

Macaques as Seed Dispersal Agents in Asian Forests: A Review

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Abstract The role of primates in seed dispersal is well recognized. Macaques (*Macaca* spp.) are major primate seed dispersers in Asia, and recent studies have revealed their role as seed dispersal agents in this region. Here, we review present knowledge of the traits that define the role of macaques as seed dispersers. The size of seeds in fruit influences whether macaques swallow (0.5–17.1 mm; median: 3.0), spit (1–37 mm; median: 7.6), or drop (8.2–57.7 mm; median: 20.5) them. Dispersal distances via defecation are several hundreds of meters (median: 259 m, range: 0–1300 m), shorter than those achieved by some mammals and birds in tropical and temperate regions. However, macaques disperse seeds by defecation at comparable distances to omnivorous carnivores, and further than passerines. Seed dispersal distance by spitting is much shorter (median: 20 m, range: 0–405 m) than by defecation. Among Asian primates, seed dispersal distances resulting from macaque defecation are shorter than those for gibbons and longer than those for langurs. The effects of seed ingestion on the percentage and speed of germination vary among both plant and macaque species. The degree of frugivory, fruit/seed handling methods, seed dispersal distance, microhabitats of dispersed seeds, and effects of dispersal on seed germination vary seasonally and interannually, and long-term studies of the ecological role of macaques are needed. Researchers have begun to assess the effectiveness of seed dispersal by macaques, secondary dispersal of seeds originally dispersed by macaques, and the effects of provisioning on seed dispersal. Future studies should also test the effects of social factors (such as age and rank), which have received little attention in studies of seed dispersal.

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Introduction

The role of animals in seed dispersal is well recognized. As many as 75% of tropical tree species produce fruits presumably adapted for animal dispersal (Howe and Smallwood 1982), and animals are estimated to move >95% of all seeds in tropical regions. Primates comprise between 25 and 40% of the frugivore biomass in tropical forests (Chapman and Russo 2007), eat large quantities of fruit, and defecate or spit out large numbers of viable seeds (Lambert 1999). Studies of primate seed dispersal have been conducted in Africa, South and Central America, and Asia since the 1980s, showing that primates remove fruit from trees and disperse seeds in forests (Andresen *et al.* 2018; Chapman and Russo 2007; McConkey 2018).

Macaques (genus *Macaca*) belong to the subfamily Cercopithecinae. They are a widely distributed primate genus, with 21 species belonging to three phyletic groups (*silenus-sylvanus*, *sinica-arctoides*, and *fascicularis* lineages) (Thierry 2007). Macaques are distributed throughout Asia, except for Barbary macaques (*M. sylvanus*), which inhabit north Africa (Table 1). Macaques have cheek pouches and multiple methods of fruit processing (Albert *et al.* 2013b). Three characteristics shared by most macaque species make them potentially important seed dispersers: 1) they are highly frugivorous (Richter *et al.* 2013; Tsuji *et al.* 2013); 2) they have longer daily path lengths and larger home ranges than other Asian primates, owing mainly to the need to frequent many feeding sites (MacKinnon and MacKinnon 1981); and 3) they are mostly semiterrestrial (Richter *et al.* 2013; Rodman 1978; Unger 1996). The *fascicularis* lineage also shows lower habitat specificity and a higher tolerance to environmental disturbance than other Asian primates (Albert *et al.* 2014; Richard *et al.* 1989). These characteristics contribute to the dispersal of seeds of various types of plant species across a diversity of habitats (Albert *et al.* 2013b).

The role of macaques as seed dispersal agents was poorly established until the 1990s (Corlett 2017); however, recent studies of seed dispersal by macaques have shown their importance as dispersers in both tropical and temperate regions and across a range of disturbance levels (Albert *et al.* 2013b; Corlett 2017). Macaques may act as dispersal agents of medium to large seeds, which may be particularly important in environments where other animals have been lost as a result of human activity, as demonstrated for guenons (*Cercopithecus* spp.) and baboons (*Papio* spp.) in Africa (Albert *et al.* 2014).

As one of the contributions to the special issue entitled “Advances and Frontiers in Primate Seed Dispersal” (Razafindratsima *et al.* 2018), we review macaque seed dispersal. First, we present the methods we used to compile data. Then, we provide an overview of macaque frugivory and seed dispersal, summarizing the characteristics that contribute to seed dispersal by macaques and comparing dispersal traits between macaques and sympatric frugivores. Next, we review spatial and temporal variation in macaque seed dispersal. Then, we review the conservation implications of macaque seed dispersal. Finally, we highlight future directions in macaque seed dispersal research.

