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

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23   ABSTRACT

24   Frugivorous vertebrates, such as primates, are important dispersal agents in tropical forests,

25   although the role of folivorous colobines is generally not considered. However, recent

26   studies reported seed dispersal by endo- and epizoochory in colobine primates, including the

27   proboscis monkey (*Nasalis larvatus*), suggesting the role colobines play in seed dispersal

28   might have been underestimated. In the Lower Kinabatangan Floodplain, in Sabah,

29   Malaysian Borneo, we investigated whether seeds were still able to germinate after being

30   ingested by proboscis monkeys. Faecal samples (n = 201) from proboscis monkeys were

31   collected between 2015 and 2017. Intact seeds belonging to eight plant species were found

32   in 77% of the faecal samples. *Nauclea* spp. was the most abundant plant species, accounting

33   for 98% of all intact seeds. This study is the first to conduct germination trials on seeds

34   defecated by proboscis monkeys. Higher germination success was recorded in ingested

35   *Nauclea* spp. seeds than in control seeds, from both ripe and unripe *Nauclea orientalis* fruits

36   (P < 0.001). Therefore, we suggest that proboscis monkeys play a role in seed dispersal, by

37   enhancing the germination success of defecated seeds, for at least some plant species. Similar

38   to other colobines, although proboscis monkeys may provide a lower contribution to seed

39   dispersal (low seed diversity over short distances) than other sympatric frugivores, this study

40   emphasises that proboscis monkeys do contribute to the dispersal of intact seeds, such as

41   *Nauclea* spp., in potentially suitable riverine habitats.

42

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

44   germination

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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

71   consumed (Garber and Lambert 1998; Norconk et al. 1998). However, primate seed

72   predators can be involved in seed dispersal by swallowing small seeds intact without

73   masticating them, by removing pericarp and seed-coat before discarding seeds (Norconk et

74   al. 1998; Barnett et al. 2012), or by seeds attaching to the animal's fur and dropping off in a

75   different location (epizoochory) (Chen et al. 2018). Indeed, the dichotomy seed predator

76   versus seed disperser has been oversimplified (Norconk et al. 1998) and many primates play

77   a number of roles, depending on the plant consumed (McConkey 2018).

78   In colobines, seed dispersal has been recorded in five species, via endozoochory (*Nasalis*

79   *larvatus* (Matsuda et al. 2013), *Trachypithecus francoisi hatinhensis* (Nguyen et al. 2013),

80   *T. auratus* (Tsuji et al. 2017) and *Presbytis* sp. (McConkey unpubl. in McConkey 2018))

81   and via epizoochory (*Rhinopithecus roxellana* (Chen et al. 2018)). Even though seed

82   germination trials were not conducted (Matsuda et al. 2013; Nguyen et al. 2013; Chen et al.

83   2018) or dispersed seeds showed low germination success (Tsuji et al. 2017), authors

84   suggested that the role colobines play in seed dispersal might have been underestimated. In

85   regard to the wide distribution and biomass of Asian and African colobines, colobine

86   primates might play a considerable role in seed dispersal of some plant species (Matsuda et

87   al. 2013; Corlett 2017; Tsuji et al. 2017).

88   Proboscis monkey (*Nasalis larvatus*) is an endangered colobine primate endemic to the

89   island of Borneo, where the species inhabits riverine, swamp and mangrove forests

90   (Meijaard et al. 2008). In riverine forest, proboscis monkey home range averages 81 ha

91   (Stark et al. 2017) and the mean daily distance travelled is 940 m (Stark 2018). Proboscis

92   monkeys highly use areas close to rivers, select sleeping sites along water and avoid sleeping

93   at the same location on consecutive nights (Stark 2018). Similar to other colobines, proboscis

