fission–fusion; 3, dispersed foraging groups.
[3] Average passage time through the digestive tract (from Lambert 1998).
[4] Estimates from passage time and path length.

Social structure can also affect primate seed shadows. Primates with more fluid social structures, such as the fission–fusion societies of spider monkeys (*Ateles* spp.) and chimpanzees (*Pan troglodytes*) and the multi-species foraging groups of capuchins (*Cebus* spp.), cover large areas in their daily ranges; and individuals in groups are often widely dispersed (Terborgh 1983, McFarland 1986). Thus, one might expect primates with fluid social structures to have a more scattered pattern of seed dispersal than species with more cohesive ones. For example, Wehncke et al. (2003) demonstrated that white-faced capuchins (*Cebus capucinus*) on Barro Colorado Island, Panama, spend only 10 min feeding in individual trees, travel between 1 and 3 km a day, and defecate seeds in small clumps throughout the day. Repeated use of the same sleeping site may alter this relationship (Fig. 31.1). Seeds defecated diurnally by spider monkeys (*Ateles paniscus*) in Peru were more widely scattered and had longer dispersal distances than did those defecated at sleeping sites, which were closer to parent trees and more clumped (Russo and Augspurger 2004). No data are available to compare the extent of clumping in seed shadows generated by primates with fluid versus cohesive social structure. However, based on the data in Table 31.1, there is no difference in the mean dispersal distances of species with fluid (e.g., spider monkeys) or dispersed (e.g., redtail monkeys) groups in

comparison to primates whose social structures are more cohesive (e.g., howler monkeys; $t = 1.024$, $p = 0.333$, $n = 12$). Furthermore, in species that do not have cohesive group structures, sex and age may influence seed shadows. In spider monkeys and woolly monkeys (*Lagothrix lagotricha*), males have greater day ranges and tend to disperse seeds longer distances than do females (Symington 1987b, Stevenson 2000, Dew 2001).

The interaction between diurnal variation in movement patterns and passage time affects both dispersal distance and the spatial distribution of seeds. For example, seeds ingested by spider monkeys (*Ateles* spp.) and woolly monkeys (*Lagothrix lagotricha*) in the morning or early afternoon tend to be dispersed the same day. In contrast, seeds ingested later in the afternoon tend to be dispersed at sleeping sites at night or the next morning (Stevenson 2000, Dew 2001, Russo 2003a). In addition, foraging movements in the morning and early afternoon tend to be faster than those in the late afternoon (Chapman and Chapman 1991). As a result, seeds ingested early in the day are likely dispersed longer distances than those ingested later (Stevenson 2000, Dew 2001, Russo 2003a).

Variation in diet can also influence seed shadows, not only by determining which fruiting species are dispersed but also because the quantity of nonfruit foods in the diet

typically increases seed passage time (Milton 1981, Kay and Davies 1994, Lambert 1998). Primates that consume substantial quantities of leaves, such as howler monkeys (*Alouatta* spp.), have greater colon volume than do similarly sized close relatives (e.g., spider monkeys [*Ateles* spp.]; Milton 1981, 1986). As a result, howler monkeys have longer passage times than do spider monkeys (Milton 1981, 1986). However, this difference does not necessarily translate into longer seed dispersal distances by howler monkeys as they tend to move slower and have smaller day ranges than do spider monkeys (Milton 1981).

Primate Responses to Traits of Fruiting Species

Primate species respond differently to traits of fruiting species, and this response generates variation in seed shadows. These traits range from those at the community level, such as the abundance and distribution of fruit resources, to those at the individual plant or patch level, such as fruit production, to those at the level of a single fruit or seed, such as seed size. Primates' responses to fruiting plant traits are mediated by many factors, including their foraging decisions, digestive anatomy, seed-handling strategies, social structure, and ranging behavior. Taken together, these plant–primate interactions determine the variation in the seed shadows that primates generate, which in turn influences plant demography and spatial distribution. Here, we consider how variations in *(1)* the distribution and abundance of fruit resources, *(2)* the characteristics of fruit patches, and *(3)* fruit and seed traits influence primates' seed shadows.

Distribution and Abundance of Fruit Resources

Primates' foraging decisions, and hence visitation and seed dispersal of fruiting species, are sensitive to the community-wide abundance and distribution of fruit resources (Agetsuma and Noma 1995, Garber and Paciulli 1997, Janson 1998). Fruit is a spatially and temporally patchy resource (Frankie et al. 1974, van Schaik et al. 1993). As such, any particular fruiting species may not be reliable, especially given the rarity of tropical plant species in general and their tendency to have supra-annual fruiting schedules (Chapman et al. 1999, in press). Such variability in fruit resources likely contributes to the often observed pattern of dietary plasticity and helps explain the great diversity of plant species that primates disperse (Chapman 1987, 1995; Chapman et al. 2002; Russo et al. in press). A comparative study of diets in spider monkeys (*Ateles* spp.) indicated that, despite their catholic diets, spider monkeys appear to prefer relatively abundant fruiting species that consistently produce annual crops (Russo et al. in press).

The community-wide abundance of fruit may also affect dispersal distances and the frequency of seed predation. During periods of community-wide fruit scarcity, daily path lengths of spider and woolly monkeys decreased and the proportion of time spent resting increased relative to periods of fruit abundance (Symington 1987b, Stevenson 2000). As

a result, dispersal distances may decrease during periods of fruit scarcity. In addition, the consumption of unripe fruit by some primates, which likely represents seed predation, often increases during periods of fruit scarcity (Kaplin et al. 1998, Stevenson 2000). Cercopithecine monkeys alternate between acting predominantly as seed spitters, seed predators, and seed defecators depending on fruit resource availability (Kaplin et al. 1998).

