

# Primate Seed Dispersal: Coevolution and Conservation Implications

COLIN A. CHAPMAN

Early studies of primates have demonstrated that many species rely heavily on fruit, and that primates constitute a large component of the frugivore biomass in tropical forests. Consequently, primates have long been thought to be important seed dispersers. It is only recently that studies have been conducted that have illustrated the complex nature of the interactions between fruit-eating primates and their food trees. Such studies have raised questions as to the causes and consequences of the intriguing differences between primate communities, the importance of other animals in the interactions (such as dung beetles and rodents that secondarily disperse seeds), how primate-plant interactions evolve, and the significance of primates in forest regeneration and conservation. Since subsistence and commercial hunting of primates has heavily impacted frugivore communities, but left the physical structure of the forest relatively unaltered, studies of primate seed dispersal have important implications for the future of forests where seed dispersers have declined or disappeared.

One central theme of primatology revolves around understanding environmental influences on primate social organization and behavior.<sup>1-4</sup> However, primates in turn affect the structure and composition of the plant communities with which they interact. One of the primary ways they accomplish this is by dispersing the seeds of many of the trees from which they feed. Until recently, surprisingly little detail has been available regarding the interactions between frugivorous primates and tropical fruit trees. However, based on the facts that pri-

mates constitute between 25 and 40% of the frugivore biomass in tropical forests<sup>5,6</sup> and that they defecate or spit out large numbers of seeds,<sup>7-11</sup> they were believed to play an important role in tropical forest regeneration and dynamics.

Recently, detailed studies of the interactions between primates and fruiting trees have provided information about the germination potential of defecated seeds,<sup>12-14</sup> the fate of dispersed seeds during the period when they are on the forest floor prior to germination,<sup>8,14</sup> and the relative importance of different frugivores in the dispersal of particular tree species.<sup>11,15-17</sup> These studies have not only highlighted the fact that the interactions between primates and tropical tree communities are complex, but have also provided evidence to strengthen arguments that primates play an important role in forest regeneration. In fact, many researchers now assert that the maintenance of frugivore populations that facilitate seed dispersal is critical for the regeneration and maintenance of tropical forest trees.<sup>11,18-21</sup>

Colin Chapman is an assistant professor of zoology at the University of Florida. Trained in both anthropology and zoology, he has focused his research on how the environment influences primates (the ecological determinants of primate group size and social organization) and on how primates influence their environment (primate seed dispersal and the fate of the dispersed seeds in pristine and degraded forests). He has conducted field work in St. Kitts and Costa Rica, and now has established a long-term research program in Kibale National Park, Uganda. [cachapman@zoo.ufl.edu](mailto:cachapman@zoo.ufl.edu)

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## THE IMPORTANCE OF PRIMATES AS SEED DISPERSERS

Given the numerical abundance of primates in tropical forests, together with the heavy reliance of many of these species on fruit (Table 1), it is not surprising that they have often been thought to play a significant role in seed dispersal. However, there is more to seed dispersal than fruit removal. The seed or seeds inside the fruit represent the reproductive potential of the plant. How a frugivore treats the seed can have a great influence on whether or not the seed is successful in becoming an adult member of the next generation. The quality of a particular seed disperser to a plant depends on a variety of factors: (1) the number of seeds dispersed away from the habitat beneath parent trees<sup>22</sup> which can be characterized by high density-dependent mortality; (2) seed processing—whether the primate defecates seeds or spits them out, and the germination potential of seeds processed in these different ways; (3) the suitability of the microsite where the seed is deposited for germination and establishment; and (4) the influence of the frugivore's actions on the probability of secondary dispersal to a suitable or unsuitable location or the probability of seed predation.

Obtaining data on all of these aspects of seed dispersal is extremely difficult. Ultimately, we are trying to determine the consequences of the disperser's actions on the fitness of the parent tree. Because most tropical forest trees have very long generation times and can produce hundreds of thousands of seeds per year, relating seed dispersal to parent fitness is often an unrealistic objective. However, studies of components of the process

**TABLE 1. Primate Communities in Different Areas and the Percentage of Fruit in Each Species' Diet (modified from Waser<sup>30</sup>)**

