

8 The Fate of Primate-dispersed Seeds: Deposition Pattern, Dispersal Distance and Implications for Conservation

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Introduction

The role of animals in seed dispersal is well recognized. Indeed, 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 are argued to be particularly important seed dispersers. Primates, for example, comprise on average between 25 and 40% of the frugivore biomass in tropical forests (Eisenberg and Thorington, 1973; 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 researchers working in South America (e.g. Garber, 1986; Julliot, 1996; Dew, 2001; Vulinec, 2002), Central America (e.g. Estrada and Coates-Estrada, 1984, 1986; Chapman, 1989), and Africa (e.g. 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).

Because primates are relatively large, arboreal mammals requiring the high levels

of soluble carbohydrates available in fruit, seed removal from trees by primates can be high. Stevenson (2000), for example, has documented that woolly monkeys (*Lagothrix lagothricha*) in Colombia disperse 25,000 seeds/km²/day. In northern Costa Rica, spider monkeys (*Ateles geoffroyi*), howler monkeys (*Alouatta palliata*) and capuchins (*Cebus capucinus*) disperse approximately 5600 large seeds/km²/day (Chapman, 1989), and in French Guiana, a single group of howler monkeys (*Alouatta seniculus*) dispersed more than 1,000,000 seeds per year from approximately 100 plant species (Julliot, 1996). These patterns hold in Africa, too, where in Kibale National Park, Uganda, Lambert (1997, 1999, unpublished) has documented that redtail monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), mangabeys (*Lophocebus albigena*) and chimpanzees (*Pan troglodytes*) either spit out or swallow the seeds of approximately 35,000 fruits/km²/day.

We have compelling evidence that primates remove large numbers of fruits from tropical trees. However, data on fruit removal and seed handling must be linked with data on post-dispersal seed fate to fully understand the relationships among primary dispersal and the origin and

maintenance of plant species diversity, tropical forest regeneration, and plant demography. Several studies illustrate this point: Balcomb and Chapman (2003), for example, recently quantified patterns of seed removal and seedling recruitment of *Monodora myristica*, a low-fecundity forest tree species in Uganda. The fruit of this species is large, with an average fruit diameter of 18.5 cm, multiple large seeds over 2 cm in length, and a very thick and difficult to penetrate pericarp (Lambert, 1997, 1999; Balcomb, 2001), suggesting dispersal by only the very largest of arboreal frugivores. Balcomb and Chapman (2003) documented fruit and seed removal of *M. myristica* during focal tree watches, quantified the fate of naturally and experimentally dispersed and fallen seeds, and monitored natural seedling, sapling, and pole densities and survivorship of this species at two Kibale sites. As predicted, large-bodied primates played a critical role in primary seed dispersal; *P. troglodytes* and *L. albigena* were the only frugivores that opened the hard-husked fruits and were estimated to disperse over 85% of the mature seeds. However, seed germination and the probability of seedling establishment were highly variable among experimental seed-deposition types within each site, as well as between sites and years, suggesting complexity beyond that which could be explained by primary dispersal of seeds by primates.

Similar complexity has been documented in a study on the long-term consequences of directed seed dispersal by black-and-white-casqued hornbills (*Ceratogymna subcylindricus*) to nests (Paul, 2000). The patterns in which *C. subcylindricus* moves seeds are analogous to what has been described at many primate sleeping sites (Julliot, 1996, 1997). In his study, Paul (2000) assessed the species composition of the advanced plant regeneration below hornbill nests that was identified 12–16 years prior (Kalina, 1988). During nesting, *C. subcylindricus* females and juveniles are sealed into tree cavities and are provisioned by males primarily with ripe fruits. During the 4-month breeding

season, numerous seeds are regurgitated or defecated below nests. Many of these seeds establish as seedlings, altering the seedling composition towards hornbill-dispersed species. All woody plants in front of 25 hornbill nests (i.e. sites receiving hornbill dispersed seeds) and behind nests (control sites) were identified. However, there was no difference in total species richness, diversity or density of hornbill-dispersed species in these two microhabitats for any size class larger than the seedling stage. Thus, directed seed dispersal to hornbill nests over a decade did not substantially alter sapling community composition at these sites.

