

# Seed Dispersal by Primates in Asian Habitats: From Species, to Communities, to Conservation



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**Abstract** Primates are among the most important seed dispersers in the habitats they occupy. Understanding the extent of, and gaps in, our knowledge of seed dispersal by Asian primates is essential, because many of these primates are extremely vulnerable to anthropogenic disturbance. In this review, I show how initial studies focused on the role of individual species in seed dispersal have expanded more recently to consider their role in the wider frugivore community. There are five functional groups of primate seed dispersers in Asia; most of our information comes from the (usually) highly frugivorous macaques and gibbons, while our understanding of the roles played by orangutans and, especially, colobines and lorises remains rudimentary. Preliminary community-wide studies suggest a pivotal role for gibbons and macaques in frugivore communities, with higher dispersal overlap with other mammals than with birds. The gaps in our knowledge are plentiful, however, including understanding fruit selection in detail, determining how seed dispersal roles might change across different habitats, evaluating the balance between mutualisms and antagonisms in orangutans and macaques, describing postdispersal processes, and documenting how habitats are impacted by changes in primate abundance and behavior.

**Keywords** Frugivory · Gibbons · Langur · Loris · Macaques · Orangutans

## Introduction

The process of seed dispersal is of fundamental importance to conserving habitats and biodiversity (Fricke *et al.* 2017; McConkey *et al.* 2012). Primates are dominant

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frugivores and herbivores in many habitats and play important, possibly essential, roles in seed dispersal (Chanthorn *et al.* 2017; Corlett 2017). Asian primates are a diverse group, ranging from the 300-g exudate-feeding loris (*Nycticebus borneanus*) to the 50–100-kg frugivorous orangutan (*Pongo* species). This diversity is reflected in how much fruit they consume, what they do with the discarded seeds and, therefore, the seed dispersal roles they perform. Asian primates also differ in their vulnerability to disturbance (IUCN 2017) and they inhabit ecosystems that are currently more threatened by anthropogenic pressure than most other regions in the world (Almeida-Rocha *et al.* 2017; Sodhi *et al.* 2004). Hence, it is imperative we understand the functional roles performed by primates and how vulnerable these roles are under current rates of disturbance.

The objective of this review was to provide a multilayered account of seed dispersal by Asian primates. My aim was to document the information that is currently available and emphasize the most important gaps in our knowledge. I examine seed dispersal at different levels: 1) seed dispersal by functional groups of primates, 2) contribution of primates to seed dispersal at a community level, and 3) intrapopulation variation in seed dispersal roles. In addition I summarize our knowledge of 4) understudied processes related to seed dispersal by Asian primates and 5) effects of disturbance on seed dispersal by Asian primates.

## Methods

I conducted an exhaustive literature review on all seed dispersal studies on Asian primates using Google Scholar and Scopus®. I used the search term “seed dispersal” in conjunction with the “genus” of each Asian primate, with the exception of the carnivorous tarsiers (Tarsiidae). Because name changes have occurred for some taxa, I also used the common name for the broad groups: orangutan, gibbon, macaque, langur, leaf-eating monkey, loris. I supplemented this information with studies reported in the gray literature. I include studies specifically addressing seed dispersal by primate taxa, as well as broader community studies. I broadened the search to include accounts of frugivory when information on seed dispersal could not be found.

To visually compare the contributions of different primate taxa I displayed their contributions on a Seed Dispersal Effectiveness Landscape (SDE; Schupp *et al.* 2010, 2017). An animal’s contribution to seed dispersal is typically evaluated according to “quantitative” and “qualitative” components (Schupp *et al.* 2010). “Quantity” is a measure of the amount of seeds dispersed, while “quality” is a measure of how likely a dispersed seed is to establish as an adult plant, taking into account seed handling, seed deposition, and germination (Schupp 1993); however, since measuring survival to adulthood is not possible for most studied plants “quality” is practically measured to an earlier dispersal stage. The SDE of an animal is the product of these quantitative and qualitative components, and can be visualized on an SDE Landscape (Schupp *et al.* 2010, 2017). Here, I define Quantity as “the percentage of fruit recorded in the diet.” I use “dispersal distance” to represent Quality since this parameter has significant influences on seed survival and seedling establishment (Swamy and Terborgh 2010; Wang and Smith 2002) and is the most consistently measured parameter in the available studies. For the quantity and quality values, I used the mean and standard deviation across available

studies. I constructed isoclines that represent the SDE (quantity  $\times$  quality) of the taxa. Since orangutans and macaques (Cercopithecinae) spit larger seeds, I include different size classes of seeds (less or greater than 10 mm in width) in the SDE landscapes; 10 mm overestimates the contributions of orangutan and macaques, but it provides the most conservative comparison with gibbons (Hylobatidae). Colobines (Colobinae) are included on the same landscape, but do not defecate seeds longer than 5 mm.

## Understanding Seed Dispersal Within “Functional Groups”

Around 90 plant-eating primate species currently live in Asian habitats (IUCN 2017). The only primates not recorded to consume some fruits in this region are the carnivorous tarsiers. Documenting the seed dispersal roles of individual species is the first step in understanding primate–seed dispersal mutualisms, and this has been the traditional approach of most studies. Because primates can often be habituated and followed, these data are (usually) relatively easy to obtain for primates compared to other animal groups, yet we currently have seed dispersal data for only 11 species (about 12% of all species) (Table I) and dietary information for several more. However, species within families, or subfamilies, have similar physiologies and will behave similarly with respect to seed dispersal. Hence, a realistic approach to assessing the roles of primates—without performing studies on all species—is to assume that species within families, or subfamilies are functionally similar in their seed dispersal role and consider these higher taxonomic categories as a functional group (Dennis and Westcott 2006). The functional groups are the orangutans, gibbons, macaques, colobines, and lorises.

More important than ensuring a large number of primate species have been studied is ensuring that each functional group has been studied across a representative range of habitats. The habitat and associated distribution of resources play a large role in determining the ranging and foraging behavior of the animals within it and, therefore, the range of fruits eaten and the subsequent distribution of the seeds (McConkey and O’Farrill 2015, 2016; Tsuji *et al.* 2013a). For example, the eastern hoolock gibbon (*Hoolock leuconedys*) that occupies montane forest in Yunnan, China consumes the lowest number of fruit species ever recorded for a gibbon species and it is folivorous during the coldest months (Fan *et al.* 2013). In comparison, the western hoolock gibbon (*Hoolock hoolock*) that inhabits Bangladesh is among the most frugivorous recorded, with 90% of its diet as fruits and figs (Hasan *et al.* 2005). Given that much more minor habitat changes have been shown to influence seed dispersal distances (McConkey and Chivers 2007; Phiphatuwannachai *et al.* 2017), it might be misleading to generalize seed dispersal roles across such divergent habitats. At present, fewer than half the habitat types occupied by Asian primates have had any seed dispersal studies (Fig. 1), and no functional groups have had detailed seed dispersal studies conducted within even half the habitats occupied (as specified by the IUCN, 2017).

### Hominidae

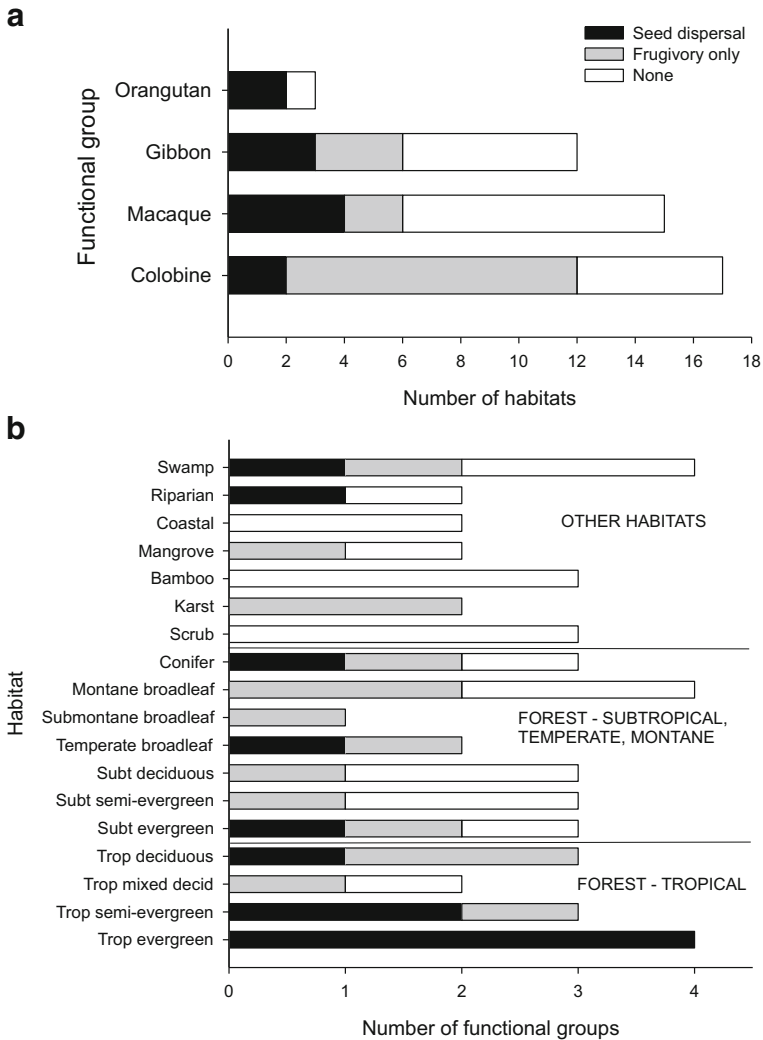
Given their large body sizes and wide ranges, orangutans have the potential to play important roles as seed dispersers (Corlett 2017), and this has generally been assumed, despite the minimal studies that have been conducted (Table I). Two orangutan species

**Table 1** Published seed dispersal studies for Asian primates arranged by functional group

Taxa	Country	Habitat	Study length (mo)	No. spp. dispersed (by seed spitting)	% feces with seeds	References
<b>Orangutan</b>						
<i>Pongo pygmaeus</i>	Malaysia	Dipterocarp forest	12 <sup>a</sup>	64	80	Ancrenaz <i>et al.</i> 2006
	Indonesia	Peat swamp	26	47 (31)	73	Nielsen <i>et al.</i> 2011; Tarsziz 2016,
<b>Gibbon</b>						
<i>Hylobates lar</i>	Thailand	Evergreen forest	6	16	100	Phiphatsuwannachai <i>et al.</i> 2017
	Thailand	Mosaic forest	6	9	84	Phiphatsuwannachai <i>et al.</i> 2017
<i>H. muelleri</i> × <i>agilis</i>	Indonesia	Dipterocarp forest	14	77	100	McConkey 2000; McConkey <i>et al.</i> 2002
<i>Nomascus concolor</i>	China	Temperate evergreen	8	27	100	Fan <i>et al.</i> 2008
<i>Symphalangus syndactylus</i>	Indonesia	Evergreen forest	1	7	–	Atmanto <i>et al.</i> 2014
<b>Macaque</b>						
<i>Macaca fascicularis</i>	Singapore	Evergreen forest	5	95 (67)		Lucas & Corlett 1998
	Indonesia	Evergreen forest	7	19	62	Tsuji <i>et al.</i> 2017
<i>Macaca fuscata</i>	Japan	Urban conifer	13	20	85	Tsuji 2011
	Japan	Temperate deciduous	12 <sup>a</sup>	35	58	Tsuji 2014; Tsuji & Morimoto 2014; Tsuji <i>et al.</i> 2011
	Japan	Temperate evergreen	10	21	87	Otani 2004; Otani & Shibata 2000
	Japan	Conifer forest	6	11	86	Enari & Sakamaki-Enari 2014
	Japan	Evergreen forest	12	26		Yumoto <i>et al.</i> 1998
<i>Macaca leonina</i>	Thailand	Seasonal evergreen	12	93	89	Albert <i>et al.</i> 2013
<i>Macaca mulatta</i>	India	Deciduous, evergreen	12	41 (24)	87	Sengupta <i>et al.</i> 2014, 2015
–Provisioned	India	Deciduous, evergreen	3		27	Sengupta <i>et al.</i> 2015
	Vietnam	Evergreen	6	16	58	Tsuji <i>et al.</i> 2013b
<b>Colobine</b>						
<i>Nasalis larvatus</i>	Malaysia	Riverine forest	13	3	32	Matsuda <i>et al.</i> 2013
<i>Trachypitecus auratus</i>	Indonesia	Evergreen	7	6	54	Tsuji <i>et al.</i> 2017

