1 **Factors influencing riverine utilization patterns in two**

2 **sympatric macaques**

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18 **Short title**: Riverine utilization patterns of two sympatric macaques

Abstract

Many species of terrestrial animals, including primates, live in varied association with the aquatic (e.g., riverine or coastal) environment. However, the benefits that each species receive from the aquatic environment are thought to vary depending on their social and ecological characteristics, and thus, elucidating those benefits to each species is important for understanding the principles of wild animal behaviour. In the present study, to gain a more complete picture of aquatic environment use, including social and ecological factors in primates, factors affecting riverine habitat utilization of two macaque species *(Macaca nemestrina* and *M. fascicularis)* were identified and qualitative comparisons were made with sympatric proboscis monkeys *(Nasalis larvatus)*, which have different social and ecological characteristics. Temporal variation in sighting frequency of macaques at the riverbanks was positively related to the fruit availability of a dominant riparian plant species and negatively related to the river water level which affects the extent of predation pressure. Riverine utilization of macaques was greatly influenced by distribution and abundance of food (especially fruit) resources, possibly in association with predation pressure. Additionally, qualitative ecological comparisons with sympatric proboscis monkeys suggest that the drivers of riverine utilization depend on the feeding niches of the species, and different anti-predator strategies resulting from their differing social structures.

Keywords

Anti-predator strategy, aquatic environment, foraging strategy, landscape of fear, southern pig-tailed macaque

Introduction

44   Animals often live in forests characterized as mosaic habitats comprising both terrestrial

45   and aquatic (e.g., riverine or coastal) environments while varying their associations with

46   the aquatic environment. In addition to direct relationships such as obtaining food from

47   the aquatic environment, e.g., bears eating salmon [1]; racoons eating mussels [2], the aquatic

48   environment has an indirect impact on terrestrial animals by bringing about

49   environmental heterogeneity. Differences in terrestrial flora, which are due to varying

50   water abundance and light intensity at the border between aquatic and terrestrial

51   environments, affect foraging behaviour of animals that use plants as a food source. In

52   addition, such boundaries restrict the distribution and movement patterns like a river-

53   barrier [3] and thus are constraints on habitat utilization. Aquatic environments are,

54   therefore, undoubtedly important for terrestrial animals across many taxonomic groups

55   and geographic areas.

56   Primates are a primary example of terrestrial animals that rely on the aquatic

57   environment. Kempf [4] presented a comprehensive review of primate aquatic behaviours

58   with the conclusions that the use of aquatic resources and the aquatic environment affect

59   various aspects of primate life, including feeding, traveling, predation avoidance, and

60   thermoregulation, although it has been noted that the represented data are inadequate to

61   draw strong conclusions. Reports of aquatic-related primate ecology have increased in

62   recent years, strongly supporting such proposed broader trends with special reference to

63   primates inhabiting flooded habitats [5]. One of the notable flooded habitats is riverine

64   forest, providing a relatively constant availability of fruits, combined with greater plant

65   diversity and higher leaf quality when compared with dryland forest, which is due to the

66   frequent supply of nutrient-rich soils in riverine forests that are exposed to seasonal

67 flooding [6,7]. Further, in contrast to dryland forest, riverine forest potentially has a better

68 light environment and more gap-specialists that have leaves containing higher protein

69 content [8]—one of the important factors influencing primate abundance [9] and dietary

70 choice e.g., [10,11]. The distinctive food conditions caused by the presence of such large-

71 scale riparian areas in forest habitat are likely to have a significant impact on primate

72 behavioural ecology, and thus riverine habitat is an ideal forest type for research

73 contributing to a fundamental understanding of primate behavioural ecology, including

74 how the aquatic environment affects primate distribution and ranging behaviours.

75   Furthermore, studying habitats in riparian environments also plays an

76 important role in understanding the landscape of fear [12,13]. Animals' responses to

77 predation risk vary over time and space; for example, they can alter their behaviour,

78 such as by changing time allocation patterns depending on the level of fear [14].