In the Neotropics, both Julliot (1996) and Chapman (1989) have documented the important role that *Alouatta* spp. (howler monkeys) can play in the primary dispersal of seeds. Yet experiments conducted in Santa Rosa National Park, Costa Rica, indicate that within 70 days of dispersal, 97.9% of seeds were removed or destroyed by spiny pocket mice (*Liomys salvini*), peccaries (*Pecari tajacu*), agoutis (*Dasyprocta punctata*) and a diversity of dung beetles (Chapman, 1989). These studies illustrate that processes acting after dispersal can substantially alter dispersion patterns generated by primary dispersers (see also Herrera *et al.*, 1994; Jordano and Herrera, 1995; Schupp and Fuentes, 1995; Kollmann *et al.*, 1998; Rey and Alcantara, 2000; Lambert, 2002) and point to the importance of quantifying seed fate.

Our objective in this review is to consider two aspects of primate primary seed dispersal that have the potential to strongly influence the roles that primates play in influencing plant demography and forest structure.

1. We consider patterns of seed deposition (i.e. scattered versus clumped; *sensu* Howe, 1989) generated by different primate species and evaluate the probable ecological consequences of these patterns.
2. We evaluate the distance primates typically move seeds away from the parent tree and the density-dependent mortality associated with parent trees.

Because they allow researchers to link primary dispersal to patterns of seed fate, such data are important for understanding the role of primates in influencing spatial structure of forests, as well as the degree to which they may exert evolutionary selection pressures on plants and seed characteristics. However, given the extreme hunting pressure that primate populations are facing throughout Neo- and Palaeotropical forests, such understanding may be moot. As such, we conclude by contextualizing these data in light of the possible cascading consequences that the removal of primate seed dispersers by hunting will have on the future composition of tree communities.

Pattern of Deposition: Scatter versus Clump Dispersal and Seed Fate

Many primate species exhibit a variety of seed handling behaviours (Corlett and Lucas, 1990; Kaplin and Moermond, 1998; Lambert and Garber, 1998; Lambert, 1999, 2002). For example, seeds themselves can be an important food for primates and, as such, are not dispersed but destroyed. Seed predation occurs in species that consume seeds seasonally, when preferred fruits are not available (e.g. *Cebus* and *Cercopithecus* spp.: Peres, 1991; Gautier-Hion *et al.*, 1993; Kaplin and Moermond, 1998; Lambert and Garber, 1998; Lambert, 1999), as well as in taxa that prefer seeds as food and exhibit adaptations in dentition (e.g. Kinzey and Norconk, 1990; Pitheciines: Kinzey, 1992) and in the gastrointestinal tract (e.g. Colobines: Kay and Davies, 1994; Oates, 1994; Lambert, 1998) for seed predation. It should be noted, however, that even morphologically adapted seed predators such as Pitheciines can be seed dispersers (e.g. Norconk *et al.*, 1998).

Under circumstances when it is fruit pulp that is the sought-out food, there remains the challenge of what to do with the seeds themselves once pulp is removed (Lambert, 1999). Protective seed coats are typically highly refractory to digestion, and seeds can be rife with secondary metabolites

(Janzen, 1971; Fenner, 1992; Chivers, 1994; Waterman and Kool, 1994). Seeds can also account for more than half of the weight of fruits consumed by primates (van Roosmalen, 1984; Garber, 1986). Swallowed seeds may thus represent a significant cost to frugivores in that they not only increase an animal's body mass, but may also displace more readily processed, nutritious digesta from the gut (Corlett and Lucas, 1990; Levey and Grajal, 1991). The seeds of fruits are thereby an unwanted mass, and the adhesive pulp must be removed and seeds discarded in some way.

Despite these constraints, seed swallowing is by far the most common means of primate seed dispersal in the Neotropics (Muskin and Fischgrund, 1981; Estrada and Coates-Estrada, 1984; Garber, 1986; Chapman, 1989; Andresen, 1999; Dew, 2001). In the Palaeotropics many primates also swallow seeds (e.g. *Papio anubis*, Lieberman *et al.*, 1979; *Pan troglodytes*, Wrangham *et al.*, 1994; Lambert, 1999); 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).

Spit or dropped seeds are likely to be deposited on the forest floor singly, as fruits are processed one by one. Swallowed seeds, however, can be deposited in either a high-density clump, or 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 (Kaplin and Moermond, 1998; Andresen, 1999; Lambert, 1999). In Cameroon, for example, Poulsen *et al.* (2001) have found that western lowland gorillas (*Gorilla gorilla*) and chimpanzees average 18 and 41 large (> 2 cm) seeds per faecal sample, respectively, while four frugivorous monkeys had large seeds/faeces averages ranging from 1.0 to 2.1 seeds.

