Chapter 10
The Seed Dispersal Niche of Gibbons in Bornean Dipterocarp Forests

Kim R. McConkey

Introduction

Most tropical rain forest plants are adapted to have their seeds dispersed by animals (Richards 1996). A profusion of birds, mammals, insects, and occasionally reptiles and amphibians consume fruits, but they differ in their ranging behavior, ability to manipulate seeds, and, hence, their seed dispersal effectiveness (van der Pijl 1982; Corlett 1998). It was assumed for many years that effective seed dispersers had close coevolutionary relationships with their selected fruit species (McKey 1980), but more recent research indicates that coevolution has generally been on a diffuse scale – between suites of dispersers and fruits (Herrera 1985). The development of close relationships are hindered by the diversity of frugivores that feed on most plant species [only rarely is a plant species dispersed by a single species (e.g., Cochrane 2003)] and by inconsistencies in frugivore foraging over time or space (Chapman and Chapman 2002), or even within a single fruiting season of a plant species [e.g., small sources may attract a different array of frugivores than large sources (Russo 2003)]. Furthermore, very few dispersed seeds produce a reproductive, adult plant with subsequent life stages overriding any subtle advantages of one dispersal mode over another (Howe and Mitiri 2004). For a frugivorous species to develop a more direct coevolutionary relationship with favored plant species, it must have a clearly defined niche in the frugivore community, providing a consistent and unique dispersal service that can have a lasting positive impact on the survival and establishment of dispersed seeds.

Effective seed dispersers should disperse many seeds (quantitative component), from multiple sources, and in a manner that maximizes the survival and subsequent germination of the seeds (qualitative component) (Schupp 1993). One of the most important aspects of seed dispersal is the removal of seeds away from the canopy of the parent plant, where there are often higher rates of seed

K.R. McConkey (✉)
E-64 Sainikpuri, Secunderabad 500094, India
e-mail: kimmcconkey@yahoo.co.nz

predation and seedling competition (Barot et al. 1999; Connell 1971; Howe and Mitiri 2004; Janzen 1970; Nathan and Muller-Landau 2000). Seed dispersal also enhances gene flow (Hamilton 1999; Nathan and Muller-Landau 2000), influences plant distribution (Levin et al. 2003; Howe and Mitiri 2004), may help colonize new sites (such as tree fall gaps) (Dalling et al. 2002; Levine and Murrell 2003), and in some cases ensures seeds reach targeted sites, which are crucial for germination (Wenny 2001).

Gibbons (Hylobatidae) are good seed dispersers in Asian rain forests. Studies throughout their distribution indicate that gibbons are consistently frugivorous (Chivers 1984; Elder this volume), swallow most seeds whole, few seeds are dropped or destroyed, and the seeds are subsequently scattered via their scats throughout their home range (Ahsan 1994; McConkey 2000; McConkey and Chivers 2007; Whitington and Treesucon 1991). Two gibbon species inhabit the forests on the island of Borneo [*Hylobates muelleri* and *H. agilis albibarbis* or *H. albibarbis*; the species status of this taxon is controversial (Chatterjee this volume)], and these apes share the forest with many other animals that consume fruit. Despite the apparent efficiency of gibbons as seed dispersers, other animals may adequately disperse the same plant taxa, thereby hindering the development of coevolutionary relationships between gibbons and the plants whose seeds they disperse.

The aim in this chapter is to evaluate the role of gibbons in seed dispersal in Bornean dipterocarp forests with respect to how this role is distinct from other frugivorous animals. First, I describe what type of fruit gibbons favor, since favored fruit species have the most potential to develop coevolutionary relationships. Second, I evaluate the likelihood of gibbons dispersing seeds from multiple individuals of a single plant species and across all fruit patch sizes. Third, the pattern of seed dispersal produced by gibbons and other animals are compared to determine whether the gibbons have a unique dispersal mode and whether this may facilitate the establishment of new individuals of favored species.

Methods

I studied seed dispersal by gibbons (*Hylobates muelleri x agilis/albibarbis*, viable hybrids of two species present in Borneo) in the dipterocarp forests at the Barito Ulu research area, Central Kalimantan, Indonesia between October 1996 and September 1997 (McConkey 1999). I use this research as a basis for evaluating the role of gibbons, while the effectiveness of other frugivores is described from the work of other authors and from observations during the above study.

Study Area and Gibbon Groups

The Barito Ulu research area occurs virtually at the geographic center of the island of Borneo (0°12'N and 114°6'E), in the watershed of the upper Barito

River. The area has a rugged, hilly to mountainous terrain, with altitude ranging from 100 to 350 m asl. Various forest types are present (including heath forest and various stages of secondary forest), but the most expansive is lowland dipterocarp forest (Mirmanto et al. 1999; Brearly et al. 2004). The mean annual rainfall from 1990 to 1997 was 3738 mm. Temperature was very equitable, with a mean maximum of 34°C and a nighttime low of 22°C.