79 Boundaries between aquatic and terrestrial environments, e.g., riverbanks, can be

80 advantageous or disadvantageous in anti-predator strategies, because they provide

81 animals with a physically heterogeneous environment. In riverine habitats, river-edge

82 trees in exposed places are preferred by primates for roosting to avoid predation,

83 because this allows detection of approaching predators [15-18]. For example, proboscis

84 monkeys (*Nasalis larvatus*) often choose sleeping sites in river-edge trees in areas with

85 narrow river widths; this provides good escape routes from terrestrial predators such as

86 clouded leopards (*Neofelis diardi*) [19-21], which generally show a nocturnal activity

87 pattern [22]. Conversely, on flooded days when water levels are extremely high, proboscis

88 monkeys remain in inland forest because of reduced predation threat, as terrestrial

89 predators are prevented from foraging on the forest floor [23]. Therefore, riverine forests

90 have temporal and spatial environmental heterogeneity, and revealing the behavioural

91   changes of animals in response to such heterogeneity can provide insight into

92   behavioural adaptation in response to fear of predators. Consequently, studying primates

93   that live in riverine habitats is ideal for elucidating their resource exploitation patterns

94   relative to anti-predator strategies; these are central components to understanding

95   various primate habitat adaptations.

96   Long-tailed macaques (*Macaca fascicularis*) and southern pig-tailed macaques

97   (*M. nemestrina*, hereafter pig-tailed macaques, unless otherwise noted) are widely

98   distributed throughout the Sundaic region of Southeastern Asia, often coexisting in a

99   broad variety of habitats [24]. Long-tailed macaques have often been reported sleeping in

100   river-edge trees [16,25,26], and van Schaik, et al. [16] indicate that multiple ecological factors

101   (food availability, temperature and predation risk) influence their riverine utilization.

102   Conversely, ecological data for pig-tailed macaques, including the northern species

103   (*Macaca leonina*) and southern pig-tailed species, are less complete [27-30], and their

104   aquatic-related behaviours are rarely reported. Rodman [31] reported that microhabitat

105   segregation occurs between the two species and that, unlike long-tailed macaques, pig-

106   tailed macaques generally do not use riverine areas. Conversely, Albert, et al. [18] noted

107   that the preference of northern pig-tailed macaques to locate their sleeping sites in river-

108   edge trees was a part of their predator avoidance strategy. In addition to predation

109   pressure, as in long-tailed macaques, food availability may affect riverine utilization in

110   pig-tailed macaques. By determining the effects of food availability on riverine forest

111   use in macaque habitat, it is possible to evaluate whether the ranging behaviour of pig-

112   tailed macaques is affected by food availability in the same way as that of long-tailed

113   macaques.

114   We examined the riverine habitat utilization patterns of sympatric long-tailed

115   and pig-tailed macaques inhabiting a secondary riverine forest on the island of Borneo.

116   At this site, it has been reported that sympatric primates, including the two study

117   macaque species, proboscis monkeys and other species, prefer to utilize river-edge trees

118   for night-time sleeping, although the frequency of riverine usage is different among

119   these sympatric primates [32]. A previous study on proboscis monkeys at the site

120   suggested that riverine preference is related to high predation pressure, but not river-

121   edge dietary choice [17,23]. However, in theory, predation risk varies with group size and

122   body weight [33-35]. The two species of macaques in this study may have different anti-

123   predator strategies from proboscis monkeys, as the macaques live in groups of multiple

124   males and females and have larger group sizes than proboscis monkeys, which live in

125   groups consisting of one male and multiple females [35,36] and have significantly different

126   body weight than the two macaque species, i.e., proboscis monkey: male, 25kg and

127   female, 14 kg; long-tailed macaque: male, 6 kg and female, 4 kg; pig-tailed-macaque,

128   male, 14 kg and female, 7 kg [37-39]. Additionally, the ranging behaviour of primate

129   species that prefer to feed on patchy and clumped food sources, e.g., fruits and flowers,

130   such as northern pig-tailed and long-tailed macaques [16,25,26], is more influenced by food

131   distribution and abundance than that of primate species that prefer to feed on ubiquitous

132   food sources (i.e., leaves), such as proboscis monkeys [40]. Therefore, for macaques, the

133   location of foraging patches may have a stronger effect on sleeping site selection.

