A KEY ROLE OF THE SOUTHERN PIG-TAILED MACAQUE *Macaca nemestrina* (Linnaeus) IN SEED DISPERSAL OF NON-CLIMBING RATTANS IN PENINSULAR MALAYSIA

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ABSTRACT

Primates play an important role in the seed dispersal of a multitude of plant species, including rattans (Calamoideae). Here, camera-trapping was used as a means of identifying mammal rattan fruit predators of two non-climbing rattan species, *Calamus castaneus* Griff. and *Daemonorops calicarpa* (Griff.) Mart., at a lowland dipterocarp forest of West Malaysia. Of a total of 25 resident frugivorous and mainly terrestrial mammal species at the study site, only Southern Pig-tailed Macaques *Macaca nemestrina* (Linnaeus) were found responsible for rattan fruit removal at ground level. Video recordings allowed the analysis of fruit handling behaviour, of which the most frequent was firstly peeling of skin and sucking of pulp, and subsequently ingesting the pulp and seeds (38.3% of N=148). Cheek pouch feeding (34.0%) and ingestion of the whole fruit (27.7%) also occurred frequently. These behaviours might not lead to the destruction of the seed and indicate seed dispersal rather than predation. As both rattan species have a low tendency to form clonal clusters, they might very much rely on animal seed dispersers for successful reproduction. This has implications for conservation efforts, as there seems to be no redundancy in seed dispersers for local acaulescent rattans, and a decline in *M. nemestrina* abundance might therefore severely affect rattan genetic diversity and population dynamics. Thus, *Macaca nemestrina* might be considered a single-species seed disperser for these two rattan species at the study site.

Keywords: acaulescent rattans, Calamoideae, *Calamus castaneus*, *Daemonorops calicarpa*, seed dispersal, seed predation, Segari Melintang Forest Reserve, Perak.

INTRODUCTION

Ninety percent of primates found in tropical regions are dependent on the forest (Mittermeier & Cheney, 1987) where they have significant effects on seed dispersal of up to 75% of plant species (Howe & Smallwood, 1982; Terborgh et al., 2002; Beckmann & Muller-Landau, 2007; Dirzo et al., 2007; Levey et al., 2002; Nuñez-Iturri & Howe, 2007; Stoner et al., 2007; Wang et al., 2007; Wright et al., 2007; Stevenson et al., 2008). Primates comprise around 40% of the frugivore biomass in tropical forests (Eisenberg & Thorington, 1973; Chapman, 1995) where they consume large quantities of fruits and defecate or spit high numbers of diverse seeds (Lambert, 1999). Moreover, they can add positive effects on seed germination, which are caused by the passage of seeds through their digestive system (Samuels & Levey, 2005; Robertson et al., 2006; González-Di Pierro et al., 2011). Seed swallowing is by far the most common means of primate seed dispersal in the Neotropics. In the Palaeotropics seed spitting by cheek-pouched monkeys (Cercopithecinae) is more common. Cheek pouches, which have nearly the same capacity as the stomach, allow monkeys to extract pulp without having to invest in digesting swallowed seeds (Lambert, 1999).

The plant-primate interaction determines the variation in seed shadows, which influences plant demography and spatial distribution. Primate seed-handling strategies depend on factors, such as the interactions between their digestive system and traits of the fruiting species, and there is a wide variation in the shape of seed shadows generated by primates (Chapman & Russo, 2007). In addition, the response of a primate to a fruiting species is mediated by many factors, such as its social structure, foraging decision, digestive anatomy, seed-handling strategy, or ranging behaviour, whereas the distribution and abundance of fruit resources influences daily foraging speeds and distances (Chapman & Russo, 2007).

There is a high variability among primate species, and according to Chapman & Russo (2007) there is no such thing as one "primate seed syndrome" for fruiting plant species. It seems that primates tend to ingest and disperse more smaller than larger seeds (Corlett & Lucas, 1990; Lambert, 1999), and more ovoid than round seeds (Garber, 1986; McConkey, 2000); and some, but not all primates, might be rather selective, for example orangutans preferred high pulp mass (Leighton, 1993), whereas Long-tailed Macaques *Macaca fascicularis* (Raffles) did not select on the basis of seed or fruit size (Corlett & Lucas, 1990). Ingested seeds may become dispersed over longer distances than spat seeds (Lambert, 1999, 2001), and spat or dropped seeds are more likely to be deposited on the forest floor singly because fruits are handled individually (Lambert, 1999).