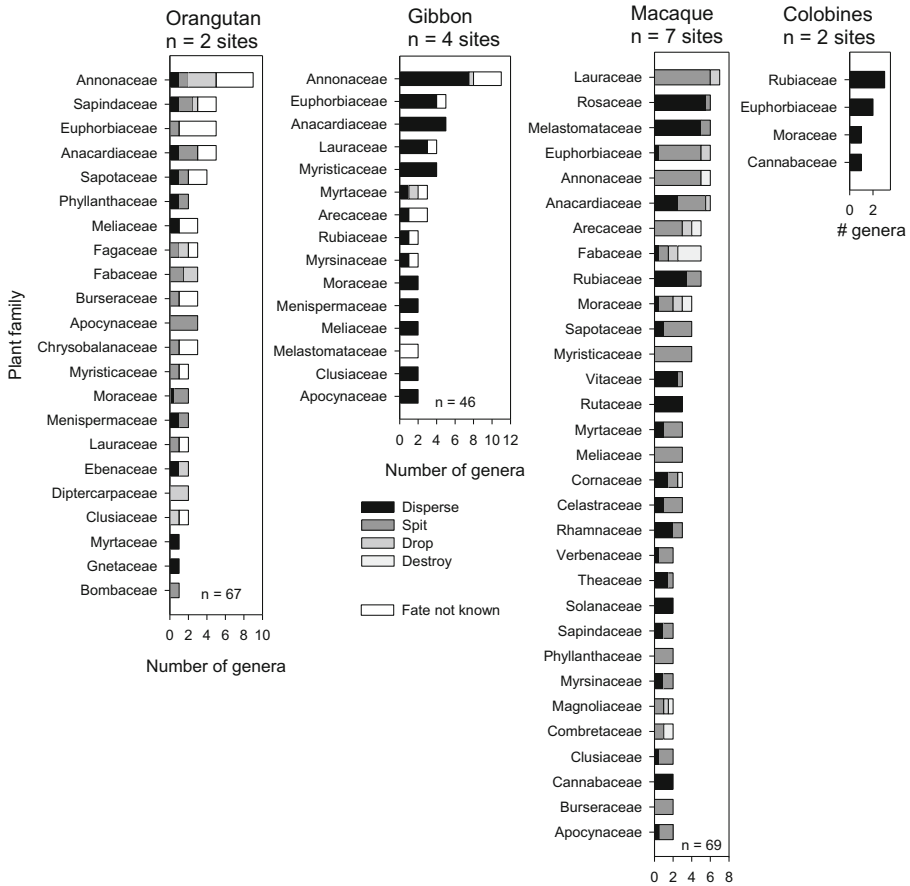
The count of species dispersed includes species dispersed by swallowing and defecation (endozoochory) and also by seed spitting (synzoochory). Species dispersed by spitting only are indicated in brackets

<sup>a</sup> Study length not specified, but covered multiple years



**Fig. 1** Habitats occupied by different primate functional groups in Asia, showing the number of frugivory or seed dispersal studies conducted. Studies arranged by **a** functional groups, and **b** habitat. Where seed dispersal studies have been completed, I assume frugivory papers are also available. Occupation of habitats was determined from primate listings on the IUCN Red List. Habitats are grouped into broad categories.

(*Pongo abelii* and *Pongo pygmaeus*) are listed as Critically Endangered (IUCN 2017), and a newly described species (*Pongo tapanuliensis*) is probably the world’s most endangered great ape (Nater *et al.* 2017). Our lack of an understanding of their seed dispersal roles could be a severe limitation to assessing the resilience of habitats following their decline. They may play significant roles in moving large-seeded fruits, which have few others dispersers (Corlett 2017)—especially in Bornean habitats that lack elephants (*Elephas maximus*) and rhinoceros (Rhinocerotidae). However, the feeding data that are available suggest that orangutans might play just as dominant roles as seed predators as they do seed dispersers (Fig. 2).



**Fig. 2** Plant families dispersed by the main functional groups of Asian primates. Figures show the number of genera in each family that are dispersed (swallowed and defecated), spat, dropped, destroyed, or eaten but the fate is unrecorded. Only plant families that have at least two genera recorded are included. If a plant genus had two dispersal modes, then a value of 0.5 was applied to each category. If the seeds were consistently destroyed and not dispersed by any primate group, the plant taxa are not shown; if they were dispersed by at least one primate group then records of seed eating are shown for the other groups.

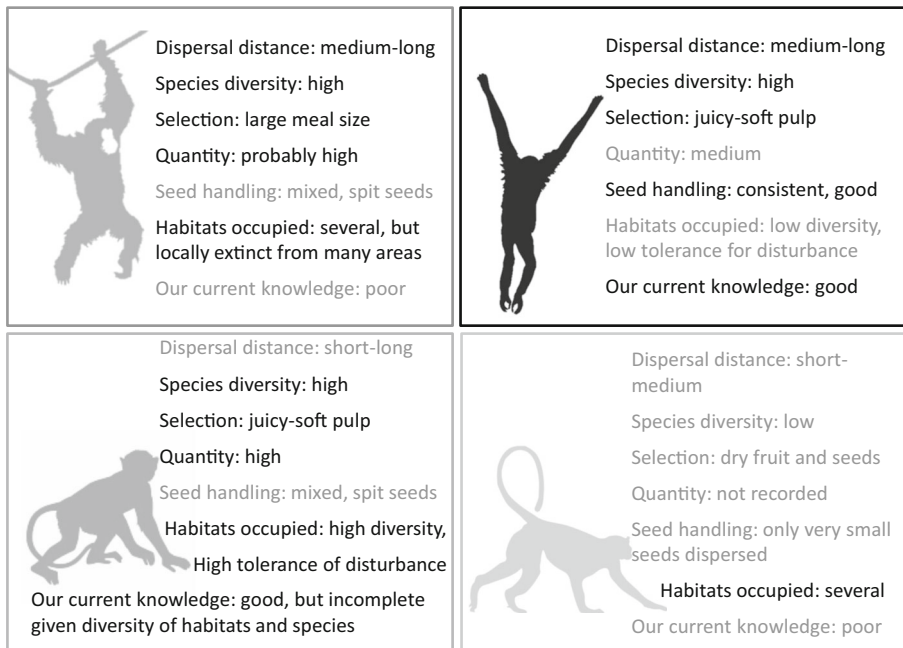
Orangutans select for meal size, in terms of large crop size and high pulp or fruit weight, rather than other fruit attributes (Leighton 1993), and they respond spatially and temporally to increases in fruit abundance, by consuming more fruit or moving into areas where fruit is most available (Kanamori *et al.* 2010, 2017). However, they are inconsistent in their seed handling, often spitting larger seeds (>15 mm wide; Galdikas 1982; Mohd-Azlan *et al.* 2015) and they are frequently seed predators (Mohd-Azlan *et al.* 2015; Nakashima *et al.* 2008); often they spit, swallow, and destroy seeds of a single plant species (Mohd-Azlan *et al.* 2015). Dispersal distances have the potential to be long for swallowed (small) seeds (>1 km) given the large ranges occupied by orangutans (Corlett 2009), and defecated seeds retain the capability to germinate (Nielsen *et al.* 2011), but even spat seeds can probably be regularly dispersed away from parent crowns (up to 75 m; Corlett 1998; Galdikas 1982). The role of orangutans

as seed dispersers and/or seed predators remains one of the largest gaps in our knowledge of primate seed dispersal in Asia, despite decades of research (Fig. 3).

A second, larger ape once occupied parts of Asia. *Gigantopithecus blacki* weighed up to 270 kg (three to five times heavier than an orangutan) and lived in northern Southeast Asia and southern China from the Pliocene to *ca.* 100,000 years ago (Corlett 2017). Stable isotope analysis suggested it had a vegetarian diet that included fruit, and that it was a forest dweller (Bocherens *et al.* 2017). Orangutans also occupied parts of the range of *Gigantopithecus* in prehistoric times (Corlett 2013), suggesting these regions are missing potentially dominant contributors to seed dispersal mutualisms.

## Hylobatidae

The four genera of gibbons are probably among the most important seed dispersers in the habitats they occupy (Fig. 3) (Corlett 2017; McConkey 2009). Gibbons are generalist frugivores, consuming and dispersing a large array of taxa (Brockelman 2011; McConkey 2000; Suwanvecho *et al.* 2017). They exhibit preferences for certain fruit types, which are primarily medium-sized (6–30 g), with soft-juicy pulp, and are thin-skinned or with a rind (McConkey *et al.* 2002); in some habitats their preferred fruit are available over long time frames or fruit asynchronously (Dillis *et al.* 2015). However, gibbons consume fruits of diverse morphologies, including dehiscent fruits predominantly dispersed by hornbills (Bucerotidae) (Savini and Kanwatanakid-Savini 2011) and tough-skinned fruits more easily accessed by large animals (Corlett 2017;



**Fig. 3** Overview of the seed dispersal roles of the four main functional groups of fruit-eating primates in Asia (excluding lorises, which have no available seed dispersal information); strengths are indicated in black font, and weaknesses in gray.

McConkey *et al.* 2015; Vogel *et al.* 2009), and appear to have no clear selection for fruit color (Corlett 2017; D'Agostino and Cunningham 2015). While gibbons consume and can disperse some of the largest fruits in the forest (McConkey *et al.* 2015), their capability is limited by the size of the seed that can be swallowed (a maximum of *ca.* 20 mm, but influenced by size of individual gibbons) (McConkey 2000) and by access to the fruit and pulp. This means that the very largest seeds—such as those of *Mangifera*—and very well-protected fruit—such as *Durio*—cannot be dispersed by gibbons (McConkey *et al.* 2002).

