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Citation for final published version:

Thiry, Valentine, Bhasin, Oriana, Stark, Danica J., Beudels-Jamar, Roseline C., Vercauteren Drubbel, Régine, Nathan, Senthilvel K. S. S., Goossens, Benoit and Vercauteren, Martine 2019. Seed dispersal by proboscis monkeys: the case of *Nauclea* spp. *Primates* 60 (5) , pp. 449-457. 10.1007/s10329-019-00736-x

Publishers page: <http://dx.doi.org/10.1007/s10329-019-00736-x>

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Title: Seed dispersal by proboscis monkeys: the case of *Nauclea* spp.

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ABSTRACT

Frugivorous vertebrates, such as primates, are important dispersal agents in tropical forests, although the role of folivorous colobines is generally not considered. However, recent studies reported seed dispersal by endo- and epizoochory in colobine primates, including the proboscis monkey (*Nasalis larvatus*), suggesting the role colobines play in seed dispersal might have been underestimated. In the Lower Kinabatangan Floodplain, in Sabah, Malaysian Borneo, we investigated whether seeds were still able to germinate after being ingested by proboscis monkeys. Faecal samples (n = 201) from proboscis monkeys were collected between 2015 and 2017. Intact seeds belonging to eight plant species were found in 77% of the faecal samples. *Nauclea* spp. was the most abundant plant species, accounting for 98% of all intact seeds. This study is the first to conduct germination trials on seeds defecated by proboscis monkeys. Higher germination success was recorded in ingested *Nauclea* spp. seeds than in control seeds, from both ripe and unripe *Nauclea orientalis* fruits ($P < 0.001$). Therefore, we suggest that proboscis monkeys play a role in seed dispersal, by enhancing the germination success of defecated seeds, for at least some plant species. Similar to other colobines, although proboscis monkeys may provide a lower contribution to seed dispersal (low seed diversity over short distances) than other sympatric frugivores, this study emphasises that proboscis monkeys do contribute to the dispersal of intact seeds, such as *Nauclea* spp., in potentially suitable riverine habitats.

Keywords: *Nauclea* spp., *Nasalis larvatus*, proboscis monkey, seed dispersal, seed germination

ACKNOWLEDGEMENTS

We are grateful to the Sabah Biodiversity Centre and the Sabah Wildlife Department for supporting our research project and allowing us to conduct this study in the Lower Kinabatangan Wildlife Sanctuary. This project would not have been possible without financial support from the FNRS (Fonds de la Recherche Scientifique), the FNRS Gustave Boël-Sofina Fellowship and the Fonds Léopold III – pour l’Exploration et la Conservation de la Nature asbl. We thank Quentin Phillipps for his precious contribution, as well as all the students and research assistants at Danau Girang Field Centre who worked with us in the field. Finally, we thank the two anonymous reviewers for their valuable comments that improved the manuscript.

INTRODUCTION

Many plant species across the globe rely on animals to disperse their seeds (Farwig and Berens 2012). In tropical forests, up to 98% of plant species bear fruits and require vertebrates, such as birds or mammals, for the dispersal of their seeds (Howe and Smallwood 1982; Terborgh et al. 2002). Largely because they represent a considerable proportion of the frugivore biomass in tropical forests, primates have long been considered as seed dispersers (Chapman 1995). When consuming fruits, primates can handle the seeds differently: feeding on the pulp and dropping or spitting out seeds; swallowing and defecating intact seeds (endozoochory); or chewing and destroying seeds (Corlett and Lucas 1990). Recent studies highlighted the important role many primate species play in seed dispersal (Razafindratsima et al. 2018), mostly by swallowing or dropping the seeds (Albert et al. 2013). However, some primate taxa, such as Asian and African colobines, were generally not included and were considered more as seed predators (Norconk et al. 1998), destroying most of the seeds they

consumed (Garber and Lambert 1998; Norconk et al. 1998). However, primate seed predators can be involved in seed dispersal by swallowing small seeds intact without masticating them, by removing pericarp and seed-coat before discarding seeds (Norconk et al. 1998; Barnett et al. 2012), or by seeds attaching to the animal's fur and dropping off in a different location (epizoochory) (Chen et al. 2018). Indeed, the dichotomy seed predator versus seed disperser has been oversimplified (Norconk et al. 1998) and many primates play a number of roles, depending on the plant consumed (McConkey 2018).