134   In the present study, to gain a more complete picture of the riverine utilization

135   patterns in the two species of sympatric macaques, we sought to 1) evaluate temporal

136   variation in their riverine usage and asses the factors affecting riverine usage, including

137   physical environment, i.e., river width and water level, and 2) describe their diets in

138   river-edge areas, with a comparison of those availability. In addition, the effects of

139   feeding niches and social structure on ranging behaviour are discussed by qualitatively

140   comparing the characteristics of riverine utilization of the two species of macaques with

141   those of proboscis monkeys reported in previous studies [17,21,23].

142

Methods

143

Study area and subjects

144

145   We performed the observations over two years from 2012 to 2014 in riverine forests along

146   the Menanggul River (average river width 0–4000 m from the river mouth: 19.9 m), a

147   tributary of the Kinabatangan River, Sabah, Borneo, Malaysia (118°30'E, 5°30'N). The

148   south side of the Menanggul River is covered extensively in natural forest, whereas the

149   north side has been deforested for oil palm plantations, except for a protected zone along

150   the river [41]. The mean minimum and maximum daily temperatures were approximately

151   24°C and 30°C, respectively, and the mean annual precipitation at the site was 2,474 mm

152   [6]. The riverine forest was inhabited by long-tailed and pig-tailed macaques, as well as

153   proboscis monkeys, silver langurs (*Trachypithecus cristatus*), Hose's langurs (*Presbytis*

154   *hosei*), maroon langurs (*Presbytis rubicunda*), Bornean gibbons (*Hylobates muelleri*) and

155   orangutans (*Pongo pygmaeus*) [32]. Long-tailed and pig-tailed macaques under observation

156   were well habituated to observers in boats, as this area is one of the main tourist attractions

157   in the region, with many boats and tourists visiting the Menanggul River since more than

158   10 years ago.

159

Data collection

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Boat-based surveys

161

162   Surveys by boat in the late afternoon are considered the most effective method for

163   studying primates, including the two sympatric macaques in this region, because they

164   often sleep in riverside trees [32]. We therefore collected data on the distribution pattern of

165   the sympatric macaques in the late afternoon (16:00–19:00) for 434 days from June 2012

166   to July 2014 via boat-based surveys. We conducted the surveys along the river at a speed

167   of approximately 4–6 km/h. When we detected a group or individual macaque, we

168   switched off the boat engine to avoid disturbing them and paddled closer to record their

169   species and numbers. We divided the river into 50-metre sections from the river mouth to

170   4,000 m inland, recording the river sections where sightings of macaques were made.

171   When group members were distributed over several sections, the section containing the

172   largest number of individuals in the visual inspection was defined as the detected section.

173

174   *Boat-based behavioural observations*

175   We collected behavioural data from the adults and subadults in both macaque species

176   during the boat-based surveys. During the observation periods, we recorded the activity

177   of all visible primates at the time of detection by scan sampling [42] over 60 days from June

178   2012 to May 2014. We divided the behaviours into seven categories: feeding, grooming,

179   moving, resting, playing, fighting and other. Food items consisted of leaves, fruits,

180   flowers and other items, and food plants were taxonomically identified *in situ*.

181

182   *Vegetation survey*

183   We established a total of 16 transects (200–500 m × 3 m) on both sides of the river at 500

184   m intervals from the river mouth to 4,000 m. The total length of the 16 transects was

185   7,150 m, and the total surveyed area was 2.15 ha. We taxonomically identified trees ≥10

186   cm in diameter at breast height (DBH) and vines ≥5 cm in diameter that were located

187 within the transects [6]. Because these data did not include herbaceous climbers, we added

188 data on *Cayratia trifolia* (Vitaceae), an important food source for macaque species (see

189 results) in case the climber was entangled in the surveyed trees/vines.

190

191 *Monthly availability survey for* C. trifolia *fruits*

192 We carried out a fruit quantity survey of *C. trifolia*, which has fleshy, juicy, dark purple

193 and nearly spherical fruits ca. 1 cm in diameter [43]. It has been reported that sympatric

194 proboscis monkey at this study site consume *C. trifolia* [40]. Early in each monthly survey

195 from July 2012 to June 2014, we travelled by boat up to 4000 m from the river mouth and

196 counted all the visible mature and young fruits of *C. trifolia* on both riverbanks. Two

197 observers independently counted the number of fruits in a section, and the average was

198 defined as the availability of *C. trifolia* in the section. We judged the degree of fruit

199 maturation by its colour, with mature fruit being purple to black and young fruit being

200 green.