Gibbons are consistently effective dispersers as they swallow and defecate seeds of almost all species, and drop or chew seeds only very rarely (Fig. 2). Because they are highly territorial, dispersal distances are confined by the boundaries of their home range and are influenced by the shape of the home range, habitat occupied, and the behavior of the individuals (McConkey and Chivers 2007; Phiphatsuwannachai *et al.* 2017). Distances of up to 1300 m have been recorded for gibbons, but more frequently average 200–400 m, and the majority of seeds are dispersed beyond 100 m (McConkey and Chivers 2007; Phiphatsuwannachai *et al.* 2017; Hai *et al.* *unpubl. data*). Gibbons have traditionally been considered to be poor dispersers across habitats, but this can occur where individual territories encompass a mosaic of habitats (Phiphatsuwannachai *et al.* 2017). Given that gibbons usually cannot maintain populations in habitats in which the canopy is not continuous (Cheyne *et al.* 2013), their dispersal role is probably confined to relatively undisturbed habitats.

### **Cercopithecidae, Subfamily Cercopithecine**

The family Cercopithecidae contains two subfamilies that exhibit very different seed dispersal capabilities, suggesting that the functional group for this family should be considered at the level of subfamily. The cercopithecines are represented solely by the genus *Macaca* (macaques) in Asia. The 21 species of macaques in Asia are spread across a very diverse range of habitats (Fig. 1), which is reflected in a very diverse range of plant species consumed and dispersed (Fig. 2) (Tsuji *et al.* 2013a) but, like gibbons, macaques prefer fruits with juicy-soft pulp (Sengupta and Radhakrishna 2015; Ungar 1995). There are seed dispersal studies for only three species, but these include studies in tropical, temperate, dry, and even urban habitats (Table I; Fig. 3). Macaques show consistency in seed treatment across these habitats; *ca.* 60–85% of feces contain small seeds (Table I), and the major exception was when the macaques were provisioned by humans (27%, Sengupta *et al.* 2015). In tropical regions the majority of seeds dispersed are spat after processing in the cheek pouches (59% and 70%; Lucas and Corlett 1998; Sengupta *et al.* 2014), while rates of seed spitting are often lower in temperate regions (Tsuji *this issue*), where seeds tend to be smaller (Moles *et al.* 2007). Macaques are also seed predators, often spitting, dispersing, and destroying seeds of a single plant species (Otani 2004). There appears to be no absolute threshold for seed sizes to be swallowed, but most species consistently swallow seeds <5 mm in diameter (Albert *et al.* 2014; Tsuji *this issue*) and inconsistently up to *ca.* 25 mm (Albert *et al.* 2013; Yumoto *et al.* 1998). The prevalence of seed spitting appears to depend more on how easy the pulp can be separated from the seed than seed size (Yumoto *et al.* 1998; Tsuji *this issue*). Terrestrial and semiterrestrial species can also disperse seeds by carrying the fruit in the hands (Albert *et al.* 2014).



Information on dispersal distances for macaques is scarce, considering that they are widely distributed and relatively common in some regions. Spit seeds frequently end up under parent crowns (McConkey and Brockelman 2011), but can reach distances of ca. 200–400 m (Albert *et al.* 2013; Tsujino and Yumoto 2009; Tsuji *this issue*). The actual distances achieved by seed spitting can be influenced by the size of the foraging group and the size of the fruit resource (which influences how long the macaques stay within the source) (Albert *et al.* 2014). Because macaques frequently forage in large groups, the sheer number of seeds dispersed at close distances to the parent tree can imply an important role for this primate in seed dispersal (McConkey and Brockelman 2011). Dispersal distances for defecated seeds have averaged 97–486 m, with maximums of 265–1300 m (Sengupta *et al.* 2014; Terakawa *et al.* 2009; Tsuji and Morimoto 2016; Tsuji *this issue*), but given the large home ranges occupied by many species (Albert *et al.* 2014), it seems likely that some populations might achieve greater dispersal distances.

### **Cercopithecidae: Subfamily Colobinae**

Colobines (Colobinae: langurs, leaf monkeys and proboscis monkeys) have been considered as seed dispersers only very recently and the available data are very limited (Fig. 3) (Matsuda *et al.* 2013; Tsuji *et al.* 2017). They digest their food in a similar way to ruminants (Kay and Davies 1994) and consume more foliage, unripe fruits, and seeds than other Asian primates (Corlett 2017; Matsuda *et al.* 2014; Tsuji *et al.* 2013a). At present, only dispersal of small seeds (<5 mm in length) has been confirmed, and for three genera: *Nasalis* (Matsuda *et al.* 2013), *Trachypithecus* (Nguyen *et al.* 2013; Tsuji *et al.* 2017; L. Ong *unpubl. data*), and *Presbytis* (K. R. McConkey *unpubl. data*) (Table I, Fig. 2), but all genera have been recorded to consume “fruit” (e.g., Dela 2007; Erb *et al.* 2012; Grueter *et al.* 2009; Hoang *et al.* 2009; Kool 1993; Ma *et al.* 2017; Marshall *et al.* 2014; Matsuda *et al.* 2009; Ungar 1995; Zhou *et al.* 2006). These studies have limited usefulness for assessing seed dispersal, because ripe fruits and unripe fruits are frequently grouped together even though the seeds will have different fates. While only small seeds appear to be dispersed internally by colobines, larger-seeded fruits might be dispersed when they are carried away from the parent crown; we lack any information on this potential role but langurs (*Semnopithecus entellus*) were reported to drop seeds “close to” as well as under parent trees in a dry forest in Northern India (Prasad *et al.* 2004).

### **Lorisidae**

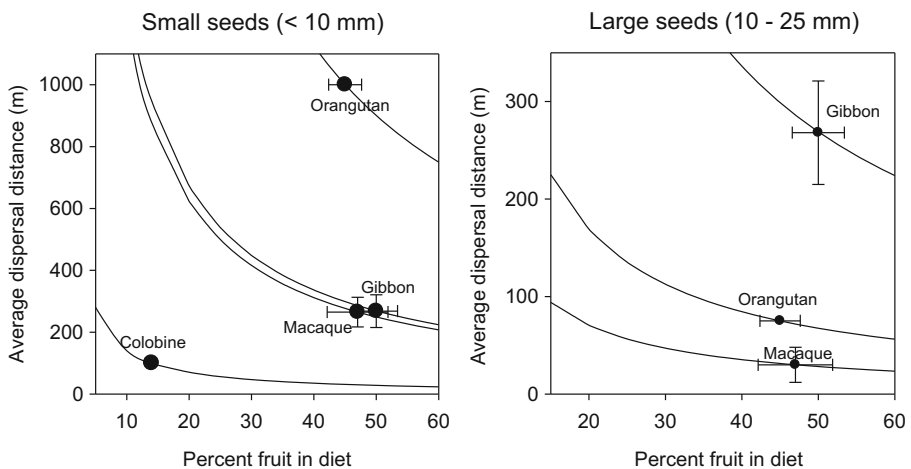
Several species of loris have been noted to consume fruits, but they are usually considered obligate exudativores (Starr and Nekaris 2013), or their diet is dominated by insectivory (Radhakrishna and Kuamara 2010). Fruits can form as low as 0.3% of the diet (*Nycticebus bengalensis*: Swapna *et al.* 2009), but several species have ca. 20% of their diet as fruit (*N. pygmaeus*, 19%: Starr and Nekaris 2013; *N. coucang*, 22.5%: Wiens *et al.* 2006; *Loris lydekkerianus*, 24%: Radhakrishna and Kumara 2010). It is likely that they eat more fruit when their preferred food items become scarce (Radhakrishna and Kuamara 2010). Fruits of several plant species have been recorded in the diet of lorises (two species, Swapna *et al.* 2009; six species, Radhakrishna and Kuamara 2010; nine

species, Wiens *et al.* 2006), with 19 species recorded in the scats of a single species (including broken seeds) (Wiens *et al.* 2006); however, some of these fruits are eaten while unripe (S. Radhakrishna *pers. comm.*), and it is unclear whether lorises can disperse viable seeds. Consumption of small-seeded plants, such as figs and *Dillenia*, suggest they could have minor contributions to the seed dispersal of some plants.

### Comparing Seed Dispersal Roles Across Taxa

The four main functional groups of frugivorous primate (orangutans, gibbons, macaques, and colobines) show different contributions to seed dispersal, when presented on a Seed Dispersal Effectiveness Landscape (Fig. 4). More plant species are potentially dispersed by macaques than any other taxa (Fig. 2), which probably reflects their wide distributions and diversity of habitats that can be occupied (Fig. 1).

For small seeds (Fig. 4a), the contributions of macaques and the gibbons are clustered together, suggesting they might play similar dispersal roles for these plants (at least in terms of the simplified view presented here). If their roles do differ it might be in terms of seed handling /digestion and factors associated with microhabitat. Colobines are unlikely to be able to match the seed dispersal contributions of the more frugivorous taxa, where they occur sympatrically. Orangutans might offer a complementary service to macaques and gibbons, as they could disperse seeds consistently longer distances, but there are no published studies on dispersal distances for orangutans and the value given here is an estimate based on movements (Corlett 2009). For larger seeds (Fig. 4b), gibbons disperse seeds consistently longer distances than orangutans and macaques (which spit seeds of this size). Overall, this suggests that gibbons are consistently reliable seed dispersers, while we might be overestimating the role of orangutans and underestimating the role of macaques, based on information that is currently available.



**Fig. 4** Comparison of functional groups of Asian primates on seed dispersal effectiveness (SDE) landscapes. Quantity is the percentage of fruit in the diet, and Quality is the dispersal distance. Where multiple studies have been performed the mean and standard error are shown. SDE landscapes are shown for small seeds, and large seeds, as orangutans and macaques exhibit different seed handling behavior for different sized seeds. Isoclines represent the SDE value of the taxa.

## Increasing Scales: The Importance of Primates in the Community

Studies of individual primate taxa are essential for understanding seed dispersal roles, but the importance of these taxa (or functional groups) cannot be evaluated until these roles are considered at the level of communities. Asian habitats still lack published community-wide network analyses, which would help assess the relative contributions of primates to seed dispersal mutualisms within communities. The most broadly studied seed dispersal communities in Asia are dry forests in India (Prasad 2010), seasonal evergreen forests in Thailand (e.g., Brodie *et al.* 2009; Chanthorn *et al.* 2017; Kitamura *et al.* 2002; McConkey and Brockelman 2011) and temperate forests in Japan (e.g., Masaki *et al.* 2012; Noma and Yumoto 1997). Community-wide information also exists for a mosaic of habitats in Kalimantan, Indonesia (e.g., Marshall *et al.* 2014), tropical semievergreen forest in Arunachal Pradesh, India (Datta and Rawat 2008), evergreen forests, Southern India (Ganesh and Davidar 2005), and dipterocarp forest in Peninsular Malaysia (L. Ong *unpubl. data*). These very different habitats exhibit interesting differences in the communities of fruit-eating animals, and it is unlikely primates play equivalent roles across habitats.