In colobines, seed dispersal has been recorded in five species, via endozoochory (*Nasalis larvatus* (Matsuda et al. 2013), *Trachypithecus francoisi hatinhensis* (Nguyen et al. 2013), *T. auratus* (Tsuji et al. 2017) and *Presbytis* sp. (McConkey unpubl. in McConkey 2018)) and via epizoochory (*Rhinopithecus roxellana* (Chen et al. 2018)). Even though seed germination trials were not conducted (Matsuda et al. 2013; Nguyen et al. 2013; Chen et al. 2018) or dispersed seeds showed low germination success (Tsuji et al. 2017), authors suggested that the role colobines play in seed dispersal might have been underestimated. In regard to the wide distribution and biomass of Asian and African colobines, colobine primates might play a considerable role in seed dispersal of some plant species (Matsuda et al. 2013; Corlett 2017; Tsuji et al. 2017).

Proboscis monkey (*Nasalis larvatus*) is an endangered colobine primate endemic to the island of Borneo, where the species inhabits riverine, swamp and mangrove forests (Meijaard et al. 2008). In riverine forest, proboscis monkey home range averages 81 ha (Stark et al. 2017) and the mean daily distance travelled is 940 m (Stark 2018). Proboscis monkeys highly use areas close to rivers, select sleeping sites along water and avoid sleeping at the same location on consecutive nights (Stark 2018). Similar to other colobines, proboscis monkeys have a large sacculated forestomach wherein food fermentation occurs (Nijboer

and Clauss 2006), and therefore, they usually avoid feeding on ripe fleshy fruits which are rich in sugar susceptible to ferment in gas, and therefore, can be deleterious for their digestive system (Waterman and Kool 1994). Proboscis monkeys mostly consume young leaves, unripe fruits and seeds (Matsuda et al. 2009) and display long gut retention times (mean retention times (MRTs) of 40 hours (Matsuda et al. 2015)).

The role of proboscis monkeys as seed dispersers has previously been suggested, based on the presence of intact seeds in 11% of monkey analysed faeces (Matsuda et al. 2013). However, until now, no known germination tests have been conducted to determine how the ingestion of seeds by proboscis monkeys would affect seed germination. We focused on seed dispersal by endozoochory and aimed to investigate whether seeds were still able to germinate after being ingested by proboscis monkeys. We predicted that (1) small intact seeds would be found in proboscis monkey faeces, as reported by Matsuda et al. (2013) and because small seeds might be less damaged by mastication and pass intact through the animal gut (Corlett and Lucas 1990; Norconk et al. 1998), and (2) due to their feeding habits (preferring unripe fruits over ripe fruits), the seeds defecated by proboscis monkeys would experience lower germination rates than control seeds (collected directly from fruits), such as reported in the colobine Javan lutung (*T. auratus*) (Tsuji et al. 2017).

METHODS

Study site

This study took place over 14 months between May to August 2015, January to May 2016, and November 2016 to March 2017, in Lots 5, 6, and 7 of the Lower Kinabatangan Wildlife Sanctuary (LKWS, 5°10'-05°50'N, 117°40'-118°30'E), Sabah, Malaysian Borneo (Fig. 1). The major forest types in the LKWS include dry lowland forests, semi-inundated and

permanent swamps, and mangrove forests (Abram et al. 2014). Forest vegetation is dominated by *Dillenia excelsa*, *Mallotus muticus*, *Colona serratifolia*, *Antidesma puncticulatum* and *Vitex pinnata* tree species. The five most abundant vine species are *Lophopyxis maingayi*, *Entada rheedii*, *Bridelia stipularis*, *Dalbergia stipulacea* and *Croton triqueter* (6.25 ha botanic plot survey, Thiry unpubl.). Daily temperatures and rainfall were measured at the research station. During the study, mean monthly rainfall was 177 (\pm SD = 121) mm. Mean minimum and maximum temperatures were 24.5 (\pm SD = 0.7) and 30.4 (\pm SD = 1.8)°C, respectively.