Differences in seed handling strategies result in primary seed deposition patterns that vary depending on fruit species, season, and the primate species handling the seeds (Kaplin and Moermond, 1998; Lambert, 1999, 2002). Because some primates spit or

defecate seeds in very low-density seed piles (Andresen, 1999) while other primate species defecate seeds into high-density seed clumps (Julliot, 1996), primates lend themselves to an evaluation of the scatter- versus clump-dispersal hypothesis suggested by Howe (1989) for all fruit-eating animals (Lambert, 2002). Howe (1989) proposed that many tree species are scatter-dispersed by small frugivores that regurgitate, spit or defecate seeds singly. These seeds recruit as isolated individuals and are unlikely to evolve 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 seeds germinate in close proximity to one another and thus evolve chemical or morphological defences against seed predators, pathogens and herbivores that act in a density-dependent fashion. These processes are proposed to reflect the spatial distribution of adults, with scatter-dispersed species being widely dispersed and clump-dispersed species being highly aggregated.

One prediction stemming from Howe's (1989) hypothesis is that seeds are likely to be in clumps if frugivores weighing greater than 3 kg disperse them. However, Lambert (1997, 1999, 2004) has demonstrated that a number of variables not related to body size can influence patterns of fruit processing and seed handling in primates in general, and *Pan troglodytes* and *Cercopithecus ascanius* in particular. For example, *C. ascanius* (adult male = 4.2 kg) consistently (77% total fruit-eating events) scatter-disperses the seeds of fruit they consume, depositing them singly within 10 m of the parent tree. Although body size is important, a combination of dental and buccal anatomy with long digestive retention times facilitates this 'scatter' pattern of seed handling and dispersal.

Others argue similarly. In his work on avian seed dispersal, Levey (1986) has suggested that, while disperser body size can be influential, other factors – such as oral and digestive anatomy and the chemical and physical treatment of seeds in the gut – have

important implications for seed treatment and the patterns in which seeds will be dispersed. For example, Levey (1986, 1987; also see Levey and Grajal, 1991) has examined methods of seed processing by nine species of tropical frugivorous birds and found that tanagers and finches masticated fruits and dropped large seeds. Manakins, on the other hand, swallowed fruit intact and dropped no seeds, despite the fact that these birds weigh significantly less than 1 kg. Those seeds that were swallowed by the birds are more likely to be dispersed some distance away from the parent tree and deposited in higher density clumps.

Moreover, Howe's (1989) hypothesis rests on one critical assumption: that the initial seed deposition pattern must persist for density-dependent factors to play a role. Given that processes acting after dispersal have the potential to obscure or even cancel patterns generated by the dispersers (Herrera *et al.*, 1994; Jordano and Herrera, 1995; Schupp and Fuentes, 1995; Kollmann *et al.*, 1998; Rey and Alcantara, 2000; Balcomb and Chapman, 2003), this assumption needs to be substantiated.

As evidenced in chapters throughout this volume, post-dispersal seed predation and secondary dispersal can dramatically affect seed survival and, ultimately, seedling recruitment and the dynamics of plant demography (Feer and Forget, 2002). Numerous studies cite the importance of rodent seed predation on the fate of dispersed seeds and tree regeneration, and this has been known for some time. For example, De Steven and Putz (1984) have documented the influence of mammalian seed predation on the recruitment of a tropical canopy tree (*Dipteryx panamensis*) on Barro Colorado Island, Panama. They documented that predation on unprotected *D. panamensis* seeds and cotyledons exceeded 90%. The authors suggest that predation by the seed-eating mammals can be so extensive that even dispersed seeds have little chance of escape (De Steven and Putz, 1984). Likewise, Forget (1992) examined seed removal and seed fate in *Gustavia superba* on Barro Colorado Island and found that, on average, 86% of the seeds were removed within 28 days.

Estrada and Coates-Estrada (1991) documented that 59% of the seeds dispersed by howler monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico, disappeared and were presumably killed within 24 h. In Kibale National Park, Uganda, 73% of seeds placed experimentally on the forest floor had disappeared after 6 months (range = 10–100% among species; Chapman and Chapman, 1996).

