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THE ROLE OF *MACACA* SPP. (PRIMATES: CERCOPITHECIDAE) IN SEED DISPERSAL NETWORKS

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ABSTRACT. — To understand the consequences of an animal extinction on the survival of a plant species, it is necessary to study the functional redundancy between seed dispersers, both diet overlap and redundancy in seed dispersal patterns and effectiveness. In the Indo-Malayan region, we observe seed dispersal networks including macaques, other primate species, hornbills, bulbuls, fruit pigeons, civets, and bats. Hornbills, gibbons, and bulbuls are effective seed dispersers and complement each other in their dispersal services. The role of *Macaca* species has been overlooked in seed dispersal network studies despite their potential importance in forest regeneration. In fact, many *Macaca* species could be effective seed dispersers. Most are frugivorous and, unlike other dispersers, can eat every fruit type, regardless of colour, fruit size, seed size, presence or lack of seed protection, and plant life form. They spit out, swallow, and drop seeds. Their long gut retention time, long daily travels, and large home ranges increase the probability that they disperse seeds as far as, if not farther than, other frugivores. Moreover, unlike other dispersers often restricted to canopy or ground, their semi-terrestriality gives them access to fruits of every forest strata. Finally, more than simply dispersing seeds, *Macaca* species may play an important role in forest regeneration because they cross both deforested and every forest type, unlike most other frugivores which are unable to use gaps or open habitats. In conclusion, macaques provide a significant complement in terms of dispersal quantity and are sometimes the only frugivores able to disperse the large or protected seeds of some plant species and may thus bring those species a vital dispersal service.

KEY WORDS. — Macaque, functional redundancy, forest regeneration, Indo-Malayan region

INTRODUCTION

Plants and animals depend on each other for their survival (Chapman & Chapman, 1995; Andresen, 1999). On the one hand, seed dispersal is a crucial process for plant reproduction. By moving far from the parent plant, the seeds can avoid competition and predation, and can reach suitable sites for germination and establishment (Janzen, 1970; Connell, 1971). On the other hand, frugivores benefit from this relation by acquiring energy through the sugar-rich flesh of fruits. By removing 70–80 % of seeds produced by canopy and sub-canopy trees, vertebrates represent the most important seed dispersal agents in forests of the paleotropical region (Howe & Smallwood, 1982; Chapman & Chapman, 1999).

The majority of fruit species are eaten by several kinds of frugivores, such as mammals and birds (Coates-Estrada & Estrada, 1988; Fleming & Williams, 1990; Nathan & Muller-Landau, 2000; Kitamura et al., 2002). The composition of seed disperser assemblages, i.e., the various species dispersing a given plant species, varies over space and time according to fruit structure, size, and abundance (Herrera, 1985). Seed shadows, i.e., the spatial distribution of seeds dispersed from a single plant (Nathan & Muller-Landau, 2000), are thus determined by the combined effects of all dispersal agents (Nathan & Muller-Landau, 2000; Jordano et al., 2007; Spiegel & Nathan, 2007; Martínez et al., 2008). A common mistake is thinking that animals with an overlapping diet in fruit species could replace each other in terms of seed dispersal if one of them was brought to extinction. However, before concluding such a redundancy in seed dispersal services, one has to look both at overlaps in consumed species and at the seed dispersal effectiveness and patterns generated by each seed disperser for every plant species (i.e., functional redundancy; Clark et al., 2001; Brodie, 2007; Loiselle et al., 2007; McConkey & Brockelman, 2011).

Many factors influence these patterns and various animal species—characterised by their specific diets, habitat use, ranging behaviours, locomotion types, and activities—may induce various seed dispersal patterns, the sum of which may increase seed dispersal quality of a plant species (Brodie, 2007; Spiegel & Nathan, 2007; Brodie et al., 2009; Schupp et al., 2010).

To understand the consequences of an animal extinction on a plant species survival, it is crucial to study the composition of frugivore assemblages at fruiting plants as well as to determine each disperser species respective role (e.g., Lambert, 1999; Poulsen et al., 2002; Brodie et al., 2009; McConkey & Brockelman, 2011; Savini & Kanwatanakid-Savini, 2011) and even to understand the structure of mutualistic networks (Fortuna & Bascompte, 2006; Bascompte & Jordano, 2007). Eventually, the knowledge of the whole process is essential for tropical forest protection because one species' disappearance could trigger cascading effects leading to the disappearance of many plant and animal species.

In this review, we first introduce the importance of seed dispersal networks in the survival of plant populations. We then focus on how *Macaca* species could play a crucial role in seed dispersers' assemblages using a review of the available information on *Macaca* species. Indeed this genus was often overlooked in seed dispersal network studies, whereas most findings highlight their potential importance in forest regeneration (Corlett, 2009). We predicted that, based on their eco-ethological characteristics, mainly their diet, seed processing techniques, and ranging behaviour, it should make them as important as other dispersing frugivores usually studied in seed dispersers' assemblages.