Table 1 Characteristics of macaque species relevant to seed dispersal

Species ^a	Common name	Social style ^b	Female body mass (kg) ^a	Habitat type	Study length (months)	% fruit in diet	Number of fruit species used as foods	Number of species whose seeds are found in feces or spat out
<i>Silenus-sylvanus</i> lineage								
<i>Macaca brunnescens</i>	Muna-Butung macaque	4	?	?	n.a.	n.a.	n.a.	n.a.
<i>M. hecki</i>	Heck's macaque	4	?	Forest	n.a.	n.a.	n.a.	n.a.
<i>M. leonina</i>	Northern pig-tailed macaque	2	6.5	Forest	12 ^c	74.6 ^c	126 ^c	90 ^c
<i>M. maurus</i>	Moor macaque	4	6.1	Forest, grassland	n.a.	n.a.	n.a.	n.a.
<i>M. nemestrina</i>	Southern pig-tailed macaque	2	6.5	Forest	29 ^d	65.9 ^e	n.a.	n.a.
<i>M. nigra</i>	Crested macaque	4	5.5	Forest	18 ^e	56.9–66.0 ^e	> 145 ^m	n.a.
<i>M. nigrescens</i>	Gorontaro macaque	4	?	Forest	12 ^{o,f}	85.1 ^e	n.a.	n.a.
<i>M. ochreata</i>	Booted (Buton) macaque	4	?	Forest	n.a.	n.a.	n.a.	n.a.
<i>M. pagensis</i> (including <i>M. siberu</i>)	Mentawai macaque	?	?	Forest	12 ^g	75.7 ^e	n.a.	n.a.
<i>M. silenus</i>	Lion-tailed macaque	3	6.1	Forest	12 ^e	67.6–79.1 ^{c,k}	16–33 ^{i,n}	18 ⁿ
<i>M. sylvanus</i>	Barbary macaque	3	11.0	Forest, shrubland, rocky areas	16 ^h	0.8–4.3 ^a	41 ^o	n.a.
<i>M. tonkeana</i>	Tonkean macaque	4	9.0	Forest	15 ^c	78.1–85.8 ^e	33–59 ^p	n.a.
<i>Sinica-arctoides</i> lineage								
<i>M. arctoides</i>	Stump-tailed macaque	3	8.4	Forest	n.a.	n.a.	n.a.	n.a.
<i>M. assamensis</i>	Assamese macaque	3	6.9	Forest	12 ^e	17.4–42.4 ^e	33 ^q	n.a.
<i>M. munzala</i>	Arunachal macaque	?	?	Forest	7 ⁱ	10.3 ^e	11 ⁱ	n.a.
<i>M. radiata</i>	Bonnet macaque	3	3.9	Forest, savanna, shrubland	14 ^e	54.5 ^e	20–40 ^f	n.a.
<i>M. sinica</i>	Toque macaque	3	3.2	Forest	> 36 ^{o,f}	75–81 ^k	23–53 ^k	n.a.
<i>M. thibetana</i>	Tibetan macaque	3	12.8	Forest, caves	n.a.	n.a.	45 ^s	n.a.
<i>Fascicularis</i> lineage								
<i>M. cyclopis</i>	Taiwanese macaque	1	4.9	Forest	12–14 ^e	42.2–75.6 ^e	37 ^t	22 ^t
<i>M. fascicularis</i>	Long-tailed macaque	2	3.6	Forest, wetland	12–18 ^e	66.7–87.0 ^e	185 ^u	19–105 ^{u,x}
<i>M. fuscata</i>	Japanese macaque	1	8.0	Forest	12–16 ^e	15.0–53.7 ^e	1–98 ^v	12–35 ^y

Table I (continued)

Species ^a	Common name	Social style ^b	Female body mass (kg) ^a	Habitat type	Study length (months)	% fruit in diet	Number of fruit species used as foods	Number of species whose seeds are found in feces or spat out
<i>M. mulatta</i>	Rhesus macaque	1	8.8	Forest, savanna, shrubland	12–24 ^c	6.2–34.1 ¹	49 ^w	43 ^z

? = unknown; n.a. = not available

^a Based on Thierry (2007)

^b Ordered mainly based on conciliatory tendency and social tolerance, which increase from grade 1 (nepotistic) to grade 4 (egalitarian) (Thierry 2007)

^c Albert *et al.* (2013a)

^d Caldecott (1986)

^e Tsuji *et al.* (2013)

^f Duration of the study was not mentioned

^g Richter *et al.* (2013)

^h Ménard and Vallet (1996)

ⁱ Mendiratta *et al.* (2009) and Kumar *et al.* (2007)

^j Erinjeri *et al.* (2015)

^k Hladik and Hladik (1972) and Dittus (1977)

^l Huang *et al.* (2015)

^m O'Brien and Kinnaird (1997)

ⁿ Umpathy and Kumar (2000)

^o Mehlman (1988)

^p Pombo *et al.* (2004) and Riley (2007)

^q Zhou *et al.* (2011)

^r Krishnamani (1994) and Ali (1986)

Zhao *et al.* (1991), described as “reproductive parts”

^s Su and Lee (2001)

^t Corlett and Lucas (1990)

^v Tsuji (2011)

^w Sengupta and Radhakrishna (2016)

^x Tsuji *et al.* (2017)

^y Tsuji (2011)

^z Sengupta *et al.* (2014)

Literature Review and Data Analyses

We conducted a web-based survey of studies quantifying the composition of the diets of Asian macaques using the ISI Web of Science (<http://apps.webofknowledge.com/>) and Google Scholar (<http://scholar.google.co.jp/>), with the key words “seed dispersal*,” “macaque*,” and “*Macaca*.” We supplemented this information with our knowledge of the published literature.

We used Spearman’s rank correlation tests to examine relationships between dispersal characteristics (seed size [mm], percentage of feces with seeds, and dispersal distance [m]), and adult female body mass (kg). We also used Spearman’s rank correlation tests to compare the number of seeds of individual plant species in a single

fecal sample, number of seed species per feces, and dispersal distance and latitude (°). We used a Mann–Whitney U test to test for differences in seed size between spat and defecated seeds. We used the χ^2 test of independence to examine the effects of ingestion on the percentage of germination and germination speed. We set α at 0.05 for all analyses.

Macaque Frugivory and Seed Dispersal: An Overview

Macaque characteristics important in seed dispersal include 1) degree of frugivory, 2) seed handling methods, 3) amount of seeds handled, 4) dispersal distances, 5) microhabitats of the deposition sites of dispersed seeds, 6) germination of dispersed seeds, and 7) secondary dispersal by dung beetles. Here we introduce our knowledge of each characteristic.

Macaques feed on various types of natural foods, including leaves, flowers, buds, bark, insects, mushrooms, and human foods (garbage, agricultural products, and provisioned foods) (Thierry 2007; Tsuji *et al.* 2013). Among these, fruit represents $48 \pm 24\%$ (mean \pm SD) of the diet across macaque species (9 species across 19 study sites) (Tsuji *et al.* 2013). Macaques eat fruit with seeds of varying size. For example, long-tailed macaques (*Macaca fascicularis*) in Bukit Timah Nature Reserve, Singapore, feed on fruits containing seeds 1–38 mm in length (Corlett and Lucas 1990), while northern pig-tailed macaques (*M. leonina*) in Khao Yai National Park, Thailand, feed on fruits containing seeds 0.1–58 mm in length (Albert *et al.* 2013a; see also Kitamura *et al.* 2002). Thus, macaques disperse various kinds of plant seeds in forests when feeding.