### Wet Forests vs. Dry Forests

Primates play central roles in seed dispersal in wet forest systems, such as tropical rain forests (Chanthorn *et al.* 2017) and the temperate forest habitats of Japan (Masaki *et al.* 2012). In tropical rainforests, primates often occur at relatively high diversity and density, which is matched by a high diversity and abundance of medium–large fleshy fruited species (Kitamura *et al.* 2002). Fruits such as these, which are mostly unavailable to birds owing to their physical structure, are most often dispersed by primates (McConkey and Brockelman 2011; McConkey *et al.* 2014, 2015). In Thailand, primates generated species-rich patterns of seed rain around their preferred food species and this pattern was still prevalent in saplings; similar patterns were not observed in bird-dispersed fruits (Chanthorn *et al.* 2017). However, habitats that have both a high primate density and a high diversity of terrestrial dispersers have not yet had published accounts. In Japan, macaques dominated the much simpler communities in terms of their contribution to seed dispersal; they dispersed 23 species compared to 13 species by the bulbul *Hypsipetes amaurotis*, while all other birds dispersed fewer than 7 species (Noma and Yumoto 1997). Masaki *et al.* (2012) found that the traits of Japanese fruits had evolved to suit mammals and not migratory birds, confirming a central role for primates in these systems.

In contrast, the dry forest communities that have been studied in India are dominated by terrestrial herbivores such as deer (Cervidae) and elephants (Prasad 2010; Sekar *et al.* 2017; Sridhara *et al.* 2016). The primate communities are limited to two taxa: langurs and macaques and the other key dispersers include frugivorous birds (Prasad and Sukumar 2010; Ramaswami *et al.* 2016; Sekar and Sukumar 2013, 2015 Sengupta *et al.* 2014). Community studies in these regions have indicated that primates occupy a less central role in seed dispersal (Prasad and Sukumar 2010; Sekar and Sukumar 2013, 2015) than has been shown in wet systems (Albert *et al. unpubl. data*). The peat swamp forests of Kalimantan appear to be another region where the contribution of primates to seed dispersal might be limited; primate-dispersed species were the most dispersal

limited while bird and bat species were the most common (Freund 2012). This might be expected given that volant animals have a clear advantage, compared to primates, in terms of mobility across a water-logged landscape.

### Primates vs. Other Taxa

Birds and primates are often the most conspicuous seed dispersing animals, and can be the easiest to collect data for. Hence, many comparisons of broad animal groups have focused on these two groups and have usually shown significant diet overlap. In Arunachal Pradesh, 45% of fruits dispersed by primates were also dispersed by hornbills (Datta and Rawat 2008); gibbon and hornbill diet overlap was 31% in Kalimantan, Indonesia (Marshall *et al.* 2009), while in Sulawesi and Sumatra they shared 45% and 41% of diet species, respectively (Kinnaird and O'Brien 2005). Although these figures help us understand frugivory—the first stage of the seed dispersal process—they do not describe actual dispersal overlap within communities. Fruit-eating animals are often generalists and consume a wide range of species to ensure their dietary requirements are met (Suwanvecho *et al.* 2017), so a high overlap between birds and primates could be expected. However, the preferences of these groups can be very different and they are important as dispersers for different subsets of these fruits (Table II); the “bird” fruits tend to be dispersed by birds, while the “mammal” fruits tend to be dispersed by mammals. Hence, “dispersal overlap” needs to be measured in terms of the relative numbers of fruits each taxa takes, and the chances of the seeds surviving and not based solely on frugivory information.

Diet and dispersal overlap between primates and other mammals might be more prevalent than with birds (Table II), but this has been considered more rarely. A good reason for the lack of comparisons until recently has been the sheer difficulty in obtaining information on these other animals, which tend to be nocturnal and are often terrestrial (and are therefore more difficult to approach). Camera traps have indicated that civets (Viverridae), bear (Ursidae), deer, and even elephants (all effective dispersers for some species) often consume similar species to some primate taxa and these are fruits not generally eaten by birds (Table II). Tree watches have also confirmed consumption of these fruits by squirrels (Sciuridae) (50% diet overlap with gibbons: Marshall *et al.* 2009), but squirrels are generally ineffective as seed dispersers (Corlett 2017; McConkey and Brockelman 2011; McConkey *et al.* 2014). Determining diet and dispersal overlap with bats has proven more difficult in this region because flying foxes (Pteropodidae)—which leave the most easily recognizable fruit remains—are often heavily hunted and/or persecuted (Aziz *et al.* 2015; Mildenstein *et al.* 2015) or presence of elephants and tigers prevent nocturnal field studies. Bats also prove difficult to capture on camera traps. However, the limited information we have about the diet of Asian fruit bats suggests overlap could be reasonable (Aziz *et al.* 2017; Boon and Corlett 1990; Hodgkison *et al.* 2003).

### Understanding Redundant and Complementary Dispersal

While a network approach that assesses the links between fruits and frugivores can provide a picture of how important a primate population might be within a community in terms of seed dispersal, the complexity within individual roles is rarely considered.

Table II Plant-focused studies that compare primates with other seed dispersing animals

Plant species	Family	Fruit, seed width (mm)	Seed dispersers							Reference		
			Orangutan	Gibbon	Macaque	Colobine	Birds	Squirrel	Civet		Bear	Deer
Mammal fruit												
<i>Dillenia indica</i>	Dilleniaceae	100, 6			+						++	Sekar & Sukumar 2013
<i>Irvingia malayana</i>	Irvingiaceae	42, 29			+						++	Ong unpubl. Data
<i>Artocarpus chaplasha</i>	Moraceae	90, 15			++			+			++	Sekar & Sukumar 2015
<i>Careya arborea</i>	Lecythidaceae	60, 20			+						++	Sekar & Sukumar 2015
<i>Platymitra macrocarpa</i>	Annonaceae	60, 18	+		+						++	McConkey et al. unpubl. Data
<i>Garcinia bentharii</i>	Clusiaceae	49, 13	++		+			+			+	McConkey et al. 2015
<i>Salacia chinensis</i>	Celastraceae	43, 14	++		++			+				McConkey et al. 2014
<i>Alphonsea boniana</i>	Annonaceae	27, 9	++		+			+				McConkey et al. 2014
<i>Nephelium melliferum</i>	Sapindaceae	26, 12	++		+			+			+	Brockelman et al. unpubl. Data
<i>Phyllanthus axillaris</i>	Phyllanthaceae	24, 11									++	Prasad & Sukumar 2010
<i>Chorospondias axillaris</i>	Anacardiaceae	23, 15	+				+				++	Brodie et al. 2009
<i>Dracontomelon dao</i>	Anacardiaceae	12, 6	++		+							Hai et al. unpubl. Data
<i>Durio zibethinus</i>	Bombacaceae	10, 3	-		++						+	Nakashima et al. 2008
Generalist fruit												
<i>Myrica rubra</i>	Myricaceae	25, 13	++		++			+				Terakawa et al. 2008
<i>Prunus javanica</i>	Rosaceae	13, 9	+		++			+			+	McConkey & Brockelman 2011
<i>Aphananthe cuspidate</i>	Cannabaceae	13, 8	-		++			+				McConkey unpubl. Data

Table II (continued)

Plant species	Family	Fruit, seed width (mm)	Seed dispersers							Reference			
			Orangutan	Gibbon	Macaque	Colobine	Birds	Squirrel	Civet		Bear	Deer	Elephant
Bird fruit													
<i>Durio graveolens</i>	Bombacaceae	9, 2	–					++	+	+			Nakashima et al. 2008
<i>Polyalthia simitarum</i>	Amonaceae	20, 14	+	+			++	++					McConkey unpubl. Data
Multiple	Myristicaceae	mixed	?	+	+	?	++	++	+	+	+	+	Kitamura & Poonswad 2013
<i>Horsfieldia amygdalina</i>	Myristicaceae	20, 16			+		++	++	+	+	+	+	McConkey unpubl. Data

Studies of plant species that are not dispersed by primates are not included. Dispersers are split into primates, birds, and other mammals and coded as to whether they are major (++) or minor (+) dispersers of the species, or seed predators (–), or fate was not known (?). Plant species are divided according to the general fruit characteristics: mammal fruits have a structure that usually prevent consumption by birds, generalist fruits are attractive to both birds and mammals, and bird fruits are dehiscent or have traits that are attractive and accessible to birds

When two taxa consume and disperse the same plant species they might be redundant as seed dispersers (so that only one taxon is required to ensure the species can regenerate) or they might play complementary roles (so that regeneration would be negatively impacted if one taxon was removed) (McConkey and Brockelman 2011; Rother *et al.* 2016). Determining whether a species plays a redundant or complementary role is quite difficult, in practice, but efforts have been made to address this at both landscape and local levels.

Traditionally, the “best” seed dispersers were considered to be those that dispersed seeds across large distances, but both local and far seed dispersal are probably required for a plant species to regenerate (Nathan 2007; Schupp *et al.* 2010); local seed dispersal ensures regeneration of the immediate population, while dispersal across long distances helps promote genetic mixing and colonization of new areas. Hence, two taxa that consume the same fruit species but disperse seeds at different average distances could have important complementary roles, rather than the taxa with more constrained dispersal being redundant (McConkey and Brockelman 2011; Rother *et al.* 2016). Hornbills and gibbons play potentially complementary roles because gibbons have a better capacity for local dispersal, while hornbills move seeds over large areas and across habitat fragments (Savini and Kanwatanakid-Savini 2011).

Redundancy and complementarity can be investigated by focusing on the seed dispersal ecology of selected plant species (Table II). These studies emphasize the importance of moving beyond species-focused approaches to measuring seed dispersal. A focus on species can produce an incomplete picture of a primate’s importance and it is essential to evaluate their role in relation to other dispersal agents. For example, macaques are often considered to be ineffective, redundant dispersers because they spit most seeds close to parent trees (Lucas and Corlett 1998); yet, the sheer volume of seeds that a large macaque group can disperse made them the most important local seed disperser for *Prunus javanica* in Thailand, with gibbons and hornbills playing complementary roles as medium- to long-distance dispersers (McConkey and Brockelman 2011). For another plant species in this forest, macaques and gibbons played complementary roles in terms of plants selected to feed and their actual effectiveness was almost equivalent despite dispersing seeds in very different ways (*Salacia chinensis*: McConkey *et al.* 2014). Other studies have shown that the role of primates might be primarily as a back-up dispersal mechanism when more efficient, but also more sporadic dispersers, are unavailable (*Dillenia indica* and macaques: Sekar and Sukumar 2013; *Garcinia bethamii* and gibbons: McConkey *et al.* 2015). In contrast, gibbons had a most likely redundant role in the dispersal of *Choreospondias axillaris* despite being regular consumers of the fruit; muntjacs (*Muntiacus muntjak*) were the only disperser that consistently moved seeds to the best microhabitats (Brodie *et al.* 2009). Overall, these studies are too few to understand the roles of different primate species at a community level. However, they suggest we should not underestimate what we do not know and consider that at times short-range, high-volume seed dispersal might be as important as long-distance, low-volume seed dispersal, or that even good seed dispersers might not provide equivalent services across all plant species.



## Decreasing Scales: Intrapopulation Variation

### Behavior is Important to Seed Dispersal

Behavioral studies are integral to primatology, providing a wealth of information with which to interpret seed dispersal behavior; yet studies of seed dispersal usually incorporate only the bare minimum of available behavioral information. Understanding the motivations of primate frugivory and seed dispersal behavior would give us a broader understanding of why variation in seed shadows exists and allow us to make predictions about how seed dispersal roles might be altered by changes such as anthropogenic disturbance.

