# Seed Dispersal

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In the habitats where they occur, frugivorous primates disperse an enormous quantity of plant seeds, often far more than many other frugivorous taxa. In a Bornean tropical forest, a single group of gibbons (*Hylobates muelleri* × *agilis*) dispersed at least 16,400 seeds per kilometer per year of 160 woody plant species. With an average per capita seed survival rate of about 8 percent, these gibbons effectively dispersed about 13 seedlings per hectare per year (McConkey 2000). The example of Bornean gibbons is not a rare one: primates play equally vital roles in the regeneration of forests in Peru, Ecuador, Panama, Costa Rica, Uganda, and elsewhere. Frugivory and seed dispersal are fundamental plant–animal interactions that have influenced the evolution and ecology of primates and of the plants whose seeds they disperse.

## Traits of Primates and Plants Influencing Seed Dispersal

Fruits are the seed-containing reproductive organs of angiosperms, and many primate species have evolved a diet primarily comprised of fruit (Lambert 2011). Frugivorous species can be found in nearly all phylogenetic lineages of primates: 64 percent of the extant species are frugivores, and 96 percent occasionally consume fleshy fruits (Gómez and Verdú 2012). Frugivores and plant species are considered to have undergone diffuse co-adaptation, leading to coordination between the characteristics of fruits and of the species that consume fruits and disperse the seeds inside them. For instance, primate-dispersed fruits often are large, yellow, orange, or brown in color, and have a hard exocarp requiring manipulation to access the nutritious mesocarp within. In contrast, bird-dispersed fruits often are smaller, red or black in color, and rarely have a hard exocarp. These and other differences in the traits of fruits dispersed by primates versus birds may be related to differences in body size, manual dexterity, and color vision. On average, primate species are larger than bird species, and so can consume larger fruits. Most birds have limited dexterity and must largely manipulate food items with the bill, whereas the dexterity of primates' feet and hands makes it energetically profitable for them to seek out food requiring more complex manipulation. Birds have trichromatic vision, enabling them to distinguish red and black fruit on a background of green leaves, whereas only some primates, such as humans, most catarrhines (Old World monkeys and apes), and some platyrrhines (New World monkeys) have trichromatic vision. While such fruit–frugivore syndromes have been broadly described, frugivorous primates display substantial dietary plasticity, which may amount to the exception that proves the rule. Nonetheless, phylogenetic analyses of the primate–plant facultative mutualism suggest that while frugivory has favored the diversification of primates, diversification was even faster if these frugivorous primates were also seed dispersers (Gómez and Verdú 2012).

Seed dispersal is often considered broadly as two processes: finding and consuming fruit and processing seeds. In finding and consuming fruit, primates make foraging decisions, often responding not only to the traits of plant species, such as the size, color, and nutritional quality of fruit, as described above, but also to the spatial distribution and abundance of fruiting plant species in a habitat, which is often patchy. Primates must choose among a variety of different potential fruit patches, that differ in accessibility and caloric and nutrient contents, and their choices must be metabolically profitable to ensure sufficient dietary resources for survival and reproduction. The foraging decisions and their energetic implications depend on a number of traits of primates that vary among lineages, including body size, social structure, digestive anatomy, locomotion,

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and vision. Several types of quantitative models have taken a mechanistic, energetic approach to describe the movement patterns arising from the foraging decisions of primates, including optimal and central-place foraging models, which often incorporate variables related to the traits of primate and plant species. These models can be contrasted with random-walk models, which make minimal assumptions about the factors influencing how primates move on the landscape. Such models of primate movement patterns, combined with information on seed passage time through the gut, can be used to model the spatial pattern of seed dispersal, or the seed shadow, produced by primates.