Countries with primate populations are losing approximately 125,000 km^2 of forest each year (Chapman & Peres, 2001) and habitat fragmentation and hunting are further reducing primate populations. The reduction in primate abundance may have severe impacts on plant communities (Redford, 1992; Chapman, 1995) as it was shown that hunted primate populations in a fragmented habitat produce altered seed dispersal patterns (Pacheco & Simonetti, 2000; Wright et al., 2000; Chapman, Chapman et al., 2003; Chapman, Lawes et al., 2003; Cordeiro & Howe, 2003). Most importantly, there is simply not enough redundancy in fruit disperser species to compensate for losses of one group, such as primates (Poulsen et al., 2002). Thus, with the loss of primate species in fragmented areas, seed dispersal rates may decrease and seed shadows may become more stereotyped, which can eventually lead to changes in plant population densities and reduction of diversity of plant communities (Chapman & Russo, 2007).

Primates are considered to be, besides hornbills, the main dispersers of rattan seeds (Calamoideae, Arecaceae) in both Southeast Asia and Africa (Corlett & Lucas, 1990; Dransfield, 2001; Sunderland, 2001). Rattans are an important component of the primary and secondary forest vegetation of Malaysia and play an important role in the rainforest ecosystem: they can act as shelter, for example for ants (Sunderland, 2004); or as food source, such as for various insect groups that feed on their pollen (Henderson, 1986; Lee, 1995; Kidyoo & McKey, 2010); and mammals or birds that feed on fruits, seeds, or fresh shoots (Sunderland & Dransfield, 2002). In Peninsular Malaysia alone, 106 species of eight genera grow in the wild (Dransfield, 1979) and of the approximately 600 rattan species that can be found worldwide, 117 are now regarded as threatened to some degree (Walter & Gillet, 1998). The threats are manifold but habitat loss due to land conversion and overexploitation of rattans for the furniture industry must be considered the most hazardous ones. Rattans use two reproductive strategies: some rattan species have a high tendency to form big clusters with multiple clonal stems, whereas other species appear solitarily or in small clusters. These are widely represented by genetically different, seed-derived individuals (Dransfield & Sunderland, 2002).

There are two commonly observed strategies of rattan fruit handling by primates: either fruits are ingested as a whole and pass through the intestinal tract with the seed intact, or the pulp is sucked and the seed spat out (Corlett & Lucas, 1990; Pritchard & Davies, 1999). However, only a few studies address the role of primates in rattan seed dispersal (e.g. Corlett & Lucas, 1990; Tutin et al., 1994; Lucas & Corlett, 1998; Sunderland, 2001) and none of these were conducted in Peninsular Malaysia. Primates are the most important dispersers of larger-seeded plant species (Howe & Smallwood, 1982; Chapman & Chapman, 1995; Chapman & Russo, 2007) and most rattan species that were found at the study site have medium- to larger-sized seeds (c. 1 cm diameter).

However, in studies on African primates where gorillas, chimpanzees, bonobos, drills and mandrills were found to use rattan fruits as a food source (Tutin et al.,1994; Sunderland, 2001), their feeding habit seemed to lead to the destruction of the seeds. These larger primate species often chew before they swallow their food and this might inhibit the germination ability of the seed (Kingdon, 1997). Feeding experiments with African rattan seeds presented to those primate species showed that only fruits of the genus *Laccosperma*, which has small seeds (1 cm x 0.6 cm), were swallowed as a whole and thus stood the chance of being dispersed intact. Bigger seeds (diameter >1.5 cm) of the genera *Eremospatha* and *Oncocalamus* were either chewed and destroyed or spat out at the site (Sunderland, 2001).

Also in Southeast Asia, primates have been found to contribute to rattan seed dispersal (Dransfield, 2001). In Singapore, Long-tailed Macaques have been observed to feed on seeds of the genera *Calamus*, *Daemonorops* and *Korthalsia* in the wild. They were found to spit out or clean and drop the majority (up to 69%) of seeds of the ripe fruits they consume. This alternative "seed spitting behaviour" might be regarded as a means of dispersing viable seeds (Corlett & Lucas, 1990; Lucas & Corlett, 1998). Despite these efforts to better understand the role of primates in rattan seed dispersal, there is still a major lack of fundamental studies dealing with rattan seed dispersal mechanisms in general and the specific interactions of primate and rattan species of Peninsular Malaysia. This study was thus aimed at identifying mammal species that play a key role in seed dispersal of local non-climbing rattan species.This was conducted by means of camera trap surveillance of fruiting rattans during a two-year survey. Both primate species and small mammals were expected to predate on ripe rattan fruits. Seed handling strategies were analysed to assess the impact on seed survival.