201

202 *Rainfall, water level and river width*

203 We measured daily rainfall every morning at base camp approximately 1.5 km from the

204 mouth of Menanggul River, using a tipping bucket rain gauge. We also recorded water

205 level and river width to evaluate the effects of river level on behaviours of the study

206 macaques. We installed a water level gauge at the mouth of Menanggul River, and

207 measured the water level at the end of the boat-based survey (17:00–19:00). We

208 measured the river width at the start and end points of each 50 m section with a laser

209 rangefinder, and the average value of the start and end points was used as a

210 representative value of the river width of the section.

211

212   *Data analysis*

213   To extract time-series characteristics of the increase or decrease in the number of *C.*

214   *trifolia* fruit, we conducted seasonal decomposition of time series by loess (STL) [44]

215   which is a filtering procedure for decomposing a seasonal times series into three

216   components: trend, seasonal, and remainder or residual.

217   We evaluated the effects of the availability of *C. trifolia* fruits, rainfall and river

218   width on the sighting frequency of the two macaque species counted during the boat-

219   based surveys, using a hierarchical Bayesian continuous-time structural equation model

220   (CtSEM). Models were fitted using the R package ctsem ver. 2.5.0 [45] with four chains

221   and 4,000 iterations. The CtSEM modelling addresses unequally spaced time intervals

222   in longitudinal data assessment. Since the number of survey days varied between

223   months and the survey days were not evenly spaced, the monthly mean values were not

224   strictly equally spaced time interval data. Through a hierarchical Bayesian framework,

225   CtSEM allows for the estimation of continuous time processes of a sample while

226   accounting for potential subject-level deviations by using population model estimates to

227   inform subject-level model priors [46]. The possible temporal autocorrelations among our

228   data are the total amount of *C. trifolia* fruits, and the monthly mean number of counted

229   macaques on each day. In addition, since there is a possibility that spatial

230   autocorrelation occurs between adjacent 50 m sections, the 500 m section was adopted

231   for examination of factors for sightings of macaques on riverbanks. As a result of the

232   evaluation of the spatial autocorrelation by Moran's *I* index, which is the most

233   commonly used coefficient in univariate autocorrelation analyses, such a trend was not

234   detected at each 500 m section for the monthly sighting frequency of the macaques, i.e.,

235   mean monthly number of counted pig-tailed (Moran *I* statistic index = −0.324 – −0.115,

236   *p* > 0.3) and long-tailed macaques (Moran *I* statistic standard deviate = −0.299 –

237   −0.085, *p* > 0.2), and availability of *C. trifolia* fruits (Moran *I* statistic standard deviate

238   = −0.224 – −0.101, *p* > 0.2). This indicates that the 500 m section is a unit that can be

239   analysed without considering spatial autocorrelation and is a suitable analytical unit for

240   subsequent analysis. Predictor and independent variables were z-standardized to build a

241   common metric. We performed the calculations using R ver. 3.6.1 [47]. In the

242   representation of the result of the model, SD refers to posterior standard deviation and

243   PCI refers to posterior credibility intervals. The PCI indicates the probability that the

244   parameter falls between the lower (2.5%) and upper (97.5%) limits.

245

246   **Results**

247   **Boat-based survey: sighting frequency of primates and consumed food items**

248   During the study period, there were a total of 3,180 detection events for six species of

249   primates, and 39,907 individuals were observed during boat-based surveys (Table 1).

250   Long-tailed and pig-tailed macaques accounted for 37.0% and 25.7% of the total

251   number of observed individuals, respectively (Table 1). We collected a total of 66 and

252   277 feeding records for pig-tailed and long-tailed macaques, respectively. Fruits and

253   flowers/buds of *C. trifolia* and *Dillenia excelsa* were by far the most important foods at

254   the riverbanks, which constituted 22.7%, and 50.9% (*C. trifolia*), and 42.4% and 18.8%

255   (*D. excelsa*) of the total feeding records in pig-tailed and long-tailed macaques,

256   respectively (Table 2).