Seeds often account for more than half of the weight of fruits consumed by primates, and so how primates treat seeds is an important foraging consideration. While some primates are granivores and consume the seeds themselves, and are thus seed predators, not seed dispersers, frugivorous primates, by definition, generally do not. They must find a way to extract the nutritious mesocarp and discard the seeds, and frugivorous primate species have evolved a diversity of ways to do this. If they are small enough, seeds can be swallowed whole and pass through the digestive tract, with the seed's endocarp protecting the plant embryo and endosperm within from damage. If the seed is too large to ingest, primates may pluck and consume bits of mesocarp from the fruit, and manually discard seeds immediately. Yet a third strategy is employed by African and Asian cheek-pouched monkeys (Cercopithecinae), which have cheek pouches with nearly the same capacity as their stomachs, allowing them to store multiple fruits and extract the mesocarp without incurring the costs of transporting ingested seeds until defecation.

Each of these different seed-processing strategies has different consequences for the shapes of seed shadows that primates generate. Seeds ingested whole may be moved long distances from the mother tree to the site of defecation, since it may take hours for seeds to pass through the gut, at which point a primate may be quite far from the location where the fruit was consumed. Some of the longest recorded seed dispersal distances, over 1 kilometer, are from primate species, such as spider monkeys (*Ateles* spp.), with large home ranges, that routinely travel long distances as they move quickly between successive food patches. While seeds that are spat out immediately are cleaned of mesocarp, which may aid germination, they may not be dispersed past the crown of the mother tree. Such seeds often suffer high predation rates from granivorous rodents that forage in the dense aggregations of seeds that fall undispersed to the ground under the mother tree's crown. Seeds carried in cheek pouches can also be dispersed relatively long distances, depending on how long it takes to process fruit within the cheek pouch, and they, along with swallowed and defecated seeds, can thus escape the high predation rates commonly experienced by undispersed seeds.

Escape from predation is considered to be one of the three principal benefits of seed dispersal to plants (Howe and Miriti 2004). Seed dispersal also enables plants to colonize different habitats. For example, pioneer tree species are those that require gaps in the forest canopy in order to reach adulthood, since they have high light requirements for survival and growth. Canopy gaps, however, are often infrequent and widely distributed in forests, and so seeds have a low probability of arriving in them unless they are also widely dispersed. A third benefit is that of seed dispersal directed to specific habitats or locations that are particularly favorable to seed and seedling survival.

Seed dispersing primates may differ in their dispersal effectiveness, which has both quantitative and qualitative components (Schupp, Jordano, and Gómez 2010). The quantity of seed dispersal depends on the number of visits made to the plant by a disperser and the number of seeds dispersed per visit. The quality of seed dispersal depends on the treatment given to a seed in the digestive system and the probability that a deposited seed will survive and become an adult (Fuzessy et al. 2016).

Many traits make some primate species effective seed dispersers. In terms of dispersal quantity, because primates often have larger bodies than many other seed-dispersing animals, an individual primate can process more seeds per day. Many primate species can also occur at high population densities, which, when combined with large body size, contributes to high quantity of seed dispersal at the population level. For example, in Amazonian Peru, the 6-

to 8-kilogram spider monkey (*Ateles paniscus*) occurs at an estimated population density of 25 individuals per square kilometer, greater than any other seed-dispersing bird species in the same forest, all of which are also much smaller in body size. Simply moving large numbers of seeds alone would not make primates effective seed dispersers, but primates are often high-quality dispersers as well. The more heterogeneous the seed shadow of a plant species is, the more likely those seeds are to enjoy the benefits of seed dispersal (Russo and Chapman 2010).