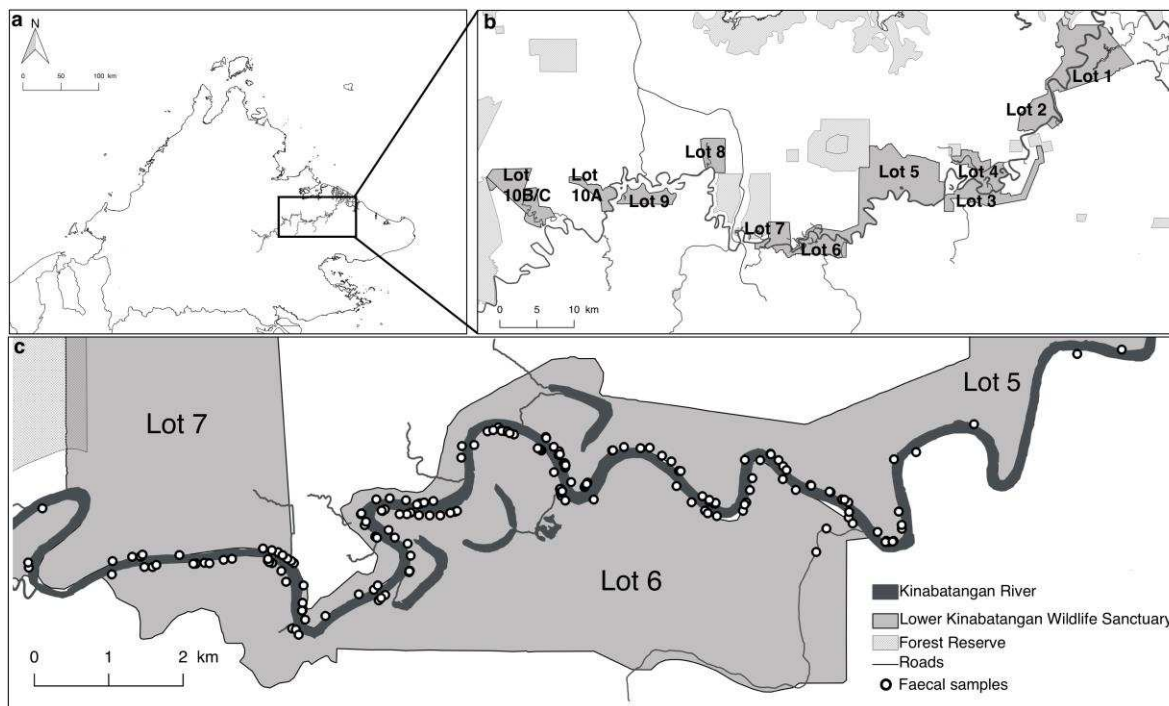


Fig. 1 Maps of the study area: **a** the State of Sabah in Malaysian Borneo with the location of the Kinabatangan River; **b** the Lower Kinabatangan Wildlife Sanctuary, with its 10 protected forest lots (dark grey) and the Forest Reserve (light grey); **c** zoom on the study site in lots 5, 6 and 7, with faecal sampling locations

Faecal sampling

In riverine habitats, proboscis monkeys generally spend their nights in trees along riverbanks (Matsuda et al. 2011). We conducted boat-based surveys in the late afternoon to look for proboscis monkeys along the Kinabatangan River. To avoid sampling the same group multiple times within the same month, we searched for proboscis monkey groups along different sections of a pre-established 21 km river transect in a month. We selected the first proboscis monkey group that we found and conducted behavioural observations until dark (instantaneous scan and ad libitum sampling). The following morning, we returned to the same trees where the group was located the previous evening and continued our observations on the same group. This allowed us to ascertain that no other diurnal primate species (long-tailed and pig-tailed macaques (*Macaca fascicularis* and *M. nemestrina*); silvered, maroon and Hose's langurs (*Trachypithecus cristatus*, *Presbytis rubicunda* and *P. hosei*); Bornean gibbons (*Hylobates muelleri*) and Bornean orangutans (*Pongo pygmaeus*)) spent the night in or neighbouring (within 10 m) proboscis monkeys' sleeping trees. In the morning, once the proboscis monkeys had left the riverside, we approached the bank to search for fresh faecal samples under the sleeping trees. Although some faeces might have fallen in the water when a sleeping tree canopy was overhanging the river, we were still able to find faecal samples most (if not all) mornings. Proboscis monkey faeces were easily identifiable, generally properly shaped and soft (Nijboer 2006) and spread out on leaves, on the forest ground or on the river bank. One single large faecal sample assumed to belong to an adult individual was collected per group and stored in an empty Falcon tube until analysis. An extra sample was collected to supply faecal matter in germination trial experiments (see treatment F2 below). When sympatric primates were within 10 m of the group, we did not collect faecal

157 samples. During the study, we collected a total of 201 proboscis monkey faecal samples
158 (mean \pm SD = 14 ± 6 faeces month⁻¹). Most faeces sampled within the same month were
159 considered to belong to distinct proboscis monkey groups that ranged in different areas along
160 the study transect.