Since the vast majority of primate field studies are relatively short-term (i.e., 1 year or less), it is difficult to assess the importance of periods of fruit scarcity. Yet, these times may be important periods of selection for both the primate dispersers and the trees. Fruit availability has been quantified in Kibale National Park, Uganda, for over 12 years (Chapman et al. in press). Over this period, temporal variation in fruit availability was high; the proportion of trees per month with ripe fruit varied from 0.1% to 15.9%. In addition, there was dramatic interannual variation in fruit availability: in 1990, on average only 1.1% of trees bore ripe fruit each month, while in 1999 an average of 6.7% of trees bore fruit each month (Fig. 31.2). If a month of fruit scarcity is defined as one with <1% of monitored trees bearing ripe fruit, there is considerable interannual variation in how often frugivores experienced food shortages (Fig. 31.2). For example, 9 of the 12 months in 1990 had <1% of the trees with fruit, while in 2000 no month had <1% of trees fruiting. This level of variability means that for a tree that fruits during a period of general community-wide fruit scarcity, the probability of its seeds being dispersed is likely very different from that in a subsequent year when a greater number of species are attempting to attract the services of dispersers.

Characteristics of Fruit Patches

Characteristics of fruit resource patches, such as size and density of fruits, affect visitation by primates (Leighton 1993). Greater numbers of ripe fruits in the nutmeg tree (*Virola calophylla*, Myristicaceae) increased both visitation and the number of seeds ingested by spider monkeys (*Ateles paniscus*,
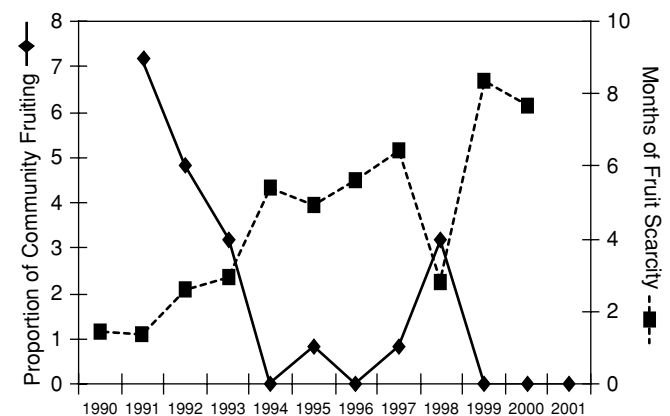

Figure 31.2 The average monthly proportion of the tree community that fruited each year in Kibale National Park, Uganda, and the number of months of fruit scarcity, defined as months with <1% of the entire population bearing fruit.

Russo 2003b). Similarly, orangutans (*Pongo pygmaeus*) preferred to forage in trees with large crop size (Leighton 1993). Furthermore, as the size of primate foraging parties increases, they tend to deplete resource patches completely, thereby increasing travel between patches (Symington 1987a, Chapman and Chapman 2000, Gillespie and Chapman 2001). Seed dispersal distances may therefore increase, all else being equal, as foraging party size increases.

Fruit and Seed Traits

Despite dietary plasticity, primates forage selectively based on traits of fruits and seeds, and these traits have been the basis of describing a primate seed dispersal "syndrome" (van der Pijl 1982, Gautier-Hion et al. 1985). Suites of traits (e.g., color, size, protection) have been interpreted as coadapted features of plants that govern the choice of fruits by dispersers. While these syndromes may be broadly meaningful, responses of different primate species to these traits are nonetheless highly variable, likely due in part to variability in the floristic composition of their habitats and interspecific interactions (Gautier-Hion et al. 1993, Chapman and Chapman 2002, Russo et al. in press). Fruits considered, based on their traits, to be primarily bird-dispersed can be extensively dispersed by primates (Julliot 1996, Russo 2003b). In fact, it may be more difficult for a plant to exclude primates as dispersers, for example, compared to birds since primates are better able to manipulate even fruits protected by hard outer coverings. Gautier-Hion et al. (1985) went so far as to say that these suites of traits exist despite an outstanding lack of specificity between fruit and consumer species. This lack of specificity has led some to question the generality of such syndromes, and they have pointed out large differences in how syndromes have been defined (Fischer and Chapman 1993). For example, based on observations in Peru, Janson (1983) described a primate syndrome as fruits that are large, yellow, orange, brown, or green with a woody outer covering, whereas based on observations in Gabon, Gautier-Hion et al. (1985) described the primate syndrome as fruits intermediate in size, bright red, orange, or yellow and either dehiscent with arillate seeds or succulent and fleshy.

Despite this controversy over the generality of syndromes, primates are obviously selective in their choice of fruits. Choice of fruiting species can be based on morphology (i.e., color, protection, size) as well as nutrient, caloric, and secondary chemical content. Bornean orangutans preferred high pulp mass per diaspore (Leighton 1993). In contrast, spider monkeys (*Ateles paniscus*) did not respond to the aril:seed ratio of the fruits of *Virola calophylla* in terms of either visitation or seed removal (Russo 2003b). Similarly, long-tailed macaques (*Macaca fascicularis*) did not appear to select fruit on the basis of seed or fruit size (Corlett and Lucas 1990), although howler monkeys (*Alouatta seniculus*, Julliot 1996) and four species of lemurs in Madagascar appeared to select fruits in part based on size (Dew and Wright 1998).