Macaques disperse seeds from parent trees mainly via swallowing and spitting, but they also drop seeds (Lucas and Corlett 1998; Yumoto *et al.* 1998). The different treatments increase the chance that seeds are dispersed to favorable sites (Kitamura *et al.* 2002). Handling methods depend on the size, shape, and hardness of fruits and seeds (Albert *et al.* 2013a; Corlett and Lucas 1990; Lucas and Corlett 1998; Yumoto *et al.* 1998). The secondary compounds of fruits influence how New World monkeys handle them (Kinzey and Norconk 1993), but such effects have not been studied in macaques. If seeds are small (median: 3.0, range: 0.5–17.1 mm, Table II) and the seeds and pulp are tightly connected, macaques swallow and disperse seeds through defecation (dispersal by ingestion). The percentage of feces containing seeds varies but was $>80\%$ in 8 of 12 sites (Table II). There are no significant relationships between macaque body mass and seed size (Spearman's rank correlation: $N=11$, $r_s=0.324$, $P=0.331$) or the percentage of feces with seeds ($r_s=-0.204$, $P=0.548$), suggesting that dispersal characteristics are determined primarily by environmental factors rather than macaque body mass. Part of the seed is sometimes crunched during mastication, with the percentage of intact seeds defecated by captive Japanese macaques ranging 4.4–78.0% (Otani 2004; Tsuji *et al.* 2010). Seeds with larger surface areas might be crunched more than smaller seeds (Otani 2010; Tsuji *et al.* 2011).

Macaques spit out larger seeds than they swallow (mean size of spit seeds: 7.9 mm, range: 1.0–37.0 mm, defecated seeds: 3.4 mm, range: 0.5–17.1 mm, Mann–Whitney U test, $U=42.5$, $P=0.009$) (Table II). They spit out seeds when moving and sometimes while feeding under the crown of the parent tree. Spitting is associated with macaques'

Table II Characteristics of seeds a) defecated and b) spat out by macaques at various study sites

Macaque species	Study site	Latitude (°)	Number of species whose sizes are measured ^a	Seed size (mm)		Percentage of feces containing seeds (N)	Number of seeds per feces		Number of plant species per feces		Dispersal distance (m)		Reference
				Mean ± SD	Range		Mean ± SD	Range	Mean ± SD	25–75th percentile	Mean ± SD	Range	
a) Defecation													
<i>Silenus-sylvanus</i> lineage													
<i>Macaca leonina</i>	Khao Yai NP, Thailand	14.08	53	3.9 ± 3.3	0.5–13.6	89.0 (335)	2054	44, 2671 ^a	1.9 ± 1.4	0.9–2.6	–	–	Albert <i>et al.</i> (2013a)
<i>Fascicularis</i> lineage													
<i>M. cyclops</i>	Fushan, Taiwan	24.77	35	2.2 ± 1.2	0.8–4.5	–	292 ± 234	0–2130	2.6 ± 2.0	0–13	97 ± 92	0–430	Chen (1999); Huang (2005)
<i>M. cyclops</i>	Kenting, Taiwan	21.95	–	–	–	98.6 (545)	941 ± 675	0–5181	2.3 ± 0.5	0–5	259 ± 265	108–350	Liu <i>et al.</i> (2012); Hsu (2014)
<i>M. fascicularis</i>	Bukit Timar, Singapore	1.66	24	3.0 ± 3.0	1–10	–	–	–	–	–	–	–	Corlett and Lucas (1990)
<i>M. fascicularis</i>	Pangandaran, Indonesia	–7.75	19	3.0 ± 1.7	0.7–6.2	61.7 (240)	832 ± 2743	1–21,513	1.4 ± 0.8	1–5	–	–	Tsuji <i>et al.</i> (2017)
<i>M. fuscata</i>	Bonbori, Japan	36.00	20	4.2 ± 2.6	1.6–11.8	84.6 (62)	342 ± 405	1–1568	1.8 ± 0.9	–	–	–	Tsuji <i>et al.</i> (2011)
<i>M. fuscata</i>	Kashima, Japan	37.75	18	2.3 ± 1.1	1.2–4.1	92.5 (107)	–	–	2.4 ± 1.5	–	–	–	Otani (2003)
<i>M. fuscata</i>	Kinkazan, Japan	38.00	35	3.0 ± 2.0	0.8–10.8	57.7 (1294)	58 ± 176	1–2392	2.0 ± 0.9	1–8	420–486 ^c	0–1300	Tsuji <i>et al.</i> (2011); Tsuji and Morimoto (2016)
<i>M. fuscata</i>	Shimokita, Japan	41.35	12	2.7 ± 1.2	1.2–4.1	78.7 (75)	–	–	1.9 ± 0.8	–	–	–	Otani (2003)
<i>M. fuscata</i>	Shirakami, Japan	40.50	21	3.5 ± 1.9	1.2–7.0	86.0 (169)	106 ± 215, 54 ± 102 ^d	–	–	–	–	–	Eitani and Sakamaki (2014)
<i>M. fuscata</i>	Yakushima, Japan	30.33	34	2.5 ± 1.7	1.1–6.4	99.2 (132)	315 ± 274	–	2.8 ± 1.4	–	–	–	Otani and Shibata (2000)
<i>M. fuscata</i>	Yakushima, Japan	30.33	23	4.8 ± 2.7	0.9–9.9	–	–	–	–	–	–	–	Yumoto <i>et al.</i> (1998)
<i>M. fuscata</i>	Yakushima, Japan	30.33	–	–	–	80.5 (87)	8.7 ± 1.1 ^b	0–48	–	–	270	20.4–634.0	Terakawa <i>et al.</i> (2008)

Table II (continued)