161

162 **Faecal analysis**

163 Within four hours of collection, the sample was weighed and cleaned with water using a 0.4
164 mm mesh strainer until all faecal matter was removed (Trolliet et al. 2016). Using a
165 stereoscope, intact seeds were extracted and grouped according to their shape, size and
166 colour, and the exact numbers of intact seeds were counted. Finally, ingested seeds were
167 identified by comparing them to a pre-established seed reference collection, containing seeds
168 from identified fruit species found in the study area. When identification was not possible
169 on site, seeds were sent to the Forest Research Centre (Sandakan, Sabah) to be identified by
170 botanical experts.

171

172 **Germination trials**

173 *Preliminary germination trials*

174 For each seed species found intact in proboscis monkey faeces, cleaned seeds (F1) were
175 placed in Petri dishes (maximum 16 seeds / Petri dish) filled with filter paper (Serio-Silva
176 and Rico-Gray 2003). Filter paper was chosen for the ease to visualise small seeds. Petri
177 dishes were placed outside at ambient temperature and in continuous shade for 60 days.
178 Seeds were checked every four days and germination event was defined as the emergence of
179 the radicle (Trolliet et al. 2016).

Advanced germination trials: Nauclea spp.

As *Nauclea* spp. seeds were found in abundance in proboscis monkey faeces, further germination trials were conducted, considering different seed treatments. To assess the effect of proboscis monkey gut passage on *Nauclea* spp. seed germination, we conducted experiments to compare the germination of ingested seeds and control seeds from fruits. *Nauclea orientalis* and *N. subdita* trees are present throughout the study site, however the seeds are morphologically indistinguishable: the fruits are brown with an irregular globular shape and contain thousands of tiny ovoid seeds measuring 1 mm long (Lim 2013). Even though fruits from both species are consumed by proboscis monkeys (Matsuda et al. 2009; Thirty unpubl.), fruit-feeding behaviour in the current study was mostly on *N. orientalis* (88% of feeding occurrences recorded at the riverside by scan sampling method). Therefore, seeds from *N. orientalis* fruits were used as experimental controls.

Based on Samuels and Levey (2005), we investigated five different treatments, which included the effect of being discarded from fruit pulp (manually extracted seeds from *N. orientalis* unripe (FR1) and ripe fruits (FR2) vs. seeds from ripe fruits with fleshy pulp (FR3)); and the chemical/mechanical effect of being ingested by proboscis monkeys (gut passed seeds, without (F1) or with (F2) faecal matter vs. manually extracted seeds (FR1 and FR2)) (Table 1). We considered two treatments for gut passed seeds to better represent natural conditions, F1 consists of defecated seeds that are freed from faecal matter (i.e., after secondary seed dispersal by dung beetles, or heavy rain washing the faecal matter away) and F2 where seeds lay inside faecal clumps.

Table 1. Categories (gut passed and control) and treatments (F1, F2, FR1, FR2 and FR3) of *Nauclea* spp. and *N. orientalis* seeds used during germination trials, set up in Petri dishes filled with forest soil.

Seed categories and treatments	Seed code in survival analyses
Gut passed seeds: <i>Nauclea</i> spp.	
F1: without faecal matter (n = 109)	F (n = 201)
F2: with faecal matter (n = 92)	
Control seeds: <i>N. orientalis</i>	
FR1: from unripe fruit (n = 104)	UF (n = 104)
FR2: from ripe fruit without pulp (n = 75)	RF (n = 153)
FR3: from ripe fruit with pulp (n = 78)	

ⁱ n = number of seeds per treatment.

Petri dishes were filled with forest soil (depth: 0.5 – 1 cm) and 16 *Nauclea* seeds of the same treatment (F1, F2, FR1, FR2 or FR3) were deposited on the soil surface of each dish. All Petri dishes were placed outside at ambient temperature and in continuous shade for 60 days (Trolliet et al. 2016) and subsequently the Petri dishes were moved into direct sunlight for 20 more days (i.e., sun conditions) (Hodgkison et al. 2003). We checked the seeds and added water every four days. To investigate the effect of the five treatments on *Nauclea* spp. seed germination, we conducted survival analyses (McNair et al. 2012) by measuring initial germination delay (the time it took for the first seed to germinate), germination speed (how many seeds germinated within four days) and total percentage of seeds that germinated at the end of the experiment (McNair et al. 2012). Survival analyses were only performed for *Nauclea* spp. (see below), as sample sizes of other seed species were too small.