I collected data for two gibbon groups (four individuals each) with adjacent home ranges (46 and 43 ha in size, respectively). My assistants and I followed each gibbon group from their waking site to their sleeping tree, for 5 days in every month for 12 months (a total of 10 days each month). I compiled gibbon diet by direct observations of the feeding gibbons and collection of food items [see McConkey et al. 2002 for more details]. I also collected scats during the follows, from which seeds were identified, counted, and then returned to the defecation location. I checked scats after 1 week and then monitored monthly until the end of the study period (4–12 months after returning scats) (see McConkey 2000, 2005a for details). Seeds that had been destroyed by insects, vertebrates, or had disappeared or germinated were recorded. I noted the removed seeds as verte-brate predation for the analysis, although some of these may have been hoarded by rodents and subsequently germinated (McConkey 2005a). There was no evidence that topography and rainfall (which was very low during the study) were responsible for the disappearance of some seeds. I determined the selection of fruit taxa by gibbons by comparing feeding data with information on the availability of plant taxa. Full methods are given by McConkey et al. (2002), and a summarized version of the resulting selection list is given in the Appendix. Although 17% of fruit feeding observations were of figs (McConkey et al. 2002), figs are not included in the analysis and subsequent discussion since they repre-sent a specially favored food item for many animal species.

I collected phenology data for 1000 trees [selected using the point-center-quarter method (Mueller-Dombois and Ellenberg 1974)] monthly during the study period. The presence of fruit (unripe, ripe), flower, and young leaf in the trees, and lianas within them, was noted (McConkey et al. 2002). I collected and examined the available fruit (general description, fruit and seed measurements) from all phenology trees and the lianas within them, and also opportunistically from other locations.

Bornean Frugivores

Many animals consume the fruits or the seeds of plants, or both, but it is reasonable to assume that animals that are primarily seed predators [e.g., langurs, rodents, some squirrel species, pigs (Corlett 1998)] are unlikely to disperse similar quantities of seeds as gibbons, even if some of the same species are dispersed. Hence, details on these animals were not collected. Similarly, gibbons feed almost exclusively in the upper strata of the forest, and arboreal and volant animals

that rarely, or never, use these strata are also excluded. Some terrestrial animals consume fallen fruit (e.g., deer, pheasants and partridges), but these animals are also excluded. Deer (mouse deer, muntjac, and sambar) can disperse small or very hard seeds, while most other seeds are destroyed (Corlett 1998). Though almost nothing is known about frugivory by terrestrial birds (Corlett 1998), their role (if one of seed dispersal rather than seed predation) is likely to have some similarities to other frugivorous birds in terms of fruit selection and handling.

In this chapter I evaluate the roles of 16 animal taxa (Table 10.1), with respect to their diet and dispersal overlap with gibbons. Some species are grouped in higher taxonomic divisions, because either the role is likely to be similar amongst species (i.e., macaques, most bird taxa) or there is inadequate knowledge to treat species separately (i.e., civets, fruit bats).

Table 10.1 Main seed dispersal agents in Bornean dipterocarp forests

Frugivore	Taxa (number of species in each group)	Seed dispersal references
Bornean orangutan	*Pongo pygmaeus*	1, 2
Gibbon	*Hylobates* (2 spp.)	3, 4
Macaque	*Macaca* (2 spp.)	2, 5
Prevost's squirrel	*Callosciurus prevostii*	6, 7, 8
Sun bear	*Helarctos malayanus*	9, 10, 11
Civets	Viverridae (approx. 4 spp.)[1]	8, 12, 13
Fruit bats	Pteropodidae (11 genera)[1]	14
Hornbills	Bucerotidae (8 spp.)	15
Barbets	Capitonidae (8 spp.)	15, 16
Pigeons	*Ducula* and *Ptilinopus*[2]	15, 17
Black magpie	*Platysmurus leucopterus*[3]	15
Green broadbill	*Calyptomena viridis*	15
Asian fairy bluebird	*Irena puella*	15
Bulbul	Pycnonotidae (approx. 16 spp.)[1]	15, 18
Leafbird	Chloropseidae (3 spp.)	15
Flowerpecker	Dicaediae (approx. 4 spp.)[1]	15

[1] Habits of taxa are not fully understood, and the exact number of frugivorous species feeding in the canopy is not known. [2] Other pigeon genera tend to be seed predators. [3] Other Corvidae may also disperse seeds, but data were only available for this species.
References: 1 – Leighton (1993); 2 – Ungar (1995); 3 – McConkey (2000); 4 – McConkey et al. (2002); 5 – Lucas and Corlett (1998); 6 – Payne (1979); 7 – Becker et al. (1985); 8 – McConkey (1999); 9 – McConkey and Galetti (1999); 10 – Wong and Servheen (2002); 11 – Fredriksson et al. (2006); 12 – Bartels (1964); 13 – Colón (1999); 14 – Hodgkison et al. (2003); 15 – Leighton (1982); 16 – Fogden (1970); 17 – McConkey et al. (2004); 18 –Weir Also see (Payne et al. 1985; MacKinnon and Phillipps 1993; Corlett 1998).

Quantity: Selection of Food Plants

Many frugivores include a diverse array of fruit and plant types in their diet, but the bulk of their feeding time is usually spent on a more limited selection of species. Selection of food plants is an important component of a frugivore's seed dispersal niche; it determines the quantity of seeds that a frugivore is likely to

disperse for a particular species when it is available and the number of sources from which they feed. Since only a very small proportion of dispersed seeds survive to adulthood (Howe and Mitiri 2004), animals that disperse many seeds of a particular species (away from the parent canopy) are more likely to disperse a seed that produces a reproductive adult than an animal that feeds sporadically on that species. Dispersal of seeds from multiple individual plants is essential for the development of coevolutionary relationships between frugivores and plants (since the animal should exert selection pressure across the plant's population) and also helps to maintain gene flow.