| Species  | Population Density (ind/km <sup>2</sup> ) | Biomass Density (kg/km <sup>2</sup> ) | % Fruit in Diet    |
|--|---|---------------------------------------|--------------------|
| <b>Krau Game Reserve, Malaysia</b>   |   |                                       |                    |
| <i>Hylobates syndactylus</i>   | 5   | 39                                    | 44. <sup>45</sup>  |
| <i>Presbytis obscura</i>   | 31  | 172                                   | 55.9 <sup>45</sup> |
| <i>Presbytis melalophos</i>  | 74  | 406                                   | 49.6 <sup>45</sup> |
| <i>Hylobates lar</i>   | 6   | 30                                    | 59.6 <sup>45</sup> |
| <i>Macaca fascicularis</i>   | 39  | 89                                    | 64.9 <sup>45</sup> |
| (+ <i>M. nemestrina</i> , <i>Nycticebus coucang</i> )  |   |                                       |                    |
| <b>Kutai Nature Reserve, Borneo</b>  |   |                                       |                    |
| <i>Pongo pygmaeus</i>  | 4   | 160                                   |                    |
| <i>Presbytis aygula</i>  | 20  | 81                                    |                    |
| <i>Macaca nemestrina</i>   | 5   | <22                                   |                    |
| <i>Hylobates muelleri</i>  | 15  | 56                                    | 62                 |
| <i>Macaca fascicularis</i>   | 15  | 34                                    |                    |
| (+ <i>Nasalis larvatus</i> , <i>Presbytis rubicunda</i> , <i>P. frontata</i> , <i>Nycticebus coucang</i> , <i>Tarsius bancanus</i> )   |   |                                       |                    |
| <b>Kibale National Park, Uganda</b>  |   |                                       |                    |
| <i>Pan troglodytes</i> <sup>b</sup>  | 2.5                                       | 85                                    | 82                 |
| <i>Colobus guereza</i>   | 58  | 317                                   | 13.6 <sup>a</sup>  |
| <i>C. badius</i>   | 300                                       | 1760                                  | 28 <sup>a</sup>    |
| <i>Cercocebus albigena</i>   | 9   | 60                                    | 58                 |
| <i>Cercopithecus mitis</i>   | 41  | 127                                   | 21–43              |
| <i>C. lhoesti</i>  | 5   | 13                                    | ?                  |
| <i>C. ascanius</i>   | 130                                       | 328                                   | 43.7               |
| <i>Perodicticus potto</i>  | 17.7                                      | 18.6                                  | ?                  |
| <i>Galago inustus</i> and <i>G. demidovii</i>  | 79.5                                      | 50.1                                  | ?                  |
| (+ <i>Papio anubis</i> )   |   |                                       |                    |
| <b>Makokou, Gabon</b>  |   |                                       |                    |
| <i>Cercopithecus neglectus</i>   | 28–38                                     | 110                                   | 77.3               |
| <i>C. nictitans</i>  | 20–40                                     | 100                                   | 72.0               |
| <i>C. pogonias</i>   | 20–25                                     | 60                                    | 82.5               |
| <i>C. cephus</i>   | 20–30                                     | 80                                    | 81.3               |
| <i>C. talapoin</i>   | 40–90                                     | 60                                    | 43.0               |
| (+ <i>Gorilla gorilla</i> , <i>Pan troglodytes</i> , <i>Papio sphinx</i> , <i>Cercocebus albigena</i> , <i>C. galeritus</i> , <i>Colobus guereza</i> , <i>Perodicticus potto</i> , <i>Galago elegantulus</i> , <i>G. alleni</i> , <i>D. demidovii</i> , <i>Arctocebus calabarensis</i> ) |   |                                       |                    |
| <b>Manu National Park, Peru</b>  |   |                                       |                    |
| <i>Ateles paniscus</i>   | 25  | 175                                   | 75 <sup>68</sup>   |
| <i>Alouatta seniculus</i>  | 30  | 180                                   | ?                  |
| <i>Cebus apella</i>  | 40  | 104                                   | 75.4               |
| <i>C. albifrons</i>  | 35  | 84                                    | 63.6               |
| <i>Saimiri sciureus</i>  | 60  | 48                                    | 82.0               |
| <i>Aotus trivirgatus</i>   | 40  | 28                                    | 75                 |
| <i>Callicebus moloch</i>   | 24  | 17                                    | 51                 |
| (+ <i>Logothrix lagotricha</i> , <i>Pithecia monachus</i> , <i>Callimico</i> , <i>goeldii</i> , <i>Saguinus imperator</i> , <i>S. fuscicollis</i> , <i>Cebuella pygmaea</i> )  |   |                                       |                    |

<sup>a</sup>Species present in the community for which data are not available; <sup>b</sup>includes unripe fruit; <sup>c</sup>Chapman and Chapman, unpublished data.

can yield enlightening results.

### Seed Removal and How Primates Process Seeds

Recently, quantification of the number of seeds processed and dispersed by primates has become available from South American forests,<sup>13,23</sup> Central American forests,<sup>7,8,14,15,24</sup> and African forests.<sup>10,11,17,25,26</sup> These studies have revealed interesting differences between primates communities. For example, in Kibale National Park, Uganda, 98.5% of chimpanzee dung samples contain seeds, with an average of 22 large seeds ( $\geq 2$  mm) per defecation.<sup>11</sup> The number of large seeds dispersed by the chimpanzee population is estimated at 369 large seeds/km<sup>2</sup>/day. In contrast, the average number of seeds per defecation for the arboreal frugivorous monkeys in Kibale is 0.37. However, given their numerical dominance, these monkeys defecate approximately 446 large seeds/km<sup>2</sup>/day. Thus, the frugivorous primate community at Kibale, with a biomass of 575 kg/km<sup>2</sup>, defecates approximately 815 large seeds/km<sup>2</sup>/day. In contrast, a primate community of northern Costa Rica (*Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus*), having a biomass of 426 kg/km, disperses approximately 5,600 large seeds/km<sup>2</sup>/day.<sup>14,27,28</sup>