Macaque species	Study site	Latitude (°)	Number of species whose sizes are measured ^a	Seed size (mm)		Percentage of feces containing seeds (N)	Number of seeds per feces		Number of plant species per feces		Dispersal distance (m)		Reference
				Mean ± SD	Range		Mean ± SD	Range	Mean ± SD	25–75th percentile	Mean ± SD	Range	
<i>M. milatta</i>	Buxa Tiger Reserve, India	25.00	15	–	–	87.1 (311)	318 ± 47	–	–	117 ± 79	29–774	Sengupta <i>et al.</i> (2014)	
<i>M. milatta</i>	Son Tra, Viet Nam	16.10	16	6.7 ± 4.4	0.9–17.1	58.2 (110)	61 ± 204	1–1232	1.3 ± 0.6	1–4	–	Tsuiji <i>et al.</i> (2013)	
b) Spat out													
Silenus-sylvanus lineage													
<i>M. leonina</i>	Khao Yai NP, Thailand	14.08	30	8.4 ± 3.8	3.7–19.3	n.a.	n.a.	n.a.	n.a.	n.a.	141–265	Albert <i>et al.</i> (2013a)	
Fascicularis lineage													
<i>M. cyclops</i>	Fushan, Taiwan	24.77	9	6.7 ± 2.2	4.1–11.1	n.a.	n.a.	n.a.	n.a.	n.a.	–	Chen (1999)	
<i>M. fascicularis</i>	Bukit Timar, Singapore	1.66	80	10.3 ± 6.3	1–37	n.a.	n.a.	n.a.	n.a.	n.a.	> 20 m	Corlett and Lucas (1990)	
<i>M. fasciata</i>	Yakushima, Japan	30.33	19	6.1 ± 2.1	2.7–9.9	n.a.	n.a.	n.a.	n.a.	n.a.	0–139	Yumoto <i>et al.</i> (1998)	
<i>M. fasciata</i>	Yakushima, Japan	30.33	–	–	–	n.a.	n.a.	n.a.	n.a.	n.a.	0–405	Tsujino and Yumoto (2009)	
<i>M. milatta</i>	Buxa Tiger Reserve, India	25.00	30	–	–	n.a.	n.a.	n.a.	n.a.	n.a.	19 ± 8	5–69 Sengupta <i>et al.</i> (2014)	

n.a. = not available

^a We excluded dry fruits from analysis^b Standard error^c Median of two plant species^d Obtained from data collected in spring (N = 81 feces) and summer (N = 89), respectively^e Obtained from four species

large cheek pouches (Murray 1975). For instance, when intragroup competition over fruits is severe, macaques put fruit in their cheek pouches (Yumoto *et al.* 1998) and spit the seeds out when they process the fruits. There is no significant relationship between the size of spat seeds and macaque body mass ($N = 4$, $r_s = -0.800$, $P = 0.333$), suggesting that the degree of seed spitting is probably determined by environmental and fruit characteristics rather than macaque body mass.

Macaques drop large seeds after feeding on the pulp (e.g., *Macaca leonina* in Khao Yai NP, Thailand: median: 23.0, range: 8.2–57.7 mm in length, Albert *et al.* 2013a). Northern pig-tailed macaques (*M. leonina*) drop or spit out 51% of the large seeds of *Garcinia benthamii* they handle under the parent crowns and drop a further 41% within 30 m (McConkey *et al.* 2015). Seeds dropped beneath the trees are predicted to have lower survival rates than seeds dropped in open areas (McConkey *et al.* 2015) because they are subject to poor sunlight exposure and nutrition, along with exposure to pathogens (Augspurger 1984). Such seeds generally fail to germinate or show lower growth rates (Gross-Camp *et al.* 2009). Thus, seed dropping by macaques does not appear to increase the fitness of plant species.

In Asia, community-wide studies of frugivory began in the 2000s and have shown that macaques remove more fruits from food trees than sympatric birds do. For instance, in Buxa Tiger Reserve, India, rhesus macaques (*Macaca mulatta*) remove ca. 62 fruits of *Artocarpus chaplasha* from the canopy per day, which is nine times more than the bird species in this region remove (Sekar and Sukumar 2015). Taiwanese macaques (*M. cyclopis*) consume two to five times more Lauraceae fruits than sympatric birds and small-sized mammals (such as squirrels and flying squirrels) (Lin 2000). In coastal forests in Yakushima, southern Japan, Japanese macaques (*M. fuscata*) consume greater amounts of fruit of *Ficus superba* than sympatric bird species (Hamada and Hanya 2016; Otani 2001; cf. Hanya 2005).

In contrast to birds, large animals remove more fruits than macaques. In the Deramakot Forest Reserve, Malaysia, Bornean orangutans (*Pongo pygmaeus*) are the major seed consumers of wild durians (*Durio graveolens* and *D. zibethinus*), whereas long-tailed macaques (*Macaca fascicularis*) handle this fruit less frequently (Nakashima *et al.* 2008). In Khao Yai National Park, Thailand, northern pig-tailed macaques (*M. leonina*) consume up to 25% of fruits of *Garcinia benthamii* produced, which is a much smaller amount than that consumed by sympatric gibbons (up to 87%) (McConkey *et al.* 2015). Thus, the amount of seeds removed by macaques is intermediate among other forest community members.

Several studies have assessed the distances to which macaques disperse seeds, both via spitting out (five studies) and via defecation (five studies) (Table II). The median dispersal distance of spat seeds was 20 m (range: 0–405 m) and showed no relationship with the body mass of macaques ($N = 5$, $r_s = -1.000$, $P = 0.333$) (Table II). Macaques spit out some seeds at distances comparable to those for other animals (such as flying foxes and rodents; Corlett 2009; Nakamoto *et al.* 2009; Reiter *et al.* 2006), although they spit out many seeds under or close to parent trees (Fig. 1a).