Social and antagonistic behaviors can have important influences on frugivory and ranging of animals, and could be included more in seed dispersal studies (McConkey and O’Farrill 2016). In Asia, these behaviors could influence the seed dispersal role of the highly social macaques. Macaques often occur in large groups but may forage in small subgroups or as part of the large group (Albert *et al.* 2014), and this dichotomy could have quite different impacts on seed dispersal roles. In large groups, hierarchies among individuals can force individuals to process fruit away from the parent tree, resulting in scattered seed shadows close to the parent tree crown (McConkey and Brockelman 2011). In contrast, when subgroups forage in scattered fruit resources they might collect a few fruits as they pass through, store them in their cheek pouches, and spit seeds while roaming to the next food resource, resulting in longer dispersal distances (McConkey *et al.* 2014). Interactions with conspecifics can also influence the seed dispersal behavior of primates in smaller groups, such as gibbons. Gibbons are highly territorial and their movement patterns are influenced by the density, location, and aggressiveness of surrounding groups (Mitani and Rodman 1979). This could have repercussions on food choice and seed shadows (Phiphatsuwannachai *et al.* 2017) and how they might be altered by disturbance and reductions in gibbon density (McConkey and O’Farrill 2016).

Individual animals within populations often make consistent differences in fruit choices (McConkey and O’Farrill 2016). This might be driven by personality or learning and means that the collective seed shadow generated by a group might be very different from that observed in individual animals. This has rarely been studied, but in Sumatra, individual female orangutans made different fruit choices, and these preferences might have been transmitted from mother to offspring by social learning (Hardus *et al.* 2013).

### Variation Within Habitats

Within landscapes, species and even individual plants do not offer identical rewards, owing either to their nutritional content or their spatial distribution (Carlo and Morales 2008; Jordano 2000; Prasad and Sukumar 2010; Worman and Chapman 2005). Clumped resources tend to attract more frugivores than scattered resources (Carlo and Morales 2008; Prasad and Sukumar 2010), while plants of a single species can vary in nutritional content across individuals, and within individuals across time (Houle *et al.* 2007; Worman and Chapman 2005). Individual primates also differ in their nutrient requirements according, for example, to their age and reproductive status (Vogel *et al.* 2017). Pioneering work on nutrition has been conducted in Africa (e.g.,



Raubenheimer *et al.* 2015; Rothman *et al.* 2011), with far fewer studies in Asia (Vogel *et al.* 2017). We do know that spatial and temporal patterns of fruit selection can have a persistent effect on seed shadows of birds (Carlo and Morales 2008), ungulates (Prasad and Sukumar 2010), and bats (Chen *et al.* 2017); hence, understanding the motivation for what to eat and when to move is an important gap in our knowledge on the seed dispersal roles of Asian primates.

## Understanding More of the Seed Dispersal Process

### Seed Dispersal Beyond Endozoochory

There is a tendency among seed dispersal researchers to focus on frugivory and seed deposition, but truly understanding the function of a seed disperser requires a broader appreciation of what seed dispersal involves. Many (if not most) primates play multiple roles: as seed predators or seed dispersers, or they might have neutral roles. Primates can also act as seed dispersers by endozoochory (swallowing the seed) or by synzoochory (carrying the seed by hand or in the mouth) and we need to consider the joint impacts of all these roles. In Asia, this is particularly relevant to macaques and orangutans, which do not treat seeds consistently (Albert *et al.* 2014; Mohd-Azlan *et al.* 2015; Tarsisz 2016) (Figs. 2 and 3). They show four different types of seed handling behavior (predation, swallowing, spitting, carrying) and often treat single plant species in multiple ways (Albert *et al.* 2013; Mohd-Azlan *et al.* 2015; Sengupta *et al.* 2014; Tarsisz 2016). Macaques, and other cercopithecines, are unique among primates in the presence and use of cheek pouches (Albert *et al.* 2013) in which they can store fruit and process it slowly, before spitting out the seeds. This is possibly reminiscent of regurgitation in birds, and can result in short- to medium-range dispersal distances (depending on movement patterns) (Albert *et al.* 2013; Tsujino and Yumoto 2009). Macaques can have pivotal roles in seed dispersal via seed spitting (McConkey *et al.* 2015; Sengupta *et al.* 2014; Tsujino and Yumoto 2009). Orangutans also spit seeds but almost nothing is known of how effective this is as a seed dispersal method. Even carrying seeds can promote seed dispersal (Albert *et al.* 2013), especially for large-seeded fruits that have fewer alternative dispersers (Kitamura *et al.* 2002). This dispersal mode is available only to terrestrial or semiterrestrial primates because arboreal primates require their hands and feet to move through the canopy; hence, again it is the macaques and orangutans that might use this method most effectively.

Seed predation can have just as profound impacts on plants as seed dispersal (Genrich *et al.* 2017; Janzen 1971). Colobines are major seed predators in Asian forests (Ganesh and Davidar 2005; Hanya and Bernard 2013; Sun *et al.* 2007), but the impact of this function on the forests is almost unexplored. In Pasoh, Malaysia, leaf monkeys were the major pre-dispersal predator of *Shorea* seeds and might play a critical role in the evolution of masting in these plants (Sun *et al.* 2007). Orangutans and macaques are both seed predators and seed dispersers, and the balance between this mutualism and antagonism is similarly unexplored, yet is potentially very important (Genrich *et al.* 2017; Otani and Shibata 2000). For example, orangutans eat dipterocarp seeds when non-dipterocarp fruits (which they can disperse) are not widely available (Curran and Leighton 2000), while in other cases they might preferentially target species for their seeds (Hayna and Bernard 2013).

## Secondary Processes

Although secondary processes on dispersed seeds are recognized as very important (Culot *et al.* 2015; Janzen 1971), relatively few studies have assessed what happens to seeds dispersed by Asian primates (Enari and Sakamaki-Enari 2014; McConkey 2005a, b). Dispersed seeds might be removed by secondary dispersers, destroyed by seed predators, be attacked by pathogens, or germinate, and the likelihood of these different fates will be strongly species-specific. In a tropical forest in Thailand, rates of seed survival in macaque and gibbon-dispersed seeds ranged from 2% to 66% and 7% to 70%, respectively, depending on the plant species and where the seeds were dispersed to (McConkey and Brockelman 2011; McConkey *et al.* 2014, 2015). These secondary stages of seed dispersal can profoundly alter seed shadows (Culot *et al.* 2015); only 11% of seeds in gibbon seed shadows in dipterocarp forest germinated and almost all dungs were visited by seed predators or dispersers (McConkey 2005a). Primate feces can act as a strong attractant for seed-eating animals, particularly rodents (McConkey 2005b). Hence, understanding how seed spitting vs. seed swallowing impacts subsequent seed survival is an important topic to explore for primate species that handle seeds in different ways.

Secondary seed dispersal can occur through seed hoarding by rodents (Muridae and Sciuridae) or seed burial by dung beetles (Scarabaeidae). The function of dung beetles in removing seeds in primate feces has been studied intensively in the Neotropics (e.g., Andresen 2002; Culot *et al.* 2015), but Asia lacks studies on a comparative scale. In the heavy snowfall forests of Japan, between 28% and 40% of seeds defecated by macaques were incorporated into the seed bank by dung beetles with rates influenced by seed size (Enari and Sakamaki-Enari 2014) and some beetle species preferentially targeted macaque feces over those from other mammals (Enari *et al.* 2016). In a rain forest in Thailand, 10% of large seeds (length > 20 mm) in gibbon dungs were removed by dung beetles (Jadejaroen 2003). Similarly, seed hoarding by rodents is an important means of secondary seed dispersal in Neotropical forests (e.g., Forget *et al.* 2002; Jansen *et al.* 2012). Hoarding is also common for some rodent–plant interactions in Asia (e.g., Wang and Ives 2017; Xiao *et al.* 2005), and rodents are common visitors to primate dungs (McConkey 2005b), but the extent of seed hoarding from primate dungs is not known.

## Choosing a Fruit

Fruit selection is another aspect of seed dispersal that has received little research attention. Selection can occur at differing scales—from choosing species, individual trees, and individual fruits within trees—and is influenced by multiple factors, including nutritional requirements; olfactory, visual, tactile, and possibly auditory, acuity; and behavioral and ecological constraints (Corlett 2011; Dominy *et al.* 2001), as well as the range of fruits actually available at any time (McConkey *et al.* 2002; Suwanvecho *et al.* 2017). Langurs select different fruit types than orangutans, macaques, and gibbons (Fig. 3), but even within the three monogastric primates differences in fruit selection were observed (Ungar 1995) and there has been little follow-up work. All Old World monkeys and apes have full trichromatic color vision, which promotes easier detection

of green-yellow-red fruits (Dominy *et al.* 2001); this has possibly occurred at the expense of reduced olfactory ability (Gilad *et al.* 2007), but we know very little about the role other senses actually play in fruit selection. Both orangutans and gibbons have been shown to track fruit supplies; orangutan density alters with fruit availability (Marshall *et al.* 2009) and social transmission also influences fruit choices (Hardus *et al.* 2013), while gibbons make targeted visits to certain trees, presumably to check fruiting status (Asensio *et al.* 2011). Location of fruiting trees by macaques and langurs has not yet been assessed, but this has been studied in cercopithecines (baboons) in Africa (Noser and Byrne 2010).

## Understanding Change

Asian primates are at high conservation risk and are among the least adaptable of the world's primate species to the extreme changes that are affecting their habitats (Almeida-Rocha *et al.* 2017); this could have serious repercussions for the ecosystems they help to maintain. Most primate taxa already inhabit severely reduced distributions (although macaques have established introduced populations in some regions; Brodie *et al.* 2017) and reduced populations, and taxa are at varying degrees of threat from hunting, habitat loss, the pet trade, and “pest” control (Corlett 2007). All orangutan species are listed as Critically Endangered (IUCN 2017), along with 25% of gibbon species and species from all other functional groups (macaques, colobines, and lorises) (IUCN 2017). Although orangutans can maintain populations in degraded forests, the severe threat from hunting, pest control, and the pet trade (Corlett 2007) ensures they are unlikely to have long-term roles in seed dispersal in these habitats. Most gibbon species are listed as Endangered (69%) and their inability to maintain populations in degraded areas in which the canopy is discontinuous suggests their excellent seed dispersal capabilities are useful only in the increasingly limited intact forests. Macaque and colobine species are listed across the range of threat levels, but they also have species considered to be at low risk, and in some instances these species are commensal with humans (Sengupta *et al.* 2015; Tsuji 2011). These taxa, particularly macaques, are perhaps the most likely primates to maintain seed dispersal services in degraded areas (Albert *et al.* 2013).

The most serious conservation concern, in terms of seed dispersal, is what might happen to habitats in which primates are locally extinct. The quantity of seeds of *Myrica rubra* dispersed on Tanegashima Island, Japan—where *Macaca fuscata* are locally extinct—was 20 times less (all dispersed by bulbuls [Pycnonotidae]) than the quantity of seeds dispersed on Yakushima Island, where the macaque still occurs (Terakawa *et al.* 2008). Although primates are among the most hunted animals in Asian forests and have been extirpated or exist in reduced populations in many forests (Corlett 2007), this is the only study to specifically address the impact the loss of primates might have; however, evidence for significant effects on seed dispersal exists at a community level. Lambir Hills National Park in Sarawak, Malaysia is severely defaunated and has lost 50% of its primate species (and 22% of all mammals); overhunting has caused pervasive changes in the spatial structure of tree populations, with animal-dispersed species showing more clustering around adult trees than seeds

dispersed abiotically (Harrison *et al.* 2013). Although these changes could not be attributed to specific animal species, the Bornean gibbon (*Hylobates muelleri*) was among the primate species lost (Harrison 2011). Similarly, the likelihood of extinction of a gibbon-dispersed species, *Milivusa horsfieldii*, was predicted to increase 10-fold if all dispersers were to become extinct from the Thailand forest (Caughlin *et al.* 2014); however, again, the contribution of gibbons compared to other dispersers (civets and bears) was not distinguished.