94   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.
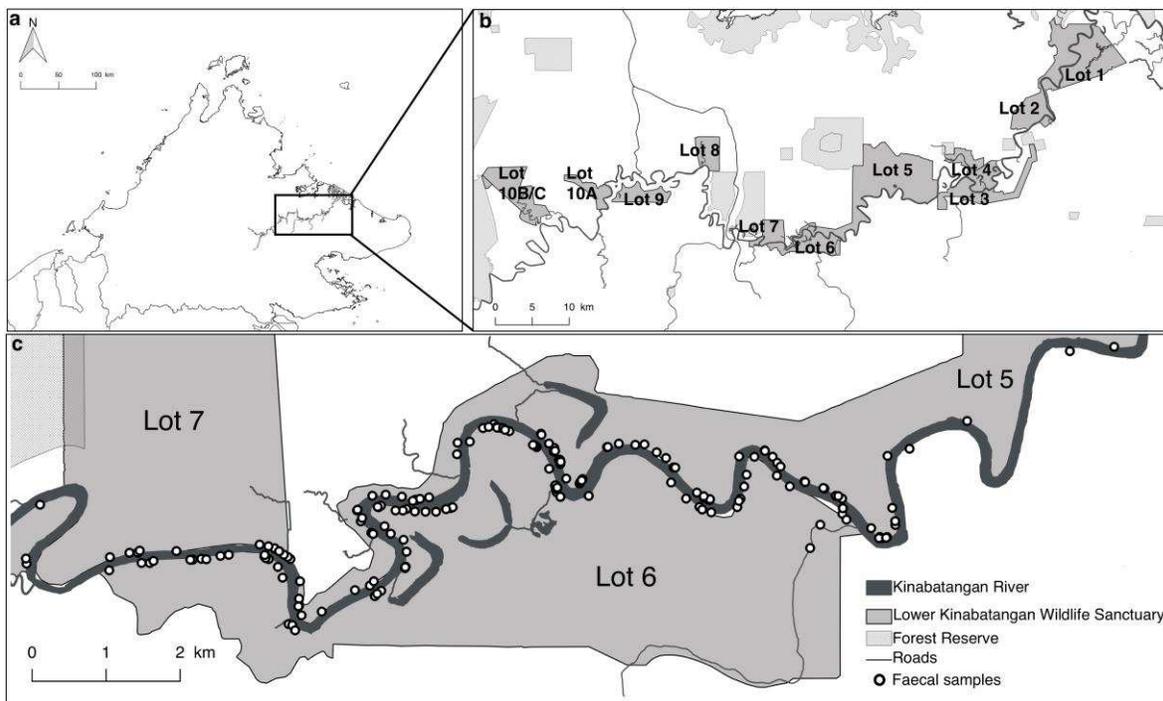
Fig. 1 Maps of the study area: **a** the State of Sabah in Malaysian Borneo with the location of the Kinabatangan River; **b** the Lower Kinabatangan Wildlife Sanctuary, with its 10 protected forest lots (dark grey) and the Forest Reserve (light grey); **c** zoom on the study site in lots 5, 6 and 7, with faecal sampling locations

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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 ± 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).

180

Advanced germination trials: Nauclea *spp.*

182 As *Nauclea* spp. seeds were found in abundance in proboscis monkey faeces, further

183 germination trials were conducted, considering different seed treatments. To assess the effect

184 of proboscis monkey gut passage on *Nauclea* spp. seed germination, we conducted

185 experiments to compare the germination of ingested seeds and control seeds from fruits.

186 *Nauclea orientalis* and *N. subdita* trees are present throughout the study site, however the

187 seeds are morphologically indistinguishable: the fruits are brown with an irregular globular

188 shape and contain thousands of tiny ovoid seeds measuring 1 mm long (Lim 2013). Even

189 though fruits from both species are consumed by proboscis monkeys (Matsuda et al. 2009;

190 Thiry unpubl.), fruit-feeding behaviour in the current study was mostly on *N. orientalis* (88%

191 of feeding occurrences recorded at the riverside by scan sampling method). Therefore, seeds

192 from *N. orientalis* fruits were used as experimental controls.