Rodents demonstrate a preference for dense seed deposits. Price and Jenkins (1986) argue that, in general, absolute numbers and rates of seed removal usually increase with seed density. Other examples support this assertion. For example, Casper (1987) analysed post-dispersal seed predation of the semi-desert annual, *Crytantha falva*, and found that after 3 to 4 days there was a consistent tendency for more seed removal from high-density seed deposits. Kasenene (1980) also found a density effect in Kibale National Park, Uganda, such that a wide variety of rodents appeared to locate and consume larger seed piles than smaller ones. Willson and Whelan (1990) found that high-density seed deposits were more likely to be detected by rodent predators than those containing only a few seeds.

Initial seed deposition patterns by primates are also disrupted by the secondary seed dispersal performed by dung beetles. Andresen (1999) investigated the fate of monkey-dispersed seeds in Peru and found that 27 species of dung beetle visited the dung of *Ateles paniscus* and *Alouatta seniculus* and buried 41% of the seeds they encountered. In Brazil, Vulinec (2002) has argued that dung beetles may be particularly important to regeneration of disturbed forest where there is high primate biomass. In Uganda, Shepherd and Chapman (1998) documented that dung beetles buried 31% of the seeds placed in experimental primate dung.

These studies suggest that clump-dispersed seeds do not remain in a clumped distribution. Other studies provide experimental data in support of this observation. Forget and Milleron (1991) experimentally investigated the fate of dispersed *Virola nobilis* seeds on Barro Colorado Island,

Panama. This aril-bearing fruit is commonly consumed by *Ateles geoffroyi* (Howe, 1981, 1993). These monkeys routinely swallow the seeds whole and defecate them in clumps. Using thread-marked seeds, these authors observed that agoutis (*Dasyprocta punctata*) scatterhoarded *V. nobilis* seeds that they found both singly or in clumps. Seed removal and seed burial rates were strongly affected by features of forest habitats, such as *V. nobilis* tree richness and/or forest age, but not by seed dispersal treatment (scattered versus clumped). Predation (mostly post-dispersal) of unburied seeds by weevils was independent of habitat and dispersal treatment.

Similarly, in the Palaeotropics Lambert (1997, 2001, 2002) determined that most primate-dispersed seeds do not remain at the site of deposition, and that post-dispersal processes dilute the effect of the initial dispersal pattern. For three of seven species that Lambert (2002) studied in Kibale National Park, Uganda, seed density did not have an effect on seed fate. For example, *Aphania senegalensis* had virtually no germinating seeds or fungal attack, and seeds in all treatments (either single seeds, five seeds in clumps or 30 seeds in clumps) were equally vulnerable to predation. Likewise, density of seed deposition did not differentially influence the fate of *Cordia abyssinica* seeds; there was virtually no germination, and seeds were highly vulnerable to fungal attack and predation, independent of treatment. Similarly, *Pseudospondias microcarpa* was highly desirable to rodents, regardless of seed treatment. For another three of the seven species, seed treatment did affect seed fate, though the effects offer little support for Howe's (1989) model. *Monodora myristica* was particularly vulnerable to fungal attack in larger clumps of seeds, suggesting adaptations to scatter dispersal. However, single seeds of this species were also more likely to be killed by rodents than were clumps of seeds. Thus, pathogens and predation in this species offset any selective advantage of the number of seeds in a seed-dispersal event – with more pathogen attack in clumps of seeds and more predation on single seeds. There were also seed

treatment effects on the fate of *Linociera johnsonii* and *Celtis durandii*, although, again, the effects did not clearly correspond to those predicted from the scatter- vs. clump-dispersal model. Both species had more seeds damaged when in higher densities. But they also had more seeds removed when in less dense seed stations. Overall, high predation swamped any effect of seed deposition patterns. Indeed, data indicate that rodent seed predation was so intense that seeds never remained in clumps long enough to produce saplings.