The hardness of the fruit's outer covering and its seed plays an important role in the foraging decisions of primates,

thereby governing which primate species disperse or prey upon seeds of a particular species. When sympatric primates compete for fruit resources, these axes of trait variation may provide means of niche separation. In Suriname and Venezuela, the bearded saki monkey (*Chiropotes satanas*) consumes significantly harder fruits than does the spider monkey (*Ateles belzebuth*, Kinzey and Norconk 1990). Furthermore, seeds masticated by saki monkeys are softer than those dispersed by spider monkeys (Kinzey and Norconk 1990). The fruit consumed by redtail monkeys (*Cercopithecus ascanius*) and mangabeys (*Lophocebus albigena*) do not differ in dietary hardness during periods of fruit abundance, but mangabeys exploited a diet more resistant to puncture than redtail monkeys during periods of fruit scarcity (Lambert et al. 2004). This suggests that it is the differences in the mechanical properties of fallback foods during periods of resource scarcity that may facilitate niche separation.

Many primates pass ingested seeds, resulting in few, if any, negative impacts on germination (Estrada and Coates-Estrada 1984, Dew and Wright 1998, McConkey 2000, Lambert 2001, Poulsen et al. 2001, Stevenson et al. 2002). However, even among primate species that rarely prey upon seeds, seed predation may nonetheless occur, albeit at low frequency, and properties of fruits and seeds influence the likelihood of seed predation. Seeds having relatively soft seed coats or that provide no pulp or aril appear more likely to be preyed upon (Corlett and Lucas 1990, Russo et al. in press). The shape and size of the seed may also influence seed handling (Chapman 1995). Primates tend to ingest and disperse more smaller than larger seeds (Corlet and Lucas 1990, Lucas and Corlet 1998, Lambert 1999, Oliveira and Ferrari 2000) and more ovoid than round seeds (Garber 1986, McConkey 2000). When pulp or aril is easily removed from the seed, gibbons (*Hylobates mulleri × agilis*) and long-tailed macaques (*Macaca fascicularis*) tend to spit seeds under the parent tree (McConkey 2000), although some observations indicate this effect may be overridden by the effect of seed size (Corlett and Lucas 1990).

The effect of fruit and seed traits on the probability of being ingested has consequences for seed shadows because seeds that are ingested by primates usually are dispersed longer distances than seeds that are spit-dispersed (Lambert 1999, 2001) (Table 31.1). Furthermore, spit or dropped seeds are likely to be deposited on the forest floor singly as fruits are processed one by one (Lambert 1999). However, swallowed seeds can be deposited either in a high-density clump or as just a few seeds, depending on animal size and position in the canopy, defecation size, and the intensity of the feeding bout during which the seeds were swallowed (Wrangham et al. 1994, Kaplin and Moermond 1998, Andresen 1999, Lambert 1999). In Cameroon, for example, Poulsen et al. (2001) found that gorillas and chimpanzees averaged 18 and 41 large (>2 cm) seeds per fecal sample, respectively, while average numbers of large seeds per fecal sample for four frugivorous monkeys were less, ranging 1.0–2.1 seeds. Some primates that largely ingest seeds, however, do not always

disperse them in clumps (e.g., *Cebus capucinus*; Wehncke et al. 2003). In addition, seeds ingested by spider monkeys (*Ateles paniscus*) that are defecated diurnally tend to be dispersed at lower densities than those that are defecated at sleeping sites (Russo and Augspurger 2004). A similar pattern has been observed for woolly monkeys (Stevenson 2000) and gorillas (Rogers et al. 1998).

Although seed size can influence the passage time of ingested seeds, this effect may not necessarily translate into dispersal distances, which also vary with seed size (Garber 1986, Stevenson 2000; but see McConkey 2000). In fact, in some primates, passage time correlates poorly with dispersal distance, primarily because movements are rarely unidirectional and because seeds dispersed at sleeping sites are retained in the gut overnight (Stevenson 2000), although in primates the relationship is positive (Garber 1986).

Because fruit pulp attracts animals that may disperse a plant's seed, it generally presents less of a challenge to ingest and digest than other primate foods (Janson and Chapman 1999). In general, most fruits are high in sugars but low in fats and protein. As a result, protein content seems to have little to do with fruit choice (Leighton 1993) since the animals often obtain protein from other sources. Immature fruits are often chemically defended against insect or mammalian herbivory, and some species continue to be defended even when the pulp is ripe (Fenner 1992, Cipollini and Levey 1997). Some fruits have evolved chemical traits that appear to restrict dispersal of seeds to a fraction of the frugivore community. For example, the chemicals that make red peppers spicy to humans and other mammals are not perceived by birds (Janson and Chapman 1999). An interesting avenue for future research would involve investigations of whether some of these apparently defensive chemicals can alter gut passage times in primates and thus dispersal distances, as in birds (Murray et al. 1994).

SEED DISPERSAL MODELS

We have a relatively underdeveloped understanding of both seed-deposition patterns created by primates and the relationship between these patterns and the primate movements and behaviors that produce them. This lack of understanding results partly from the difficulty of quantifying complex movement patterns that often occur over large spatial scales. It does, however, hamper our quantification of the effect of primate dispersal agents on plant population and community dynamics. Modeling approaches have proven useful in describing seed-dispersal curves (App. 31.1), as well as the seed shadows generated by primates.

Two modeling approaches, inverse and mechanistic models, have made fundamental contributions to understanding seed dispersal (Nathan and Muller-Landau 2000). The inverse-modeling approach estimates parameter values for dispersal functions that result in the best fit to seed-dispersal data from seed traps, given a model of dispersal, or *dispersal*

kernel (App. 31.1), describing the seed shadow of individual, mapped parent trees (Ribbens et al. 1994, Clark et al. 1999). One limitation of inverse modeling is that it does not directly incorporate information about the behavior of dispersal agents and therefore does not provide an explicit link between seed-deposition patterns and disperser behavior. Furthermore, seed dispersal by more terrestrial primates cannot be assessed using seed traps. In addition, there are logistic difficulties in applying this approach to primates that range over large spatial scales (e.g., chimpanzees). Thus, inferences based on inverse modeling of the role of primate dispersers in plant population and community dynamics are limited.