193 Based on Samuels and Levey (2005), we investigated five different treatments, which

194 included the effect of being discarded from fruit pulp (manually extracted seeds from *N.*

195 *orientalis* unripe (FR1) and ripe fruits (FR2) vs. seeds from ripe fruits with fleshy pulp

196 (FR3)); and the chemical/mechanical effect of being ingested by proboscis monkeys (gut

197 passed seeds, without (F1) or with (F2) faecal matter vs. manually extracted seeds (FR1 and

198 FR2)) (Table 1). We considered two treatments for gut passed seeds to better represent

199 natural conditions, F1 consists of defecated seeds that are freed from faecal matter (i.e., after

200 secondary seed dispersal by dung beetles, or heavy rain washing the faecal matter away) and

201 F2 where seeds lay inside faecal clumps.

202

203   **Table 1.** Categories (gut passed and control) and treatments (F1, F2, FR1, FR2 and FR3) of

204   *Nauclea* spp. and *N. orientalis* seeds used during germination trials, set up in Petri dishes

205   filled with forest soil.

Seed categories and treatments	Seed code in survival analyses
Gut passed seeds: *Nauclea* spp.	
F1: without faecal matter (n = 109)	F (n = 201)
F2: with faecal matter (n = 92)	
Control seeds: *N. orientalis*	
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)	

206   [i] n = number of seeds per treatment.

207

208   Petri dishes were filled with forest soil (depth: 0.5 – 1 cm) and 16 *Nauclea* seeds of the same

209   treatment (F1, F2, FR1, FR2 or FR3) were deposited on the soil surface of each dish. All

210   Petri dishes were placed outside at ambient temperature and in continuous shade for 60 days

211   (Trolliet et al. 2016) and subsequently the Petri dishes were moved into direct sunlight for

212   20 more days (i.e., sun conditions) (Hodgkison et al. 2003). We checked the seeds and added

213   water every four days. To investigate the effect of the five treatments on *Nauclea* spp. seed

214   germination, we conducted survival analyses (McNair et al. 2012) by measuring initial

215   germination delay (the time it took for the first seed to germinate), germination speed (how

216   many seeds germinated within four days) and total percentage of seeds that germinated at

217   the end of the experiment (McNair et al. 2012). Survival analyses were only performed for

218   *Nauclea* spp. (see below), as sample sizes of other seed species were too small.

219

Statistical analyses

221 *Advanced germination trials:* **Nauclea *spp.***

222 Analyses were conducted with R (version 3.4.3) with a statistical significance of P < 0.05

223 (R Development Core Team 2017). We performed time-to-event analyses (survival analysis)

224 on *Nauclea* spp. germination data (McNair et al. 2012), using the *survival* package

225 (Therneau 2015) to fit Kaplan-Meier survival functions. Survival curves were then plotted

226 using the *survimer* package (Kassambara et al. 2017). Finally, log-rank tests were performed

227 to assess the homogeneity of multiple survivor functions and to conduct pair-wise

228 comparisons of different seed treatments (McNair et al. 2012).

229

230 RESULTS

231 A high proportion (77.1%) of the analysed faecal samples (155 out of the 201) contained

232 intact seeds, with seeds being recorded each month of the study. There were 28,452 intact

233 seeds from at least eight different plant species found in 77.1% of the faecal samples (Table

234 2). All species were small-seeded, with most seeds measuring less than 2 mm in length,

235 except for *Antidesma puncticulatum* (2-5 mm), Unknown sp. B (2-5 mm) and *Bridelia*

236 *stipularis* (5-8 mm). The number of seeds ranged from 0 to 2,408 per sample, with an average

237 of 141 ± 262 seeds per sample. Accounting for 98% of all intact seeds and found in 70.1%

238 of the faecal samples, *Nauclea* spp. were the most abundant seed species, followed by an

239 unidentified species (Unknown sp. A, recorded in 14.4% of faeces). Other species were

240 observed less frequently, on average in 3.2 ± 2.3% of the faeces (Table 2). Chewed (broken)

241 seeds were not considered: due to the small seed size we would not have been able to

242 distinguish or identify them.