Dispersal distances via defecation are estimated by combining the gut passage time (33–60 h, Chang *et al.* 2016; Liu *et al.* 2012; Tsuji *et al.* 2010) and the animals' ranging pattern (e.g., Tsuji and Morimoto 2016), by measuring the distances between defecation sites and the closest conspecific tree (e.g., Sengupta *et al.* 2014) or by comparing the genotypes of seedlings to putative parents (Terakawa *et al.* 2008). The latter is likely to

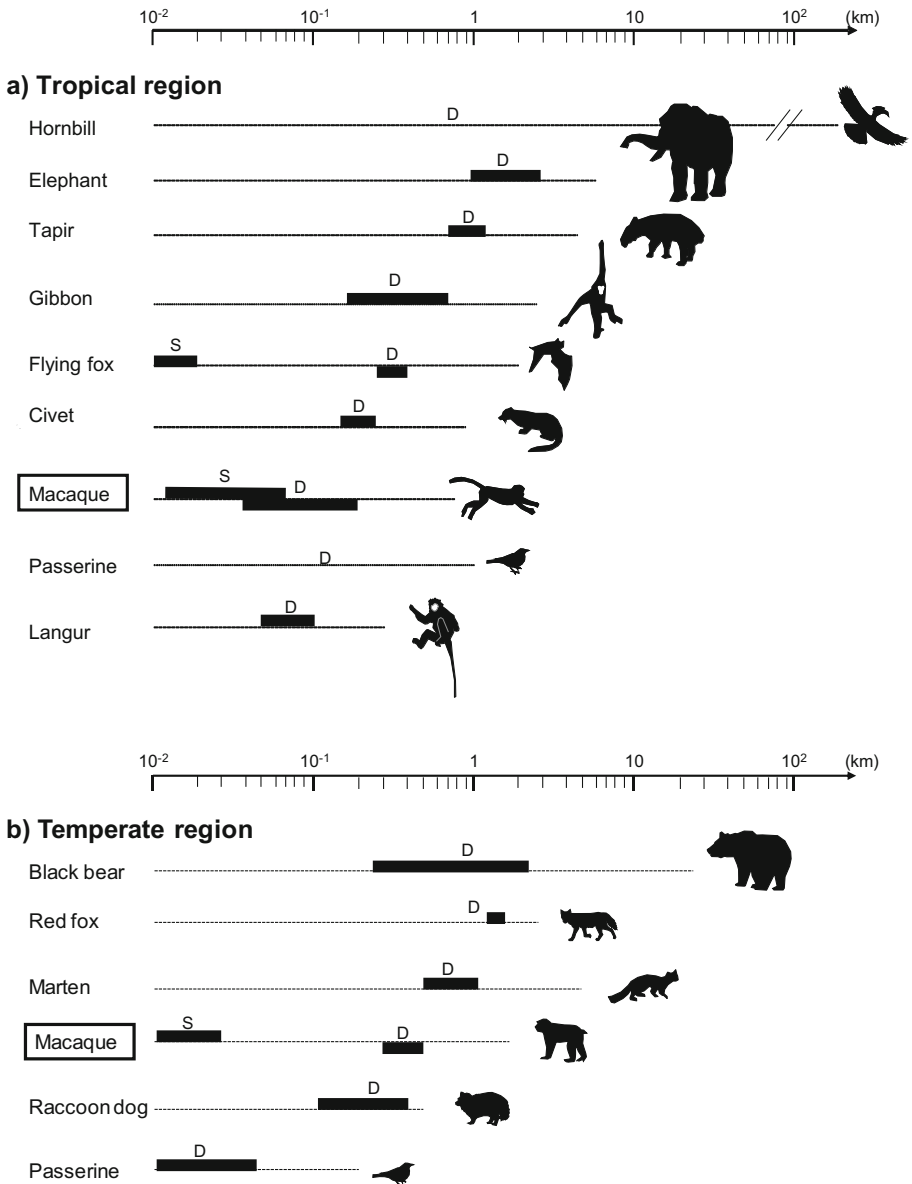


Fig. 1 Interspecific variation in seed dispersal distances (km, with a logarithmic scale) of forest-dwelling animals in Asia. Thin lines represent the whole range; thick lines represent the range of the most frequent dispersal distances of target animal species (shown in source article). S and D represent dispersal distance via spitting out and defecation, respectively. Sources: Kitamura (2011) (hornbill); Campos-Arceiz *et al.* (2008), and Sekar *et al.* (2015) (elephant); Campos-Arceiz *et al.* (2012) (tapir); McConkey and Chivers (2007) (gibbon); Nakamoto *et al.* (2009) (flying fox); Nakashima and Sukor (2010) (civet); Sengupta *et al.* (2014) and Tsuji and Morimoto (2016) (macaque); Corlett (2009) and Fukui (1995, 1996) (passerine); Tsuji *et al.* (2017) (langur); Koike *et al.* (2011) (black bear); González-Varo *et al.* (2013) (red fox); Tsuji *et al.* (2016) (marten); Sakamoto and Takatsuki (2015) (raccoon dog).

be the most accurate approach. The median seed dispersal distance via defecation was 259 m (range: 0–1300 m, different methods combined) and is not significantly related to body mass ($N = 5$, $r_s = 0.264$, $P = 0.668$) (Table II). Variation in gut passage time across macaque species is not likely to affect dispersal distances, because macaques usually stay in the core area of their home range (Go 2010; O'Brien and Kinnaird 1997; Santhosh *et al.* 2015; Tsuji and Takatsuki 2004). Instead, seed dispersal distances are probably related to home range size, which, in turn, is probably affected by group size and the availability of food resources (Mehlman 1989; Takasaki 1981).

The recent accumulation of studies of animal seed dispersal enables us to make interspecific comparisons. Seed dispersal distances via macaque defecation are shorter than those of Asian elephants (*Elephas maximus*: Campos-Arceiz *et al.* 2008; Sekar *et al.* 2015), Malayan tapirs (*Tapirus indicus*: Campos-Arceiz *et al.* 2012), hornbills and flying foxes (by defecation) (Corlett 2009; Kitamura 2011; Nakamoto *et al.* 2009) in tropical regions (Fig. 1a), and shorter than those of Asiatic black bears (*Ursus thibetanus*: Koike *et al.* 2011), martens (*Martes* spp.: González-Varo *et al.* 2013; Tsuji *et al.* 2016), and red foxes (*Vulpes vulpes*: González-Varo *et al.* 2013) in temperate regions (Fig. 1b). In tropical regions, seed dispersal distances via spitting and defecation overlap, but this is not the case in temperate regions (Fig. 1). Seed dispersal distances via macaque defecation are comparable to those of civets (*Paradoxurus hermaphroditus*: Nakashima and Sukor 2010), raccoon dogs (*Nyctereutes procyonoides*: Sakamoto and Takatsuki 2015), and small- and medium-sized forest passerines (Corlett 2009). Among Asian primates, seed dispersal distances via macaque defecation are shorter than those of gibbons (McConkey and Chivers 2007) and longer than those of langurs (Tsuji *et al.* 2017).