General Fruit Types

Broad categories in fruit types are frequently used for distinguishing frugivore preferences (van der Pijl 1982). These categories are based on the observed preferences of, mainly, birds, primates, and bats for certain fruit colors and pulp types and also on their ability to process certain fruit morphologies. Most birds, for example, are unable to remove a thick rind (Fogden 1970), so are limited to consuming fruit that is dehiscent or with a thin edible skin. Birds also tend to prefer pulp that is rich in lipids, which are usually avoided by primates (and other mammals) (Corlett 1998). Consistent differences in the colors of different fruit types are probably related to the visual capabilities of the respective animals, rather than an active preference for color [e.g., fruits favored by night-foraging bats tend to not change color on ripening (Hodgkison et al. 2003)].

   A simplified version of fruit types is given below. These divisions describe the "average" fruit eaten by most Asian birds and primates (Kitamura et al. 2002; Leighton 1982; Leighton 1993; McConkey 1999; McConkey et al. 2002; Ungar 1995), reflecting the preferences of primarily pulp-eating (and seed dispersing) animals, rather than those species that consume seeds and exhibit different choices [e.g., langurs (Ungar 1995)]. Alternative fruit types are consumed by birds and primates to varying degrees (Chapman and Russo 2007), but frugivores are likely to visit more sources and disperse more seeds of favored species. A bat fruit type is not defined, since the only distinguishing feature of such fruits appears to be color (Hodgkison et al. 2003). Fruit that appear to be bat-dispersed at Barito Ulu are included in the "other" category. This category includes a variety of fruit-types, which are not typically, bird, primate, or generalist.

   Bird fruit: Lipid-rich aril, dehiscent capsule, or berry or drupe with a thin skin, often red, blue, or black in color (e.g., *Myristica* spp.). A second type of bird fruit is also frequently described: small, sugary fruit with a thin skin and small seed(s) (e.g., *Hydnocarpus anomala, Macaranga* spp.).

Primate fruit: Sweet or sour, with juicy pulp and a thick rind, often orange-yellow in color; frequently, with a single large seed (e.g., *Willughbeia* spp., *Nephelium rambutan-ake, Zizyphus sulvensis*).

Generalist fruit: Sweet juicy pulp, with a thin skin and medium-sized seed(s), usually orange-yellow in color. These are frequently grouped with primate fruit, but the absence of a rind makes them accessible to a wider variety of frugivores (e.g., *Prunus javanica, Rourea minor*).

Gibbons are unspecialized frugivores, consuming fruits from a wide range of taxa (Marshall et al. this volume), but at Barito Ulu the favored taxa [over-selected: amount of time spent feeding on species is greater than expected by the species' abundance in the forest (McConkey et al. 2002)] almost always displayed fruit traits associated with primate fruit (Fig. 10.1). Generalist fruit had a weaker tendency to be over-selected, while bird fruit were eaten rarely and were usually under-selected or not eaten by gibbons. Lianas may be particularly important for gibbons. Almost all consumed liana fruit were over-selected and most lianas included in their diet had primate fruit (70% of liana species). The gibbons were more likely to forage at multiple individuals of plant species with primate fruit each month, than for species with generalist or bird fruit (Kruskal-Wallis, $H = 17.05$, $P = 0.0002$; Fig. 10.2).

At Barito Ulu I observed 19 fruiting tree and liana species (Appendix) eaten by gibbons and displaying one of the three types of fruit. Only plant sources actually visited by gibbons were watched and the number of hours spent watching each species was low (7–26 h each; watches were mainly in the mornings); however, some general patterns can be seen in the foraging behavior of different animals when the plant species are grouped into fruit types (primate fruit, $n = 112$ h; generalist fruit, n = 82 h; bird fruit, n = 90 h). Primate fruits were consumed almost exclusively by gibbons, while bird fruits (small sweet berries rather than the lipid-rich drupes, which were virtually ignored by the gibbons
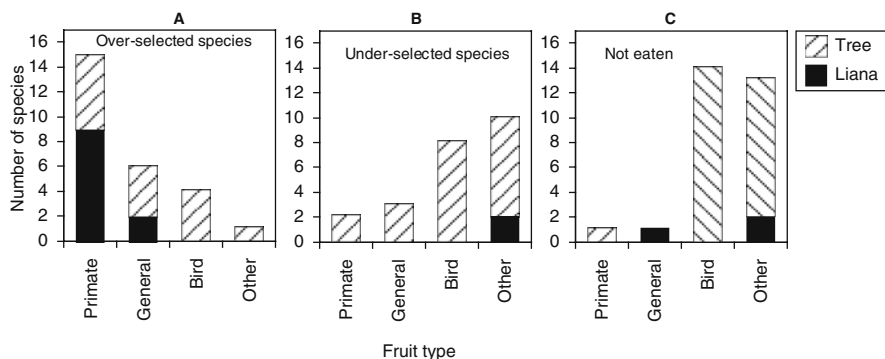

Fig. 10.1 Number of species (**a**) over-selected, (**b**) under-selected, and (**c**) not eaten by gibbons at Barito Ulu according to fruit and plant types (*n* = 79 species). Species listed as "not eaten", exclude those with fruits lacking an edible pulp