SEED DISPERSAL NETWORKS

Mutualistic networks. — A true mutualistic interaction between two species has long been considered as existing only when both received a benefit from, and were strictly dependent on, this interaction (Stoner & Henry, 2008). However, today it is increasingly accepted that mutualism may involve real networks of interacting species (Bascompte et al., 2003; Jordano et al., 2003; Bascompte & Jordano, 2006; Brodie, 2007) and it is frequent to observe interaction networks in which a particular plant species relies on some frugivores for seed dispersal, whereas these frugivores depend on other plant species during periods of fruit scarcity (Kaplin et al., 1998). Given these complex networks, it is difficult to predict the effects of the disappearance of one particular species on the other interactants. Consequently, understanding the functioning of these networks is necessary for the establishment of adequate conservation plans, which is all the more important since the maintenance of these interactions and of the associated species is critical for the regeneration of tropical forests (Chapman et al., 1992b; Chapman, 1995; Chapman & Chapman, 1996; Loiselle et al., 2007). Understanding these networks' function requires the study of each participant eco-ethological characteristics, mainly focusing on their foraging behaviour, which is the "main mechanism driving seed dispersal" (Jordano & Godoy, 2002, p. 315).

Seed size: large seeds, large dispersers. — Ideally, seeds dispersed into degraded areas should include early-, mid-, and late-successional species. While growing, pioneer species, such as shrubs, quickly form a shady and humid environment essential to the survival and growth of mid- and late-successional species. However, Duncan & Chapman (1999) showed that 99.9% of seeds recovered in a deforested agricultural area were early-successional species already present and fruiting on the site. This seems logical since these species often produce larger numbers of seeds compared with mid- and late-successional species (Duncan & Chapman, 2002). Hence, the most important role of frugivores appears: the seed dispersal of mid- and late-successional species, mainly large-seeded species characteristic of the ultimate stage of succession (Parrotta et al., 1997; Kaplin & Moermond, 1998). Large-seeded species are better competitors than small-seeded species as they have better survival probabilities and are more competent in establishment (Murali, 1997). But these advantages cannot counteract the fact that they are poorer colonisers (Dominy & Duncan, 2005) as their dispersal can only be realised by a few groups of large frugivores (Corlett, 1998; Kitamura et al., 2002), such as large birds and mammals. Indeed, the maximum size of seeds dispersed by any animal species depends on its gape (Forest Restoration Research Unit, 2006) and also on the size of its body. Consequently the number of frugivore species that serves a given plant species declines with seed size (Chapman et al., 1992a; Kitamura et al., 2002; Peres & van Roosmalen, 2002). Large-seeded species are thus more threatened than others as they depend on a restricted number of seed dispersers thought to be vulnerable to extinction, due to selective hunting (Kitamura et al., 2002; Chapman et al., 2009) and to habitat loss or degradation (Corlett, 1998; Kitamura et al., 2002; Melo et al., 2010). The disappearance of their dispersers could bring large-seeded species to extinction because of the low probability of finding seed dispersers with a similar role.

Many studies highlight the role of birds and bats in seed dispersal (Fleming & Heithaus, 1981; Herrera, 1984; Medellin & Gaona, 1999) but others maintain that primates are essential within dispersers' assemblages (Wrangham et al., 1994; Dew & Wright, 1998; Garber & Lambert, 1998; Poulsen et al., 2001; Lambert & Chapman, 2005). Specifically, primates are particularly apt at dispersing large-seeded or hard-husked fruit species, which may be inaccessible to smaller taxa, or may be hard to process (Kaplin & Lambert, 2002; Chapman & Russo, 2007).

MACAQUES: OVERLOOKED ASSOCIATES

Tropical forests of the Indo-Malayan region share many of the same families and genera of animals (Corlett, 1998). Thus, it is common to observe networks of potentially effective seed dispersers, including macaques (one or several species), some other primate species (mainly arboreal ones, e.g., langurs, gibbons), hornbills, bulbuls, fruit pigeons, civets, and bats (Phua & Corlett, 1989; Corlett, 1998; Lucas & Corlett, 1998; Borries et al., 2002; Ganesh & Davidar, 2005; Srivastava, 2006; McConkey & Brockelman, 2011; Savini & Kanwatanakid-Savini, 2011). Other frugivores, such as elephants, deer, bovids, tapirs, and bears may complete the network, depending on the area. Three *Macaca* species are exceptions according to the habitat and climate where they live. *M. fuscata* lives in Japanese temperate forests where the climate varies with altitude from sub-tropical, warm temperate to cool temperate, tending to sub-alpine. *M. fuscata* is thus part of a different seed dispersal network only made by birds (mainly thrushes, pigeons and bulbuls; Noma & Yumoto, 1997), and deer (*Cervus nippon yakushimae*). *M. sylvanus*, the only species outside tropical Asia, lives in the Atlas Mountains of Algeria and Morocco with a small population of unknown origin in Gibraltar. It is also the only macaque species to be highly herbivorous and granivorous. Another species, *M. thibetana*, has much of its range outside the Indo-Malayan region and may be found in tropical, sub-tropical as well as temperate forests.