The difference in the number of seeds defecated relative to the biomass of the communities can be attributed, in part, to the fruit processing techniques used by the different species. The fruit-eating primate has three options: swallow the fruit with the pulp and seed, and defecate the seed intact; clean the pulp off the seed and subsequently spit out the seed; or break the seed and digest its contents.<sup>9</sup> For a primate, swallowing the seed has the disadvantage of forcing the animal to carry the hard indigestible seed in its stomach until it can be passed. Some species of primates (e.g., *Pithecia pithecia* and *Chiropotes satanas*) are specialized seed predators<sup>29</sup> and other species (e.g., *Cercocebus albigena*) break and digest seeds on occasion.<sup>30</sup> However, this is not a common foraging strategy in the primate order, probably because seeds typically are protected both chemically and mechanically.<sup>9</sup> Therefore,

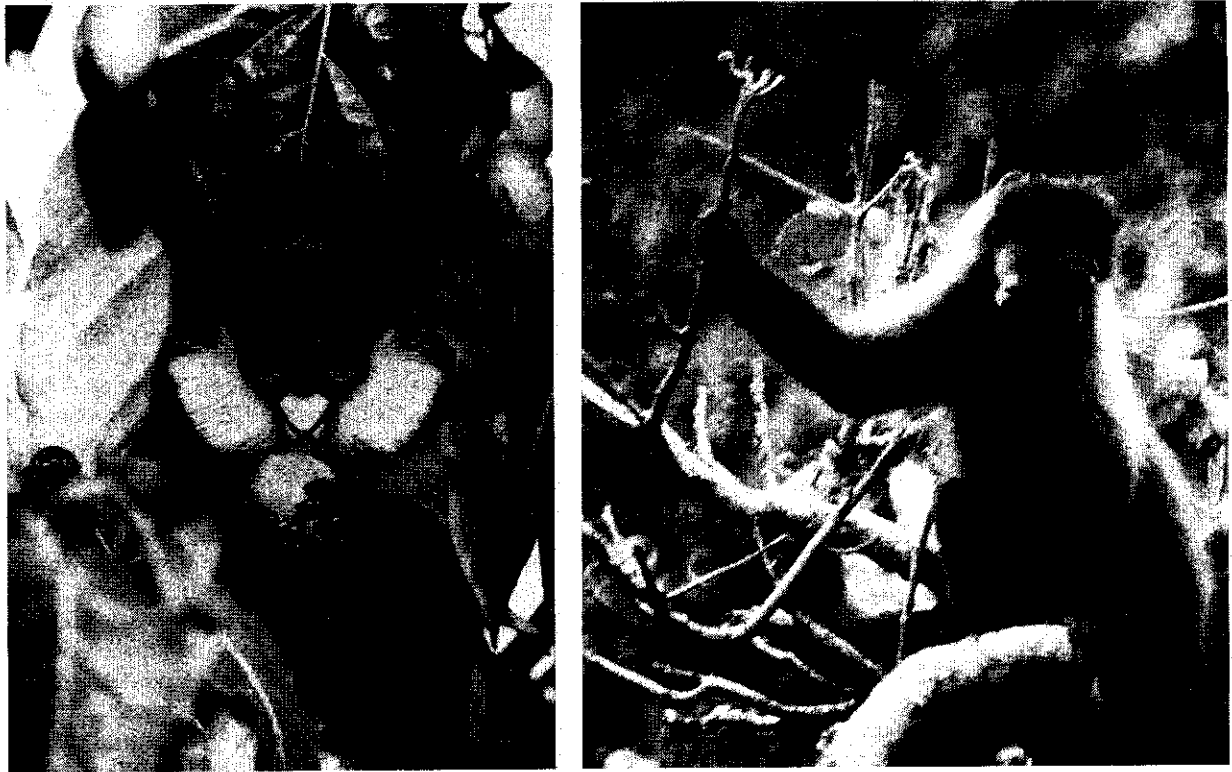


Figure 1. A redtail monkey (*Cercopithecus ascanius*) and a mangabey (*Cerecocebus albigena*) from Kibale National Park, Uganda. These monkeys often put a large number of fruits in their cheek pouches. Later the fruit is processed in the mouth, the fruit pulp is removed, and seeds are spit out.