257

Vegetation characteristics and food availability

259 We marked 1,645 trees and 497 vines (180 species, 125 genera, 52 families) along our

260 16 trails (for details, see [6]). *Cayratia trifolia* was entangled in only four of 1,645 marked

261 trees (0.24%), and was located in well-lit forest gaps caused by fallen trees. Conversely,

262 *C. trifolia* was clearly more abundant along the riverbanks, and was found in 12.5%–

263 72.5% of all 50-m river sections in each monthly survey. Contrary to the distribution

264 pattern of *C. trifolia*, *D. excelsa* was more abundant inside the forest: of 98 *D. excelsa*

265 plants in the vegetation transects, 84 (86%) were found in the inland forest (>50 m from

266 the riverbanks). The tendency was the same for *Mallotus muticus* (120 of 149 in the

267 inland forest), which was the third most common plant in feeding records of pig-tailed

268 and long-tailed macaques; *Albizia corniculate* (22 of 28 in the inland forest) and *Ficus*

269 spp. (20 of 23 in the inland forest), which were the fourth and fifth most common in the

270 feeding records of pig-tailed macaques; and *Antidesma thwaitesianum* (27 of 28 in the

271 inland forest) and *Xylosma sumatrana* (53 of 67 in the inland forest), which were the

272 fourth and fifth most common in the feeding records of long-tailed macaques.

273 The mean monthly number of counted *C. trifolia* fruits on the riverbanks was

274 23,283.7 (SD ±19,707.3; range 1,844–78,505). The mean monthly numbers of young and

275 mature fruits were 22,795.0 (±19,260.0; 1,806–76,002) and 488.6 (±572.4; 38–2,503),

276 respectively. STL based on the number of counted fruits in each monthly survey clarified

277 that the *C. trifolia* fruit availability seasonally fluctuated (Fig. 1). Fruit availability

278 declined in the middle of 2013 and then increased again, and tended to increase and

279 decrease every 4–6 months.

280

281 **Factors affecting temporal variation in sighting frequency of macaques**

282 The mean and 95% PCI of T_0 mean parameters (Table 3), representing the relationship

283 between the subject's initial states with their later states throughout the latent process,

284 were 0.408 (−0.089, 0.911), 0.313 (−0.199, 0.783) and 0.270 (−0.230, 0.805) for the

285 sighting frequency of pig-tailed and long-tailed macaques and *C. trifolia* fruits,

286 respectively. This indicated that there was no tendency for each parameter to increase or

287 decrease substantially over time, because for all parameters zero falls within the PCIs.

288 The manifest mean parameters (Table 3) represent the average level of the processes,

289 reflecting the intercepts of the sighting frequency of pig-tailed and long-tailed macaques

290 and availability of *C. trifolia* fruits.

291 The regression coefficients of the monthly mean sighting frequency of

292 macaques and monthly availability of *C. trifolia* fruits within each section denoted the

293 temporal autoregressive effects (Fig. 2); *C. trifolia* fruits had a temporal autocorrelation

294 that lasted approximately three months, but sighting frequency of macaques had no such

295 autocorrelation.

296 To assess the effects of the monthly availability of *C. trifolia* fruits on the

297 monthly mean sighting frequency of pig-tailed and long-tailed macaques, we evaluated

298 the drift parameters representing the cross effects (Table 3). The positive values showed

299 that the *C. trifolia* fruits had a positive effect on the sighting frequency of pig-tailed

300 (mean = 1.560, SD = 0.653, PCI = [0.131, 2.710]) and long-tailed (mean = 0.850, SD =

301 0.148, PCI = [0.581, 1.168]) macaques throughout the study period, indicating that

302 more macaques were sighted in areas where *C. trifolia* fruits were abundant.

303 Conversely, the sighting frequency of macaques did not affect the availability of *C.*

304 *trifolia* fruits. Additionally, the positive values indicated that the sighting frequency of

305   both macaques had positive effects on each other (pig-tailed to long-tail macaques,

306   mean = 0.984, SD = 0.367, PCI = [0.356, 1.802]; long-tailed to pig-tailed macaques,

307   mean = 0.753, SD = 0.281, PCI = [0.272, 1.373]).