Some disperser species' networks have been better studied than others. Seed dispersal by hornbills (Kitamura et al., 2002; Kitamura et al., 2004a; Kitamura et al., 2006), gibbons (Whitington, 1990; Kitamura et al., 2002; Brodie et al., 2009) and bulbuls (Kitamura et al., 2002; Khamcha, 2009), and the network interaction between several of them (McConkey & Brockelman, 2011; Savini & Kanwatanakid-Savini, 2011) have been well studied and we know that beyond being simply effective seed dispersers alone (Corlett, 2002), these taxa may also complement each other in their dispersal services (McConkey & Brockelman, 2011; Savini & Kanwatanakid-Savini, 2011). Gibbons seem to be prevalent as they disperse many plant species (Table 1), including fruit with hard covers and flesh attached to seeds that hornbills are unable to eat (Kanwatanakid, 2000; Kitamura et al., 2004b). However, due to their small home ranges (Table 1), gibbons disperse seeds over a small area (Savini & Kanwatanakid-Savini, 2011). Hornbills are less frugivorous (Kanwatanakid-Savini et al., 2009) and disperse fewer seed species (Table 1), but over a larger area during non-breeding seasons, and are able to consume dehiscent fruits usually ignored by gibbons (Savini & Kanwatanakid-Savini, 2011). Bulbuls seem to be similar to gibbons in that they disperse many seed species over small areas (Khamcha, 2009). However, they have a very short gut retention time which decreases the probability of harmful scarification of the ingested seeds and they forage in the lower to middle strata of the canopy (Khamcha, 2009). Moreover, contrary to gibbons and large hornbills, they only disperse small-seeded species (Khamcha, 2009).

Other species could be essential parts of the seed dispersal assemblages found in the Indo-Malayan region. Some herbivores have been shown to provide effective dispersal services to plant species with particular requirements. For instance, muntjacs (*Muntiacus muntjak*) are the most effective dispersers for *Choerospondias axillaris* (Anacardiaceae) seeds in Khao Yai National Park, Thailand (Chanthorn & Brockelman, 2008; Brodie et al., 2009), although deer seem to be mostly seed predators (Corlett, 1998). Indian rhinoceros (*Rhinoceros unicornis*) may be the major dispersal agent for *Trewia nudiflora* (Euphorbiaceae) seeds, in Chitwan, lowland Nepal (Corlett, 1998). Elephants (*Elephas maximus*) could also play a vital role for some plant species, like their African relatives, *Loxodonta africana* (Chapman et al., 1992b; Babweteera et al., 2007). But these species still need to be studied as seed dispersers, along with sambars (*Cervus*

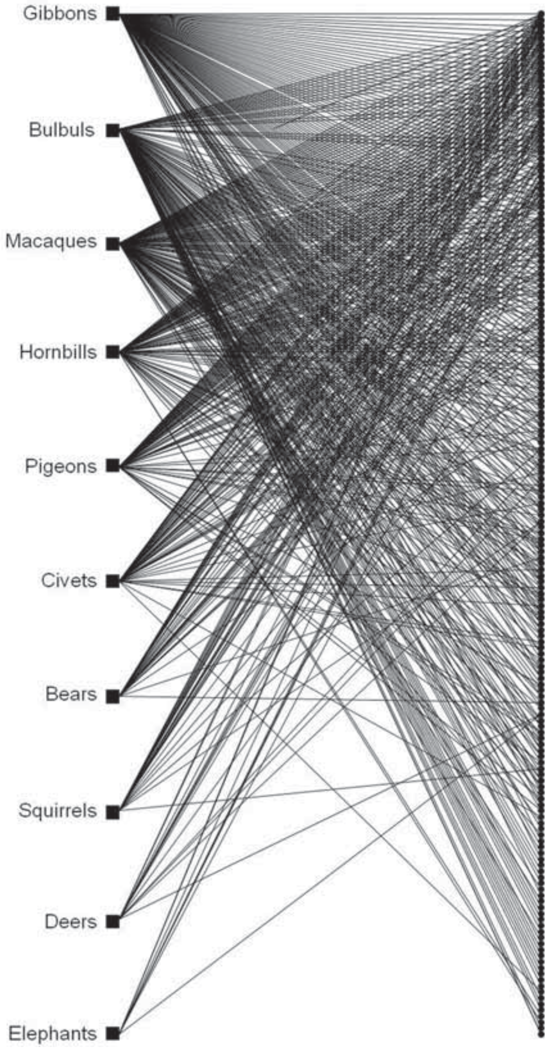

Fig.1. Bipartite graph depicting a plant-animal mutualistic network involving 10 frugivores (left) and 170 of the plant species (right) they disperse at Khao Yai National Park, Thailand. The list of plant species is based on Kitamura et al. (2002), then the list of frugivores dispersing each species has been completed thanks to data from bin Kassim (1987), Kitamura et al. (2005), Datta & Rawat (2008), Brockelman (2009), McConkey & Brockelman (2011), Albert et al. (2013), Ngoprasert (2012), Khamcha (pers. comm.), Latinne (pers. comm.), Martmoon (pers. comm.).