The environmental conditions of sites where seeds are deposited affect the germination and growth of seedlings because of differences in soil nutrition, vegetation, sunlight, and moisture (Dalling 2005). Japanese macaques (*Macaca fuscata*), for example, spit out seeds of *Myrica rubra* on a hill that is the preferred habitat of this tree species (Tsuji and Yumoto 2009). This may be an example of “directional dispersal,” in which dispersal agents take seeds to nonrandom places that are well suited for establishment and growth (Howe and Smallwood 1982). In comparison, southern pig-tailed macaques (*M. nemestrina*) spit seeds out at random, resulting in lower germination success and survival rates of seeds when compared with seeds dispersed by sympatric civets (Nakashima *et al.* 2010). This observation suggests that the degree of directed dispersal by macaques is site or species specific.

Birds, flying foxes, and gibbons defecate from the tree canopy, scattering seeds out of the feces and onto the ground (Phua and Corlett 1989; Whitten 1982). In comparison, because of their mostly semiterrestrial nature (e.g., Richter *et al.* 2013), macaques frequently defecate on the ground (Albert *et al.* 2013a; Nishikawa and Mochida 2010; Tsuji *et al.* 2011), resulting in seeds remaining within the feces (Otani 2010). This difference implies that seeds dispersed by macaques are clumped, increasing their vulnerability to pathogens and predation by granivores (Andresen 2002; Howe 1989; Nishikawa and Mochida 2010).

When fruit passes through the gut, the pulp is removed. Pulp inhibits most seeds from germinating, so this removal enhances germination and/or increases the speed of germination and growth (Traveset 1998; Yagihashi *et al.* 1998). Chewing and gastric acids scarify the seeds and curtail dormancy when seeds pass through an animal's gut

(Campos-Arceiz and Blake 2011; Fuzessy *et al.* 2016; Yagihashi *et al.* 1998). The effects of ingestion on seeds vary among plant species, even when they are swallowed by the same macaque species (Table III).

Seeds in feces can be secondarily dispersed by other animals, especially dung beetles (Andresen 2005). Seed removal and burial by dung beetles might increase plant fitness by preventing seed predation (Andresen 2002; Estrada and Coates-Estrada 1991). In the cool temperate region of Japan, 14 dung beetle species (8 dwellers and 6 tunnelers) use macaque feces (Enari *et al.* 2011, 2013). Future studies should examine to what extent seeds defecated by macaques are secondarily dispersed by dung beetles and to what extent these postdispersal events influence the effectiveness of seed dispersal. Furthermore, it is important to determine how the characteristics of feces and seeds influence secondary dispersal processes and, consequently, seed fate.

Spatiotemporal Variation in Seed Dispersal Characteristics

Seed dispersal characteristics of macaques may vary spatially, across habitats, and temporally, across seasons and years. This means that we should be cautious in generalizing findings obtained from a single study site, season, or year.

The degree of frugivory varies in macaques, being lower at higher latitudes (Tsuji *et al.* 2013). Fruit production is also lower at high latitudes (Moles *et al.* 2009), fruit size is smaller at higher latitudes (Moles *et al.* 2007), and the percentage of fruits that are fleshy (lower at higher latitudes) (Herrera 2002; Otani 2005; Willson *et al.* 1989) varies regionally. We examined whether these differences are reflected in regional variation in macaque seed dispersal characteristics. At lower latitudes, the number of seeds per feces is significantly greater than that at higher latitudes (Spearman's rank correlation test, $r_s = -0.783$, $P = 0.017$) (Fig. 2c). However, we found no significant relationship between the size of spat seeds and latitude ($r_s = -1.000$, $P = 0.083$) (Fig. 2b), and no significant correlations with other characteristics (percentage of feces with seeds: $r_s = -0.091$, $P = 0.797$ [Fig. 2a], size of defecated seeds: $r_s = -0.155$, $P = 0.649$ [Fig. 2b], seed species per fecal deposition: $r_s = 0.347$, $P = 0.327$ [Fig. 2d], dispersal distance of defecated seeds: $r_s = 0.700$, $P = 0.233$ [Fig. 2e], and dispersed distance of spat seeds: $r_s = -0.500$, $P = 1.000$ [Fig. 2e]). This implies that regional variation in forest productivity and fruit size do not affect the majority of seed dispersal characteristics.

Frugivory in macaques can change seasonally and is closely associated with fruit availability. For instance, the degree of fruit eating increases when fruit availability is high (Hanya 2004; Lucas and Corlett 1991). In Japan, the degree of frugivory (except for figs) in Japanese macaques (*Macaca fuscata*) declines in winter (Hamada and Hanya 2016; Otani 2003; Tsuji *et al.* 2011) when fruit availability is lower (Tsuji *et al.* 2015) and the relative importance of birds as seed dispersers increases (Hamada and Hanya 2016; Noma and Yumoto 1997). In comparison, in tropical regions, some types of fruits are available year-round, and the importance of macaques as seed dispersers is stable (Albert *et al.* 2013a; Lucas and Corlett 1998; Tsuji *et al.* 2017).

Studies of other animals have shown that long-term temporal changes in the environment affect seed dispersal characteristics. For example, guenons (*Cercopithecus* spp.) and Bornean orangutans (*Pongo pygmaeus*) are frugivorous but eat seeds in fruit-

Table III A summary of the effects of macaque ingestion on the percentage of seeds that germinate and germination speed