the first and second options are more commonly employed. The difference in the number of seeds defecated per day by primates in African and Central American forests may reflect the fact that Old World monkeys have cheek pouches<sup>10</sup> (Fig. 1). The cheek pouches of cercopithecine monkeys can hold about as much as the animal's stomach.<sup>10</sup> Thus, a monkey often picks fruit rapidly, stuffing it into the cheek pouches, then retreats to a safe location or initiates other activities. The monkey takes each fruit from its cheek pouch into its mouth, cleans off the pulp, then spits out the seed. Rowell and Mitchell<sup>10</sup> have presented evidence that the seeds defecated by capuchin monkeys (*Cebus capucinus*) are deposited in feces anywhere from 200 to 1,000 m from a parent tree, whereas seeds carried in the cheek pouches of redtail monkeys (*Cercopithecus ascanius*) typically are spit out 30–50 m from the parent tree. Little is known about the effects of these different strategies on the relative success of seeds and the spatial distributions of resulting trees. However, there is evidence that seeds dispersed even short

distances from the parent tree may have a much greater chance of success than do seeds that fall or are deposited directly under the tree. Over a 28 week period, Schupp<sup>31</sup> documented approximately 93% mortality among *Faramaea occidentalis* seeds under the parent crown, but only 76% mortality among seeds 5 m away from the parent tree.

#### Fate of Dispersed Seeds

Once fruits have been eaten and the seeds are either spit out or defecated, they must first escape seed predators or be secondarily dispersed, and then be capable of germination and establishment. To understand the significance of fruit removal by primates, it is necessary to quantify the fate of dispersed seeds. To assess the relative importance of different primary dispersers and to understand the selective pressure primates place on the food tree species, it is necessary to understand the quality of the deposition site. Some species or populations may defecate in locations that are highly suitable for seed germination and establishment, but others may not. For

example, seeds deposited in large numbers directly under trees in which primates repeatedly sleep may have a low probability of survival relative to seeds dispersed while animals are traveling or seeds deposited at sleeping sites used only once. The proportion of seeds deposited in these different ways will influence the strength of the selective pressure exerted on the plant species.

The microsite at which animals defecate varies between species and between populations of the same species. In some populations of spider monkeys, for example, the majority of the community congregates at night at a fixed sleeping site, while other populations may have a number of fixed sleeping sites, and still other populations may not congregate at all.<sup>32</sup> In general, little is known about variation in the suitability of locations where primates deposit seeds. This is an exciting avenue for future research.

Estrada and Coates-Estrada<sup>24</sup> found that the majority ( $\geq 90\%$ ) of seeds dispersed by howler monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico, were destroyed by rodents. At

Santa Rosa National Park, Costa Rica, 97.9% of the seeds placed out at experimental stations were removed or killed 70 days after the stations had been established.<sup>14</sup> In Kibale National Park, Uganda, when the seeds of six fruiting tree species were placed on the forest floor, they disappeared at an average rate of 73% within 6 months.<sup>17</sup> However, in Kibale the pattern of disappearance was bimodal: some species of seeds had a very low probability of disappearance (e.g., that for *B. wilsoniana* was 10%), whereas other species had an extremely high probability of removal (e.g., that for *Pseudospondias microcarpa* was 100%). In a Kibale study, only 6 of 3,170 seeds placed at experimental stations in the forest germinated, only 2 of these became established, and only 1 survived for four years. This probability of seed survival is not surprising, considering that even tree species with large seeds—for example, *Pseudospondias microcarpa*, which has a seed length of 16.2 mm—commonly bear more than 30,000 fruits per tree per year.<sup>17</sup>

In all the previously mentioned studies, rodents were considered to be major seed predators. The majority of the seeds rodents handle presumably are killed, although detailed studies of the fate of these seeds are lacking. Dung beetles may play a particularly significant role in secondary seed dispersal. Some dung beetles roll primate dung, containing seeds up to 5 m from the site of deposition.<sup>24</sup> Dung beetles will incorporate seeds that have a diameter as large as 16.2 mm into their dung balls (Shepherd and Chapman, unpublished data). Burrowing and ball-rolling dung beetles bury seeds at depths ranging from 2.5 to 12 cm. The removal and burial of these seeds is thought to be beneficial because the seeds are less likely to be found by rodents.<sup>24</sup>

All studies of secondary seed dispersal have demonstrated a large amount of variation between species in the rate of seed removal from primate dung. This suggests that the selective pressures affecting a plant may involve traits that are responses to the pressures of both primary and secondary dispersers. For example, it seems reasonable to speculate that selection may favor seeds that are ovate and

elongate, like many pills. Seeds of this shape would have sufficient volume to encourage initial growth of the seedling. Their elongated shape would also increase the likelihood that the seed would be swallowed. However, it is also conceivable that elongated seeds,

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as compared to round seeds of similar volume, would have a lower probability of being incorporated in the dung beetle's ball. Investigations of how specific seed traits influence primary and then secondary seed dispersal will prove to be an intriguing area of future study.