Table 1. Characteristics of various dispersal agents found in the Indo-Malayan region.

	Gibbons (14 spp.)	Hornbills (small/large)	Bulbuls	Pigeons	Civets (11 spp.)	Deer (15 spp.)	Bears (3 spp.)	Elephants (1 sp.)
No fruit species	84[b]	71[b]	118[b]	62[b]	56[b]	46[b]	13[b]	9[b]
Fruit colour	Red, black, yellow-orange[a, b]	Red, black, purple[a, b]	Red, purple, black[b]	Red, purple, black[b]	Red, black, yellow[b]	Red, black, yellow[b]	Red, purple, black, yellow[b]	Yellow[b]
Seed processing	Swallow	Spit out (swallow very small seeds)	Swallow	Swallow	Swallow	Swallow	Swallow	Swallow
Seed dispersed/ Total ingested	90%[a]	100%[a]	—	—	—	—	—	75%[g]
Maximum diameter of ingested seed (mm)	19[b]	Spit out: 35 Swallow: 0,05[a]	13[b]	20[b]	17[b]	28[b]	13[b]	23[b]
Seed passage time (min)	900–3000[p]	Sallow: 83 (up to 600) Spit out: 67[a]	5–122[k]	20–530[q]	156[i]	—	186–2640[j]	558–6828[g]
Seed dispersal distance (m)	100–1,000[d]	1,000–10,000[d]	Up to 454[c]	>10,000[d]	1,000–10,000[d]	1,000–10,000[d]	Up to 22,000[j]	Up to 57722[g]
Deposition pattern	Clumped Scattered	Scattered	Scattered	Scattered	Clumped	Clumped	Clumped	Clumped
Germination percentage	95.5%[a]	95.8%[a]	—	—	—	—	44-63%[n]	60%[e]
Dispersal of arboreal shrubs	No[b]	No[b]	Yes[b]	—	—	—	—	No[b]
Biomass (kg km^{-2})	105[a]	38.7[a]	11.1[c]	—	—	14–117[f]	5–15[o]	–
Home range size (ha)	25[a]	100 (small) 800–4200 (large)[a]	2.2[c]	—	300–1,700[l]	—	1,000–18,000[m]	5,000–100,000 ha[h]
Travel (m day^{-1})	1300[a]	4,500(small) 8,500–11,000 (large)[a]	—	—	—	—	—	1,000-2,000[g]
Foraged canopy strata	Outer to emergent[a]	Emergent (large) Middle (small)[a]	Lower to middle[c]	—	—	Ground[b]	—	Ground[b]
Forest type	Primary[a]	Primary Secondary[a]	Primary Secondary[k]	—	—	Primary Secondary	Primary Secondary	Primary Secondary
Seed accumulation	Sleeping sites Fruiting trees Travel pathways	Nesting sites (breeding season) Roosting sites (non-breeding season) Travel pathways	Nesting sites Roosting sites	—	—	—	—	Travel pathways

[a](Savini & Kanwatanakid-Savini, 2011), [b](Kitamura et al., 2002), [c](Khamcha, unpublished data), [d](Corlett, 2009), [e](Kitamura et al., 2007), [f](Brodie et al., 2009), [g](Campos-Arceiz et al., 2008), [h](Sukumar, 2006), [i](Nakashima & Sukor, 2009), [j](Koike et al., 2011), [k](Weir & Corlett, 2007), [l](Rabinowitz, 1991), [m](Kozakai et al., 2011); [n](Koike et al., 2008); [o](Ngoprasert et al., in revision); [p](McConkey, 2000); [q](Corlett, 1998)

unicolor), or gaurs (*Bos gaurus*). Even some frugivore species have long been overlooked in seed dispersal network studies, such as bats (but see Mello et al., 2011), due to their nocturnal habits, or macaques, although *Macaca* is one of the most widespread genera of non-human primates.

Thus, data are lacking and studies on macaque seed dispersal habits come mainly from the Khao Yai National Park (Thailand; *M. leonina*), the Yakushima island (Japan; *M. fuscata*), Singapore (*M. fascicularis*) and Hong Kong (*M. fascicularis*, *M. mulatta*), with some other rare studies from Malaysia (*M. fascicularis*), Taiwan (*M. cyclopis*), and Western Ghats (India*; M. silenus*). However, given their diet, seed processing techniques, and ranging behaviour, many *Macaca* species could be effective seed dispersers (Corlett, 2002; McConkey & Brockelman, 2011).