Species	Study site	% Germination			Germination speed			Reference	
		Positive	Negative	Neutral	Positive	Negative	Neutral		
<i>Silenus-sylvanus</i> lineage									
<i>Macaca leonina</i>	Khao Yai, Thailand	0	7	12	$\chi^2 = 8.1, df=2, P=0.017^*$	3	6	10	$\chi^2 = 2.0, df=2, P=0.364$ Albert <i>et al.</i> (2013a)
<i>Fascicularis</i> lineage									
<i>M. cyclopis</i>	Fushang, Taiwan	2	5	3	$\chi^2 = 0.7, df=2, P=0.710$	1	3	2	$\chi^2 = 0.5, df=2, P=0.766$ Cheng (2002)
<i>M. fascicularis</i>	Pangandaran, Indonesia	0	1	0	-	1	0	0	Tsuji <i>et al.</i> (2017)
<i>M. fuscata</i>	Yakushima, Japan	3	0	1	$\chi^2 = 2.0, df=2, P=0.364$	-	-	-	Yumoto <i>et al.</i> (1998)
<i>M. fuscata</i>	Yakushima, Japan	8	2	2	$\chi^2 = 2.7, df=2, P=0.264$	3	3	3	$\chi^2 = 1.0, df=2, P=1.000$ Otani and Shibata (2000)
<i>M. mulatta</i>	Buxa Tiger Reserve, India	5	1	13	$\chi^2 = 6.3, df=2, P=0.042^*$	8	0	8	$\chi^2 = 6.4, df=2, P=0.041^*$ Sengupta <i>et al.</i> (2014)

Figures represent the numbers of plant species whose percentages of germination (or germination speed) are higher than (positive), lower than (negative), or the same as (neutral) those of control seeds

* $P < 0.05$

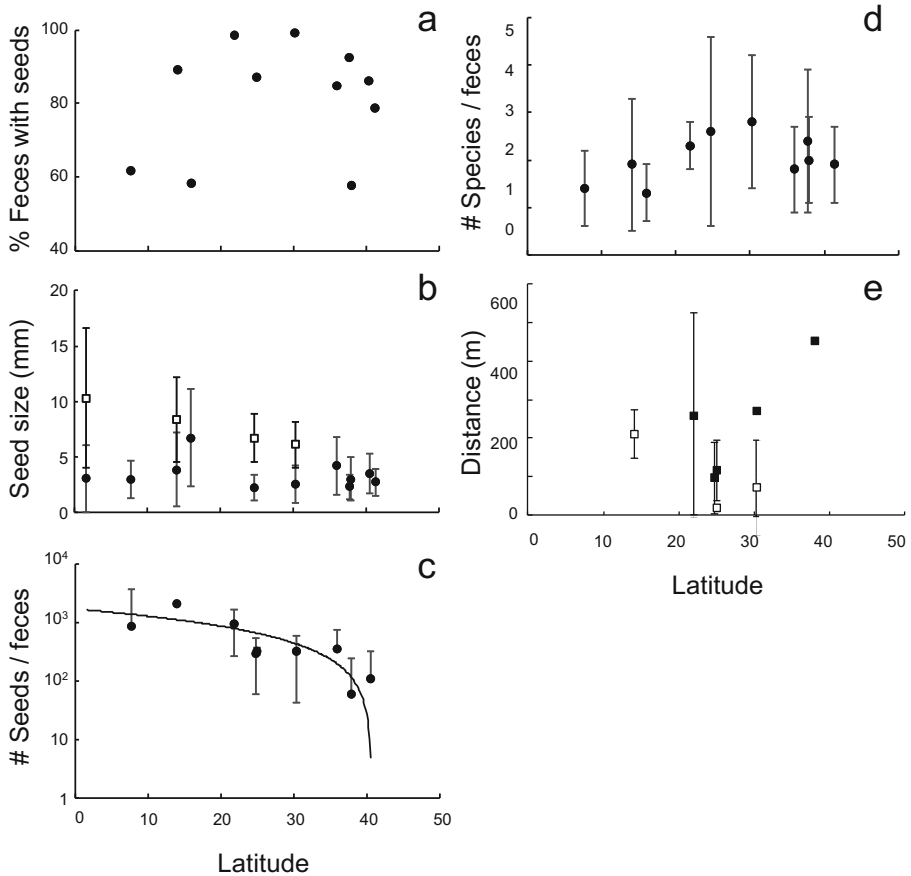


Fig. 2 Relationship between latitude (°) (absolute value) and **(a)** percentage of feces with seeds, **(b)** seed size (mean \pm SD), **(c)** number of seeds per single feces (mean \pm SD, logarithmic scale), **(d)** number of seed species per single feces (mean \pm SD), and **(e)** dispersal distance (mean \pm SD) in macaques. Filled circles represent dispersal via defecation, open squares dispersal via spitting.

scarce years (Kaplan and Moermond 1998; Leighton 1993). Information on this topic with respect to macaques is limited. Japanese macaques did not disperse seeds at different distances across a 2-year period (Tsuji and Morimoto 2016). However, the percentage of feces with seeds, seed diversity, and the percentage of intact seeds in feces changed across a 5-year study (Tsuji 2014). Interannual variation in seed dispersal characteristics depends on the amount of fruits, the combination of available fruits, and the availability of nonfruit items (Leighton 1993; Tsuji 2014). Therefore, conclusions about the role of macaques as dispersal agents based on single-year studies should be treated with caution.

Conservation Implications of Seed Dispersal by Macaques

At present, most macaque species are abundant, and they are rarely subjects of conservation concern. In fact, macaques are persecuted as pests at many sites (Albert

et al. 2014; Saraswat *et al.* 2015). Recent studies have shown that macaques are likely to maintain the distribution and demography of plants and aid the recovery and regeneration of vegetation (Terakawa *et al.* 2009). Other studies have shown negative effects of provisioning on macaque seed dispersal (José-Domínguez *et al.* 2015; Sengupta *et al.* 2015).

We can determine the importance of macaques as seed dispersal agents by comparing the plant characteristics in forests where primates are extant and locally extinct. For example, fruit removal by birds was similar on two neighboring islands in Japan, one of which is inhabited by macaques (Yakushima) and the other where macaques are absent from forests but were the sole mammalian dispersers on the island before becoming extinct as a result of hunting and forest destruction (Tanegashima). This suggests that birds cannot compensate for the absence of macaques in seed dispersal (Terakawa *et al.* 2009). The absence of macaques can also affect community structure. For example, the biomass and diversity of dung beetles was much lower in a forest without Japanese macaques compared to a forest with macaques (Enari *et al.* 2013). This suggests that regional differences in dung beetle diversity might be caused by the extinction of macaques in the last century (Enari *et al.* 2013). The effects of macaques on forest vegetation are only expected to become clear over a scale of several hundred to several thousand years, owing to an extinction debt, in which long-lived plants reproduce at much longer scales than the animals dispersing them, and animals become extinct long before the contribution of the adult population becomes apparent (Kuussaari *et al.* 2009).