Many other factors can alter how primates contribute to habitat maintenance, but these have been studied in only a handful of primate species in Asia. Reductions in primate density, changes in resource availability and habitat structure, and alteration in community composition can all change the frugivory and seed dispersal behavior of primates (McConkey and O’Farrill 2015, 2016). Resource availability, for example, is a strong determinant of primate diet and ranging. Provisioning by humans has changed the movement patterns, intergroup competition, and seed dispersal role of at least two macaque species (José-Domínguez *et al.* 2015; Sengupta *et al.* 2015). Under provisioning, rhesus macaques (*Macaca mulatta*) ate less fruit, moved less, and deposited most seeds on the road where germination was impossible (Sengupta *et al.* 2015). Macaques might be particularly vulnerable to changes in seed dispersal behavior given the behavioral flexibility of most groups (Albert *et al.* 2013), and any habitat or resource change could potentially enhance or decrease their role (McConkey and O’Farrill 2016). Changes in community composition have also been shown to alter the role of macaques. In Singapore, macaques have shifted a trophic level, eating more fruit now than before, possibly as a response to a reduction in competitors for that fruit (Gibson 2011).

## Conclusions

There are five functional groups of seed-dispersing primates in Asia. Gibbons are consistently effective dispersers, while colobines are predominantly seed predators, with orangutans and macaques playing dual roles (Fig. 3). Very little is known about the role of lorises, but they may play dual roles, or be predominantly seed predators. The importance of these roles is likely to be habitat specific, so it is essential that studies incorporate a range of habitat types and consider the seed dispersing “niche” of the primate within the wider frugivore community. Orangutans have the potential to act as long-distance seed dispersers for small to medium seeds, while gibbons are consistently medium-range dispersers for all swallowed seeds; dispersal distances achieved by macaques are extremely variable but they have the capacity for consuming large quantities of fruit. There are many gaps in our knowledge on primate seed dispersal in Asia; these include understanding the role of behavior in seed dispersal, fruit selection at different scales, postdispersal processes, and the combined impacts of dual functions (predators and dispersers). In the future, we must consider the role primates play at the level of the frugivore community and as a dynamic system that can be altered by natural and anthropogenic disturbances; only then can we determine how critical primates are for habitat persistence and the extent to which their roles are threatened by disturbance.

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### Compliance with Ethical Standards

**Conflict of Interest** The author declares that she has no conflict of interest.

## References

- Albert, A., Hambuckers, A., Culot, L., Savini, T., & Huynen, M.-C. (2013). Frugivory and seed dispersal by Northern pigtailed macaques (*Macaca leonina*), in Thailand. *International Journal of Primatology*, *34*, 170–193.
- Albert, A., McConkey, K. R., Savini, T., & Huynen, M. C. (2014). The value of disturbance-tolerant cercopithecin monkeys as seed dispersers in degraded habitats. *Biological Conservation*, *170*, 300–310.
- Almedia-Rocha, J. M., Peres, C. A., & Oliveira, L. C. (2017). Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. *Biological Conservation*, *215*, 30–38.
- Ancrenaz, M., Lackman-Ancrenaz, I., & Elahan, H. (2006). Seed spitting and seed swallowing by wild orangutans (*Pongo pygmaeus morio*) in Sabah, Malaysia. *Journal of Tropical Biology & Conservation*, *2*, 65–70.
- Andresen, E. (2002). Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, *27*, 257–270.
- Asensio, N., Brockelman, W. Y., Malaivijitnond, S., & Reichard, U. H. (2011). Gibbon travel paths are goal oriented. *Animal Cognition*, *14*, 395–405.
- Atmanto, A. D., Dwi, B. S., & Nurcahyani, N. (2014). Peran siamang sebagai pemencar biji di resort way kanan Taman Nasional Way Kambas Lampung. *Jurnal Sylva Lestari*, *2*, 49–58.
- Aziz, S. A., Clements, G. R., Peng, L. Y., Campos-Arceiz, A., McConkey, K. R., et al (2017). Elucidating the diet of the island flying fox (*Pteropus hypomelanus*) in Peninsular Malaysia through Illumina Next-Generation Sequencing. *PeerJ*, *5*, e3176.
- Aziz, S. A., Olival, K. J., Bumrungsri, S., Richards, G. C., & Racey, P. A. (2015). The conflict between Pteropodid bats and fruits growers: Species, legislation and mitigation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 377–426). Cham: Springer.
- Bocherens, H., Schrenk, F., Chaimanee, Y., Kullmer, O., Mörike, D., et al (2017). Flexibility of diet and habitat in Pleistocene South Asian mammals: Implications for the fate of the giant fossil ape *Gigantopithecus*. *Quaternary International*, *434*, 148–155.
- Boon, P. P., & Corlett, R. T. (1990). Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae). *Malayan Nature Journal*, *42*, 251–256.
- Brockelman, W. Y. (2011). Rainfall patterns and unpredictable fruit production in seasonally dry evergreen forest and its effects on gibbons. In W. J. McShea, S. Davies, & N. Phumpakphan (Eds.), *The unique ecology and conservation of tropical dry forests in Asia* (pp. 195–216). Washington, DC: Smithsonian Institution Press.
- Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Functional differences within a guild of tropical mammalian frugivores. *Ecology*, *90*, 688–698.
- Brodie, J. F., Helmy, O., Pangau-Adam, M., Ugiek, G., Froese, G., et al (2017). Cross the (Wallace) line: Local abundance and distribution of mammals across biogeographic barriers. *Biotropica*. <https://doi.org/10.1111/btp.12485>.
- Carlo, T. A., & Morales, J. M. (2008). Inequalities in fruit-removal and seed dispersal: Consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology*, *96*, 609–618.

- Caughlin, T., Ferguson, J. M., Lichstein, J. W., Zuidema, P. A., Bunyavejchewin, S., & Levey, D. J. (2014). Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Journal of the Royal Society B*, *282*, 20142095.
- Chanthom, W., Wiegand, T., Getzin, S., Brockelman, W. Y., & Nathalang, A. (2017). Spatial patterns of local species richness reveal importance of frugivores for tropical forest diversity. *Journal of Ecology*, *00*, 1–11. <https://doi.org/10.1111/1365-2745.12886>.
- Chen, S.-F., Shen, T.-J., Lee, H.-C., Wu, H.-W., Zeng, W.-T., et al (2017). Preference of an insular flying fox for seed figs enhances seed dispersal of a dioecious species. *Biotropica*, *49*, 511–520.
- Cheyne, S. M., Thompson, C. J. H., & Chivers, D. J. (2013). Travel adaptations of Bornean agile gibbons *Hylobates albibarbis* (Primates: Hylobatidae) in a degraded secondary forest, Indonesia. *Journal of Threatened Taxa*, *5*, 3963–3968.
- Corlett, R. T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. *Biological Reviews*, *73*, 413–448.
- Corlett, R. T. (2007). The impact of hunting on the mammalian fauna of tropical Asian forests. *Biotropica*, *39*, 292–303.
- Corlett, R. T. (2009). Seed dispersal distances and plant migration potential in East Asia. *Biotropica*, *41*, 592–598.
- Corlett, R. T. (2011). How to be a frugivore (in a changing world). *Acta Oecologica*, *37*, 674–681.
- Corlett, R. T. (2013). The shifted baseline: Prehistoric defaunation in the tropics and its consequences for biodiversity conservation. *Biological Conservation*, *163*, 13–21.
- Corlett, R. T. (2017). Frugivory and seed dispersal by vertebrates in tropical and subtropical Asia: An update. *Global Ecology and Conservation*, *11*, 1–22.
- Culot, L., Huynen, M. C., & Heymann, E. W. (2015). Partitioning the relative contribution of one-phase and two-phase seed dispersal when evaluating seed dispersal effectiveness. *Methods in Ecology and Evolution*, *6*, 178–186.
- Curran, L. M., & Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed production of mast-fruited dipterocarpaceae. *Ecological Monographs*, *70*, 101–128.
- D'Agostino, J., & Cunningham, C. (2015). Preliminary investigation of flexibility in learning color-reward associations in gibbons (Hylobatidae). *American Journal of Primatology*, *77*, 854–868.
- Datta, A., & Rawat, G. S. (2008). Dispersal modes and spatial patterns of tree species in a tropical forest in Arunachal Pradesh, north-east India. *Tropical Conservation Science*, *1*, 163–185.
- Dela, J. D. S. (2007). Seasonal food use strategies of *Semnopithecus vetulus nestor* at Panadura and Piliyandala, Sri Lanka. *International Journal of Primatology*, *28*, 607–626.
- Dennis, A. J., & Westcott, D. A. (2006). Reducing complexity when studying seed dispersal at community scales: A functional classification of vertebrate seed dispersers in tropical forests. *Oecologia*, *149*, 620–634.
- Dillis, C., Beaudrot, L., Feilen, K. L., Clink, D. J., Wittmer, H. U., & Marshall, A. J. (2015). Modeling the ecological and phenological predictors of fruit consumption by gibbons (*Hylobates albibarbis*). *Biotropica*, *47*, 85–93.
- Dominy, N. J., Lucas, P. W., Osorio, D., Yamashita, N., & Duncan, B. W. (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology*, *10*, 171–186.
- Enari, H., Koike, S., & Sakamaki-Enari, H. (2016). Ecological implications of mammal feces buried in snow through dung beetle activity. *Journal of Forest Research*, *21*, 92–98.
- Enari, H., & Sakamaki-Enari, S. (2014). Synergistic effects of primates and dung beetles on soil seed accumulation in snow regions. *Ecological Research*, *29*, 653–660.
- Erb, W. M., Borries, C., Lestari, N. S., & Hodges, J. K. (2012). Annual variation in ecology and reproduction of wild simakobu (*Simias concolor*). *International Journal of Primatology*, *33*, 1406–1419.
- Fan, P. F., Ai, H. S., Fei, H. L., Zhang, D., & Yuan, S. D. (2013). Seasonal variation of diet and time budget of Eastern hoolock gibbons (*Hoolock leuconedys*) living in a northern montane forest. *Primates*, *54*, 137–146.
- Fan, P., Huang, B., & Jiang, X. (2008). Seed dispersal by black crested gibbons (*Nomascus concolor*) in the Wuliang Mountains, Central Yunnan. *Acta Theriologica Sinica*, *28*, 232–236.
- Forget, P. M., Hammond, D. S., Milleron, T., & Thomas, R. (2002). Seasonality of fruiting and food hoarding by rodents in neotropical forests: Consequences for seed dispersal and seedling recruitment. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation*. Wallingford: CABI.
- Freund, C. (2012). *Assessing the role of seed dispersal in peat swamp forest regeneration*. MSc thesis, Columbia University, New York.