MACAQUES IN ASIAN SEED DISPERSAL NETWORKS

Diet. — Macaques are omnivorous-frugivorous primates, i.e., they eat fruits, but also leaves, flowers, shoots, roots, invertebrates, and small animals in variable quantities (Maruhashi, 1980; Caldecott, 1986; Kurup & Kumar, 1993; Krishnamani, 1994; O'Brien & Kinnaird, 1997; Su & Lee, 2001; Rowe & Myers, 2011; Schülke et al., 2011). The percentage of fruit in the diet, usually higher than other food items, depends on the particular macaque species—from relatively low (10–32% in *M. fuscata*; Agetsuma & Nakagawa, 1998) to very high (85% in *M. nigrescens*; Rowe & Myers, 2011)—but may also show intra-specific variations, depending on habitat and provisioning (e.g., in *M. fuscata*: 15% in provisioned troops [Son, 2003] and 88% in unprovisioned ones [Wheatley, 1980]), and seasonal variations (Hanya et al., 2003; Table 2). The number of fruit species included in the macaques' diet is species-specific but often higher than for other sympatric frugivores (Tables 1, 2; Corlett, 1998).

Fruit species eaten are not restricted to the so-called 'primate fruits', those with large seeds, orange-brown colour, and a protective rind (Corlett, 1998). Macaques eat various fruit types, including dehiscent and indehiscent fruits, protected or not, and of every colour, contrary to other mammals tending to avoid dehiscent fruits that are preferred by birds (Lucas & Corlett, 1998; Kitamura et al., 2002), unprotected fruits preferred by other frugivores (Corlett, 1998), and yellow fruits preferred by other mammals (Kitamura et al., 2002).

Studies focused on macaque seed dispersal seem to show that they may disperse very small (e.g., *M. fascicularis*: 0.2 mm; Lucas & Corlett, 1998), as well as very large seeds (e.g., *M. cyclopis*: up to 16.7 mm for swallowed seeds, Chen, 1999; *M. fascicularis*: up to 30 mm for spat out seeds and 51.3 mm for dropped seeds, Lucas & Corlett, 1998; *M. fuscata*: up to 26 mm for swallowed seeds and 40 mm for spat out seeds, Otani, 2004), such as deer, but contrary to other frugivores which are more restricted to some seed sizes (e.g., small seeds for most birds and bats, and large seeds for elephants; Kitamura et al., 2002; Lucas & Corlett, 1998).

Moreover, they feed on small as well as very large fruits (e.g., 2.4–84.3 mm in *M. leonina*; Kitamura et al., 2002), the latter excluding seed dispersal by all birds but hornbills and fruit pigeons (Corlett, 1998). Thus, in some areas where macaques are the only large frugivores, they may be essential for the dispersal of medium- and large-sized fruits, e.g., *M. fuscata* on Yakushima island (Noma & Yumoto, 1997), and *M. fascicularis* in Singapore and Hong Kong (Corlett, 1996; Lucas & Corlett, 1998). In Khao Yai National Park, several large-seeded plant species, such as *Platymitra macrocarpa*, *Nephelium melliferum*, *Baccaurea ramiflora*, *Lansium domesticum* (Kitamura et al., 2005) and *Prunus javanica* (McConkey & Brockelman, 2011) have been shown to be mainly dispersed by primates (*Macaca leonina* and *Hylobates lar*). On Yakushima island, *M. fuscata* could be, along with resident fruit pigeons, an essential seed disperser for large-fruited plant species and species fructifying in summer, such as *Myrica rubra* (Myricaceae). Indeed, they are resident on the island and feed on fruits all-year long contrary to most bird species only present in winter (Noma & Yumoto, 1997).

Finally, macaques eat fruits produced by all plant life forms (i.e., tall and small trees, lianas, shrubs, and herbs; Lindburg, 1977; Caldecott, 1986; Chen, 1999; Ramachandran & Joseph, 2000; Kitamura et al., 2002; Kumar et al., 2007) while other frugivores usually ignore small trees and shrubs, necessary for forest succession, and deer and elephants only eat the fallen fruits of tall trees (Kitamura et al., 2002).