Fig. 10.2 Mean percentage
(+ 1 sd) of plant species
consumed by Barito Ulu
gibbons each month for
which gibbons use multiple
sources. Species are divided
according to fruit-type
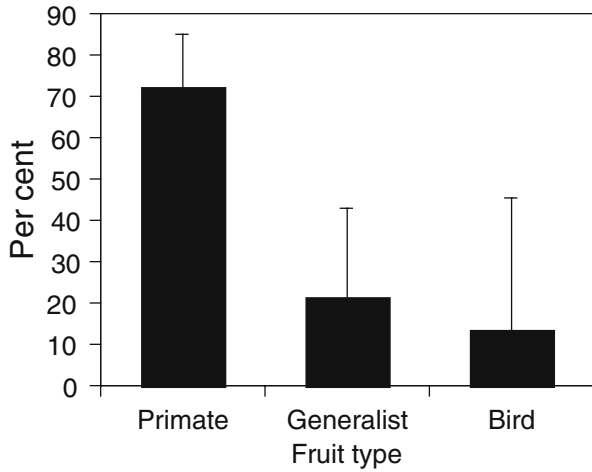
during the study period) were consumed mainly by small birds (bulbuls, Asian
fairy bluebirds, flowerpeckers) (Fig.10.3). Gibbons provided an inconsistent
dispersal service for these species as they fed on few available sources
(Fig. 10.2).

In West Kalimantan, gibbons exhibited the highest diet overlap with Prevost's
squirrel, orangutans, and macaques (Marshall et al. this volume). Prevost's
squirrels have an unspecialized diet (Marshall et al. this volume) and were
observed feeding at 10 of the 13 plant species exhibiting primate fruits that
were watched in the present study. This high diet overlap with gibbons, however,
does not reflect a high dispersal overlap since Prevost's squirrels removed few
fruits (Fig. 10.3) and were also noted to feed in some species when unripe or they
actually consumed the seeds rather than the pulp (Marshall et al. this volume).
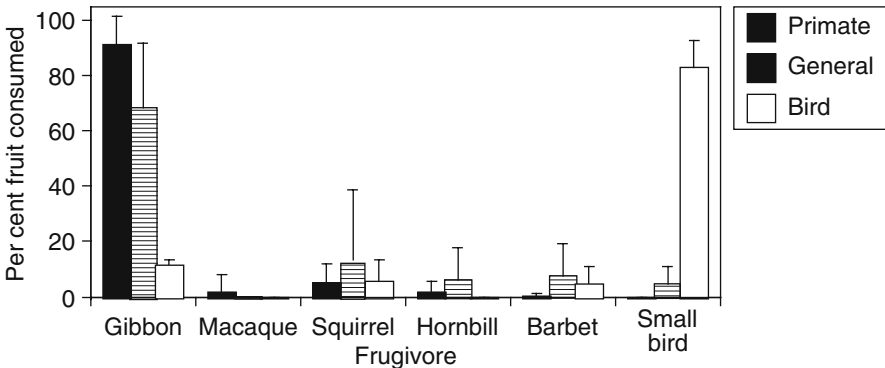
Fig. 10.3 Estimated mean percent fruit (+ 1 sd) consumed by different frugivores from plants
displaying three fruit-types and watched at Barito Ulu

Long-tailed macaques were at low density at Barito Ulu and orangutans and pig-tailed macaques were very rare (McConkey and Chivers 2004). Hence, their virtual absence during the plant observations will reflect these low densities rather than fruit choice. Differences in fruit preferences between these primates have been noted in Sumatra (Ungar 1995); orangutans consistently preferred larger fruit to the other two primate species and were more likely to consume fruits that had a hard husk, dry pericarps or were unripe. In contrast, macaques preferred small fruit and were more likely to consume dry fruit than gibbons. Lastly, gibbons showed less preference for fruit size, but had a strong preference for ripe fruits with a fleshy pericarp and low pH value. Despite these differences, all three primate taxa consume many of the same favored plant species (primate fruit) and dispersal overlap may be substantial.

Hornbills and barbets were noted to have significant diet overlap with gibbons in West Kalimantan (Marshall et al. this volume), and they also visited some of the 19 plant taxa watched in the present study (Fig. 10.3). Of the taxa with primate fruit, however, only four species ($n = 13$ species watched) were visited by hornbills and one species by barbets, suggesting these species primarily target fruits with a different morphology to that favored by gibbons (Leighton 1982). Similarly, the seasonally frugivorous sun bears consume many fruit species also eaten by gibbons (Fredriksson et al. 2006; McConkey and Galetti 1999; Wong and Servheen 2002). However, many of the favored taxa [e.g., *Syzigium, Santiria, Dacryodes, Durio* (Fredriksson et al. 2006)] are either inaccessible to gibbons (because of a hard husk or very large seed) or exhibit traits that make them unattractive to gibbons; hence, while significant diet overlap may occur, the favored species are likely to differ. This means that the plant species for which overlap exists may not be sought over multiple seasons and multiple individuals by hornbills, barbets, and sun bears.

Relatively less is known about the fruit choices of bats and civets, although they are good seed dispersers for some plant species. Civets feed on primate fruit, but may use other fruit types as well including the species not known to be eaten by gibbons (Bartels 1964; Colón 1999; McConkey 1999; Rabinowitz 1991). Many species are noted to be opportunistic frugivores, consuming fruit seasonally (Rabinowitz 1991). Some bat species select a distinct type of fruit (Hodgkison et al. 2003), but are more likely to include primate fruit in their diet than bird fruit, indicating some overlap will exist (Banack 1998; Hodgkison et al. 2003; Meehan et al. 2005). Although this overlap has not been documented in Borneo, the main fruits targeted by bats appear not to be favored by gibbons (Hodgkison et al. 2003).