METHODS

Study Site

The study site was located at the Western edge of the Segari Melintang Forest Reserve (SMFR), Manjung District, Perak, Peninsular Malaysia (4°19-20’N, 100°34-36’E) (Fig. 1). The SMFR originally comprised 4,566 ha (in the 1960s) but in 2010 only about 2,720 ha remained. 408 ha of the SMFR are strictly protected as a Virgin Jungle Reserve (VJR). The rest is a logged-over, regenerated Permanent Forest Reserve (PFR). Vegetation within the SMFR consists of coastal lowland mixed dipterocarp forest and areas with alluvial freshwater swamp forest, which are temporarily flooded. To the exclusion of a few emergents, the maximum height of the closed canopy is about 40 m and the SMFR extends from 20 m to 250 m above sea level (Wiens & Zitzmann, 2003).

Camera trap survey

In order to identify rattan fruit consumers, ripe infructescences of *Calamus castaneus* Griff. and *Daemonorops calicarpa* (Griff.) Mart. were video monitored with motion-triggered infrared cameras specially designed for wildlife monitoring (Bushnell® Trophy Cam™). Altogether 15 individuals of *C. castaneus* were video monitored over a total time span of 13 months, and five fruiting individuals of *D. calicarpa* over three months. Videos triggered by approaching animals were recorded for 15 seconds with a 2-second interval allowing identification of fruit handling behaviour. Visitors were identified to species level by the authors, who at this same time also ran a long-term mark-and-recapture study for small mammals in the area, and were thus very familiar with the local small mammal species that are sometimes difficult to identify (Ruppert et al., 2012). The number and duration of visits of all animals were recorded. Video monitoring of rattan infructescences was performed continuously from July 2010 until December 2010 and again during several other fruiting events until the end of 2013. Camera trap locations comprised an area of around 1.5 km^2.

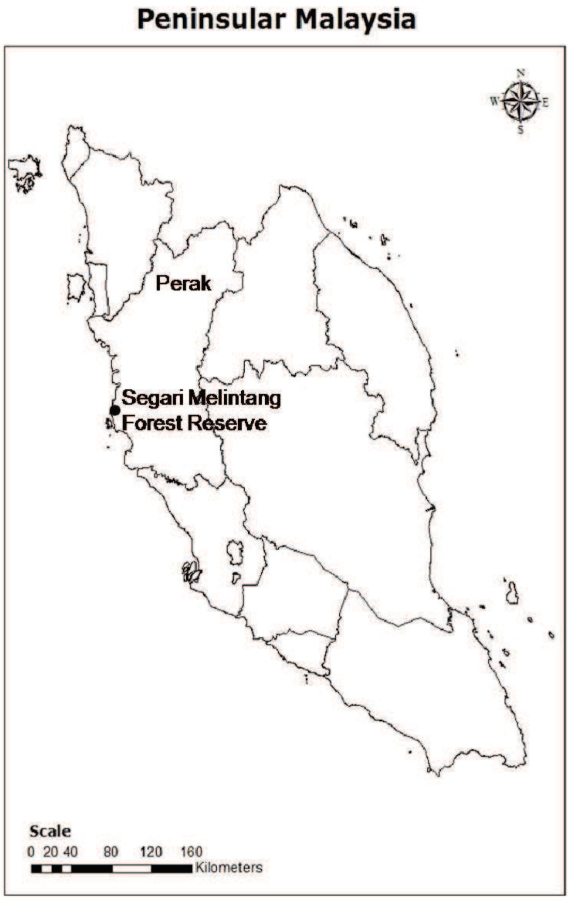

Fig. 1. Location of the Segari Melintang Forest Reserve, Manjung District, Perak, Peninsular Malaysia.