Seed processing. — Seeds may be swallowed, spat out, or dropped (Corlett & Lucas, 1990; Lucas & Corlett, 1998; Chen, 1999; Kitamura et al., 2002) depending on seed species. When swallowed, they are retained for a long duration in the gut as, like most cercopithecines, macaques have a long gut retention time. In *Macaca fuscata yakui*, Otani (2004) estimated an average retention time of 39.1 ± 3.3 h for the consumption of *Eurya emarginata* seeds, and Tsuji (2010) estimated an average retention time reaching 54 h. In *Macaca cyclopis*, Chen (1999) recorded an average retention time of 36.4 ± 5.4 h. This is significantly higher than most other dispersers (Kitamura, 2007; Khamcha, 2009; Savini & Kanwatanakid-Savini, 2011), but comparable to gibbons (15–50 h; McConkey, 2000; Savini & Kanwatanakid-Savini, 2011), bears (3.1–44 h; Koike et al., 2011), or even elephants (9.3–113.8 h; Kitamura et al., 2007; see Table 1). Thus, they may potentially disperse seeds far from the parent plant. Moreover, if a long retention time is often considered as potentially harmful for ingested seeds, many studies have shown that gut treatment by primates was mostly neutral (Traveset, 1998) and this seems to be the case for macaque species (Chen, 1999; McConkey & Brockelman, 2011; Albert et al., 2013).

Macaques defaecate individually—contrary to gibbons defaecating in group—but mainly from low branches or on the ground where they spend the largest amount of their day time (Table 2). Thus, their cohesive dungs are unlikely to be broken up during the fall, leaving seeds highly clumped

Table 2. Characteristics of *Macaca* species.

Macaca species	Common name	Home range (ha)	Daily range (m day^{-1})	No fruit species	% fruit (seeds incl.) in diet
M. arctoides	Stump-tailed	—	—	—	—
M. assamensis	Assamese	95–500[a]	1900[a]	—	42.2[v]
M. cyclopis	Formosan rock	130[a]	2065[a]	51[k]–66[j]	52[w]
M. fascicularis	Long-tailed	7–300[a]	1900[b]	185[l] 88.31[y]	15 (Provisioned)[x]
M. fuscata	Japanese	214–797[a]	1218[a]	45[m, n]	19.5–40.3[z]
M. hecki	Heck's	—	—	—	
M. leonina	Northern pigtailed	83–347[a]	690–2240[a]	126[o]	41 (Semi-provisioned)[o] 65.9[aa]
M. maura	Moor	20[a]	—	—	—
M. mulatta	Rhesus	130–1340[c]	1050–3500[c]	28[p]	65–70[p]
M. munzala	Arunachal	11–28[h]	1500[h]	11[h]	68[h]
M. nemestrina	Southern pigtailed	62–828[d]	902–2960[d]	146[q]	74.2[q]
M. nigra	Celebes crested	175–341[a]	1750–3140[a]	145[r]	60–70.7[r]
M. nigrescens	Gorontalo	—	515–1240[a]	—	85.1[a]
M. ochreata	Booted	29–85[g]	—	—	66[bb]
M. pagensis	Pagai Island	—	—	—	
M. radiata	Bonnet	2–500[a]	710–1300[a]	16[s]	53.9[s]
M. siberu	Siberut	530[a]	—	—	50[a]
M. silenus	Lion-tailed	131[e]	750–2500[e]	33[t]	92.9[a]
M. sinica	Toque	41[a]	500–2000[a]	—	67[a]
M. sylvanus	Barbary	200–720[a]	2000–9000[a]	12[cc]–42[dd]	33[a]
M. thibetana	Milne-edwards'	500[a]	—	<26[ee]	<60[ee]
M. tonkeana	Tonkean	67–143[f]	707–1500[i]	58[u]	68.2–81.2[u]

[a](Rowe & Myers, 2011); [b](Wheatley, 1980); [c](Makwana, 1978); [d](Caldecott, 1986); [e](Kurup & Kumar, 1993); [f](Riley, 2007); [g](Astaras & Waltert, 2010); [h](Kumar et al., 2007); [i](Pombo et al., 2004); [j](Chen, 1999); [k](Su & Lee, 2001); [l](Lucas & Corlett, 1998); [m](Hanya, 2004); [n](Maruhashi, 1980); [o](Albert et al., 2013); [p](Lindburg, 1977); [q](Caldecott, 1986); [r](O'Brien & Kinnaird, 1997); [s](Krishnamani, 1994); [t](Umapathy & Kumar, 2000); [u](Riley, 2007); [v](Schülke et al., 2011); [w](Chang, 1999); [x](Son, 2003); [y](Wheatley, 1980); [z](Agetsuma & Nakagawa, 1998); [aa](Choudhury, 2008); [bb](Priston, 2005); [cc](Ménard, 1985); [dd](Ménard & Vallet, 1986); [ee](Zhao et al., 1991)

by sometimes up to several hundreds (Lucas & Corlett, 1998; Otani, 2004), contrary to birds, bats, and arboreal primate faeces, which usually shatter before reaching the ground (Phua & Corlett, 1989; Corlett, 1998). This clumped deposition may have harmful consequences for seeds prone to density-dependent pathogens or predators (Howe, 1989). However, *M. silenus* and *M. sinica* are exceptions which, due to their arboreal habits, may defaecate from higher heights and increase the probability that faeces will scatter by falling through vegetation.