Seed size is another fruit characteristic that limits fruit consumption by some species. Progressively larger seeds limit dispersers due to the inability of small frugivores to manipulate large seeds, while it is often inefficient for large frugivores to forage on small fruits (Corlett 1998; Kitamura et al. 2006). The fruit types frequently have some trends in seed size (i.e., primate fruit tend to be larger-seeded than sugary bird fruit), but often a range of seed sizes is present (Corlett 1998; Kitamura et al. 2006). Gibbons are able to swallow seeds up to

21 mm wide (McConkey 2000) and 44% of diet species had seeds 10–20 mm wide (McConkey 1999). The smaller birds, macaques, and bats are unable to disperse seeds of this size by endozoochory (although macaques and bats spit larger seeds) (Fig. 10.4). Orangutans, civets, sun bears, and several bird taxa can disperse seeds of this size and greater; but, if we combine fruit choice and seed size, only orangutans are potentially regular endozoochoric dispersers of the species favored by gibbons.

Patch Size

Although gibbons feed on plants of all sizes within the forest overstorey (median dbh [diameter at breast height] of food trees at Barito Ulu was 18 cm; range 7–60 cm), they are often noted to be well adapted for foraging among plants with small fruit crops (Chivers 1984) and may be important seed dispersers of small fruiting plants that produce primate fruit. Orangutans were noted previously to be the only regular endozoochoric dispersers of species favored by gibbons, but orangutans in Borneo showed strong preferences for fruit available in large patches (Leighton 1993; Marshall et al. this volume), and appeared to actually avoid small patches (<22 cm dbh) despite the availability of primate fruit that appeared suitable for orangutan consumption (Leighton 1993). An important aspect of this tendency is that smaller fruit patches are frequently lianas. Leighton (1993) found that lianas produced fruit patches less than half the size of average tree species. Sun bears also appeared to
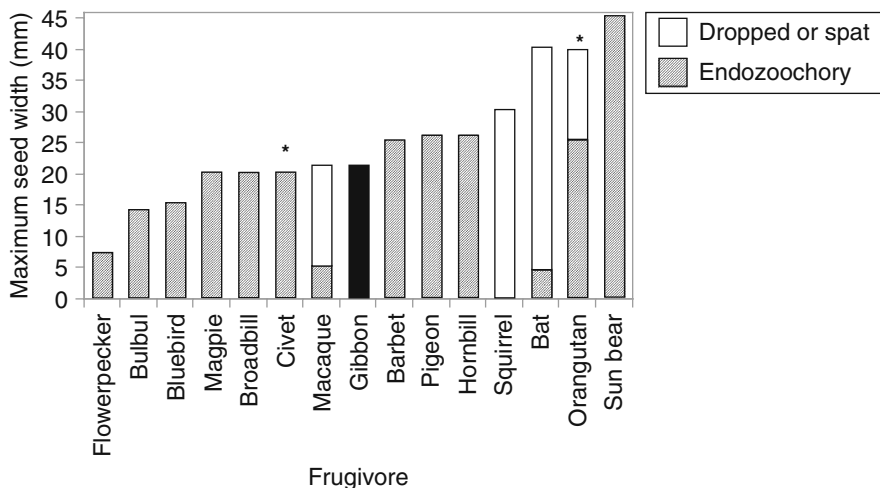
Fig. 10.4 Maximum width of seeds dispersed by Bornean frugivores (up to a maximum width of 40 mm). Bars indicated by *may be an underestimate as there was little published information on dispersed seeds or gape width available for the species. References are given in Table 10.1

preferentially feed in large fruit patches in East Kalimantan and only rarely consumed liana fruit (Fredriksson et al. 2006). All other frugivores addressed in the present study appear to forage frequently in small patches (Fogden 1970, Hodgkison et al. 2003; Leighton 1982; McConkey 1999; Payne 1979; Marshall et al. this volume).

The ability of gibbons to subsist on smaller fruit patches than orangutans (whose seed dispersal niche has a high overlap) has important consequences for seed dispersal. If gibbons are specifically targeting certain plant species that are always small, then they may be the only frugivorous primates offering a regular endozoochoric seed dispersal service for that species. Some plant species may offer both large and small fruit patches; while the large fruit patches may be visited regularly by both primate species, the small fruit patches may only regularly attract gibbons (but field studies have yet to be done to test this). Because the gibbons may be the only effective dispersers of a subset of individuals of these species, they would be important for ensuring the genetic variation of the species is maintained.

Quality: Primary Seed Shadow and Post-Dispersal Processes

Once a seed has been swallowed by a gibbon and deposited in the forest within their scats, it faces several obstacles before it can germinate and establish as a seedling. At Barito Ulu, 1470 gibbon-dispersed seeds (>4 mm wide) were monitored over 1 year and only 11% of seeds germinated (McConkey 2005a). Seed predation [including seeds that disappeared (McConkey 2005a)] was the most significant cause of seed death, killing 88% of seeds (<1% seeds did not germinate). Seed predation has been recognized as a major cause of seed death in tropical forests (Hulme 1998) and the primary granivores in Asia are rodents, pigs, deer, and various insect species (Blate et al. 1998; Curran and Webb 2000; Ickes et al. 2001; Kitamura et al. 2006; McConkey 2005b). Although the primary seed shadow (pattern of seed fall) formed by frugivores often has little lasting impact on the chance of a seed germinating (Jordano and Herrera 1995; Rey and Alcántara 2000), there are some ways in which frugivores may influence the survival probability of seeds.