Fruiting events of rattans

Calamus castaneus produced fruits non-seasonally throughout the year and one individual would exhibit different fruiting stages (ripe, unripe, budding, flowering) all at the same time (Fig. 2C). *Daemonorops calicarpa* on the other hand is a hapaxanthic species, meaning that individuals only flower and fruit once in their lifetime and die subsequently (Fig. 2A) (Dransfield, 1979). Thus, recorded fruiting events of *D. calicarpa* at the study site occurred far more seldom than those of *C. castaneus*. Both species have fruits and seeds that are similar in size (seed: 1 cm x 1 cm) (Fig. 2B).

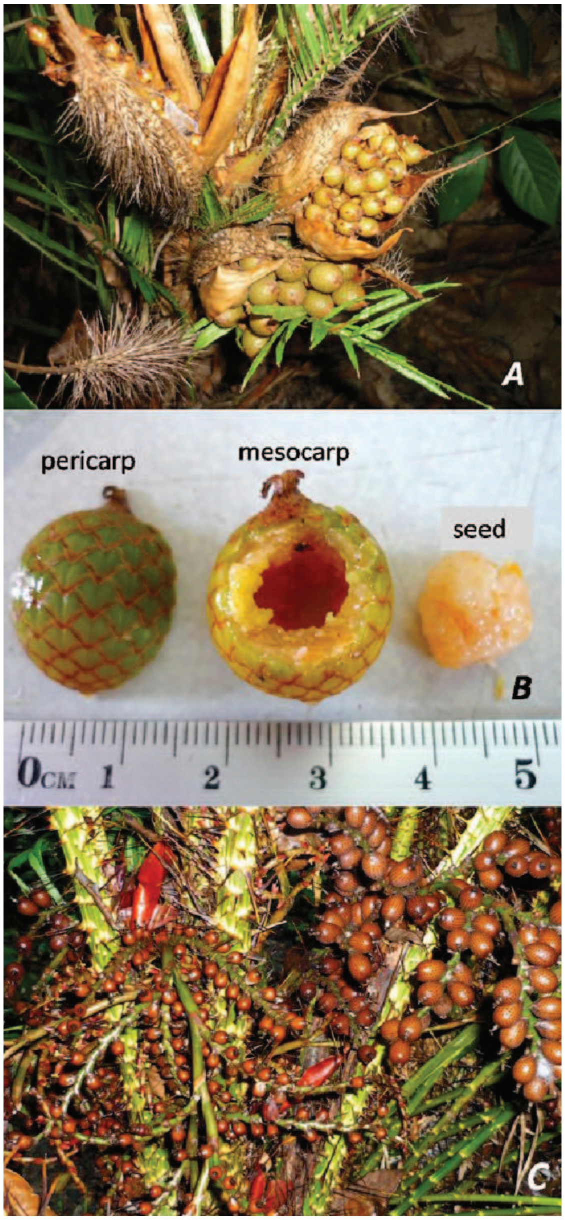

Fig. 2. (A) Infructescence of *Daemonorops calicarpa* (Griff.) Mart. (B) Fruit of *D. calicarpa* with pericarp, mesocarp and seed. (C) Infructescence of *Calamus castaneus* Griff. with different development stages (ripe, unripe, budding, flowering).

RESULTS

Frugivorous mammals at the study site

A total of 25 frugivorous diurnal and nocturnal mammal species (Table 1) were identified at the study site during the study period, either by camera trapping or live trapping (Ruppert et al., 2012). More species are probably present but escaped detection, for example several species of Sciuridae and Muridae that inhabit higher forest strata, or were missed due to low abundance.

Rattan fruit monitoring

During the video surveillance of ripe rattan infructescences a total of 485.1 minutes video footage was triggered by forest-dwelling animals moving by the infrared-sensor of the cameras. The majority of species in these recordings showed no interest in the rattan fruits, and individuals of some species (e.g. *M. fascicularis*, *Tupaia glis* [Diard], *Callosciurus notatus* [Boddaert]) would examine the fruits but subsequently not take any.

In all recorded footage, no other species but *M. nemestrina* was found responsible for any single recorded rattan fruit removal event. The species was recorded handling fruits for a total of 39.3 minutes, which corresponds to 8.1% of the overall recording time (Fig. 3).