### Germination

Evidence suggests that the seeds primates disperse that are not found by rodents or secondarily dispersed by dung beetles probably are capable of

germination if the conditions are right. When researchers take seeds from primate dung and attempt to germinate them in controlled settings, evidence typically suggests that the passage through the frugivore gut has improved the rate of germination and reduced latency to germination (but see <sup>12</sup>). Lieberman et al.<sup>33</sup> were able to germinate seeds from 59 plant species collected from baboon dung in Ghana. They found that ingestion improved germination success over that of fresh seeds in 3 of the 4 species tested. Garber<sup>13</sup> experimentally planted seeds defecated by *Saguinus mystax* and *S. fuscicollis*, and found a 70% germination success rate. Estrada and Coates-Estrada<sup>7</sup> obtained a germination success rate of 57% with seeds from dung of the howlers (*Alouatta palliata*) at Los Tuxtlas, Mexico; this was an increase of 22% over the germination of control seeds collected from the tree. In all of the 10 fruiting tree species tested in the Kibale Forest, passage of seeds through the chimpanzee gut improved the rate of germination and reduced latency to germination.<sup>11</sup> Similarly, Idani<sup>34</sup> tested the germination potential of 17 species of seeds that had been passed by bonobos and found a 77% rate of germination success, with 50% of the species showing enhanced germination success as compared with controls. For the primate community of Santa Rosa National Park, Costa Rica, approximately 60% of the seeds collected from primate dung germinated under experimental conditions.<sup>14</sup> In this study, however, the three different techniques used to germinate seeds produced significantly different germination success rates, suggesting that caution should be used when comparing absolute values of germination success and latency to germination.

Discussions such as this one give the impression that primates are highly efficient seed dispersers, but in reality they often are very wasteful during the time they feed in a tree. For example, Howe<sup>15</sup> established that 66% of the fruits of *Tetragastris panamensis* were either dropped or spontaneously fell under parent trees. Similar observations have been made regarding the feeding behavior of vervet mon-

keys.<sup>1,35</sup> Seeds fallen or deposited under a parent tree are subjected to increased density-dependent mortality associated with high levels of seed predation and pathogen attack.<sup>22</sup>

### COEVOLUTION BETWEEN PRIMATES AND TROPICAL TREES

Early comparative studies suggested that fruit traits such as color, size, and protection evolved in response to selection by frugivore dispersers as covarying character complexes or dispersal syndromes. However, seed dispersal studies have produced little empirical support for tight coevolutionary relationships between plants and their dispersers.<sup>36-38</sup> Moreover, recent comparative studies have produced conflicting results.<sup>24,39</sup> Numerous factors may limit the potential for coevolution between plants and their animal dispersers. These include inequality in the evolutionary life spans of plant and animal taxa; differences in the generation lengths of plants and their dispersers; extensive gene flow between plant populations; weak selective pressures on dispersers; ecological variables outside the control of the parent plant (e.g., the influence of other fruiting plants and dietary variability among the dispersers population); unpredictability of germination sites; secondary dispersal; and the lack of evolutionary plasticity in fruit traits.<sup>37-39</sup> In addition, fruit traits may occur in response to other selection pressures or may perform more than one function. For example, it has been suggested that green fruits reduce the energetic costs of reproduction because they are capable of photosynthesis<sup>40</sup> and that red coloration protects fruits from arthropod predators through crypsis.<sup>41</sup>

Studies in Gabon illustrate the lack of specificity between frugivore and plant species. Of 112 fruit species in the diets of ruminants, monkeys, and rodents, 35% were eaten by these three taxa and at least 70% by two taxa.<sup>26</sup> Further, during 61.5 hours of observation of *Trichilia gilgiana*, 22 species, including 2 ruminants, 9 rodents, 10 birds, and 2 monkey species, ate fruit from the tree. A similar diversity of visitors has been documented during tree watches in Kibale Forest, Uganda.<sup>17</sup>

Gautier-Hion et al.<sup>42</sup> have done an

excellent study that illustrates how dietary variability among the disperser community can result in weak selective pressure on fruit traits. They studied the diets of two species of *Cercopithecus* monkeys of the superspecies mona: *C. pogonias* in Gabon and *C. wolfi* in Zaire. They found that *C. pogonias* is primarily a fruit-pulp eater and plays an important part in seed dispersal, whereas *C. wolfi* is primarily a seed predator. These dietary differences over such a small geographical

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scale (1,050 km apart) illustrate that closely related primates can exert very different selective pressures on plant species.

Weak selection pressure on fruit traits will also result if primates have highly flexible diets and thus are not reliable dispersers. The high degree of dietary flexibility that has been observed in many primate species can be characterized by distinct shifts between different food categories (e.g., from fruit to leaves.<sup>27,43-46</sup> For example, Chapman<sup>45</sup> found that spider monkeys (*Ateles geoffroyi*) in Costa

Rica shifted from a frugivorous diet (100% of their feeding time spent eating fruit) to a folivorous diet (86.3% of their feeding time spent eating leaves). Waser<sup>30</sup> documented a number of examples of annual variation in the diet of mangabeys (*Cercocebus albigena*). For example, he observed mangabeys feeding on the leaves of *Platycerium* in 1971, but not again until 1974, although these leaves were available during the intervening years.