308   Of the time-dependent/independent variables, we detected neither significantly

309   positive nor negative effects of the monthly rainfall or river width on the mean monthly

310   sighting frequency of both macaque species and the availability of *C. trifolia* fruits,

311   while the water level had a negative effect on those factors (Table 3).

312

Discussion

314   We found that ecological factors influenced the riverine habitat utilization of the two

315   sympatric macaque species in this study. One of the important factors was the availability

316   of *C. trifolia,* which was also the most consumed plant species by the macaques; their

317   temporal variation in sighting frequency at the riverbanks was positively related to the

318   abundance of *C. trifolia* fruits. Conversely, a previous study of proboscis monkeys at this

319   study site reported that food availability is not a fundamental factor for explaining their

320   riverine habitat utilization patterns in the late afternoon [17]. Differing dietary preference in

321   relation to the digestive physiology between the two macaque species and proboscis

322   monkeys may have created this inconsistency. Hindgut-fermenting primates (e.g.,

323   macaques) generally show a stronger preference for fruits than foregut-fermenting

324   primates (e.g., proboscis monkeys), allowing the latter to exploit a diet of leaves in greater

325   quantities [48,49]. Indeed, *C. trifolia* fruits are not the most preferred food by proboscis

326   monkeys at this study site [40].

327   Predation pressure may also be a factor that affects riverine habitat utilization

328   patterns for the two macaque species in this study, which was also shown for proboscis

329   monkeys [17]. The landscape of fear is an important driver of prey habitat utilization [50].

330   Although it is generally difficult to evaluate predation pressure on primates because of

331   how rare it is to directly observe cases of attempted or successful predation [34,51],

332   behavioural responses to predator presence were reported to have more far-reaching

333   consequences for prey ecology than the actual killing of individuals [12]. Indeed, despite

334   the abundance of food resources when studying these macaques, their use of riverbanks

335   was mainly limited to the late afternoon [17,32]; one reason for this could be related to their

336   nocturnal anti-predator strategy.

337   According to previous reports [20,25,30,52-54], clouded leopards (*Neofelis diardi*),

338   crocodiles (*Crocodylus porosus* and *Tomistoma schlegeli*), and pythons (*Python* spp.) may

339   be significant potential predators of macaques of any age or sex at this study site. It was

340   previously reported that proboscis monkeys were attacked by clouded leopards when they

341   were in trees [19]. Therefore, the studied macaques should also be exposed to a threat of

342   predation by clouded leopards, which generally show a strongly nocturnal activity pattern

343   [22], when the macaques sleep in trees during the night time; during this time, there is no

344   predation threat from crocodiles. As pythons also tend to move and search for prey during

345   the night, even in trees [55], threats of predation on macaques by pythons may be similar to

346   those by clouded leopards and may be predictable.

347   Riverine habitat utilization in the late afternoon and during sleeping periods at

348   night provides more effective protection against attacks from terrestrial predators such as

349   clouded leopards, because they can only approach the macaques from the landward side.

350   Indeed, several studies reported the use of riverine refugia by long-tailed and northern

351   pig-tailed macaques [16-18], possibly to reduce predation risk from such terrestrial predators.

352   Alternatively, the openness of the river banks may pose another problem: vulnerability to

353   predation by raptors. However, raptors that prey on adult diurnal primates are considered

354   to be absent from Southeast Asia [56], probably because there are few large raptor species

355   [57]. According to literature reviews [58,59], in the case of immature primates (e.g., infants and

356   juveniles), potential predators in the study area may include raptors such as black eagles

357   (*Ictinaetus malayensis*), crested serpent-eagles (*Spilornis cheela*), and bat hawks

358   (*Macheiramphus alcinus*) [19]. However, predation upon any primates by these animals was

359   not seen at the study site; thus, their predation pressure on macaques may be less

360   prominent. Therefore, late afternoon and night-time use of the riverbanks by macaques

361   may be a response to fear of nocturnal predators. Further studies that include longer-term

362   direct observations and nocturnal observations would provide direct data on predation

363   (e.g., capture rate, loss rate of group members, and contextual data such as age, sex, and

364   social status of prey) and degree of fear of macaques (e.g., vigilance behaviour inland and

365   on river banks). Such information could provide explicit insight into the nature of the

366   landscape of fear.