Intentional and nonintentional provisioning and dependence on agricultural products affect macaque ranging, feeding habits, and population parameters (Ilham *et al.* 2017; Koganezawa and Imaki 1999; Sha and Hanya 2013). Provisioned macaques bite people and are more likely to forage on crops, resulting in their becoming pests (Priston and McLennan 2013). Provisioning may affect seed dispersal characteristics, such as frequency of dispersal event and dispersal distance. For instance, in India, provisioned rhesus macaques (*Macaca mulatta*) feed less on fruit, which, in turn, reduces the percentage of feces with seeds and the frequency of spitting out seeds. The home range size of provisioned animals also decreases, leading to shorter seed dispersal distances (Sengupta *et al.* 2015). Furthermore, the frequency of defecation on roads, which are not suitable for germination, increases with provisioning, reducing dispersal effectiveness (Sengupta *et al.* 2015). In Khao Yai National Park, Thailand, the home range size of provisioned northern pig-tailed macaques (*M. leonina*) is smaller than that of nonprovisioned macaques, leading to reduced seed dispersal distances (José-Domínguez *et al.* 2015).

To date, little attention has been paid to macaque conservation. Future studies should place stronger emphasis on quantifying how extinction of macaques would affect forest structure and how provisioning affects seed dispersal characteristics through effects of macaque behavior.

Future Challenges

Information on the seed dispersal characteristics of macaques has accumulated over the past two decades. It is now time to shift our interest to more advanced research

questions. In this section, we suggest two challenges for the study of macaque seed dispersal: the evaluation of macaque seed dispersal effectiveness (SDE) and the evaluation of individual variation on seed dispersal characteristics.

Evaluation of SDE

Most studies of seed dispersal by macaques have described seed diversity and predispersal behavior (degree of frugivory, fruit handling, and ranging). To address how macaques contribute to seed dispersal within the frugivore–plant network, we need information on the extent of frugivory, the amount of fruit removed per feeding bout, the degree of seed destruction, and the effects of gut passage on germination and growth. Such information allows us to calculate SDE (Schupp 1993; Schupp *et al.* 2010) and compare it with that of other sympatric animals (Albert *et al.* 2013a). If two sympatric animals have similar SDEs, one species could replace the role of the other species. Systematic studies of macaque SDE have been conducted in Khao Yai NP, Thailand. In the case of the woody plant *Prunus javanica*, the quality of dispersal (measured as the survival rate of seedlings) by northern pig-tailed macaques was lower than that of other frugivores (gibbons, hornbills, and birds). However, macaques dispersed more seeds so they had the highest SDE (McConkey and Brockelman 2011). These results suggest that other animals could not replace the role of macaques if they disappeared. However, in the case of a liana species, *Salacia chinensis*, macaque and gibbon SDEs are comparable, although the two genera exhibit different foraging and movement behaviors (McConkey *et al.* 2014). Finally, in case of the large fruited *Garcinia benthamii*, the SDEs of macaques and squirrels were much lower than those of gibbons (and perhaps elephants) (McConkey *et al.* 2015). At other study sites, information on seed dispersal characteristics has been collected with respect to the seed dispersal capacity of carnivores (Kitamura 2011; Koike *et al.* 2011; Nakashima *et al.* 2010), flying foxes (Nakamoto *et al.* 2009; Reiter *et al.* 2006), and mega herbivores (Campos-Arceiz *et al.* 2008, 2012; Sekar *et al.* 2015) over the last 10 years (Corlett 2017; Tsuji *et al.* 2016). Future studies should evaluate macaque SDE at these sites, to evaluate the relative contribution of macaques as seed dispersal agents in Asian forest ecosystems.

Effects of Individual Differences on the Characteristics of Dispersed Seeds

The feeding behavior of macaques varies within a group, for example with age, sex, and social rank (Thierry 2007). Seed dispersal studies have rarely considered the effects of such interindividual variation, and seed dispersal characteristics of animals are typically averaged. Future studies should focus on understanding how interindividual variation affects the dispersal characteristics of seeds. For example, when intragroup competition over food is stronger (e.g., in certain seasons or years), subordinate animals might leave feeding sites immediately (Tsuji and Takatsuki 2012; van Noordwijk and van Schaik 1987), enhancing the degree of cheek pouch dispersal. In comparison, the intact rate of seeds defecated by dominant individuals might decline, because they remain at feeding sites for longer, and chew the seeds inside the fruits. Life history traits might also affect seed dispersal. For example, lemurs usually disperse seeds up to ca. 100 m, but long-distance dispersal (>500 m) might also occur, when animals transfer to

other groups or new environments (Razafindratsima *et al.* 2013). Male macaques also immigrate into other groups, stay alone, and/or form all-male groups (Sprague *et al.* 1998; van Noordwijk and van Schaik 1985). Females sometimes establish subgroups (Sugiura *et al.* 2011) or emigrate (Tsuji and Sugiyama 2014), and this might also affect seed dispersal distances and germination.

The structuring of macaque societies ranges from “nepotistic” (*fascicularis* lineage) to “egalitarian” (*silenus-sylvanus* lineage) (Thierry 2007). This reflects the intensity of intragroup competition, which may also lead to interindividual variation in activity including frugivory. Interindividual variation in frugivory and seed dispersal characteristics may not exist in egalitarian macaque groups, owing to infrequent competition over fruits. Future studies should explore how variation in macaque social systems affects seed dispersal. To do so, we need information on frugivory and seed dispersal characteristics of egalitarian macaques, for which little information is available (Table 1).

Knowledge of the role of macaques in seed dispersal has expanded over the last 20 years, but our understanding of the ecological role of macaques in natural ecosystems and of the effects of individual or interspecific variation on seed dispersal is still insufficient. By tackling these two challenges, we will be able to evaluate the macaque’s ecological role more precisely. The issue of individual variation may be generalizable to other animals and would provide a new perspective to the study of animal ecology.

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