Statistical analyses

Advanced germination trials: Nauclea spp.

Analyses were conducted with R (version 3.4.3) with a statistical significance of $P < 0.05$ (R Development Core Team 2017). We performed time-to-event analyses (survival analysis) on *Nauclea* spp. germination data (McNair et al. 2012), using the *survival* package (Therneau 2015) to fit Kaplan-Meier survival functions. Survival curves were then plotted using the *survminer* package (Kassambara et al. 2017). Finally, log-rank tests were performed to assess the homogeneity of multiple survivor functions and to conduct pair-wise comparisons of different seed treatments (McNair et al. 2012).

RESULTS

A high proportion (77.1%) of the analysed faecal samples (155 out of the 201) contained intact seeds, with seeds being recorded each month of the study. There were 28,452 intact seeds from at least eight different plant species found in 77.1% of the faecal samples (Table 2). All species were small-seeded, with most seeds measuring less than 2 mm in length, except for *Antidesma puncticulatum* (2-5 mm), Unknown sp. B (2-5 mm) and *Bridelia stipularis* (5-8 mm). The number of seeds ranged from 0 to 2,408 per sample, with an average of 141 ± 262 seeds per sample. Accounting for 98% of all intact seeds and found in 70.1% of the faecal samples, *Nauclea* spp. were the most abundant seed species, followed by an unidentified species (Unknown sp. A, recorded in 14.4% of faeces). Other species were observed less frequently, on average in $3.2 \pm 2.3\%$ of the faeces (Table 2). Chewed (broken) seeds were not considered: due to the small seed size we would not have been able to distinguish or identify them.

244 **Table 2.** List of intact seeds recorded in proboscis monkey faeces (n = 155) collected between
 245 2015 and 2017

Intact seeds (family and species)		Number of faecal samples containing intact seeds	Range of number of seeds per faecal sample	Seed length (mm)
Moraceae	<i>Ficus racemosa</i>	15	1 - 23	< 2
Moraceae	<i>Ficus septica</i>	8	1 - 21	< 2
Phyllanthaceae	<i>Antidesma puncticulatum</i>	3	2 - 7	2 - 5
Phyllanthaceae	<i>Bridelia stipularis</i>	5	1 - 12	5 - 8
Rubiaceae	<i>Nauclea</i> spp.	141	1 – 2408	< 2
Unknown	Unknown sp. A	29	1 - 120	< 2
Unknown	Unknown sp. B	2	1 - 4	2 - 5
Unknown	Unknown spp. ⁱ	6	1 - 55	NA

246 ⁱ Unknown spp. refers to a combination of several indistinguishable seeds, different from
 247 Unknown sp. A and B.

248

249 Germination trials

250 *Preliminary germination tests*

251 Seeds of six plant species germinated after passing through the gut of proboscis monkeys
 252 (Table 3, no germination tests could be conducted with *A. puncticulatum* and Unknown
 253 spp.).

254

255 **Table 3.** Germination fate of intact seeds after ingestion by proboscis monkeys.

Seed species	Yes	No	NA	Total
<i>Bridelia stipularis</i>	1	0	35	36
<i>Ficus racemosa</i>	19	43	0	62
<i>Ficus septica</i>	8	0	0	8
<i>Nauclea</i> spp.	114	53	8	175

Unknown sp.A	12	46	5	63
Unknown sp.B	1	0	2	3

ⁱ NA refers to failure occurring during germination experiments (i.e., insect damage, humidity conditions, etc.)

Advanced germination tests: Nauclea spp.

For reasons of clarity, different seed treatments were grouped when homogeneity tests were not significantly different and did not influence differently the fate of tested seeds. F is the combination of the treatments F1 and F2 (Log Rank: $\chi^2 = 0$, $df = 1$, $P = 0.993$), RF is the combination of FR2 and FR3 (Log Rank: $\chi^2 = 0.3$, $df = 1$, $P = 0.592$) and UF refers to FR1 (Table 1).