Hence, seeds deposited in clumps by primates rarely remain aggregated, suggesting that plant adaptations to particular modes of primary seed deposition are unlikely. None the less, the seed traits proposed by Howe (1989) to be associated with patterns of primary deposition (i.e. scattered or clumped dispersal) appear to exist, although, given the diluting effects of post-dispersal processes, these attributes are probably a result of other factors such as forest microhabitat specialization. For example, the features proposed to be adaptations to scatter dispersal are also traits that favourably dispose seeds to recruiting in forest gaps, while traits proposed to be adaptations to clump dispersal are attributes that facilitate germination and establishment in forest understorey. Species adapted to establishment in large clearings have small seeds to promote wide dispersal, and require high light levels and temperatures for germination and growth (Fetcher *et al.*, 1985; Denslow, 1987; Vázquez-Yanes and Orozco-Segovia, 1993). They also grow rapidly (Kitajima, 1994, 1996), have rapid leaf turnover and, as a result, invest little in secondary metabolites that are presumed to act as deterrents to herbivory (Coley *et al.*, 1985). Conversely, some species do well in forest understorey. These species tend to be larger seeded, can germinate in relatively low light conditions, have a slow rate of growth, invest heavily in seed defences against herbivory, and consequently survive well in the understorey (Coley *et al.*, 1985; Kitajima, 1996; Connell and Green, 2000; Rose and Poorter, 2002).

Seed Dispersal Distance

Additional factors to primary seed deposition, such as the probability of seed survival over time relative to the distance from the parent plant, have been argued to influence plant recruitment and forest structure. Janzen (1970) and Connell (1970) suggested that dispersal away from the parent enhances survival by removing offspring from mortality factors acting in a density- or distance-dependent fashion. The so-called Janzen–Connell model has resulted in speculation regarding the relative fitness advantage to parent trees by primates that spit seeds versus swallow seeds. Indeed, primate seed handling – in combination with patterns of day range and habitat use – directly influences the distance that seeds are removed from parent trees. For example, assuming that fruit pulp is removed soon after a fruit is removed from the tree, spit and dropped seeds are more likely to be deposited in close proximity to the parent tree compared to seeds that are carried in the gut for some time (Rowell and Mitchell, 1991; Chapman, 1995; Lambert, 1999; Kaplin and Lambert, 2002). Data from Uganda (Lambert, 1999) and Kenya (Rowell and Mitchell, 1991) on seed spitting by *Cercopithecus* spp. suggest that seeds are spat out an average distance of 10 m from the parent tree (range 1–100 m). This stands in contrast to Neotropical ceboids – seed swallowers – that defecate seeds much longer distances away from parent trees; average distances range between 151 and 390 m, with a range that – in the case of *Ateles paniscus* (Russo, 2003) – can be up to 1119 m away from parent trees (Estrada and Coates-Estrada, 1984; Garber, 1986; Zhang and Wang, 1995; Julliot, 1996; Stevenson, 2000; Dew, 2001).

Beyond seed handling, habitat use also strongly influences seed shadow and two seed-swallowing primate species in the same habitat will create dissimilar seed shadows as a result of their daily ranging and foraging. In general, primates that travel widely in a day will deposit seeds over a greater area than primates that more intensively exploit a smaller day range. For

example, in Kibale National Park, Uganda, redtail monkeys (*C. ascanius*) travel an average of 1178 m and use a total range area of 49 ha very intensively (Lambert, 1999). Over a several-day period they often re-visit trees, and will also use multiple resources from the same tree (e.g. fruit, seeds, leaves, insects). Sympatric *P. troglodytes*, on the other hand, range widely in a day, often moving from one large-fruited tree to another and feeding along the way on terrestrial herbaceous vegetation. Although determining total day range for chimpanzees is extremely difficult, they can move up to 4–5 km/day, and use a range with an area of up to 2220 ha (Chapman and Wrangham, 1993; Lambert, 1997). These data suggest that, while there is high fruit diet overlap between these two species, they create very different seed shadows as a consequence of overall foraging strategy and habitat use, in addition to differences in seed handling.

Sympatric howler monkeys (*Alouatta* spp.) and spider monkeys (*Ateles* spp.) offer another example. *Alouatta palliata* spends from 28.5 to 50% of its feeding time consuming fruit and is reported to disperse the seeds of several plant species (Estrada and Coates-Estrada, 1984; Chapman, 1988a,b, 1989). However, howlers often spend many hours in the same feeding tree and range from only 10 to 893 m in a day. Chapman (1988b) found that *A. palliata* can stay in close proximity to individual feeding trees for up to 14 days, leaving these trees only to make short excursions. *Ateles geoffroyi* is highly frugivorous (up to 77.7% of feeding time) and is known to disperse many seeds (Chapman, 1989). The ranging patterns of this species suggest that seeds in the dung are unlikely to be defecated below the parent tree and are instead moved throughout the forest in a widely dispersed pattern. Further support of these observations comes from Peru, where Andresen (1999) has found that *Ateles paniscus* spent 22% of its time travelling, while *Alouatta seniculus* spent 9% of its time travelling. *A. seniculus* spent significantly more time in each fruiting tree than the spider monkeys (125 versus 41 min) and as a consequence most defecations were large and contained large aggregations of

seeds over smaller areas than those seed dispersed by *A. paniscus*.