243

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	*Ficus racemosa*	15	1 - 23	< 2
Moraceae	*Ficus septica*	8	1 - 21	< 2
Phyllanthaceae	*Antidesma puncticulatum*	3	2 - 7	2 - 5
Phyllanthaceae	*Bridelia stipularis*	5	1 - 12	5 - 8
Rubiaceae	*Nauclea* 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
Bridelia stipularis	1	0	35	36
Ficus racemosa	19	43	0	62
Ficus septica	8	0	0	8
Nauclea 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 ± 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).
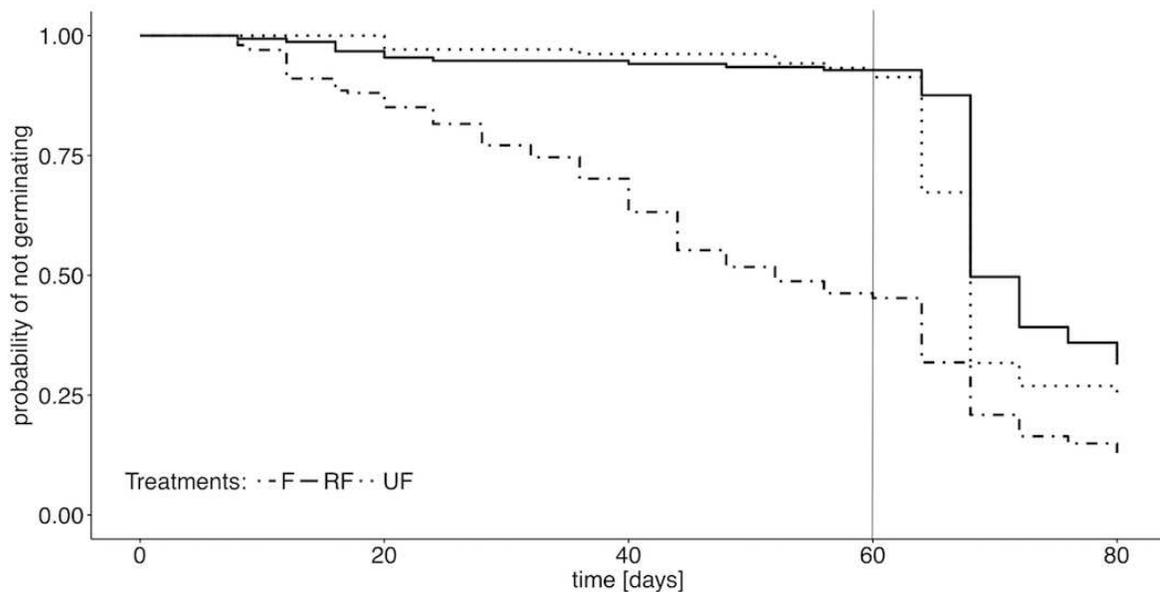
276

277　**Fig. 2** Germination curves of seeds growing under shade conditions (60 d) followed by sun

278　exposure (20 d) for three treatments; F = *Nauclea* spp. seeds ingested by proboscis monkeys

279　(n = 201), RF = seeds from ripe *N. orientalis* fruits (n = 153), and UF = seeds from unripe

280　*N. orientalis* fruits (n = 104); Each dip in the survival curve represents a germination event.

281

282　DISCUSSION

283　Our study demonstrated that proboscis monkeys do play a role in seed dispersal. We

284　recorded the presence of intact seeds in their faeces each month, with 77.1% of analysed

285　faecal samples containing seeds. As proboscis monkeys avoid ripe fruits and select unripe

286　fruits (Matsuda et al. 2009), we suggest the small intact seeds are from unripe fruits. Our

287　results contrast with previous studies that reported a low presence (only 11% of faeces in

288　three months out of a 13-month study) (Matsuda et al. 2013) or an absence of seeds in

289　proboscis monkey faeces entirely (Ranglack and Yeager 1986). Moreover, our study

14

290   reported higher seed diversity (eight species) in comparison to Matsuda et al. (2013), who

291   identified seeds belonging to only three plant species (*Ficus globosa*, *Antidesma*

292   *thwaitesianum* and *N. subdita*). We reported similar densities of *Ficus* and *A. puncticulatum*

293   (the updated name for *A. thwaitesianum)* seeds in proboscis monkey faeces (1 - 23 and 2 - 7

294   seeds per sample, respectively) as Matsuda et al. (2013) in Sukau, a study site located 30 km

295   downstream from ours. However, we recorded remarkably higher densities of *Nauclea* spp.