On a spatial scale, large dietary differences between neighboring primate groups<sup>47,48</sup> or groups living only a few hundred kilometers apart<sup>49</sup> are not uncommon. For example, one group of *Cebus capucinus* spent 81% of their feeding time eating fruit and only 17% of that time eating insects, whereas a neighboring group was heavily reliant on insects (44%) and ate less fruit (53%).<sup>48</sup> The majority of these dietary differences between the neighboring groups was unrelated to differences in the availability of specific fruiting tree species.<sup>48</sup> If there is gene flow between the plant populations that these different primate populations are affecting, such spatial variability in primate diets will result in weak selection pressure on fruit traits.

In order to propose that coevolution between primates and fruiting plants has resulted in selection for specific fruit traits, we must be able to demonstrate that there have been reciprocal evolutionary changes in the interactants.<sup>50</sup> Data from the fossil record, although incomplete, suggest that fruit traits often have remained constant while primate communities have changed dramatically. Fleshy angiosperm fruits first appeared in the Late Cretaceous<sup>51</sup> and their modern families were well established by the early to middle Eocene.<sup>52</sup> The fruits of living *Taxus* species seem essentially identical to those of *Paleotaxus*, a relative that was living 175 million years ago.<sup>38</sup> This implies that aspects of fruit morphology have remained relatively constant for millions of years. Although fleshy fruits may have evolved multiple times in a variety of ecological circumstances,<sup>53</sup> it seems probable that a succession of primate communities have encountered morphologically similar fruits.

Primates may still play a roll in determining fruit structure, but this may occur at a more general level than has been postulated. For example, Janson<sup>54</sup> has proposed that macroevolutionary patterns of change in fruit morphology may be influenced by plant frugivore interactions. His analysis of transitions among fruit characters, using a Markov model to estimate transition probabilities, indicates that transitions from unhusked to husked forms are more likely than the reciprocal transition. Janson suggests that this may be the result of differences in the foraging behavior of birds and mammals. Mammals feed on both husked and unhusked fruits, whereas birds feed almost exclusively on unhusked fruits.<sup>23</sup> This difference, he suggests, provides a selection pressure favoring the transition from unhusked to husked fruits, while a reciprocal selection pressure associated with avian dispersal is never applied to husked fruits.

Although evidence suggests few tight coevolutionary relationships between primates and the seeds they disperse, one possible exception is the relationship between *Cola lizae* and gorillas. Tutin et al.<sup>16</sup> determined that gorillas are the only important disperser of this species, that *C. lizae* seeds found in gorilla dung have a high germination success rate, and that survival of seedlings is significantly better in dung at nest sites than in other areas of the forest. Although present-day dependency on a single disperser does not necessarily require a coevolutionary relationship between the plant and the seed disperser,<sup>55</sup> studies of such highly interdependent systems are of importance in understanding factors that both limit and promote mutual dependency. It is interesting that no such highly interdependent system has been documented for chimpanzees, in spite of intensive studies of their seed dispersal abilities.<sup>11,34,56</sup> As has been suggested with highly interdependent dispersal systems involving elephants,<sup>21</sup> the large size of the seeds of *C. lizae* (35 mm long) may eliminate all but the largest-bodied seed dispersers. Regardless of whether or not specific fruit traits are the result of coevolution between primates and fruits, primate-plant inter-

actions do influence the fitness of both interactants, shape primate behavior, and affect forest structure and composition.

### PRIMATE CONSERVATION AND THE PRESERVATION OF TROPICAL FORESTS

The need for greater understanding of the role primates play in dispersing the seeds of tropical trees has taken on a degree of urgency as a result of the recent decline of many frugivore populations. It is critical that this urgency does not overshadow the need for quantitative studies describing the interactions between primates and tropical fruiting trees, and that management plans are not prematurely based on inadequate information.

It is readily apparent that the loss of

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### The most susceptible species to hunting are large-bodied frugivores, and these species may be particularly important seed dispersers.

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tropical forest is a central conservation issue. Much effort has been invested in understanding the extent of forest conversion, the factors contributing to its loss, and possible solutions to decrease the rate of destruction. However, human activities in forests are not limited to the cutting of trees. Subsistence and commercial hunting affect large tracts of forest while leaving their physical structure relatively unaltered, at least in the short term.<sup>57</sup> For example, subsistence hunting by 230 inhabitants of three small villages in Ecuador results in the killing of approximately 3,165 mammals, birds, and reptiles annually.<sup>58</sup> In the interior of Surinam, primates account for as much as 25% of the meat eaten by local people.<sup>59</sup> Unfortunately, there is little understanding of how these

hunting activities alter the processes governing the maintenance and long-term sustainability of forest ecosystems. For example, large primates, which may play particularly significant roles in the dispersal of large-seeded tropical trees, often are a preferred target for hunters.<sup>11,60</sup> Wrangham et al.<sup>11</sup> demonstrated that although chimpanzees (*Pan troglodytes*) constitute only 1.4% of the primate frugivore population by number and 14.2% of the primate frugivore biomass, they are responsible for approximately 45.3% of the seeds defecated by frugivorous primates.