How Seeds Are Deposited

There are two main ways in which frugivores deposit seeds on the forest floor (Table 10.2). Seeds may be swallowed and later regurgitated or defecated (endozoochory), or they may be spat or dropped after the pulp is consumed. Endozoochory is usually the most efficient form of dispersal, as seeds have a better chance of being deposited away from the parent canopy (Corlett 1998) and germination is frequently enhanced (Traveset and Verdú 2002). Dispersed

Table 10.2 Main dispersal modes by different frugivore taxa (for seeds greater than 4 mm wide)

Seed treatment	Scatter-dispersal	Clumped-dispersal Multiple species	Single species
Spat or dropped	Fruit bats[1]		Fruit bats[1] Macaques[2] Squirrels[2]
Endozoochory	Birds	Gibbons (small clumps) Orangutans (large clumps)	Civets (small clumps) Sun bear (large clumps)

[1]Fruit bats drop many seeds under fruiting crowns, or at feeding roosts, but a significant number are also scatter-dispersed.
[2]Most seeds are spat or dropped under parent trees

seeds also vary according to whether they are scattered singly or deposited in clumps, and seed clumps may be small or large, mono- or multispecific. The respective benefits of these dispersal modes are not clearly understood, but seeds dispersed singly or in small fecal clumps are usually more efficient dispersal modes than seeds dispersed in large fecal clumps or spat or dropped singly around the fruiting tree, since the latter frequently suffer high rates of seed predation or seedling competition (Willson and Whelan 1990; Pizo and Simao 2001). Limited evidence also suggests different plant species show physical and chemical adaptations to different broad forms of dispersal [i.e., scatter (single seeds) and clumped (many seeds) dispersal (Howe 1989; Blate et al. 1998)], and it is possible that the seeds of a particular fruit type may have higher survival, due to intrinsic qualities, if dispersed in the mode of the frugivore that favors them.

At Barito Ulu, gibbons dispersed by endozoochory the seeds of 81% of consumed fruit species (McConkey 2000). The remaining species were eaten while unripe, destroyed, or dropped under the parent crown. The seeds of consumed liana species were more likely to be dispersed (90% of liana species in the gibbons' diet had their seeds dispersed, $n = 40$) than the seeds of consumed tree species (72% of tree species, $n = 94$; Chi-square $= 5.6$, $p < 0.05$). These seeds were deposited in multispecific, small clumps containing between 1 and 51 seeds (seeds greater than 3 mm in length only; mean $= 7$ seeds) and up to 6 species (mean $= 2$ species) (McConkey 2000). Seed clumping was reduced by the scattering of scats as they fell through the canopy and seeds were occasionally buried by dung beetles [1% of defecated seeds 4–9 mm wide (McConkey 1999)].

In Borneo, eight other frugivorous taxa can disperse seeds up to 20 mm wide by endozoochory (Fig. 10.4), but only some arboreal mammals dispersed seeds in clumps (Table 10.2). Seed depositions of orangutans are most similar to gibbons since they also produce multispecific clumps, but orangutans destroy more seeds than gibbons and they spit rather than swallow some seeds [of any species (Rijksen 1978)]. Clump size is also much larger in orangutans [median of

111 seeds (Galdikas 1982)], with potential negative effects on seedling survival. Hence, gibbons produce a unique seed shadow in terms of seed deposition.

No evidence is available to assess whether the unique dispersal mode of gibbons is specifically beneficial to those plant species that they favor (compared to dispersal modes of other frugivores); however, through their behavior, gibbons positively influenced seed survival of over-selected species in their diet (McConkey unpubl. data). Since gibbons fed more in over-selected species, the scats subsequently produced contained fewer seed species. At Barito Ulu, this led to a significantly lower chance of vertebrate seed predation and a higher chance of germination for over-selected species [21% seed survival for over-selected species, compared to 5% for under-selected (McConkey 2005a)]. Hence, gibbons can have a direct influence on the post-dispersal fate of selected species.

Where Seeds Are Deposited

Effective seed dispersers remove seeds from the parent canopy and deposit them some distance (often cited as at least 5–10 m) away in sites that are suitable for germination (Howe and Smallwood 1982; Howe and Mitiri 2004). Long-distance seed dispersers (dispersal distances >100 m) are often of particular importance since they help to maintain higher levels of gene flow and are likely to disperse seeds across a wider variety of sites (Cain et al. 2000; Nathan and Muller-Landau 2000).

The gibbons at Barito Ulu dispersed > 90% of seeds more than 100 m from parent plants and <1% were dispersed under parent plants (McConkey and Chivers 2007). Mean dispersal distances exceeded 300 m for both studied groups with a maximum distance of >1000 m; hence, they are effective, regular, long-distance seed dispersers. Due to their behavior of visiting many fruiting trees in a day, 27% of scats were deposited under a fruiting tree of any species and 3.6% under conspecific plants (McConkey 2000); but these actually conveyed an advantage to seeds as seed predation (on defecated seeds) was lower in this region, probably due to the abundance of alternative foods (McConkey 2005a). There were no other obvious patterns in where gibbons deposited seeds.