Homogeneity tests showed that the different treatments influenced the fate of seeds exposed to shade and sun conditions (Log Rank: $\chi^2 = 79.5$, $df = 2$, $P < 0.001$). We observed that ingested seeds (F) had a higher probability of germination (day 80: 87% of seeds had germinated) than control seeds from unripe fruits (UF) (Log Rank: $\chi^2 = 29$, $df = 1$, $P < 0.001$; day 80: 76%) and ripe fruits (RF) (Log Rank: $\chi^2 = 63$, $df = 1$, $P < 0.001$; day 80: 69%). Moreover, we observed that UF seeds had a higher percentage of germination than RF seeds (Log Rank: $\chi^2 = 6.3$, $df = 1$, $P < 0.05$). Finally, ingested seeds (F) showed a shorter initial germination delay (mean \pm SD: 46 ± 21 d) than RF (65 ± 15 d) and UF (65 ± 11 d) seeds, as well as an increased germination speed (at day 60: 108 F seeds had already germinated, as opposed to only 10 RF and 7 UF seeds) (Fig. 2).

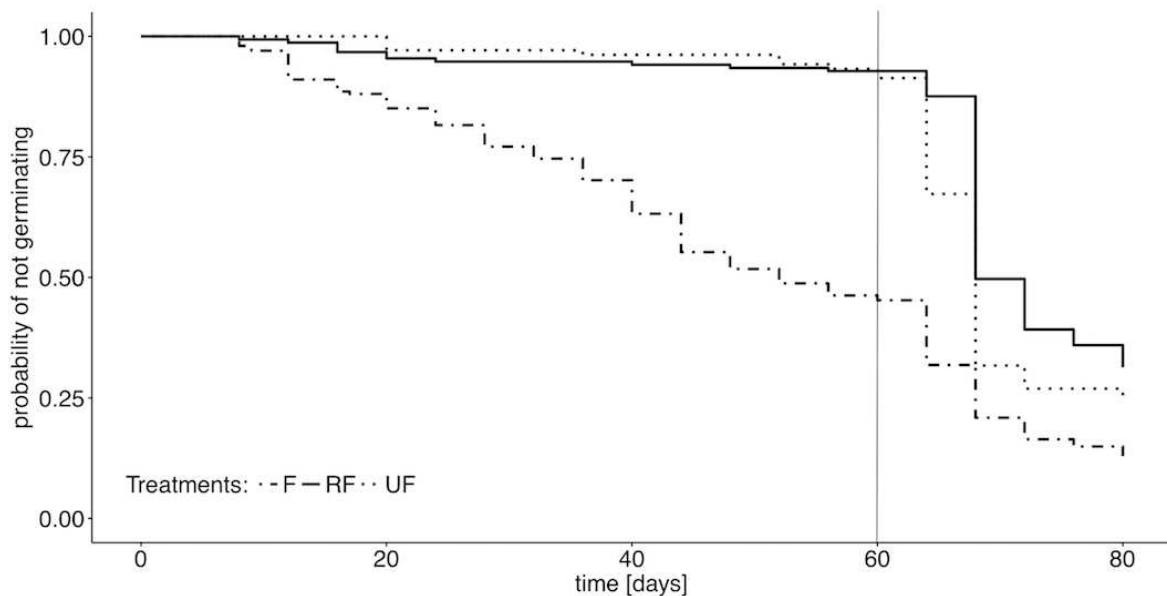


Fig. 2 Germination curves of seeds growing under shade conditions (60 d) followed by sun exposure (20 d) for three treatments; F = *Nauclea* spp. seeds ingested by proboscis monkeys (n = 201), RF = seeds from ripe *N. orientalis* fruits (n = 153), and UF = seeds from unripe *N. orientalis* fruits (n = 104); Each dip in the survival curve represents a germination event.