Mechanistic models predict seed-deposition patterns directly from the traits of plants and their dispersal agents (Nathan and Muller-Landau 2000). Basic mechanistic models predict seed dispersal distances based on the passage time and movement rates of primates (Wehncke et al. 2003). However, such models do not incorporate ecological data on the directionality of movements and behaviors of primates that often cause them to disperse seeds repeatedly in the same locations, such as sleeping sites. Hence, models based on seed passage or handling times likely underestimate clumping of primate-dispersed seeds. To understand the link between primate activity and seed-deposition patterns, more complex mechanistic models need to be developed. These models should be structured based on spatially explicit field observations of the behavior and movement patterns of primates combined with data on the fecundity of mapped parent trees. One such model has been developed for spider monkeys (*Ateles paniscus*) dispersing *Virola calophylla* in Peru (Russo 2003a). It demonstrated that the seed deposition pattern of *V. calophylla* displayed considerable spatial heterogeneity as a direct result of spider monkeys' behavior of dispersing some seeds in a scattered pattern and others in a highly clumped pattern. This heterogeneity was reflected in the multimodality of the seed-dispersal curve, which was long-tailed and did not display a monotonic decrease with distance from the source tree. Thus, the shape of the seed-dispersal curve was a direct consequence of primate dispersal processes, highlighting the need to incorporate primate behavior directly in seed-dispersal models.

The inter- and intraspecific variation in primate traits combined with their interactions with traits of fruiting species suggests that primates produce a diversity of seed shadows. Few studies have quantified primate-generated seed shadows in relation to these characters, but it is this linkage that will illuminate the effect of primate seed dispersal on plant populations and communities.

SEED DISPERSAL, PLANT POPULATION, AND COMMUNITY ECOLOGY: A REVIEW OF THEORY AND CONCEPTS

Seed dispersal influences plant ecological processes in many ways, primarily because it results in colonization of potential

recruitment sites and establishes the initial template of off-spring spatial distribution. First, the spatial extent of seed dispersal restricts the suite of potential sites for recruitment (Howe and Smallwood 1982). Second, recruitment of seedlings and saplings often depends on the initial spatial pattern of seed dispersal, such as when survival depends on the distance from a conspecific adult or density of seeds, seedlings, and/or saplings (Janzen 1970, Connell 1971). Such non-random survival produces spatial patterns of juvenile and adult plants that differ from what would result simply from random or uniform thinning of the initial template of dispersed seed (Augspurger 1983). As a result, the spatial pattern of dispersed seeds and the consequences of that pattern for seed and seedling survival affect the density and spatial distribution of recruits (Hubbell 1980, McCanny 1985). Furthermore, theory suggests that, when survival is negatively density-dependent, spatial variation in density among subpopulations can modulate population fluctuations at larger scales (Chesson 1996, 1998). In the case of seed dispersal, as seeds become more clumped, the number of seeds surviving to the seedling stage decreases, with negative consequences for seedling population growth rate (P. Chesson and S. E. Russo unpublished data). Large-scale spatial variation in seed densities resulting from seed dispersal by primates can thereby influence the demographic stability of plant populations. Thus, studies of primate seed dispersal should be designed to estimate variance in seed density as well as the dispersal processes that produce it. Third, the availability and spatial distribution of sites suitable for establishment combined with the interaction between the environment and a plant's *regeneration niche* (Box 31.1) (Grubb 1977) can determine the spatial pattern of seedling and sapling recruitment. This is likely particularly critical for small-seeded and light-demanding species that recruit best in gaps (Dalling and Hubbell 2002, Dalling et al. 2002) but also for larger-seeded, shade-tolerant species that have, for example, elevation- or soil-related habitat requirements (Webb and Peart 2000).

At the community level, the spatial distribution of individual plants mediates intra- and interspecific interactions, such as competition and density-dependent mortality; and the balance of these interactions affects species coexistence (Pacala and Tilman 1994, Chesson 2000). Limitations on seed dispersal, for example, may promote species coexistence if the inability of a better competitor to disperse to a particular site permits poorer competitors to establish there instead (Levin 1974, Tilman 1994, Hurtt and Pacala 1995). If such dispersal limitation occurs on a community-wide basis, then competitive exclusion and loss of species from a community may be slowed, thereby contributing to the maintenance of plant species diversity (Hurtt and Pacala 1995). In addition, theory has suggested and simulations have demonstrated that the spatial scale of seed dispersal affects properties of plant communities, in particular species richness and the shapes of species accumulation curves and rank abundance distributions at community and regional scales (Hubbell 2001, Chave et al. 2002). Thus, understanding the role of seed dispersal in the development of spatial pattern in plant populations is critical to explanations of the structure of plant communities (Levin 1974, Tilman 1994, Hurtt and Pacala 1995, Chesson 2000).

At landscape and larger scales, long-distance seed dispersal mediates the colonization of new habitats (Howe and Smallwood 1982; Cain et al. 2000, 2003). Although long-distance dispersal is notoriously difficult to document (Nathan et al. 2003), it nonetheless has important implications for migration of plant species under global climate change (Cain et al. 2000, Clark et al. 2003), rates of population spread of invasive species (Clark et al. 2003), and recolonization of fragmented or degraded habitats (Duncan and Chapman 1999, Kaplin and Lambert 2002). Long-distance seed dispersal by primates could occur with wide-ranging species like chimpanzees (*Pan troglodytes*) and mandrills (*Mandrillus sphinx*), when young animals disperse to new groups and carry seeds in their guts from their natal home range, and during seasonal movements.