Seed shadows are defined by the distances that seeds are moved, the habitats where they are deposited, and the spatial aggregation of seeds when they are deposited (that is, whether they are scattered or clumped). Seed and seedling survival is often negatively density dependent, being lower in areas with high densities of seeds, and positively distance dependent, being higher for seeds that are dispersed away from a conspecific. Many primate species have large home ranges, so individuals move over long distances each day, often through several vegetation types, generating longer seed dispersal distances and depositing seeds in multiple habitats. The mode of seed processing, as described above, the size and movement rates of foraging parties, and behaviors such as repeated use of sleeping sites or latrines influence the spatial aggregation of seed deposition. Primates have a diversity of social structures (Berman 2011), which influences foraging and movement patterns and home range sizes (Sussman and Garber 2011). Some of the longest dispersal distances and most heterogeneous seed shadows are generated by primates with a fission–fusion society, such as the large communities of spider monkeys (*Ateles* spp.) and chimpanzees (*Pan troglodytes*), in which parties of individuals join and splinter repeatedly during foraging. The fission–fusion society can be contrasted with other social systems. Few primate species have a social structure consisting of a single female with her offspring, as in the nocturnal prosimians. Combined with their generally smaller body size, frugivorous prosimians disperse fewer seeds shorter distances and over a narrower range of habitats. More common is monogamy, as in the gibbons (Hylobatidae), or polygyny, as in howler monkeys (*Alouatta* spp.), baboons (*Papio* spp.), and gorillas (*Gorilla* spp). In these complex societies, adult males and females and juveniles have different roles, and hence different foraging and movement patterns. For instance, in the fission–fusion societies of spider monkeys and chimpanzees, the diurnal movements of adult males are often more extensive than those of other community members, as they search for females in estrus. To the extent that individuals of different ages, sexes, or social status of a primate species vary in their foraging and movement patterns, further heterogeneity in the seed shadow is produced.

## Conservation Implications of Primate Seed Dispersal

Worldwide, rampant hunting and habitat destruction and fragmentation threaten many populations of primates and create habitats emptied of animals, especially large-bodied primates. Declines in primate populations come at a time when their seed-dispersal services are desperately needed for plant communities to respond to global anthropogenic stressors (McConkey et al. 2012), and so it is more urgent than ever to understand seed dispersal by primates. Many of the characteristics of seed shadows generated by primates, as summarized above, make them not only effective seed dispersers, but also particularly critical in the regeneration of plant communities. Primates often use disturbed habitats, and so facilitate regeneration in fragmented landscapes by moving seeds long distances between multiple habitats, such as between mature and early successional vegetation. Due to their often large body size and manual dexterity, primates are especially important for the recruitment of plant species producing large seeds or hard-husked fruits, many of which are too big or difficult to manipulate to be dispersed by other animals. Moreover, the degree of dietary frugivory increases with body size, suggesting that the most frugivorous species can disperse the largest seeds over large home ranges. While their seed deposition patterns may be clumped, which often reduces per capita seed and seedling survival, the quantity of seeds that they disperse generally exceeds that of most other dispersal agents in the same community, which may ultimately enable more seedlings to survive in terms of absolute numbers (Russo and Augspurger 2004). The dietary flexibility of primates means that they often can provide highly effective dispersal services to many plant species. For example, among South American primates, frugivorous species consumed fruit from 4 to 267 plant species (Hawes and Peres 2014). This flexibility may help mitigate the "few winners and many losers" effect that has been observed to predominate in edge-dominated habitats of hyperfragmented landscapes, in which late-successional plant species are replaced by a small set of early-successional species (Tabarelli, Peres, and Melo 2012).

SEE ALSO: Body Size and Scaling; Bushmeat; Cheek Pouches; Color Vision of Primates; Deforestation; Dispersal; Ecological Communities; Ecological Morphology; Energetics; Fission–Fusion; Foraging Strategies; Forest Regeneration (Role of Primates in); Frugivory; Group Movements (and Collective Decision Making); Grouping Patterns; Habitat Fragmentation; Habitat Restoration; Habitat Use; Home Range; Social System (Social Structure)

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## ABSTRACT

Frugivorous primates disperse the seeds of an enormous number of plant species in a wide variety of vegetation types across the globe. This facultative mutualism has contributed to the species and functional diversification of primates, in addition to influencing the reproductive ecology of plant species producing fleshy fruits. By generating heterogeneous seed shadows often characterized by the dispersal of seeds long distances, into multiple habitats, and with varying degrees of spatial aggregation, primates are often effective seed dispersers that are critical to the regeneration of plant communities, especially in an era of rapid global change.

## KEYWORDS

diet; ecology; ecosystems