DISCUSSION

Our study demonstrated that proboscis monkeys do play a role in seed dispersal. We recorded the presence of intact seeds in their faeces each month, with 77.1% of analysed faecal samples containing seeds. As proboscis monkeys avoid ripe fruits and select unripe fruits (Matsuda et al. 2009), we suggest the small intact seeds are from unripe fruits. Our results contrast with previous studies that reported a low presence (only 11% of faeces in three months out of a 13-month study) (Matsuda et al. 2013) or an absence of seeds in proboscis monkey faeces entirely (Ranglack and Yeager 1986). Moreover, our study

reported higher seed diversity (eight species) in comparison to Matsuda et al. (2013), who identified seeds belonging to only three plant species (*Ficus globosa*, *Antidesma thwaitesianum* and *N. subdita*). We reported similar densities of *Ficus* and *A. puncticulatum* (the updated name for *A. thwaitesianum*) seeds in proboscis monkey faeces (1 - 23 and 2 - 7 seeds per sample, respectively) as Matsuda et al. (2013) in Sukau, a study site located 30 km downstream from ours. However, we recorded remarkably higher densities of *Nauclea* spp. seeds (1-2,408 seeds per faecal sample) in comparison to the low *N. subdita* seed densities reported in Sukau (1-23 seeds per sample) (Matsuda et al. 2013). Finally, we recorded *Bridelia stipularis* seeds in five faecal samples, while Matsuda et al. (2013) did not. The observed disparities in seed species diversity, density and monthly presence in proboscis monkey faeces between both studies might be the result of differences in plant (fruit) composition and availabilities. High numbers of plant species are reported in both study sites (n=180 in Matsuda et al. (2009), and n=201 in this study). However, as vegetation survey methods differed between studies (trail transects (Matsuda et al. 2009) and botanic plots (Thiry unpubl.)), plant availabilities are difficult to compare. Results more probably differ between studies because the methods used to examine the content of faecal samples were different. Indeed, in Matsuda et al. (2013), faecal samples were analysed manually with forceps and a magnifying glass, without draining faecal matter away, and this method may have missed seeds, while our approach with a strainer may be more appropriate to record the presence of small seeds. Although proboscis monkeys are also known as seed predators (e.g., consumed seeds of the unripe *Ficus binnendijkii* fruit were never found in faeces) (Matsuda et al. 2013), we did not monitor proboscis monkeys the whole day, and therefore were not able to record whether other consumed seeds were absent from their faeces (i.e., chewed seeds).

Even though the role of proboscis monkeys in seed dispersal has previously been suggested (Matsuda et al. 2013), the present study is the first to detail the germination of seeds ingested by this colobine species. We found that six of the eight seed species examined were able to germinate after passage through the gut of proboscis monkeys. While statistical tests could not be performed on the germination data of five of the seed species, survival analyses conducted with the most abundant small-seeded species, *Nauclea* spp., indicated that seeds ingested by proboscis monkeys exhibit higher germination success (87%) than seeds from control fruits (both ripe and unripe). This result differs from a previous study on another colobine, the Javan lutung (*T. auratus*), where lower germination success (only 5%) was observed in defecated *Ficus* spp. seeds than in control seeds (10%), suggesting that lutungs are not efficient fig dispersers (Tsuji et al. 2017). In our study, differences are particularly striking under shade conditions (first 60 days) where the seeds ingested by proboscis monkeys started to germinate earlier and faster than the seeds extracted from fruits: at d 60, 54% of ingested seeds had already germinated, as opposed to only 7% of the control seeds (from ripe and unripe fruits). A possible explanation for this germination pattern could be that seeds ingestion increases seed-coat permeability and enhances gas exchange and water absorption (Barnea et al. 1990). Pulp removal is also reported to be beneficial, as fruit flesh may inhibit germination (Evenari 1949), although we did not observe any difference between FR2 and FR3 treatments (control seeds without and with pulp). Additionally, faecal matter surrounding ingested seeds has been suggested to have a fertilising effect and to promote seedling growth (Traveset et al. 2001). On the other hand, faecal matter may promote fungal and/or bacterial growth, that could in turn prevent seedling establishment (Meyer and Witmet 1998). The presence of faecal matter appeared to be neutral in our study, as F1 and

F2 treatments (ingested seeds without and with faecal matter, respectively) did not differ significantly.

We observed that UF seeds (control seeds from unripe fruits) had a higher probability of germination than RF seeds (control seeds from ripe fruits) by the end of the germination experiment (d 80: 60 days of shade followed by 20 days of sun exposure). Although counterintuitive (Arthur 1985), higher or similar germination success of seeds from unripe fruits, compare with mature fruits, has been reported (Foster 1977; Arditti et al. 1981; Cruz-Tejada et al. 2018). In the case of *N. orientalis* (used for control treatments), this could be an advantage to benefit from seed dispersal by animals that preferentially feed on unripe fruits, such as colobines (Davies et al. 1988; Dasilva 1994; Matsuda et al. 2009; Hanya and Bernard 2012; Ehlers Smith et al. 2013).