Macaques, due to their cheek pouches, may spit out seeds. In every macaque species, the cheek pouches are highly developed (Murray, 1975). This can be due to their extensive use, during which monkeys store large amounts of fruits and seeds and, thus, increase the probability of seed dispersal. Although they spit out many seeds under the parent trees (McConkey & Brockelman, 2011)—a behaviour also seen in other dispersers such as flying foxes (Corlett & Lucas, 1989)—a significant percentage of seeds are spat out beyond the crown edge (McConkey & Brockelman, 2011). Macaques also drop seeds but this technique seems to be mainly used for very large-seeded fruits (Lucas & Corlett, 1998; Albert et al., 2013).

Due to the generally non-destructive process of seed-handling, macaques are able to disperse seeds up to several hundred meters (Huang, 2005; Tsujino & Yumoto, 2009; Albert et al., 2013), much like gibbons (Corlett, 2009), and sometimes up to 2.4 km (Chen, 1999), a distance comparable to dispersal by hornbills, bulbuls, and civets (Corlett, 2009; D. Khamcha, unpublished data). Although seed dispersal by macaques has frequently been associated with high proportions of seeds spat under parent trees (Corlett & Lucas, 1990; Lambert, 1999, 2001), high removal rates have been documented for some plant species (McConkey et al., unpublished data).

The proportion of seed species destroyed by macaques seems to be low given seed destruction is encountered mainly in two cases: predation on seeds of Fagaceae and feeding on immature fruits (Lindburg, 1977; Maruhashi, 1980; O'Brien & Kinnaird, 1997; Corlett, 1998; Lucas & Corlett, 1998; Otani, 2004; Hanya, 2005).

Ranging behaviour. — Macaques are all semi-terrestrial, with *M. silenus* and *M. sinica* being arboreal. This enables them to survive in poor forests with scarce and scattered food sources. Terrestrial travels between arboreal food sources are rapid and energy efficient (Rodman, 1979). This travelling mode enables them to use an increased diversity of food sources including fallen fruits (Caldecott et al., 1996) to which arboreal species do not have access. Macaques thus have the possibility to forage in all strata of the forest canopy whereas other frugivores are either canopy dwellers or terrestrial animals that only eat fallen fruits (Kitamura et al., 2002). This is probably why most macaques are able to live in primary and secondary forests.

Macaques, while foraging, continuously progress across the smaller home ranges of other species included in their own home range (e.g., langurs). They quickly harvest the highest quality foods as they pass on to other food patches (Caldecott, 1986). The fast terrestrial travels of macaques, along with a long daily range (from 500–3140 m/day; Rowe & Myers, 2011), induce usually large home ranges (from 20–1340 ha; Rowe & Myers, 2011), increasing the probability that seeds will be dispersed far from the parent tree, and often farther than where seeds would be dispersed by most frugivorous birds (except hornbills), which have small home ranges (Hanya, 2005).

Finally, macaques are tolerant to human disturbance (Albert, 2012), and may cross disturbed areas, even urbanised areas for some species (Makwana, 1978; Maruhashi, 1980; O'Brien & Kinnaird, 1997; Lucas & Corlett, 1998; Sinha, 2001; Kumar et al., 2007; Riley, 2007). Their seed dispersal role may be essential to the regeneration of secondary forests in these areas (Corlett, 1998; Lucas & Corlett, 1998) as few frugivores may survive in disturbed forests, except bulbuls (Corlett, 1998) which disperse only small seeds. However, the effectiveness of seed dispersers, via the reforestation of degraded areas, always depends on the proximity of natural habitats providing enough fruits for a sufficient seed contribution.

Study case: the Khao Yai National Park. — Khao Yai National Park (KYNP; 2,168 km²) is the first park of Thailand, established in 1962. It situated at 130 km NE of Bangkok and its elevation ranges from 250–1326 m a.s.l. Its area is mainly covered by a moist evergreen forest and the climate is monsoonal.

In KYNP, seed dispersal by hornbills (*Anthracoceros albirostris, Anorrhinus austeni, Aceros undulates*, and *Buceros bicornis*; Kitamura et al., 2002; Kitamura et al., 2004a; Kitamura et al., 2006), gibbons (*Hylobates* spp.; Whitington, 1990; Kitamura et al., 2002; Brodie et al., 2009) and bulbuls (*Pycnonotus* spp., *Hypsipetes* spp., and *Alophoixis* spp.; Kitamura et al., 2002; Khamcha, 2009) and the network interaction between several of them (McConkey & Brockelman, 2011; Savini & Kanwatanakid-Savini, 2011) have already been studied. Other frugivores may also disperse seeds—pigeons, squirrels, civets, bears, deer, and elephants among others—but important associates in the seed dispersal network could be northern pigtailed macaques, *Macaca leonina*.