A number of studies of specific tree species that have examined the survival of seedlings under parent trees have found little or no recruitment under parent trees.<sup>22</sup> For example, Howe et al.<sup>61</sup> found that 99.96% of *Virola surinamensis* fruit that drop under the parent are killed within only 12 weeks. Similarly, Schupp<sup>31</sup> documented the survival of only 7% of *Farama occidentalis* seeds under the parent crown within 30 weeks, in comparison to the survival of 24% of the seeds 5 m away from the tree. However, other studies have revealed relatively small differences between the probability of survival of seeds under parent trees and those dispersed from it.<sup>62</sup> Such conflicting results make it difficult to predict the consequences of frugivore declines on plant biodiversity. Studies such as those by Leigh et al.<sup>63</sup> and Bierregaard et al.<sup>64</sup> illustrate the initial loss of tree biodiversity that results when populations are restricted to "islands" with reduced disperser and seed predator faunas. However, the times over which these studies have been carried out (1913–1980 and 1979 to present) are short relative to the life span of the tree species. In addition, a number of factors are involved in the reduction of species numbers on such islands.

A recent study attempted to estimate the potential loss in plant biodiversity that would result if all frugivore seed dispersers were hunted out of an area and fruit just fell to the forest floor under the parent.<sup>65</sup> This study identified all the seedlings, saplings, and poles growing directly under the canopy of 5 adult trees of 25 species. For tree species with large

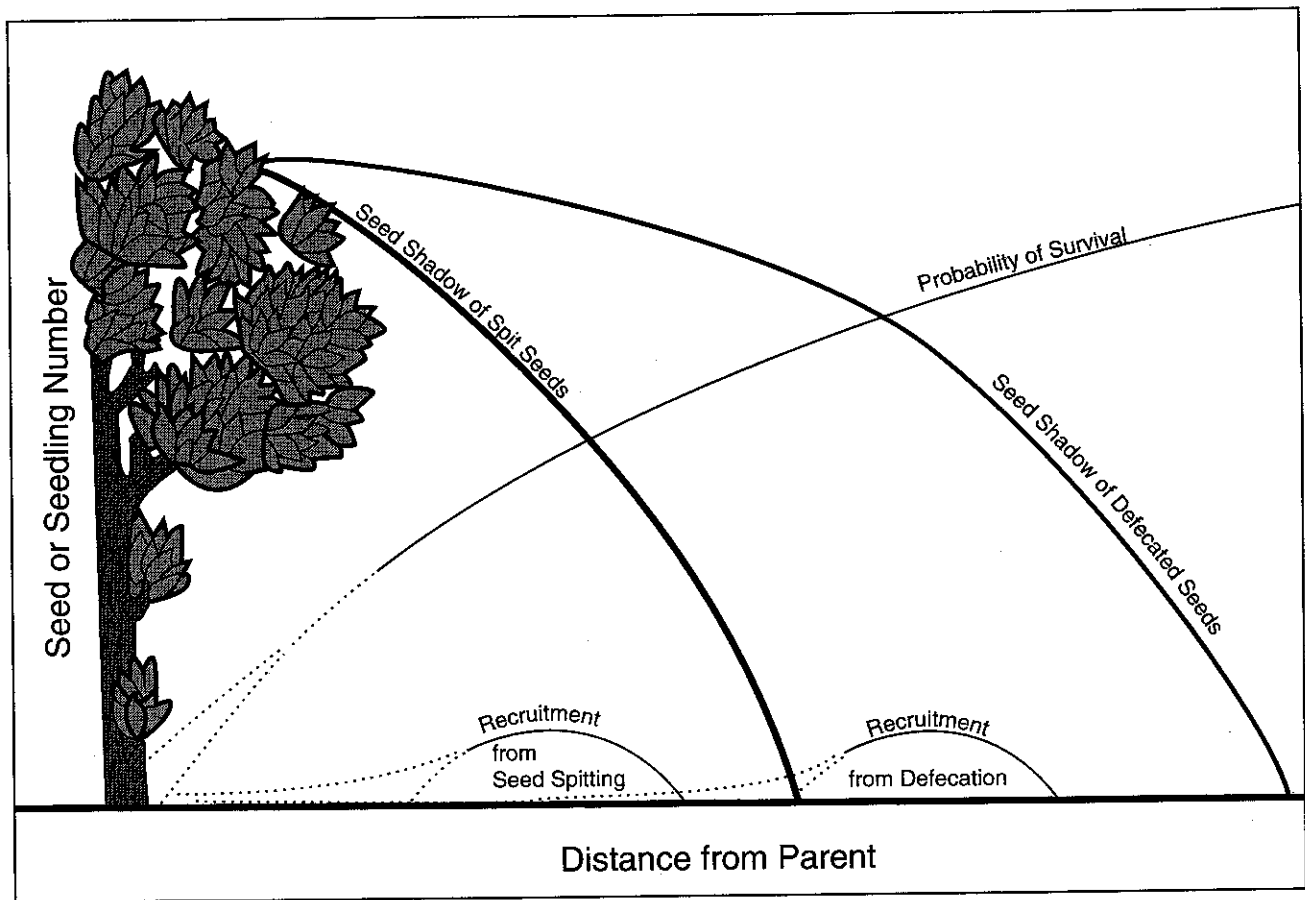


Figure 2. A hypothetical illustration of the seed shadow, the probability of seed survival, and the recruitment curves that would result from seeds that are primarily spit out, as in the Old World, and seeds that are primarily defecated, as in the New World. The dotted lines with respect to the probability of survival and recruitment curves illustrate the reason for debate about the likelihood that seeds can survive under the parent's canopy (see ref. 65).