- Fricke, E. C., Tewksbury, J. J., Wandrag, E. M., & Rogers, H. S. (2017). Mutualistic strategies minimize coextinction in plant-disperser networks. *Proceedings of the Royal Society B*, *284*, 20162302.
- Galdikas, B. M. F. (1982). Orangutans as seed dispersers at Tanjung Puting, Central Kalimantan: Implications for conservation. In L. E. M. de Boer (Ed.), *The orangutan: Its biology and conservation* (pp. 215–219). The Hague: Dr W. Junk.
- Ganesh, T., & Davidar, P. (2005). Fruiting phenology and pre-dispersal seed predation in a rainforest in southern western Ghats, India. In J. L. Dew & J. P. Boubli (Eds.), *Tropical fruits and frugivores: The search for strong interactors* (pp. 137–152). Dordrecht: Springer.
- Genrich, C. M., Mello, M. A. R., Silveira, F. A. O., Bronstein, J. L., & Paglia, A. P. (2017). Duality of interaction outcomes in a plant–frugivore multilayer network. *Oikos*, *126*, 361–368.
- Gibson, L. (2011). Possible shift in macaque trophic level following a century of biodiversity loss in Singapore. *Primates*, *52*, 217–220.
- Gilad, Y., Wiebe, V., Przeworski, M., Lancet, D., & Pääbo, S. (2007). Correction: Loss of olfactory receptor genes coincides with the acquisition of full trichromatic vision in primates. *PLoS Biology*, *5*, e148.
- Grueter, C. G., Li, D., Ren, B., Wei, F., & van Schaik, C. P. (2009). Dietary profile of *Rhinopithecus bieti* and its socioecological implications. *International Journal of Primatology*, *30*, 601–624.
- Hanya, G., & Bernard, H. (2013). Functional response to fruiting seasonality by a primate seed predator, red leaf monkey (*Presbytis rubicunda*). *Tropical Ecology*, *54*, 383–395.
- Hardus, M. E., de Vries, H., Dellatore, D. F., Lameira, A. R., Menken, S. B. J., & Wich, S. A. (2013). Socioecological correlates of inter-individual variation in orangutan diets at Ketambe, Sumatra. *Behavioral Ecology and Sociobiology*, *67*, 429–437.
- Harrison, R. D. (2011). Emptying the forest: Hunting and extirpation of wildlife from tropical nature reserves. *Bioscience*, *61*, 919–924.
- Harrison, R. D., Tan, S., Plotkin, J. B., Slik, F., Detto, M., et al (2013). Consequences of defaunation for a tropical tree community. *Ecology Letters*, *16*, 687–694.
- Hasan, M. K., Feeroz, M. M., Islam, M. A., Kabir, M. M., Begum, S., et al. (2005). Food and feeding behavior of hoolock gibbon *Bunopithecus hoolock hoolock* in a semi evergreen forest of Bangladesh. *Bangladesh Journal of Life Sciences*, *17*, 43–49.
- Matsuda, I., Higashi, S., Otani, Y., Tuuga, A., Bernard, H., & Corlett, R. T. (2013). A short note on seed dispersal by colobines: The case of the proboscis monkey. *Integrative Zoology*, *8*, 395–399.
- Hoang, M. D., Baxter, G. S., & Page, M. J. (2009). Diet of *Pygathrix nigripes* in southern Vietnam. *International Journal of Primatology*, *30*, 15–28.
- Hodgkison, R., Balding, S. T., Zubaid, A., & Kunz, T. H. (2003). Fruit bats (Chiroptera: Pteropodidae) as seed dispersers and pollinators in a lowland Malaysian rain forest. *Biotropica*, *35*, 492–502.
- Houle, A., Chapman, C. A., & Vickery, W. L. (2007). Intra-tree variation in fruit production and implications for primate foraging. *International Journal of Primatology*, *28*, 1197–1217.
- IUCN (2017). The IUCN Red List of Threatened Species. Version 2017–1. <http://www.iucnredlist.org> Accessed 23 Aug 2017.
- Jadejaroen, J. (2003). *Post-dispersal of seeds in feces of white-handed gibbons (Hylobates lar) by dung beetles (Coleoptera: Scarabeidae)*. MSc Thesis. Bangkok: Mahidol University.
- Jansen, P. A., Hirsch, B. T., Emsens, W. J., Zamora-Gutierrez, V., Wikelski, M., & Kays, R. (2012). Thieving rodents as substitute dispersers of megafaunal seeds. *PNAS*, *109*, 12610–12615.
- Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, *2*, 465–492.
- Jordano, P. (2000). Fruits and frugivory. In M. Fenner (Ed.), *Seeds: The ecology of regeneration in plant communities* (2nd ed., pp. 125–166). Wallingford: CABI.
- José-Domínguez, J. M., Savini, T., & Asensio, N. (2015). Ranging and site fidelity in northern pigtailed macaques (*Macaca leonina*) over different temporal scales. *American Journal of Primatology*, *77*, 841–853.
- Kanamori, T., Kuze, N., Bernard, H., Malim, T. P., & Kohshima, S. (2010). Feeding ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley, Sabah, Malaysia: A 3-year record including two mast fruitings. *American Journal of Primatology*, *72*, 820–840.
- Kanamori, T., Kuze, N., Bernard, H., Malim, T. P., & Kohshima, S. (2017). Fluctuations of population density in Bornean orangutans (*Pongo pygmaeus morio*) related to fruit availability in the Danum Valley, Sabah, Malaysia: A 10-year record including two mast fruitings and three other peak fruitings. *Primates*, *58*, 225–235.
- Kay, R. N. B., & Davies, A. G. (1994). Digestive physiology. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution*. Cambridge, Cambridge University Press.

- Kinnaird, M. F., & O'Brien, T. G. (2005). Fast foods of the forest: The influence of figs on primates and hornbills across Wallace's Line. In J. L. Dew & J. P. Boubli (Eds.), *Tropical fruits and frugivores*. Dordrecht: Springer.
- Kitamura, S., & Poonswad, P. (2013). Nutmeg-vertebrate interactions in the Asia-Pacific region: importance of frugivores for seed dispersal in Myristicaceae. *Tropical Conservation Science*, 66, 608–636.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., et al (2002). Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia*, 133, 559–572.
- Kool, K. M. (1993). The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. *International Journal of Primatology*, 14, 667–700.
- Leighton, M. (1993). Modeling dietary selectivity by Bornean orangutans: Evidence for integration of multiple criteria in fruit selection. *International Journal of Primatology*, 14, 257–313.
- Lucas, P. W., & Corlett, R. T. (1998). Seed dispersal by long-tailed macaques. *American Journal of Primatology*, 45, 29–44.
- Ma, C., Fan, P-F., Zhang, Z-Y., Li, J-H., Shi, X-C., & Xiao, W. (2017). Diet and feeding behavior of a group of 42 Phayre's langurs in a seasonal habitat in Mt. Gaoligong, Yunnan, China. *American Journal of Primatology*, e22695. <https://doi.org/10.1002/ajp.22695>.
- Marshall, A. J., Ancrenaz, M., Brearley, F. Q., Fredriksson, G., Ghaffar, N., et al (2009). The effects of forest phenology and floristics on populations of Bornean and Sumatran orangutans: Are Sumatran forests more productive than Bornean forests? In S. A. Wich, S. Utami, T. Mitra Setia, & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 97–117). New York: Oxford University Press.
- Marshall, A. J., Beaudrot, L., & Wittmer, H. U. (2014). Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. *International Journal of Primatology*, 35, 1178–1201.
- Masaki, T., Takahashi, K., Sawa, A., Kado, T., Naoe, S., et al (2012). Fleshy fruit characteristics in a temperate deciduous forest of Japan: How unique are they? *Journal of Plant Research*, 125, 103–114.
- Matsuda, I., Tuuga, A., Hashimoto, C., Bernard, H., Yamagiwa, J., et al (2014). Faecal particle size in free ranging primates supports a 'rumination' strategy in the proboscis monkey (*Nasalis larvatus*). *Oecologia*, 174, 1127–1137.
- Matsuda, I., Tuuga, A., & Higashi, S. (2009). The feeding ecology and activity budget of proboscis monkeys. *American Journal of Primatology*, 71, 478–492.
- McConkey, K. R. (2000). Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. *American Journal of Primatology*, 52, 13–29.
- McConkey, K. R. (2005a). The influence of gibbon primary seed shadows on post-dispersal seed fate in Central Kalimantan, Indonesia. *Journal of Tropical Ecology*, 21, 255–262.
- McConkey, K. R. (2005b). Influence of faeces on seed removal from gibbon dung in a dipterocarp forest in central Borneo. *Journal of Tropical Ecology*, 21, 117–120.
- McConkey, K. R. (2009). The seed dispersal niche of gibbons in Bornean dipterocarp forests. In D. J. Whittaker, S. M. Lappan, & T. Geissmann (Eds.), *The gibbons: New perspectives on small ape socioecology and population biology* (pp. 189–210). New York: Springer Science+Business Media.
- McConkey, K. R., Aldy, F., Ario, A., & Chivers, D. J. (2002). Selection of fruit by gibbons (*Hylobates muelleri* × *agilis*) in the rain forests of Central Borneo. *International Journal of Primatology*, 23, 123–145.
- McConkey, K. R., & Brockelman, W. Y. (2011). Non-redundancy in the dispersal network of a generalist tropical forest tree. *Ecology*, 92, 1492–1502.
- McConkey, K. R., Brockelman, W. Y., & Saralamba, C. (2014). Mammalian frugivores with different foraging behavior can show similar seed dispersal effectiveness. *Biotropica*, 46, 647–651.
- McConkey, K. R., Brockelman, E. Y., Saralamba, C., & Nathalang, A. (2015). Effectiveness of primate seed dispersers for an "over-sized" fruit *Garcinia benthamii*. *Ecology*, 96, 2737–2747.
- McConkey, K. R., & Chivers, D. J. (2007). Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology*, 23, 269–275.
- McConkey, K. R., & O'Farrill, G. (2015). Cryptic function loss in animal populations. *Trends in Ecology & Evolution*, 30, 182–189.
- McConkey, K. R., & O'Farrill, G. (2016). Loss of seed dispersal before the loss of seed dispersers. *Biological Conservation*, 201, 38–49.
- McConkey, K. R., Prasad, S., Corlett, R. T., Campos-Arceiz, A., Brodie, J. F., et al (2012). Seed dispersal in changing landscapes. *Biological Conservation*, 146, 1–13.