367   Contrary to the anti-predator strategy observed in proboscis monkeys, in which

368   they select sleeping sites in areas with narrow river widths [19,20], river width was not a

369   significant factor that predicted the sighting frequency of macaque species at the

370   riverbanks in this study. Although the two species of macaques were rarely observed

371   swimming in the river during this study, river crossing at narrower river sections have

372   been more commonly observed in proboscis monkeys [21,60]; this may be why river width

373   was not detected as a significant factor for the macaques. Both macaque species live in

374   larger groups with more males than proboscis monkeys [35,36], and larger groups are

375   generally more vigilant and are capable of detecting predators from longer distances,

376   which potentially reduces predation risk [33,61]. Therefore, the benefit of sleeping on the

377 riverbanks for the macaques may simply be the vantage point for detecting approaching

378 terrestrial predators like clouded leopards and pythons, rather than ease of crossing the

379 river. Additionally, to gain a better understanding of our riverine anti-predator hypothesis,

380 further studies should evaluate the differences and similarities of predation vulnerability

381 levels between the two macaque species in terms of their differences in

382 arboreality/terrestriality levels and riverine utilization frequency on the basis of accurate

383 population density estimates in the habitat. Furthermore, many studies emphasized the

384 importance of food resource proximity for sleeping site choice by various primate species

385 e.g., [18,30,62,63-66]. We do not deny the possibility that selecting sleeping sites on riverbanks

386 may also have a secondary effect of minimizing the macaques' foraging and traveling

387 costs by sleeping near their feeding areas (i.e., areas abundant in *C. trifolia*).

388   Echoing our observation of the negative effect of river level on macaque sighting

389 frequency at the riverbanks, Matsuda, et al. [23] noted such an effect in proboscis monkeys

390 at this study site; they suggested that this occurred because of reduced predation threats,

391 as terrestrial predators such as clouded leopards are prevented from foraging by deep

392 water covering the forest floor. For the macaques, the negative effect of river level could

393 be caused by decreased attractiveness of the dominant food resources on the riverbanks.

394 Because *C. trifolia* was mostly distributed along lower parts of the riverbanks at this study

395 site, these plants were under water or near the surface of the river when the water level

396 was high. The macaque species in this study may hesitate to forage for *C. trifolia* fruits

397 under such circumstances because of the risk of aquatic predator attacks, despite the

398 reduced terrestrial predator threat due to high-level river water. Indeed, while feeding on

399 *C. trifolia* fruits on low branches (1–3 m above the river), an adult male long-tailed

400 macaque was preyed upon by an estuarine crocodile (*Crocodylus porosus*) [20] at our study

17

401   site. As a result, the increased risks associated with *C. trifolia* foraging because of aquatic

402   predators may have diminished the value of *C. trifolia* as a food resource, and this led to

403   a low sighting frequency of the macaques. Additionally, high water levels may simply

404   make access to the riverbanks more difficult for both macaque species, although this is

405   unlikely: both macaque species were affected by water level, even though long-tailed

406   macaques are more arboreal than pig-tailed macaques [67].

407   This study showed that riverine utilization by pig-tailed and long-tailed

408   macaques was greatly influenced by temporal variation in food resource abundance and

409   predation pressure. In addition, qualitative comparisons of sympatric proboscis monkeys

410   suggested that the drivers of riverine utilization depend on the feeding niches of the

411   species and variations in how they cope with predation pressure due to differences in

412   behavioural patterns and social structure. The sighting frequency of both macaques in the

413   riverine habitat had a positive effect, and their dietary patterns in the riverine habitat were

414   similar; this indicated that their feeding niche separation is ambiguous, especially on the

415   riverbanks, although microhabitat segregation has been reported in these two closely

416   related, coexisting macaque species in East Kalimantan [26,31].

417   It should be noted, however, that we cannot deny the possibility of the

418   microhabitat segregation of these two macaque species in the inland habitat where they

419   were not observed for this study. Co-occurrence of these two macaque species on the

420   riverbanks at our study site may be due to the distinctive distribution of the food resource

421   *C. trifolia*. In fact, the sighting frequency of the macaques had no effect on the subsequent

422   abundance of *C. trifolia* fruits. This indicates that the fruits were super-abundant;

423   therefore, the effect of foraging by macaques on fruit abundance was nearly negligible.