The predictions stemming from the early Janzen (1970) and Connell (1970) articles have been seminal in the history of seed dispersal research and have strongly influenced assessments of primate seed dispersers. For example, some authors have implied that having seeds dispersed by primates further distances away from the parent tree is better in terms of the plant's fitness (Stevenson, 2000; Dew, 2001). However, the degree to which it is necessary for seeds to escape distance- and density-dependent effects near the parent is unclear. A number of species-specific studies examining seedling survival under parent trees have found little or no recruitment under parent trees (Augsburger, 1983, 1984). Howe *et al.* (1985) found that 99.96% of *Virola surinamensis* (also known as *V. nobilis*) fruit that drop under the parent are killed within only 12 weeks. Similarly, Schupp (1988) documented 7% survival of *Faramea occidentalis* seeds under the crown in 30 weeks, in comparison to 24% survival 5 m away from the parent tree. However, other studies reveal relatively small differences in the probability of survival between seeds under parent trees and those dispersed away (De Steven and Putz, 1984; Condit *et al.*, 1992; Chapman and Chapman, 1995, 1996). For example, Chapman and Chapman (1996) investigated primate-dispersed trees in Kibale National Park, Uganda, and found that in *Mimusops bagshawei* seed survivorship increases when dispersed away from adult conspecifics. *Uvariopsis congensis*, on the other hand, experienced 56% more seed predation when dispersed away from parent trees versus seeds directly under a parent tree. Thus, as more demographic and ecological data are garnered on the fate of seeds and seedlings in tropical forests, it is evident that there exists large interspecific variation in the degree to which density-dependent factors influence seed fate.

The Janzen–Connell model has resulted in speculation regarding the relative fitness advantage to parent trees by primates that spit seeds versus swallow seeds and the generalization that seed-swallowing primates

are better dispersers (Sussman, 1995; Stevenson, 2000; Dew, 2001). However, given the range in seed survivorship patterns that have been documented for tropical tree species, broad generalizations of 'good' versus 'bad' primate seed dispersal distances are not tenable. For example, many tree species have specific requirements for germination and growth and tend only to be found in particular habitats (e.g. moist valley bottoms, hillsides) suggesting that long-distance dispersal would result in seeds being carried to unsuitable habitats. Lambert (2001) has found that having seeds spat out near parent trees can be highly favourable for tree species in Kibale National Park, Uganda. For example, redbtail monkeys (*Cercopithecus ascanius*) in Kibale feed extensively on the ripe fruits of *Strychnos mitis* during some years and some seasons. The monkeys consumed fruits at a rate of approximately two per minute and almost always spit out intact seeds under the crown of the parent tree or within a few metres. *S. mitis* seeds clearly benefited from monkey processing. Eighty-three per cent of seeds spat out by redbtails germinated, while only 12% of the unprocessed fruits survived to germination. Because pulp remained on the seeds, unprocessed fruits were also more likely to be attacked and damaged by seed predators and fungal pathogens. Thus, although seeds were dispersed under or near parent trees, a distance which might be deleterious for some tropical tree species (e.g. *Caseraia corymbosa*: Howe, 1977), for *S. mitis*, *C. ascanius* fruit processing appears to be beneficial – at least at the seed and seedling stage. This indicates the difficulty in generalizing the services of a disperser across tree species.

Conservation Implications

As we have demonstrated, seeds dispersed by primates rarely remain in their primary deposition sites; primates are thus unlikely to exert selection for seed characteristics. We have also indicated that it is