Seed dispersal at all scales has consequences for population genetics of plants. Ecological mechanisms affecting gene movement play an important role in the development of genetic structure; and in seed plants, gene movement is accomplished by pollen and seed dispersal (Loveless and Hamrick 1984, Sork et al. 1999). Although gene flow from pollen movement can be extensive (Loveless and Hamrick 1984), genetic structure nonetheless may develop within populations as a result of nonrandom patterns of seed dispersal (Epperson and Alvarez-Buylla 1997, Schnabel et al. 1998, Hu and Ennos 1999). Genetic structure has important evolutionary consequences for plants, including effects on viability selection through herbivore- or pathogen-mediated effects on survival (Augspurger and Kelly 1984, Schmitt and Antonovics 1986, Sork et al. 1993), levels of inbreeding depression (Ellstrand and Elam 1993), and effective population size, which influences the dynamics of genetic change (Hedrick 2000).

Population genetic theory predicts that the more spatially restricted seed dispersal is, the more likely plant populations are to develop local genetic differentiation (Wright 1943, Loveless and Hamrick 1984). Many primates disperse seeds long distances, and those that are large-bodied can move large quantities of seeds (McConkey 2000, Stevenson 2000, Dew 2001, Poulsen et al. 2001, Russo 2003a). Such gene flow would homogenize plant genetic variation at large scales and reduce the probability of local differentiation of plant populations, thus decreasing the probability of the formation of tight coevolutionary relationships (Herrera 2002).

As detailed above, primates have high functional diversity in terms of the seed-dispersal services they provide. The diversity and heterogeneity of seed shadows they generate means that primate–plant interactions have the potential to influence nearly every aspect of plant population and community ecology.

CONSEQUENCES OF VARIATION IN SEED-DEPOSITION PATTERNS

As demonstrated thus far, many factors influence the initial seed shadows that primates generate. The spatial distribution of dispersed seeds has important consequences for plants in terms of demography and the spatial pattern of recruitment. Two aspects of seed dispersal that warrant special consideration are the scatter versus clump dispersal dichotomy (Howe 1989) and the distances that seeds are dispersed from parent trees.

Scatter Versus Clump Dispersal

Because some primates spit or defecate seeds in low-density seed piles and other primate species defecate seeds into high-density seed clumps, primates lend themselves to an evaluation of the scatter versus clump dispersal hypothesis suggested by Howe (1989) for all fruit-eating animals. Howe (1989) proposed that many tree species are scatter-dispersed by small frugivores that regurgitate, spit, or defecate seeds singly. These offspring recruit as isolated individuals and are unlikely to experience selection for resistance to herbivores, pathogens, or other sources of density-dependent seed or seedling mortality. In contrast, other species are dispersed by large frugivores that deposit large numbers of seeds in a single location. Howe (1989) proposed that these clump-dispersed seeds germinate in close proximity to one another and thus evolve chemical or morphological defenses against seedling predators, pathogens, and herbivores that act in a density-dependent fashion. These processes should therefore be reflected in the spatial distribution of adults, with scatter-dispersed species being random or widely dispersed and clump-dispersed species being highly aggregated.

Howe's (1989) hypothesis rests on one critical assumption: that the initial seed-deposition pattern persists after the seed stage so that density-dependent factors can play a role in determining the spatial pattern of recruitment. Given that processes acting after dispersal may alter patterns generated by the dispersers (Herrera et al. 1994, Jordano and Herrera 1995, Schupp and Fuentes 1995, Kollman et al. 1998, Rey and Alcantara 2000, Balcomb and Chapman 2003), this assumption should be evaluated.

Postdispersal seed predation and secondary dispersal (App. 31.1) can dramatically affect seed survival and, ultimately, seedling recruitment and the dynamics of plant demography (Feer and Forget 2002). In the Paleotropics, Lambert (1997, 2001, 2002) experimentally determined that most seeds do not remain at the site of deposition and that postdispersal processes obscure the initial seed-deposition pattern. Numerous studies cite the importance of rodent seed predation on the fate of dispersed seeds and tree regeneration. For example, DeSteven and Putz (1984) documented the influence of mammalian seed predation on the recruitment of a tropical canopy tree (*Dipteryx panamensis*, Leguminosae) on Barro Colorado Island, Panama. They found that predation of unprotected *D. panamensis* seeds and seedlings exceeded 90% and suggested that predation by seed-eating mammals can be so extensive that even dispersed seeds have little chance of escape (DeSteven and Putz 1984). At Santa Rosa National Park, Costa Rica, 98% of the seeds placed at experimental stations were removed or killed within 70 days (Chapman 1989a). In Peru, 99% of seeds of *Virola calophylla* that had been naturally dispersed by spider monkeys (*Ateles paniscus*) or had fallen below the parent tree were preyed upon within 15 months (Russo and Augspurger 2004).

Initial seed deposition patterns by primates can also be altered by secondary seed dispersal by dung beetles and rodents that cache seeds. Andresen (1999) investigated the fate of monkey-dispersed seeds in Peru and found that 27 species of dung beetle visited the dung of spider monkeys (*Ateles paniscus*) and howler monkeys (*Alouatta seniculus*) and buried 41% of the seeds they encountered. In Uganda, Shepherd and Chapman (1998) documented that dung beetles buried 31% of the seeds placed in experimental primate dung. Clumps of seeds found in chimpanzee defecations rarely remain at the site of deposition after a single day (C. A. Chapman personal observation).