- Mildenstein, T., Tanshi, I., & Racey, P. A. (2015). Exploitation of bats for bushmeat and medicine. In C. C. Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 325–375). Cham: Springer.
- Mitani, J. C., & Rodman, P. S. (1979). Territoriality: The relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology*, *5*, 241–251.
- Mohd-Azlan, J., Pail, T., & Silang, S. (2015). A preliminary study of fruit handling by captive Bornean orangutans *Pongo pygmaeus pygmaeus* and the effects on seed germination. *Asian Primates Journal*, *5*, 40–44.
- Moles, A., Ackerly, D., Tweddle, J. C., Dickie, J. C., Smith, R., et al (2007). Global patterns in seed size. *Global Ecology and Biogeography*, *16*, 109–116.
- Nakashima, Y., Lagan, P., & Kitayama, K. (2008). A study of fruit-frugivore interactions in two species of durian (*Durio*, Bombacaceae) in Sabah, Malaysia. *Biotropica*, *40*, 255–258.
- Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., de Manuel, M., et al (2017). Morphometric, behavioral and genomic evidence for a new orangutan species. *Current Biology*. <https://doi.org/10.1016/j.cub.2017.09.047>.
- Nathan, R. (2007). Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. In A. J. Dennis, E. W. Schupp, R. J. Green, & D. A. Westcott (Eds.), *Seed dispersal: Theory and its application in a changing world* (pp. 252–276). Wallingford: CABI.
- Nguyen, H., Bai, B., & Li, N., Pan, Y., & Lu, C. (2013). Fruit diet, selectivity and seed dispersal of Hatinh langur (*Trachypithecus francoisi hatinhensis*). *Acta Ecologica Sinica*, *33*, 110–119.
- Nielsen, N. H., Jacobsen, M. W., Graham, L. L. B., Morrogh-Bernard, H. C., D'Arcy, L. J., & Harrison, M. E. (2011). Successful germination of seeds following passage through orang-utan guts. *Journal of Tropical Ecology*, *27*, 433–435.
- Noma, N., & Yumoto, T. (1997). Fruiting phenology of animal-dispersed plants in response to winter migration of frugivores in a warm temperate forest on Yakushima Island, Japan. *Ecological Research*, *12*, 119–129.
- Noser, R., & Byrne, R. W. (2010). How do wild baboons (*Papio ursinus*) plan their routes? *Animal Cognition*, *13*, 145e155.
- Otani, T. (2004). Effects of macaque ingestion on seed destruction and germination of a fleshy fruited tree, *Eurya emarginata*. *Ecological Research*, *19*, 495–501.
- Otani, T., & Shibata, E. (2000). Seed dispersal and predation by Yakushima acaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. *Ecological Research*, *15*, 133–144.
- Phiphatsuwannachai, S., Westcott, D. A., McKeown, A., & Savini, T. (2017). Inter-group variability in seed dispersal by white-handed gibbons in mosaic forest. *Biotropica*. <https://doi.org/10.1111/btp.12499>.
- Prasad, S. (2010). *Seed dispersal in the tropical dry forests of Mudumalai, Southern India*. PhD thesis, Indian Institute of Science.
- Prasad, S., Chellam, R., Krishnaswamy, J., & Goyal, S. P. (2004). Frugivory of *Phyllanthus emblica* at Rajaji National Park, northwest India. *Current Science*, *87*, 1188–1190.
- Prasad, S., & Sukumar, R. (2010). Context-dependency of a complex fruit–frugivore mutualism: Temporal variation in crop size and neighborhood effects. *Oikos*, *119*, 514–523.
- Radhakrishna, S., & Kumara, H. N. (2010). Behavioural variation in the Mysore slender loris *Loris lydekkerianus lydekkerianus*. *Current Science*, *99*, 1226–1232.
- Ramaswami, G., Kaushik, M., Prasad, S., Sukumar, R., & Westcott, D. (2016). Dispersal by generalist frugivores affects management of an invasive plant. *Biotropica*, *48*, 638–644.
- Raubenheimer, D., Machovsky-Capuska, G. A., Chapman, C. A., & Rothman, J. M. (2015). Geometry of nutrition in field studies: An illustration using wild primates. *Oecologia*, *177*, 223–234.
- Rother, D. C., Pizo, M. A., & Jordano, P. (2016). Variation in seed dispersal effectiveness: The redundancy of consequences in diversified tropical frugivore assemblages. *Oikos*, *125*, 336–342.
- Rothman, J. M., Raubenheimer, D., & Chapman, C. A. (2011). Nutritional geometry: Gorillas prioritize non-protein energy while consuming surplus protein. *Biology Letters*, *7*, 847–849.
- Savini, T., & Kanwatanakid-Savini, C. (2011). Feeding overlap and seed dispersal efficiency between sympatric hornbills and gibbons in Thailand. *The Raffles Bulletin of Zoology*, *24*, 115–122.
- Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, *107*(108), 15–29.
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist*, *188*, 333–353.
- Schupp, E. W., Jordano, P., & Gomez, J. M. (2017). A general framework for effectiveness concepts in mutualisms. *Ecology Letters*, *20*, 577–590.

- Sekar, N., Lee, C.-L., & Sukumar, R. (2017). Functional nonredundancy of elephants in a disturbed tropical forest. *Conservation Biology*. <https://doi.org/10.1111/cobi.12907>.
- Sekar, N., & Sukumar, R. (2013). Waiting for Gajah: An elephant mutualist's contingency plan for an endangered megafaunal disperser. *Journal of Ecology*, *101*, 1379–1388.
- Sekar, N., & Sukumar, R. (2015). The Asian elephant is amongst the top three frugivores of two tree species with easily edible fruit. *Journal of Tropical Ecology*, *31*, 385–394.
- Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2014). Seed dispersal by rhesus macaques *Macaca mulatta* in Northern India. *American Journal of Primatology*, *76*, 1175–1184.
- Sengupta, A., McConkey, K. R., & Radhakrishna, S. (2015). Primates, provisioning and plants: Impacts of human cultural behaviours on primate ecological functions. *PLoS One*, *10*(11), e0140961.
- Sengupta, A., & Radhakrishna, S. (2015). Fruit trait preference in rhesus macaques (*Macaca mulatta*) and its implications for seed dispersal. *International Journal of Primatology*, *36*, 999–1013.
- Sodhi, N. S., Kph, L. P., Brook, B. W., & Ng, P. K. L. (2004). Southeast Asian biodiversity: An impending disaster. *Trends in Ecology & Evolution*, *19*, 651–600.
- Sridhara, S., McConkey, K. R., Prasad, S., & Corlett, R. T. (2016). Frugivory and seed dispersal by large herbivores of Asia. In F. S. Ahrestan & M. Sankaran (Eds.), *The ecology of large herbivores in South and Southeast Asia* (pp. 121–150). Ecological Studies 225). Dordrecht: Springer.
- Starr, C., & Nekaris, K. A. I. (2013). Obligate exudativory characterizes the diet of the pygmy slow loris *Nycticebus pygmaeus*. *American Journal of Primatology*, *75*, 1054–1061.
- Sun, I.-F., Chen, Y.-Y., Hubbell, S. P., Wright, S. J., & Noor, N. S. M. D. (2007). Seed predation during general flowering events of varying magnitude in a Malaysian rain forest. *Journal of Ecology*, *95*, 818–827.
- Suwanvecho, U., Brockelman, W. Y., Nathalang, A., Santon, J., Matmoon, U., et al. (2017). High interannual variation in the diet of a tropical forest frugivore. *Biotropica*. <https://doi.org/10.1111/btp.12525>.
- Swamy, V., & Terborgh, J. W. (2010). Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *Journal of Ecology*, *98*, 1096–1107.
- Swapna, N., Radhakrishna, S., Gupta, A. K., & Kumar, A. (2009). Exudativory in the Bengal slow loris (*Nycticebus bengalensis*) in Trishna Wildlife Sanctuary, Tripura, Northeast India. *American Journal of Primatology*, *71*, 1–9.
- Tarszisz, E. (2016). *The ecophysiology of seed dispersal by orangutans in Bornean peat swamp forest*. PhD Thesis. Australia: University of Wollongong.
- Terakawa, M., Isagi, Y., Matsui, K., & Yumoto, T. (2009). Microsatellite analysis of the maternal origin of *Myrica rubra* seeds in the feces of Japanese macaques. *Ecological Research*, *24*, 663–670.
- Terakawa, M., Matsui, K., Hamada, T., Noma, N., & Yumoto, T. (2008). Reduced dispersal effectiveness in the large-seeded tree *Myrica rubra* in the absence of the Japanese macaque on Tanegashima Island, Japan. *Japanese Journal of Conservation Ecology*, *13*, 161–167.
- Tsuji, Y. (2011). Seed dispersal by Japanese macaques (*Macaca fuscata*) in western Tokyo, central Japan: A preliminary report. *Mammal Study*, *36*, 165–168.
- Tsuji, Y. (2014). Inter-annual variation in characteristics of endozoochory by wild Japanese macaques. *PLoS One*, *9*, 08155.
- Tsuji, Y., Hanya, G., & Grueter, C. C. (2013b). Feeding strategies of primates in temperate and alpine forests: Comparison of Asian macaques and colobines. *Primates*, *54*, 201–215.
- Tsuji, Y., & Morimoto, M. (2016). Endozoochorous seed dispersal by Japanese macaques (*Macaca fuscata*): Effects of temporal variation in ranging and seed characteristics on seed shadows. *American Journal of Primatology*, *78*, 185–191.
- Tsuji, Y., Ningsih, J. I. D. P., Kitamura, S., Widayati, K. A., & Suryobroto, B. (2017). Neglected seed dispersers: Endozoochory by Javan lutungs (*Trachypithecus auratus*) in Indonesia. *Biotropica*, *49*, 539–545.
- Tsuji, Y., Sato, K., & Sato, Y. (2011). The role of Japanese macaques (*Macaca fuscata*) as endozoochorous seed dispersers on Kinkazan Island, northern Japan. *Mammalian Biology*, *76*, 525–533.
- Tsuji, Y., Van Minh, N., Kitamura, S., Van, N. H., & Hamada, Y. (2013a). Seed dispersal by wild rhesus macaques (*Macaca mulatta*) in Son Tra Nature Reserve, central Vietnam: A preliminary report. *Vietnamese Journal of Primatology*, *2*, 65–73.
- Tsujino, R., & Yumoto, T. (2009). Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. *Journal of Animal Ecology*, *78*, 119–125.
- Ungar, P. S. (1995). Fruit preferences of four sympatric primate species at Ketambe, northern Sumatra, Indonesia. *International Journal of Primatology*, *16*, 221–245.

- Vogel, E. R., Alavi, S. E., Utami-Atmoko, S. S., van Noordwijk, M. A., Bransford, T. D., et al (2017). Nutritional ecology of wild Bornean orangutans (*Pongo pygmaeus wurmbii*) in a peat swamp habitat: Effects of age, sex and season. *American Journal of Primatology*, 79, 1–20.
- Vogel, E. R., Haag, L., Mitra-Setia, T., van Schaik, C. P., & Dominy, N. J. (2009). Foraging and ranging behavior during a fallback episode, *Hylobates albibarbis* and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical Anthropology*, 140, 716–726.
- Wang, B., & Ives, A. R. (2017). Tree-to-tree variation in seed size and its consequences for seed dispersal versus predation by rodents. *Oecologia*, 183, 751–762.
- Wang, B. C., & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution*, 17, 379–386.
- Wiens, F., Zitzmann, A., & Huseein, N. A. (2006). Fast food for slow lorises: Is low metabolism related to secondary compounds in high-energy plant diet? *Journal of Mammalogy*, 87, 790–798.
- Worman, C. O., & Chapman, C. A. (2005). Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology*, 21, 689–697.
- Xiao, Z., Zhang, Z., & Wang, Y. (2005). Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologica*, 28, 221–229.
- Yumoto, T., Noma, M., & Maruhashi, T. (1998). Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 39, 325–338.
- Zhou, Q., Wei, F., Li, M., Huang, C., & Luo, B. (2006). Diet and food choice of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. *International Journal of Primatology*, 27, 1441–1460.