In our study of pigtailed macaques at the KYNP, we observed a diet composed of fruits, leaves, animals, shoots, piths, flowers, and fungi (Albert et al., 2013). However, they prefer to eat fruits when available (Albert et al., 2013) such as some other macaque species (Hanya et al., 2003; Corlett, 2004). They consume 126 species, indehiscent and dehiscent fruits of every colour produced by all plant life forms (tall and small trees, lianas, shrubs, and herbs; Kitamura et al., 2002; Albert et al., 2013). Consequently, they can disperse almost as many plant species as hornbills and bulbuls, from very small (0.4 mm in length) to very large seeds (up to 57.7 mm in length; Albert et al., 2013). The studied pigtailed macaques spat out seeds up to 265 m (Albert et al., 2013), but this distance is still short compared to dispersal by gibbons and hornbills (Corlett, 2009).

Their high adaptability enables them to exploit every forest type, i.e. primary forests but also grasslands, shrublands, and secondary forests (Albert et al., 2013). This latter characteristic may be essential in forest succession as *M. leonina* appears to be an effective seed disperser for many plant species and can bring seeds from primary to secondary forests (Albert et al., 2013).

CONCLUSIONS

Several frugivore species known to be effective seed dispersers coexist with macaques. However, macaques could be equally able as seed dispersers. They eat fruits in quantity, which implies the potential dispersal of many seeds. Thus, they may defaecate as many, or even more, seeds than gibbons (McConkey & Brockelman, 2011), for example, which are considered to be very good seed dispersers in forests of the Indo-Malayan region. Macaques eat a high number of species, more than other frugivores, which may increase the dilution of seeds carried out during digestion. Indeed, if a greater number of species is consumed, a more restricted number of seeds of the same species is found in the same dung. Thus, clumping is less important and the dispersal of better quality. Like gibbons (McConkey, 2000), their gut seems to process seeds with care. They have cheek pouches, which enable them to store and transport seeds away from the parent tree before spitting out the seeds. They have large home ranges, larger than some other primate species considered to be good seed dispersers, such as gibbons (Savini, 2005). But, more than simply dispersing seeds, some *Macaca* species may play an important role in various succession stages during forest regeneration given they cross a range of forest types within the same day (primary and secondary forests), and even deforested areas, contrary to gibbons unable to use gaps or open habitats. They move fast on the ground, which increases dispersal distances. They eat fruits of plant species belonging to all plant life forms present in the forest. According to Kitamura et al. (2002), pigtailed macaques and bulbuls are the only seed dispersers consuming the fruits of arboreal shrubs in KYNP. However these shrubs play a central role at the beginning of succession because they enable the future establishment of sun-intolerant species, particularly with a supply of shade and moisture on the floor. Moreover, they belong to the rare large frugivores still present in the Indo-Malayan region, and are potentially able to disperse large seeds. However, many primary forest species are characterised by their large seeds. After enabling shrub establishment, macaques are part of the only frugivorous species able to bring seeds of primary forest trees. In the same way, macaques could be vital dispersers for some pioneer species remaining as mature plants in primary forests. Their seedlings might not survive in closed forests, and would need to be dispersed in open areas that few disperser species can cross.

In conclusion, we believe *Macaca* species are important associates in the seed dispersal assemblage found in forests of the Indo-Malayan region because they may disperse most plant species usually more efficiently dispersed by birds, bats, gibbons, or civets (Corlett, 1998; Kitamura et al., 2002; Kitamura et al., 2005), and, thus, provide a significant complement in terms of dispersal quantity. Moreover, within assemblages of dispersing frugivores, they are sometimes the only one able to disperse seeds of some species, mainly large-seeded or protected species (Corlett, 1998), and may thus bring them a vital dispersal service. Macaques could be the last, but not least element of a necessary seed dispersal network.

However, several studies have highlighted the threats faced by some macaque species (habitat loss or degradation, overhunting, etc.; Eudey, 2008) and their extinction could disrupt seed dispersal networks they are engaged in, such as it has already been shown for other disperser species (McConkey et al., 2012).

This kind of network between a primate and other frugivores is not unique to Asia as we can observe similar networks in Africa and South America. Indeed, African frugivore networks often include cercopithecine species (mainly *Cercopithecus* spp., but also *Papio* spp. and *Lophocebus* spp.), other primate species (mainly chimpanzees), hornbills, fruit pigeons, bulbuls, sturnids, and bats (Poulsen et al., 2002; Forget et al., 2007; Kirika et al., 2008; Lambert, 2010). In South America, cercopithecines are absent but other primate species (*Ateles* spp., *Alouatta* spp., and *Saguinus* spp.) take part of networks including also thrushes, toucans, deer, and bats (Howe, 1983; Russo, 2003; Nuñez-Iturri & Howe, 2007; Terborgh et al., 2008; Culot, 2009). These species seem to complement each other in seed dispersal service in the same way as in Asian frugivore networks.

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