Secondary seed dispersal by rodents, which cache seeds for future consumption, may also alter the initial seed-deposition pattern. However, an important consideration is that the relatively short distances that seeds are secondarily dispersed may not result in substantial modification of the primary seed shadow (Wenny 1999, Brewer and Webb 2001, Russo in press). Larger rodents, such as agouchies (*Myoprocta agouchy*), may secondarily disperse seeds up to 124 m away from their original location, although most distances were 20 m or less (Jansen et al. 2002). The dominant effect of secondary dispersal by dung beetles and rodents may be mediated by the burial that can increase seed survival (Andresen 2001, Brewer 2001), rather than the actual movement of the seeds. Andresen and Levey (2004) documented that burial of seeds by dung beetles decreased the probability of seed predation by rodents by threefold and increased the probability of establishment by two-fold. Further quantification of how secondary dispersal modifies primate seed shadows in terms of seed distribution and survival are clearly needed; particularly, more emphasis needs to be placed on distinguishing rodent seed predation from secondary dispersal.

Some experimental studies suggest that whether seeds are scatter- or clump-dispersed may not always predictably influence seed fate. Forget and Milleron (1991) investigated the fate of experimentally dispersed *Virola surinamensis* seeds on Barro Colorado Island, Panama. Using thread-marking methods, these authors observed that agoutis (*Dasyprocta punctata*, a large rodent) scatter-hoarded *V. surinamensis* seeds that they found both singly and in clumps. Seed-removal and seed-burial rates were strongly affected by features of forest habitats, such as *V. surinamensis* tree abundance and/or forest age, but not by seed-dispersal treatment (scattered

versus clumped). Predation of unburied seeds by weevils was independent of habitat and dispersal treatment.

Although some experimental studies suggest that clump-dispersed seeds may not remain in a clumped distribution, a different picture emerges when the fate of seeds that were naturally dispersed by primates is linked to the spatial distributions of plants in later life stages. In a study of *Virola calophylla* in Peru, a clumped pattern of seed deposition was generated by the key dispersal agent, the spider monkey (*Ateles paniscus*) (Russo and Augspurger 2004), which dispersed 92% of all dispersed seeds of this tree species (Russo 2003b). The initially clumped seed-deposition pattern was largely maintained through recruitment to the sapling stage. The density of seedlings and saplings was highest where seed fall was greatest, that is, underneath *V. calophylla* parents and at the sleeping sites of spider monkeys. This clumped pattern was maintained even though per capita seed survival to 15 months at these two dispersal site types was the lowest, relative to seeds that spider monkeys dispersed diurnally at low density. In addition, per capita seed survival was negatively dependent on the density of *V. calophylla* seeds and positively dependent on their distance from the nearest female *V. calophylla* tree. Therefore, the clumped recruitment pattern of seedlings and saplings arose despite considerable distance- and density-dependent seed mortality. Thus, spatially aggregated seed dispersal by spider monkeys appeared to play a dominant role in the spatial structuring of this tropical tree population. The interesting challenge that remains is to determine under what conditions the initial seed-deposition pattern generated by primates will persist and what conditions will cause its disruption. The balance likely lies in the strength of distance- and density-dependent mortality at the seed and seedling stages relative to the spatial scale and strength of seed clumping and in the propensity of primates to disperse seeds to habitats consistent with a plant species' regeneration niche, in addition to interactions with a plant species' competitors and mutualists.

Given that many primates use one or a small number of sleeping sites repeatedly over a number of years (Anderson 1984, Chapman 1989b, Chapman et al. 1989, Julliot 1997, Russo and Augspurger 2004), these sites are clearly areas of high seed deposition. A similar pattern of repeated defecation may also exist for feeding trees or any other frequently used location (McConkey 2000, Schupp et al. 2002). Such patterns have led some researchers to speculate that defecation at such sites may alter the distribution of adult trees, depending on how many other dispersers contribute to the seed shadow of a tree species. For example, Milton (1980) suggested that the clumped pattern of seeds dispersed by howler monkeys (*Alouatta palliata*) could account for the patchy distribution of food trees in the animals' home ranges. Lieberman et al. (1979) suggested that by defecating near sleeping sites, baboons (*Papio anubis*) increase the concentration of food plants within their core area. However, these studies have not examined the long-term fate of seeds dispersed to sleeping sites, particularly after the seedling and sapling stages. Thus,

speculating on the impact of these activities with respect to adult distributions is premature. A study done near hornbill nests, large fruit-eating African birds, that examined the long-term fate of seeds deposited near nests found that directed seed dispersal to nests over a decade did not substantially alter sapling community composition at these sites (Paul 2001).

Seed-Dispersal Distance

Janzen (1970) and Connell (1971) suggested that dispersal away from the parent plant enhances survival by removing offspring from mortality factors (e.g., competition, predation, pathogens) acting in a distance- or density-dependent fashion. In one community, negative density-dependent effects on seedling recruitment have been found for every one of the 53 species examined (Harms et al. 2000), but evidence supporting distance- and density-dependent effects is mixed (Clark and Clark 1984, Condit et al. 1992, Hille Ris Lambers et al. 2002, Hyatt et al. 2003). These ideas have led to investigations examining the consequences of primates dispersing seed different distances away from the parent plant (Stevenson 2000, Dew 2001).