Fruit handling strategies

During different recording events, a total of 41 different *M. nemestrina* individuals (including adult males and females, as well as subadults and juveniles) were found foraging on rattan fruits. Together they picked 148 different fruits. The most common fruit handling behaviour was: (1) peeling or opening the pericarp with teeth to get access to the mesocarp, and subsequently (2) sucking the pulp and ingesting the seed (38.3%). Cheek pouch feeding (34.0%) and ingestion of the whole fruit (27.7%) also occurred frequently. In only 2.1% of the recordings, picked fruits were discarded or seeds were spat out at site (Table 2). Juveniles not distinguishable by sex (34.4%) and adult males (29.3%) were most frequently recorded on rattans (Table 2), however adults males and females picked the most fruits (38.5% and 30.4%, respectively) (Fig. 4). During several examinations of the forest floor under fruiting rattans, opened fruits were found where the pulp and seeds had been removed and possibly ingested by primates (Fig. 5). No seeds were found at the site.

DISCUSSION

This study highlighted the importance of *M. nemestrina* for rattan seed dispersal in forests of the Malay Peninsula. Here, the fruits of two abundant, non-climbing (or acaulescent) rattans with low clustering ability (Dransfield, 1979), *C. castaneus* (here: 6.1 stems ha^{-1}) and *D. calicarpa* (here: 3.1 stems ha^{-1}), were found to be consumed solely by one primate species at the study site. Despite the presence of four other primate species and over 16 terrestrial obligate-frugivorous small mammal species, *M. nemestrina* alone was found responsible

Table 1. List of frugivorous mammal species observed at the study site during the study period.

ENGLISH NAME	SCIENTIFIC NAME
Muridae	
Sundaic Lenothrix	*Lenothrix canus* Miller, 1903
Chestnut White-bellied Rat	*Niviventer fulvescens* (Gray, 1847)
Red Spiny Red	*Maxomys surifer* (Miller, 1900)
Whitehead's Spiny Rat	*Maxomys whiteheadi* (Thomas, 1894)
Rajah Spiny Rat	*Maxomys rajah* (Thomas, 1894)
Polynesian Rat	*Rattus exulans* (Peale, 1848)
Malaysian Field Rat	*Rattus tiomanicus* (Miller, 1900)
Annandale's Rat	*Rattus annandale* Bonhote, 1903
House Rat	*Rattus rattus* (Linnaeus, 1758)
Long-tailed Giant Rat	*Leopoldamys sabanus* (Thomas, 1887)
Sciuridae	
Plantain Squirrel	*Callosciurus notatus* (Boddaert, 1785)
Prevost's Squirrel	*Callosciurus prevostii* (Desmarest, 1822)
Pale Giant Squirrel	*Ratufa affinis* (Raffles, 1821)
Black Giant Squirrel	*Ratufa bicolor* (Sparrman, 1778)
Shrew-faced Ground Squirrel	*Rhinosciurus laticaudatus* (Müller, 1840)
Low's Squirrel	*Sundasciurus lowii* (Thomas, 1892)
Tupaiidae	
Pen-tailed Treeshrew	*Ptilocercus lowii* Gray, 1848
Common Treeshrew	*Tupaia glis* (Diard, 1820)
Tragulidae	
Lesser Mousedeer	*Tragulus kanchil* (Raffles 1821)
Viverridae	
Common Palm Civet	*Paradoxurus hermaphroditus* (Pallas, 1777)
Lorisidae	
Sunda Slow Loris	*Nycticebus coucang* (Boddaert, 1785)
Cercopithecidae	
Dusky Langur	*Trachypithecus obscurus* (Reid, 1837)
Long-tailed Macaque	*Macaca fascicularis* (Raffles, 1821)
Southern Pig-tailed Macaque	*Macaca nemestrina* (Linnaeus, 1766)
Hylobatidae	
Agile Gibbon	*Hylobates agilis* F. Cuvier, 1821

Fig. 3. Juvenile *Macaca nemestrina* (Linnaeus) picking and ingesting fruits of *Calamus castaneus* Griff. (<1m above ground; still images taken from video of camera trap).

Table 2. Rattan fruit handling behaviour of different *Macaca nemestrina* (Linnaeus) individuals (N=41).