Endozoochory frequently results in seeds being deposited away from parent plants and, consequently, many other Bornean frugivores are also capable of dispersing seeds to considerable distances. Regular long-distance dispersers include hornbills (Whitney et al. 1998; Holbrook and Smith 2000) and probably orangutans, sun bears, and large fruit bats (*Pteropus* spp.). No dispersal distances are currently available for orangutans, but they are probably on average greater than those for gibbons. Although day ranges of the two primates are similar (if not smaller for orangutans), home ranges of orangutans are usually much larger (McConkey 2005c), and the tendency of gibbons to encircle their home range within a single day reduces potential seed dispersal distances (McConkey and Chivers 2007). Sun bears have large home ranges

(approximately 14 km^2), with day ranges exceeding 1 km (Wong 1997). Assuming long gut retention times, they can potentially disperse seeds long distances; however, when favored plants are fruiting, they may confine their movements to that area for several days (Wong 1997) forming a very clumped seed shadow (McConkey and Galetti 1999). Dispersal distances for Asian *Pteropus* fruit bats are also unavailable, but on Pacific archipelagoes they are capable of carrying large fruit for distances exceeding 1 km (Banack 1996).

Several other frugivores are likely to disperse seeds beyond 100 m occasionally, but most seeds will be deposited closer to fruiting trees. *Ducula* pigeons deposited most seeds away from parent plants, but usually within 50 m, in a Pacific archipelago (McConkey et al. 2004). Bulbuls in Hong Kong regularly dispersed seeds within 100 m of fruiting trees, with maximum dispersal distances of over 1000 m (Weir and Corlett 2007). Macaques spit large seeds and the vast majority are deposited under fruiting trees (Lucas and Corlett 1998). The extra handling time macaques require for primate fruit results in more seeds being spat under tree crowns (90% of handled seeds) compared to 60% for one generalist species (McConkey et al. unpubl. data). Nevertheless, some seeds are deposited at least 40 m from fruiting trees, with the potential for greater distances (McConkey et al. unpubl. data). Little is known about the seed shadow produced by most other Bornean mammals. Some civet species have large home ranges compared to gibbons (Colón 2002; Grassman Jr. et al. 2005; Joshi et al. 1995; Rabinowitz 1991), and civets regularly deposit seeds away from fruiting trees (Bartels 1964; McConkey 1999); however, the use of "latrines" by some species causes seed clumping (Corlett 1998) and home ranges are often reduced when food is abundant (Rabinowitz 1991; Joshi et al. 1995). Many smaller bird species (including barbets and broadbills) feed for prolonged periods in fruiting trees (Lambert 1989), and with their short retention times probably disperse most seeds under the tree (Pratt and Stiles 1983). Squirrels appear to be very poor distance dispersers, with seeds deposited no more than 10 m from fruiting crowns (Becker et al. 1985; McConkey et al. unpubl. data).

What Is the Seed Dispersal Niche of Gibbons?

Gibbons may be the main seed dispersers for primate fruit found in small patches (Fig. 10.5) and may be particularly important for the dispersal of lianas bearing primate fruit. Seeds of all plant types are dispersed in a unique manner – small, multispecific scats – and are almost always dispersed away from parent trees, frequently at long distances. It is not clear whether this unique seed shadow conveys a strong advantage to gibbon-dispersed seeds over other dispersal modes, but, in terms of fruit choice, only macaques appear to favor the types of fruit and plants for which gibbons are most suited and macaques are inefficient seed dispersers (Fig. 10.5). The larger mammals (orangutans and sun bears) tend to avoid small sources, while the smaller mammals and birds show no specialization for primate fruit. This means that (1) other animals probably
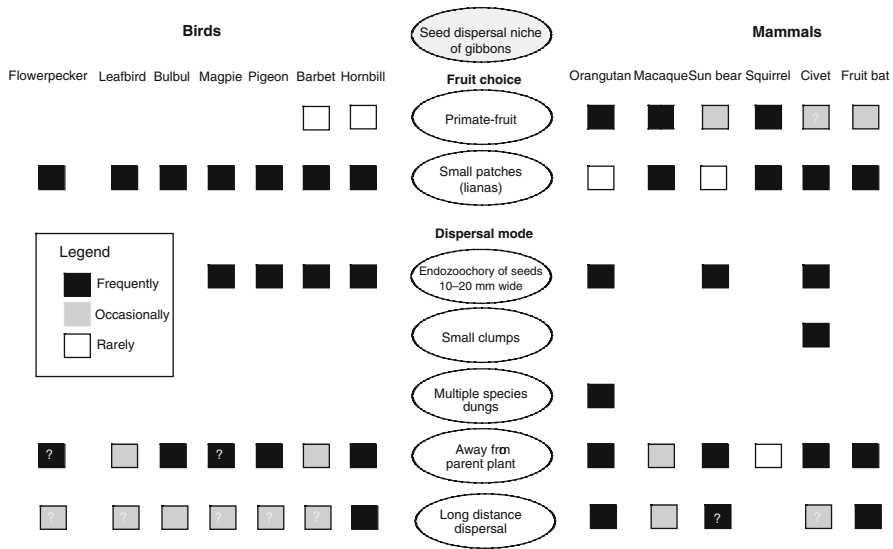
Fig. 10.5 Summary of the seed dispersal niche of gibbons and its overlap with the fruit choice and dispersal modes of other frugivores in Borneo

consume and disperse much smaller quantities of seeds than gibbons, (2) it is unlikely that any other animals would seek multiple sources of such plants, and, therefore, do not exert selection pressure across the plants' population, and (3) other animals may not feed consistently on the species across multiple fruiting seasons.