fleshy fruits adapted for dispersal by large frugivores, the loss of frugivores would affect all species that could not recruit (generate new individuals) under parent trees. It is difficult to state conclusively if seedlings of a particular species can or cannot recruit under adult conspecifics. It is possible that, for some unknown reason, recruitment of a particular species is not occurring in an area or occurs only under specific conditions that arise only occasionally over a long time. However, the presence or absence of seedlings and saplings under adult conspecifics does provide an initial assessment of the extent of loss of biodiversity that might result from a significant reduction in populations of seed dispersers. On the basis of the presence or absence of seedlings and saplings under adults, Chapman and Chapman<sup>65</sup> estimated that 60% of the 25 tree species they sampled could potentially be lost if

all frugivores were removed. Because the growth and survival of saplings are

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**An understanding of what happens to seeds that primates spit out or deposit in their dung on the forest floor is essential to quantify the intensity of the selective pressure that primates exert on their food trees.**

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often negatively affected by growing under a conspecific adult,<sup>66</sup> this estimate may be conservative.

Based on our understanding of co-evolution between frugivores and

fruiting tree species, it is unlikely that the overhunting and removal of a single frugivorous primate species will cause local extinctions of plant species, for most plant species do not depend on a single species of disperser. However, the most susceptible species to hunting are large-bodied frugivores, and these species may be particularly important seed dispersers.<sup>11</sup> This discussion of the role of primates in structuring tropical forests illustrates that research in this area not only addresses academic issues, but is a forceful argument for the preservation of primate communities.

**CONCLUSIONS AND THE NEXT GENERATION**

From an initial understanding that primates often spend large periods of time feeding on the fruits of tropical forest trees and that they constitute a major proportion of the frugivore



biomass in tropical forests, we have recently begun to unravel the complex nature of the interactions involved. However, each new discovery has demonstrated that an understanding of the evolutionary processes structuring these complex interactions will demand investigations of the fate of dispersed seeds and the spatial and temporal variability in fruit-processing strategies.

An understanding of what happens to seeds that primates spit out or deposit in their dung on the forest floor is essential to quantify the intensity of the selective pressure that primates exert on their food trees. Recent studies have generated a myriad of interesting questions: what role do dung beetles and rodents play after seeds have been defecated or spit out by primates? For fruits that primates commonly feed on, is there selection for seed traits that encourage dung beetle processing or discourage rodent predation? What are the effects of the different ways that primates process seeds? What is the effect of high levels of spatial and temporal variability in primate diets on the selection pressure exerted on fruit structure and composition?

The area that may prove most profitable as a means of increasing our understanding of the selective pressures operating in primate-seed dispersal interactions is comparisons among communities. What are the consequences of having communities dominated by dispersers that spit seeds versus communities that primarily defecate seeds? If cercopithecine monkeys with cheek pouches spit out the majority of seeds they process, while all New World primates typically disperse seeds by defecating them, are there radical differences in the selective pressures exerted by the primate communities on the different continents (Fig. 2)? For tree species that rely heavily on primates to disperse their seeds, the differences between defecating seeds and spitting seeds may result in very different distribution patterns for adult trees. Even given high mortality resulting from the density of seeds near the parent plant, one would predict that Old World trees would be more closely clumped than would trees in South-

Central America. Correspondingly, there might be selection for traits associated with dispersal by seed spitting. For instance, the effect of seed size may not be as limiting a factor for a primate that processes fruits in its cheek pouches and spits out the seed as it is for a primate that ingests the seed. However, large seed size may facilitate recruitment near the parent because the associated energy stores could permit regrowth after pathogen or herbivore attack. Thus, for congeneric species one might predict that seeds would be larger in the Old World than in the New World. Mack,<sup>67</sup> in a comparison of fruit size in eight pantropical plant families, found that species in the Old World had larger fruits than did species in the New World. He attributed this to the presence of larger animals in the Old World. An alternative explanation may involve selection resulting from differences between the continents with respect to the proportion of seeds processed and spit out as opposed to the proportion defecated.

Recent investigations of primates as seed dispersers have suggested that they play important roles in the forest ecosystems they inhabit. However, each new discovery has illustrated the complexity of the systems we are studying and has given rise to a variety of new and exciting avenues for future research.

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