Behavior **# ID of the individual[1]**	**Pick fruit & discard**	**Peel pericarp**	**Suck pulp & ingest**	**Spit seed**	**Ingest as whole**	**Put in cheek pouch**	**n**
SA♂	-	1, 2, 16, 21	1, 2, 16	-	16, 40	21	4
SA♀	-	-	-	-	-	-	0
A♀	37[2]	4, 13, 25, 34, 35, 37	4, 25, 34, 35, 37	-	4, 5	13, 25, 30, 34	7
A♂	-	11, 14, 18, 28, 29, 36	11, 14, 18, 28, 29, 36, 38	28	11, 14, 18	3, 7, 9, 11, 12, 22	12
Juv♀/♂	-	19, 26, 27, 31, 32, 36	19, 26, 27, 31, 32, 36	-	6, 33, 36, 39, 41	10, 20, 23, 24	14
Unidentified	-	17, 20	17, 20	-	8, 15	17	4
Frequency of behaviour	1	24	23	1	13	16	

[1] ID numbers refer to numerical order of recorded individuals on camera trap.

[2] #37 picked whole infructescence and discarded some fruits and ingested others.

for rattan fruit removal and ingestion. Similar findings might be expected in forests of Peninsular Malaysia with similar mammal species composition. It should be pointed out that the study site lacks any bigger herbivorous mammal species, like tapirs or elephants. Effects of macaques on seed dispersal might thus vary in forests where competition for fruits is higher (also in regard to the presence of orangutans in Borneo or Sumatra).

According to the IUCN Red List *Macaca nemestrina* is classified as Vulnerable (Richardson et al., 2008) and its possible role as the single species seed disperser for acaulescent rattan species may have far-reaching consequences for conservation efforts, also from the plant perspective. It might be argued that, whilst having a low clustering ability, the high output of fruits, especially in *C. castaneus* (see Fig. 2C), and the high abundance *C. castaneus* point towards an effective seed dispersal strategy, likely facilitated by *M. nemestrina* at the study site.

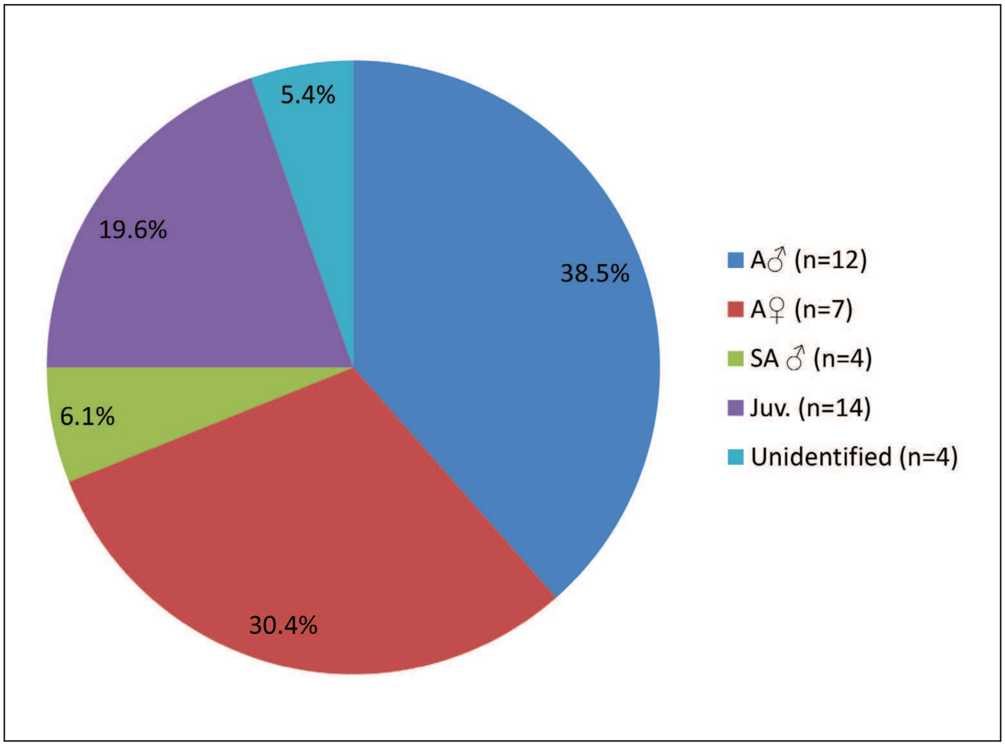

Fig. 4. Total number of rattan fruits (N=148) ingested by *Macaca nemestrina* (Linnaeus) according to age and sex.