Primates disperse seeds to a range of distances, depending in part on seed handling. Seeds that are dispersed through spitting are on average moved only a few meters from the parent tree, whereas those defecated are often moved hundreds of meters from the parent (Fig. 31.1, Table 31.1). However, the effect of seed-dispersal distance on the probability of a seed germinating and surviving will likely be variable and species-specific. For example, several species-specific studies examining seedling survival under parent trees have found little or no recruitment under parent trees (Augspurger 1983, 1984), whereas other studies reveal relatively small differences in the probability of survival between seeds under parent trees and those dispersed farther away (Condit et al. 1992; DeSteven and Putz 1984; Chapman and Chapman 1995, 1996). Howe et al. (1985) found nearly complete mortality (99.96%) within only 12 weeks for *Virola surinamensis* fruit that dropped under the parent. Similarly, Schupp (1988) documented only 7% survival of *Faramea occidentalis* seeds under the crown over 30 weeks in comparison to 24% survival 5 m away from the parent tree. In contrast, Chapman and Chapman (1996) investigated primate-dispersed trees in Kibale National Park, Uganda, and found that *Uvariopsis congensis* experienced 56% more seed predation when dispersed away from parent trees versus directly under a parent tree.

Hence, dispersal by primates away from parent trees may not always guarantee a higher probability of seed survival. Per capita survival of *Virola calophylla* seeds at the sleeping sites where spider monkeys disperse large numbers of seeds is just as low as it is underneath parents (Russo and Augspurger 2004). Although sleeping sites were distant from the nearest female *V. calophylla* tree, the high seed densities that occur there appear to attract seed predators, indicating

that distance- and density-dependent mortality can have independent effects on seed survival. In fact, the effect of seed density on seed survival was stronger than that of distance. Thus, for seeds being dispersed to sleeping sites, the value of being dispersed from a parent is reduced in this system.

Understanding whether the strength of distance- or density-dependent survival varies with scale is critical for evaluating the significance of variation among primate species in seed-dispersal distance, particularly that associated with different seed-handling strategies. At least one study has found that the strength of distance- and density-dependent survival drops off dramatically once seeds are beyond the parent crown (Schupp 1988). Furthermore, seed predators, the agents of distance- and density-dependent survival, are likely to respond to different scales of variation of their food resources, depending on their own natural history (Schupp 1992).

Evidence points to substantial interspecific variation in the degree to which distance and density dependence influence seed fate, the scale at which they do so, and the degree to which these factors act independently. Studies should not only determine whether density and distance have separate, significant effects but also quantify and compare the strength of each. Possibly a more significant implication of variation in dispersal distances is a seed's increasing ability to colonize new habitats with increasing dispersal distance (Howe and Smallwood 1982). Newly colonized habitats provide either favorable or unfavorable conditions for establishment, so the underlying spatial arrangement of habitats in a landscape and the degree to which primates cross ecotone boundaries may influence whether longer dispersal distances result in increased seed survival and seedling establishment.

CONSERVATION IMPLICATIONS

Cumulatively, countries with primate populations are losing approximately 125,000 km^2 of forest annually (Chapman and Peres 2001). Other populations are affected by forest degradation (logging and fire), habitat fragmentation, and hunting (Peres 1990; Chapman et al. 2003a,b). Significant reductions in population densities of primates are likely to have far-reaching consequences for plant populations and communities (Redford 1992, Chapman 1995, Chapman and Chapman 1995). Although there have been few empirical documentations of seed dispersal–mediated effects of hunting and fragmentation on plant recruitment, existing evidence points to altered patterns of seed dispersal in hunted compared to nonhunted populations (Pacheco and Simonetti 2000, Wright et al. 2000) and to reduced seed dispersal following habitat fragmentation (Chapman et al. 2003a,b; Cordeiro and Howe 2003). Persistence of primates even in fragmented habitats can, however, facilitate regeneration, particularly when primate dispersers cross habitat boundaries and disperse seeds to a habitat different from that in which they were ingested, as has been documented in black-

handed tamarins (*Saguinus midas niger*) (Oliveira and Ferrari 2000). Chapman et al. (2003a) found that there was movement of seeds among forest fragments in western Uganda by large-bodied dispersers, particularly chimpanzees and hornbills (*Ceratogymna subcylindricus*).

Available evidence also suggests that, although there can be overlap in the assemblages of fruiting species that different agents disperse, this overlap may not be enough to promote redundancy when a group of dispersers, such as primates, is lost as a result of hunting or other disturbance (Poulsen et al. 2002). Furthermore, density compensation by smaller primates when population densities of larger primates fall, if it occurs (Peres and Dolman 2000), is unlikely to make up for the decline in functional diversity of dispersal services. Thus, with the loss of primate dispersal agents, rates of seed dispersal may inevitably decrease and seed shadows may become more stereotyped, to the extent that decreases in species richness correlate with decreases in the functional diversity of disperser services. Whether this results in changes in plant populations and communities depends on the dynamics of postdispersal survival underneath parent trees versus at sites where primates would have dispersed seeds. For example, in Uganda and Bolivia, reduced numbers of large-bodied primates were correlated with lower seedling densities of large-seeded forest trees species (Chapman and Onderdonk 1998, Pacheco and Simonetti 2000) and greater seedling aggregation around parent trees (Pacheco and Simonetti 2000). In contrast, in Mexico and Panama, seedling densities were higher in areas with depleted mammalian communities (Dirzo and Miranda 1991, Wright et al. 2000).

Several authors have argued that the role of primates as seed dispersers is probably particularly important for large-seeded or hard-husked fruit species, which may be inaccessible to smaller, arboreal taxa (Andresen 2000, Kaplin and Lambert 2002). The conservation of primates is therefore argued to be critical to maintaining effective seed dispersal of such species (Andresen 2000). However, in most situations, variation in postdispersal seed fate makes it very difficult to predict accurately how a particular tree species will respond to the removal of its primate dispersers. Thus, if models are developed to predict changes in plant populations and communities with the loss of primate dispersal services, they must account not only for changes in the seed shadow but also for the resulting alterations in the transition probabilities between seed, seedling, sapling, and adult stages; the spatial component of these transitions; and the consequences for interspecific interactions among plants.