296   seeds (1-2,408 seeds per faecal sample) in comparison to the low *N. subdita* seed densities

297   reported in Sukau (1-23 seeds per sample) (Matsuda et al. 2013). Finally, we recorded

298   *Bridelia stipularis* seeds in five faecal samples, while Matsuda et al. (2013) did not. The

299   observed disparities in seed species diversity, density and monthly presence in proboscis

300   monkey faeces between both studies might be the result of differences in plant (fruit)

301   composition and availabilities. High numbers of plant species are reported in both study sites

302   (n=180 in Matsuda et al. (2009), and n=201 in this study). However, as vegetation survey

303   methods differed between studies (trail transects (Matsuda et al. 2009) and botanic plots

304   (Thiry unpubl.)), plant availabilities are difficult to compare. Results more probably differ

305   between studies because the methods used to examine the content of faecal samples were

306   different. Indeed, in Matsuda et al. (2013), faecal samples were analysed manually with

307   forceps and a magnifying glass, without draining faecal matter away, and this method may

308   have missed seeds, while our approach with a strainer may be more appropriate to record the

309   presence of small seeds. Although proboscis monkeys are also known as seed predators (e.g.,

310   consumed seeds of the unripe *Ficus binnendijkii* fruit were never found in faeces) (Matsuda

311   et al. 2013), we did not monitor proboscis monkeys the whole day, and therefore were not

312   able to record whether other consumed seeds were absent from their faeces (i.e., chewed

313   seeds).

314   Even though the role of proboscis monkeys in seed dispersal has previously been suggested

315   (Matsuda et al. 2013), the present study is the first to detail the germination of seeds ingested

316   by this colobine species. We found that six of the eight seed species examined were able to

317   germinate after passage through the gut of proboscis monkeys. While statistical tests could

318   not be performed on the germination data of five of the seed species, survival analyses

319   conducted with the most abundant small-seeded species, *Nauclea* spp., indicated that seeds

320   ingested by proboscis monkeys exhibit higher germination success (87%) than seeds from

321   control fruits (both ripe and unripe). This result differs from a previous study on another

322   colobine, the Javan lutung (*T. auratus*), where lower germination success (only 5%) was

323   observed in defecated *Ficus* spp. seeds than in control seeds (10%), suggesting that lutungs

324   are not efficient fig dispersers (Tsuji et al. 2017). In our study, differences are particularly

325   striking under shade conditions (first 60 days) where the seeds ingested by proboscis

326   monkeys started to germinate earlier and faster than the seeds extracted from fruits: at d 60,

327   54% of ingested seeds had already germinated, as opposed to only 7% of the control seeds

328   (from ripe and unripe fruits). A possible explanation for this germination pattern could be

329   that seeds ingestion increases seed-coat permeability and enhances gas exchange and water

330   absorption (Barnea et al. 1990). Pulp removal is also reported to be beneficial, as fruit flesh

331   may inhibit germination (Evenari 1949), although we did not observe any difference between

332   FR2 and FR3 treatments (control seeds without and with pulp). Additionally, faecal matter

333   surrounding ingested seeds has been suggested to have a fertilising effect and to promote

334   seedling growth (Traveset et al. 2001). On the other hand, faecal matter may promote fungal

335   and/or bacterial growth, that could in turn prevent seedling establishment (Meyer and

336   Witmet 1998). The presence of faecal matter appeared to be neutral in our study, as F1 and

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

338   significantly.

339   We observed that UF seeds (control seeds from unripe fruits) had a higher probability of

340   germination than RF seeds (control seeds from ripe fruits) by the end of the germination

341   experiment (d 80: 60 days of shade followed by 20 days of sun exposure). Although

342   counterintuitive (Arthur 1985), higher or similar germination success of seeds from unripe

343   fruits, compare with mature fruits, has been reported (Foster 1977; Arditti et al. 1981; Cruz-

344   Tejada et al. 2018). In the case of *N. orientalis* (used for control treatments), this could be

345   an advantage to benefit from seed dispersal by animals that preferentially feed on unripe

346   fruits, such as colobines (Davies et al. 1988; Dasilva 1994; Matsuda et al. 2009; Hanya and

347   Bernard 2012; Ehlers Smith et al. 2013).

348   Seed density has been reported to negatively affect germination success (Barnea et al. 1992).

349   Therefore, when high density of seeds are found in faecal samples, such as in our present

350   study, intra- and interspecific competition may occur between seeds, affecting seedling

351   survival and establishment (Loiselle 1990; Traveset et al. 2007). However, being consumed

352   by frugivores might still benefit plant species bearing multi-seeded fruits, such as *Nauclea*

353   or *Ficus* species. Indeed, faecal clumps may contain lower seed densities than the multi-

354   seeded fruit itself, reducing seed competition and potentially enhancing germination (Barnea

355   et al. 1992).