problematic to generalize a primate species' effectiveness as a seed disperser according to whether they disperse seeds far from (via swallowing) or close to (via spitting) parent trees. None the less, primates move literally billions of seeds in forests around the tropics every day and consequently have the capacity to influence numerous post-dispersal processes and initiate innumerable chains of ecological interactions. Yet, given the precipitous decline in primate populations around the world (Chapman and Peres, 2001), garnering more data to unravel these processes may soon be a luxury. Subsistence and commercial hunting can have profound impacts on forest animal populations, while leaving the physical structure of the original forest largely unaltered (Peres, 1990; Wilkie *et al.*, 1992). Wildlife harvest can be a major source of food for many local communities around the tropics, and primates are often prime targets. For example, a market survey in two cities in Equatorial Guinea, West Africa with a combined human population size of 107,000 recorded 4222 primate carcasses for sale over 424 days (Fa *et al.*, 1995). Peres (1990) documented that a single family of rubber tappers in a remote forest site of western Brazilian Amazonia killed more than 200 woolly monkeys (*Lagothrix lagotricha*), 100 spider monkeys (*Ateles paniscus*) and 80 howler monkeys (*Alouatta seniculus*) over a period of 18 months. Peres (2000) calculated the total game harvest in the Brazilian Amazon by multiplying these values by the size of the zero-income rural population in the entire region. Using the values presented for primates, we estimate that 3.8 million primates are consumed annually in the Brazilian Amazon (range in estimates: 2.2–5.4 million). As dramatic as these figures are, they probably underestimate actual hunting-induced mortality. Harvest estimates from market surveys do not include primates that are consumed in villages (Lahm, 1993). In the Democratic Republic of Congo, 57% of primates are eaten in the villages and do not make it to the market, and, in Liberia, primates were

more valuable in rural than urban areas (Colell *et al.*, 1994).

The fact that primates are often both preferred targets in the bushmeat trade and important seed dispersers has led researchers to evaluate the cascading effects of their removal on future forest regeneration and structure (Howe, 1984; Pannell, 1989; Chapman and Chapman, 1995). Chapman and Chapman (1995), for example, estimated the potential loss in plant biodiversity that would result if all large-bodied seed dispersers such as cercopithecines and apes were removed from Kibale National Park, Uganda, resulting in fruit dropping below parent trees rather than being dispersed. On the basis of presence or absence of seedlings and saplings under adults, they concluded that 60% of the 25 tree species they studied would ultimately be lost if primates were removed. Similarly, Chapman and Onderdonk (1998) evaluated intact forest with complete primate communities and fragments around Kibale in which there were no primate seed dispersers. They found fewer seedlings, fewer species, and a higher percentage of small-seeded species in the forest fragments. Other studies corroborate these findings and demonstrate that changes in disperser abundances are associated with changes in seedling densities (Dirzo and Miranda, 1991; Pacheco and Simonetti, 1998; Wright *et al.*, 2000) as well as spatial patterns of seedling recruitment (Pacheco and Simonetti, 1998). However, as there are evident differences in responses to dispersal removal, we clearly have much to learn. 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, 1998) and higher seedling aggregations around parent trees (Pacheco and Simonetti, 1998). In contrast, in Mexico and Panama, seedling densities were higher in areas with depleted mammalian communities (Dirzo and Miranda, 1991; Wright *et al.*, 2000).

In summary, in this review we have documented that seeds are handled by

primates in different ways (swallowed or spit), are deposited in different distributions (scattered or clumped), and are subsequently differentially affected by secondary seed dispersers and seed predators. In addition, different primate species disperse seeds in varying distances away from parent trees, and the susceptibility of species to density- or distance-dependent factors is highly variable. There is some evidence that increases in the abundance of some primate species may offset the population declines in other species caused by hunting (Peres and Dolman, 2000). However, if current populations of seed-dispersing primates are hunted to the point of regional decline, it is difficult to argue, *a priori*, whether other species can fulfil this role in an ecologically equivalent fashion, if at all. Several authors have argued that the role of primates as seed dispersers may be 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 thus key to maintaining effective seed dispersal of some species (Andresen, 2000; Entwistle *et al.*, 2000). However, in most situations, variation in post-dispersal seed fate probably makes it impossible to make predictions concerning how a specific tree species will respond to the removal of its primate disperser.

Acknowledgements

Our projects in Kibale have been supported by a Makerere University Grant for Biological Research, Sigma Xi, the American Society of Primatologists, the University of Oregon, the Wildlife Conservation Society, the National Geographic Society, and National Science Foundation Grants (SBR-9617664, SBR-990899). We thank the Government of Uganda, the National Parks Service, and Makerere University for permission to work in Kibale National Park. We thank Lauren Chapman for providing helpful comments on this manuscript.

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Seed Fate

Predation, Dispersal and Seedling Establishment

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2005

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