There might be several reasons why other primate or small mammal species at the study site did not engage in rattan fruit removal. For the more arboreal primate species (*Hylobates agilis* F. Cuvier, *Trachypithecus obscurus* Reid and *M. fascicularis*) low-growing rattans of the understorey vegetation might simply be growing outside their preferred niche. However, there were several recordings showing *M. fascicularis* and *T. obscurus* sitting next to fruiting rattans on the ground. One video showed the attempt of one *M. fascicularis* individual to reach for some rattan fruits, but it was chased away by an adult male *M. nemestrina* already present at the site. This does point towards competition for ground resources between these two species, where *M. nemestrina* seems to dominate this habitat type (Caldecott, 1986). On the other hand, peaceful interactions between groups of both species, resulting in mixed-species foraging cohorts, even leading to playful interactions between subadult members of both species, could be frequently observed (N. Ruppert, pers. obs.).

So there might also be other reasons unknown to the authors for why *M. fascicularis* could not be recorded feeding on rattan fruits at the study site. Slow lorises *Nycticebus coucang* (Boddaert), which are nocturnal and thus inhabit another ecological niche, could be expected to feed on ripe fruits (Wiens & Zitzmann, 2003). They were frequently recorded on videos monitoring Dull Bertam Palm (*Eugeissona tristis* Griff.) flowers at the study site (F. Wiens, in litt.) but not a single individual was caught on camera near rattans, for reasons unknown. Also nocturnal and diurnal rodents could not be associated with rattan fruit removal, which might be due to the seed size that is presumably too big to be handled by small mammal species (P.-M. Forget, pers. comm.). In general, not many studies on *M. nemestrina* have been conducted in the wild (e.g. Caldecott, 1986; Oi, 1990). These primates live in multi-male multi-female groups with a group number of up to 80 individuals (Caldecott, 1986). Usually higher ranking males gain prior access to food sources. Groups often split up during daily foraging tours, and adult males might wander solitarily over longer daily distances than females and juveniles (Caldecott, 1987). Here, it was shown that adult males contributed most to rattan fruit removal, and might thus also carry seeds over longer distances than females, who do not leave their group. Adults, in contrast to subadults, were responsible for the majority of 69% of rattan fruit removal.

Fig. 5. Examples of discarded rattan fruits (here *Calamus castaneus* Griff.) on the forest floor around fruiting rattan clumps. Pictures show the opened pericarp with pulp and seeds removed. No seeds were found on site.

Preliminary data on a habituated group of *M. nemestrina* at the study site indicates that the group travels between 1.5 km and 3.5 km (average 1,880 m) per day, with a mean travelling speed of 420 m h-1 during the active period" However, gut passage time between the sexes and age may differ, which complicates the prediction of dispersal distances, but there hardly exists any literature for this on wild macaques (e.g. Corlett, 2009 mentioned seed dispersal distances by macaques ranging between 10 m to 100 m). A study on captive *Macaca fuscata* (Blyth) indicated a mean retention time of larger seeds of 37-54 hours (Tsuji et al., 2010) with 4.4% of ingested seeds passing through the GI tract intact (Otani, 2004). Wild *Macaca leonina* (Blyth) ingested the seeds of at least 15 fruit species in Khao Yai, Thailand where some seeds were dispersed and others predated (Latinne et al., 2008). There, a variety of fruits were dispersed by over 25 different animal species, including macaques, but no close relationship between a particular fruit plant and a frugivore was found (Kitamura et al., 2002).

In order to study the impact of *M. nemestrina* on seed dispersal, more studies including experiments on gut passage time, daily foraging distances and effects of gut passage on seed germination correlated to gender and age must be conducted in the future. These preliminary results point towards a role of *M. nemestrina* as seed disperser rather than predator for acaulescent rattans. The fact that only *M. nemestrina* was found to consume rattan seeds does put extra weight on the need of acting towards protection of these primates. As there seems to be no redundancy in seed dispersal agents for non-climbing rattans, a decline in *M. nemestrina* abundance might directly influence rattan population dynamics and lead to an erosion of their genetic diversity.

ACKNOWLEDGEMENTS

This study was part of NR's PhD-project on the population dynamics of rattans, which was financed by USM Postgraduate Grant 1001/PBIOLOGI/843098, University Research Grant 1001/PBIOLOGI/811131 and Ministry of Higher Education Fundamental Research Grant 203/PBIOLOGI/6711223. The authors acknowledge the Perak Forestry Department for issuing respective permits. NR would like to thank Antje Engelhardt and another anonymous reviewer for valuable comments on the manuscript.

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