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APPENDIX 31.1. GLOSSARY

Dispersal kernel: A probability density function describing the probability of a seed being deposited per unit area at locations measured with respect to the parent plant. See also Nathan and Muller-Landau (2000).

Endozoochory: Seed dispersal in which seeds are transported inside an animal. For primates, this can occur when seeds are ingested into the gut and passed (*defecation dispersal*) or when seeds are processed in cheek pouches and later spat (*spit dispersal*).

Regeneration niche: A term coined by Grubb (1977) referring to the biotic and abiotic requirements that ensure a high probability of success in the replacement of one mature individual of a plant species by another mature individual of that species. When seeds of a species are dispersed to a habitat outside of its regeneration niche, these seeds have a low probability of germinating, establishing seedlings, or reaching adulthood.

Seed density: The number of seeds in a unit area. Seed density is often used as an indicator of the extent to which dispersed seeds are clumped (higher seed density in a small area) or scattered (lower seed density in that area). See Howe (1989).

Seed dispersal: The movement of seeds away from a parent plant. *Primary seed dispersal* for animal-dispersed seeds refers to the movement of the seed away from the parent by the first dispersal agent, aside from gravity. *Secondary dispersal* refers to subsequent movement of seeds after they have been dispersed by primary dispersal. Secondary dispersal is often by dung beetles (Scarabeidae). When primary dispersal agents defecate seeds, dung beetles accidentally roll seeds up in the dung balls in which they lay their eggs, moving the seeds short distances and burying them in the process. Secondary dispersal also occurs by rodents that cache seeds under the leaf litter or soil (scatter-hoarding and larder-hoarding) for later consumption (see *seed predation*). However, some seeds cached by rodents escape predation because they are not relocated and are, thus, dispersed.

Seed-dispersal curve: The frequency distribution of distances that seeds are moved from the parent plant. Seed-dispersal curves may also be expressed in terms of the density of seeds in annuli (rings) of a particular width surrounding a parent plant, which accounts for the area over which seeds are deposited at each distance from a parent.

Seed-dispersal distance: The straight-line distance a seed travels away from its parent.

Seed passage time: The amount of time that a seed takes to pass through the gut of its animal dispersal agent.

Seed predation: The consumption of seeds, in particular the endosperm, cotyledons, or embryo, rendering the seed, by definition, nonviable for germination. Seed predation is often by either arboreal or terrestrial birds and mammals (particularly rodents) but also by insects that lay eggs inside

seeds, where the larvae develop and consume the seed, or by pathogens, such as fungi.

Seed shadow: The spatial distribution of seeds dispersed from a single plant. Seed shadows from multiple individuals may be summed over an area to represent the spatial distribution of seeds for a population of plants

32

Predation on Primates
Past Studies, Current Challenges, and Directions for the Future

Lynne E. Miller and Adrian Treves

INTRODUCTION

Predation has long been thought to be a major selective pressure shaping the morphology and behavior of primates (Alexander 1974, Cheney and Wrangham 1987, Clutton-Brock and Harvey 1977, Crook and Gartlan 1966, Eisenberg et al. 1972, Goss-Custard et al. 1972, Rodman 1973, van Schaik 1983, Struhsaker 1969, Terborgh and Janson 1986). However, the many challenges of studying primate predator–prey interactions have limited our ability to make rigorous tests of hypothetical relationships. Several reviews have noted the paucity of reliable data on patterns of predation (Boinski and Chapman 1995; Boinski et al. 2000; Isbell 1994; Janson 1998; Treves 1999, 2000). Certainly, more data become available every year, but they still often represent anecdotal accounts rather than systematic studies of interacting variables; therefore, this chapter will again be a call for further attention to this important area of research. It is important because our efforts to understand current primate behavior and past primate evolution will benefit from understanding the subtle nuances of how and when predators exert directional selection and when predation is minor relative to other selective pressures.

This chapter begins with a brief review of the reports of predation on primates, along with some caveats about using such data for quantitative analyses. We then move on to methodological issues, including the challenges of studying predator–primate interactions, and experimental protocols that might allow researchers to tease apart the impact of multiple

selective forces. From there, we will discuss the growing body of data regarding the behaviors associated with predation risk, including the formation of social groups; manipulation of foraging, sleeping, and ranging patterns; and vigilance and alarm calling. This discussion will include reference to the variables that may mediate an individual's vulnerability to predation, which may in turn influence its willingness to take risks. By this approach, we hope to encourage multifactorial analyses of predator–primate interactions and, thus, begin to develop a more realistic model of this complex relationship. The chapter will close with a brief discussion of the role of humans as predators of nonhuman primates, addressing the extent to which humans represent a special category of predators. Although hard data on predator–primate interactions are few, there is an enormous body of literature on the myriad factors related to predation. In a chapter of this length, it is impossible to review all of these studies; thus, our aim is to provide an overview of current issues, along with a review of classic and recent publications in each area.

ACCOUNTS OF PREDATOR–PRIMATE INTERACTIONS

There is a substantial body of reports of predatory attacks on primates. Recent publications have summarized these accounts (Boinski et al. 2000, Treves 1999). Table 32.1 presents an updated list of prey and predator taxa. We have included accounts of successful and unsuccessful attacks, along with a few data based upon scat and nest debris (though we recognize that these remains may represent scavenging behavior rather