356   The presence of *N. orientalis* seeds has already been recorded in the faeces of another

357   colobine primate, the Javan lutung (*T. auratus*) in Indonesia (Tsuji et al., 2017). In our study

358   site, silvered langurs (*T. cristatus*) are also known to consume *N. orientalis* fruits. Colobines

359   are not the only mammals consuming *N. orientalis* fruits, as other frugivores, such as the

360   Bornean bearded pig (*Sus barbatus*), large flying fox (*Pteropus vampyrus*), long-tailed

361   macaque or Bornean orangutan, also feed on these fruits, underlying the potential existence

362   of a wide community of *N. orientalis* dispersers (Bhasin, unpubl.). The relative contribution

363   of colobines to seed dispersal may be lower than that of other sympatric frugivorous animals

364   (i.e., macaques, gibbons, hornbills, etc.), mostly as they disperse low diversity of seeds over

365   short distances (Tsuji et al. 2017, McConkey 2018). However, in regard to the wide

366   distribution and large biomass of colobines in Asian and African forests (Matsuda et al.

367   2013), they could potentially be important seed dispersers for some plant species. Moreover,

368   as colobines mostly target unripe fruits and disperse seeds over shorter distances (i.e., < 100

369   m in Javan lutung (Tusji et al. 2017)), we believe they can provide a complementary service

370   to other frugivores (i.e., gibbons) consuming ripe fruits and dispersing seeds over longer

371   distances (i.e., up to 1.3 km in gibbon (McConkey 2018)). As *N. orientalis* naturally occurs

372   along riverbanks (Azmi 1998, Boland et al. 2006), we suggest that riverine seed deposition

373   by proboscis monkeys is suitable for *Nauclea* spp. In addition, as proboscis monkey sleeping

374   trees are often located along water (Stark, 2018), secondary seed dispersal might also occur

375   by hydrochory: when branches overhang the river, proboscis monkey faeces may fall in the

376   water, float away until reaching a bank and potentially establish seedlings in a distant

377   suitable riverine habitat. *N. orientalis* seed dispersal by water has already been reported

378   along the Ord River in Australia (Pettit & Froend 2001). These results suggest that *N.*

379   *orientalis* has more than one dispersal mechanism (polychory).

380   It is of interest to note that we often recorded large numbers of faecal samples under

381   proboscis monkey sleeping trees, which may attract a vast guild of secondary seed dispersers

382   (e.g., dung beetles) (Shepherd and Chapman 1998) or seed predators (e.g., rodents)

383   (Andresen and Levey 2004). Although faecal samples were collected shortly after being

384   defecated, dung beetles were often already observed in proboscis monkey faeces. Therefore,

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

386 seeds.

387 To conclude, our study emphasises that the role proboscis monkeys play in seed dispersal

388 has been underestimated thus far. Proboscis monkeys should be considered as seed

389 dispersers, at least of some plant species. First, they prefer to feed on unripe fruits over young

390 leaves during certain times of the year (Matsuda et al. 2009). They then defecate large

391 numbers of tiny intact seeds, which can improve the germination success of some plant

392 species, such as those of *Nauclea* spp. And finally, in regard to their long MRTs (Matsuda

393 et al., 2015), daily ranging movements and sleeping site selection close to rivers (Stark,

394 2018), we suggest that proboscis monkeys contribute to the dispersal of intact seeds, away

395 from the parent plant, in potentially suitable riverine habitats.

396

397 COMPLIANCE WITH ETHICAL STANDARDS

398 **Funding**

402

403 **Conflict of Interest**

404 The authors declare that they have no conflict of interest.

405

406 **Ethical approval**

407   No direct contacts with animals were conducted during this research and ethical aspects of

408   the research protocols have been approved by the FNRS committee and Sabah Biodiversity

409   Council.

410

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