Gibbons regularly feed on, and disperse the seeds of, many other plant species that are not primate fruits. Since the seeds of these plants appear intact in the gibbons' feces, it may be assumed that they are also effective dispersers of these plants. It is unlikely coevolutionary relationships can develop though, since they feed inconsistently on these species – during years when more favored species are available, it is possible they ignore these species completely and they are less likely to consume fruit from multiple sources. Moreover, seeds from nonfavored species had much higher predation rates in the gibbons' feces than those from favored species, indicating gibbons may be less suited for their dispersal.

Gibbons satisfy several requirements necessary for the development of coevolutionary relationships with their food plants. Fruit is the favored food item of all gibbon species [although some populations rely more heavily on leaves (Elder this volume)] and the seeds of most diet species are dispersed effectively by endozoochory. There is almost no variation in their treatment of seeds within species (few seeds are dropped while foraging, and there have been no records of significant seed damage on swallowed seeds). They also appear to be best suited for specific fruit/plant types, of which they feed on selectively when

available, use multiple sources, and which have very few other effective dispersers. Finally, gibbons produce a unique seed shadow, although the importance of this is not yet understood.

Appendix

Selection of plant taxa consumed by gibbons at Barito Ulu. Only plant taxa that are dispersed by gibbons are shown. Taxa are arranged in approximate order of preference[1]. Plants that were watched at Barito Ulu are indicated by an asterix.

Taxa	Family	Source	Fruit type
Over-selected			
Liana sp. 16*	Unidentified	Liana	Primate
Gnetum spp.*	Gnetaceae	Liana	Primate
Garcinia spp.*	Clusiaceae	Tree	Primate
Artabotrys lanuginosa	Annonaceae	Liana	Primate
Diospyros puncticuolsa	Ebenaceae	Tree	Primate
Tetrastigma trifoliolatum	Vitaceae	Liana	Primate
Zizyphus sulvensis	Rhamnaceae	Liana	Primate
Strychnos colubrine	Loganiaceae	Liana	Primate
Erycibe maingayi	Convolvulaceae	Liana	Primate
Nephelium rambutan-ake	Sapindaceae	Tree	Primate
Zizyphus horsfieldii	Rhamnaceae	Liana	General
Calamus spp.*	Arecaceae	Liana	Primate
Willughbeia sp.*	Apocynaceae	Liana	Primate
Polyalthia glauca	Annonaceae	Tree	General
Prunus javanica	Rosaceae	Tree	General
Parkia javanica	Fabaceae	Tree	Other
Cryptocarya crassinervis	Lauraceae	Tree	Primate
Xanthophyllum flavescens	Polygalaceae	Tree	Other
Artocarpus spp.*	Moraceae	Tree	General
Eugenia spp.	Myrtaceae	Tree	Other
Dillenia borneensis	Dilleniaceae	Tree	Other
Blumeodendron elateriospernum	Euphorbiaceae	Tree	Primate
Litsea ferruginea	Lauraceae	Tree	General

(continued)

Taxa	Family	Source	Fruit type
Macaranga sp. 1	Euphorbiaceae	Tree	Bird
*Rourea minor**	Connaraceae	Liana	General
*Aglaia ganggo**	Meliaceae	Tree	Primate
Neutral or under-selected			
Beilschmiedia dictyoneura	Lauraceae	Tree	Other
Xanthophyllum amoenum	Polygalaceae	Tree	Other
Adinandra dumosa	Theaceae	Tree	Other
Mangifera sp. 1	Anacardiaceae	Tree	Other
Embelia coriaceae	Myrsinaceae	Tree	Bird
*Hydnocarpus anomala**	Flacourtiaceae	Tree	Bird
Litsea angulata	Lauraceae	Tree	Other
Baccaurea spp.	Euphorbiaceae	Tree	Bird
Xerospernum norohanum	Sapindaceae	Tree	Primate
Vitis imperialis	Vitaceae	Liana	Other
*Pternandra rostrata**	Melastomataceae	Tree	Bird
Artobotrys rosea	Annonaceae	Tree	Primate
Prunus arborea	Rosaceae	Tree	General
Zizyphus angustfolius	Rhamnaceae	Tree	General
Diospyros dictioneura	Ebenaceae	Tree	General
Xanthophyllum sp. 2	Polygalaceae	Tree	Other
Ashtonia excelsa	Euphorbiaceae	Tree	Bird
Polyalthia lateriflora	Annonaceae	Tree	Bird
Erycibe impressa	Convolvulaceae	Liana	Other
Xanthophyllum stipitatum	Polygalaceae	Tree	Other
Palaquium sp.	Sapotaceae	Tree	Other
Polyalthia sumatrana	Annonaceae	Tree	Bird
Myristica spp.	Myristicaceae	Tree	Bird

[1]Actual selection ratios were calculated for three time periods differing in fruit abundance (high, medium, low). Hence, order is determined by calculated ratios as well as consistency in selection (McConkey et al. 2002).

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