Seed density has been reported to negatively affect germination success (Barnea et al. 1992). Therefore, when high density of seeds are found in faecal samples, such as in our present study, intra- and interspecific competition may occur between seeds, affecting seedling survival and establishment (Loiselle 1990; Traveset et al. 2007). However, being consumed by frugivores might still benefit plant species bearing multi-seeded fruits, such as *Nauclea* or *Ficus* species. Indeed, faecal clumps may contain lower seed densities than the multi-seeded fruit itself, reducing seed competition and potentially enhancing germination (Barnea et al. 1992).

The presence of *N. orientalis* seeds has already been recorded in the faeces of another colobine primate, the Javan lutung (*T. auratus*) in Indonesia (Tsuji et al., 2017). In our study site, silvered langurs (*T. cristatus*) are also known to consume *N. orientalis* fruits. Colobines are not the only mammals consuming *N. orientalis* fruits, as other frugivores, such as the Bornean bearded pig (*Sus barbatus*), large flying fox (*Pteropus vampyrus*), long-tailed

macaque or Bornean orangutan, also feed on these fruits, underlying the potential existence of a wide community of *N. orientalis* dispersers (Bhasin, unpubl.). The relative contribution of colobines to seed dispersal may be lower than that of other sympatric frugivorous animals (i.e., macaques, gibbons, hornbills, etc.), mostly as they disperse low diversity of seeds over short distances (Tsuji et al. 2017, McConkey 2018). However, in regard to the wide distribution and large biomass of colobines in Asian and African forests (Matsuda et al. 2013), they could potentially be important seed dispersers for some plant species. Moreover, as colobines mostly target unripe fruits and disperse seeds over shorter distances (i.e., < 100 m in Javan lutung (Tusji et al. 2017)), we believe they can provide a complementary service to other frugivores (i.e., gibbons) consuming ripe fruits and dispersing seeds over longer distances (i.e., up to 1.3 km in gibbon (McConkey 2018)). As *N. orientalis* naturally occurs along riverbanks (Azmi 1998, Boland et al. 2006), we suggest that riverine seed deposition by proboscis monkeys is suitable for *Nauclea* spp. In addition, as proboscis monkey sleeping trees are often located along water (Stark, 2018), secondary seed dispersal might also occur by hydrochory: when branches overhang the river, proboscis monkey faeces may fall in the water, float away until reaching a bank and potentially establish seedlings in a distant suitable riverine habitat. *N. orientalis* seed dispersal by water has already been reported along the Ord River in Australia (Pettit & Froend 2001). These results suggest that *N. orientalis* has more than one dispersal mechanism (polychory).

It is of interest to note that we often recorded large numbers of faecal samples under proboscis monkey sleeping trees, which may attract a vast guild of secondary seed dispersers (e.g., dung beetles) (Shepherd and Chapman 1998) or seed predators (e.g., rodents) (Andresen and Levey 2004). Although faecal samples were collected shortly after being defecated, dung beetles were often already observed in proboscis monkey faeces. Therefore,

further research should investigate the post-dispersal fate of proboscis monkey dispersed-seeds.

To conclude, our study emphasises that the role proboscis monkeys play in seed dispersal has been underestimated thus far. Proboscis monkeys should be considered as seed dispersers, at least of some plant species. First, they prefer to feed on unripe fruits over young leaves during certain times of the year (Matsuda et al. 2009). They then defecate large numbers of tiny intact seeds, which can improve the germination success of some plant species, such as those of *Nauclea* spp. And finally, in regard to their long MRTs (Matsuda et al., 2015), daily ranging movements and sleeping site selection close to rivers (Stark, 2018), we suggest that proboscis monkeys contribute to the dispersal of intact seeds, away from the parent plant, in potentially suitable riverine habitats.

COMPLIANCE WITH ETHICAL STANDARDS

Funding

This study was funded by FNRS (2014 – 18100, 2016 - 16755), FNRS Gustave Boël-Sofina Fellowship (2016) and Fonds Léopold III – pour l’Exploration et la Conservation de la Nature asbl. (2014 - 14.118).

Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical approval

No direct contacts with animals were conducted during this research and ethical aspects of the research protocols have been approved by the FNRS committee and Sabah Biodiversity Council.

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