424   The presence of super-abundant food would mitigate feeding competition and allow the

425 two macaque species to co-occur on the riverbanks. Tracking macaque groups into the

426 inland forest during other times of the day would reveal the importance of riverine

427 habitats in the diet of these species and provide further insights into the mechanisms of

428 coexistence. In addition to feeding competition, future studies should evaluate the effects

429 of competition for sleeping trees to elucidate coexistence mechanisms in sympatric

430 macaques, as we observed the two macaque species both sharing a sleeping tree and

431 competing for a sleeping tree.

432

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453

Author contributions

455 YO, GH and IM conceptualized the initial idea; YO and IM performed the data

456 collections; AT, HB, AW and JT arranged the data collection in the wild; YO performed

457 and interpreted the statistical analyses; YO and IM drafted the manuscript; all authors

458 contributed to the final version of the manuscript.

459

Competing interests

461 The authors declare that they have no competing interests.

462

Data availability statement

464 Data in support of the findings of this study are available from the corresponding

465 authors by reasonable request.

466

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657

Table and Figure legends

658

659   Table 1. Summary of detection events and the number of individuals sightings during

660   boat-based surveys (n = 434 days).

661   Table 2. Food items and parts consumed by southern pig-tailed and long-tailed

662   macaques with their observed frequency during boat-based surveys.

663   Table 3. Means, standard deviations (SD) and posterior credibility intervals (PCI) of the

664   CtSEM model. Asterisks (*) indicate that zero does not falls within the PCIs, i.e.,

665   positive or negative effects are indicated.

666   Figure 1. Decomposition plot of abundance of *Cayratia trifolia* fruits based on Seasonal

667   decomposition of time series by loess (STL). Numbers of *C. trifolia* fruits are

668   represented on the y-axis. Trend and seasonality indicate a relatively steady

669   increase or decrease over time, and a pattern that repeats, respectively.

670   Figure 2. Auto-regressive effects plotted for time intervals of $0 < \Delta t < 10$ months.

671   Parameters represent within-section persistence of the number of *Cayratia trifolia*

672   fruits, and the sighting frequency of pig-tailed and long-tailed macaques over time.

673   Solid lines represent auto-regressive effects for the number of *C. trifolia* fruits

674   over time, and dashed lines represents auto-regressive effects for the sighting

675   frequency of pig-tailed (a) and long-tailed macaques (b).

Table 1. Summary of detection events and the number of individual sightings during boat-based surveys (n = 434 days).

	Pig-tailed macaque	Long-tailed macaque	Proboscis monkey	Silver langur	Maroon langur	Orangutan
Total number of discovery event (times)	442	1357	1278	44	1	67
Total number of individual sighting (head)	10257	14785	14393	344	6	122
Averaged individual sighting (head/day ±SD)	23.63 ±24.07	34.07 ±23.05	33.16 ±23.86	0.79 ±2.67	0.01 ±0.29	0.28 ±0.91

Table 2. Food items and parts consumed by southern pig-tailed and long-tailed macaques with their observed frequency during boat-based surveys.

Species	Type	Pig-tailed macaque		Long-tailed macaque	
		Number of observation time	%	Number of observation time	%
Albizia corniculata	fruit	1	1.52		
	unkown	1	1.52		
Antidesma thwaitesianum	flower			10	3.61
	fruit			2	0.72
	leaf			1	0.36
Baccaurea stipulata	fruit	1	1.52		
Cayratia trifolia	fruit	15	22.73	141	50.90
	leaf			9	3.25
Dillenia excelsa	flower	24	36.36	45	16.25
	fruit	4	6.06	7	2.53
	leaf			2	0.72
	unkown			1	0.36
Eichhornia crassipes	stem			2	0.72
Ficus sp.	fruit	2	3.03	4	1.44
Gnetum gnemonoides	fruit			1	0.36
Mallotus muticus	flower	1	1.52	3	1.08
	fruit	3	4.55	8	2.89
	leaf	1	1.52	7	2.53
	unkown			1	0.36
Nauclea subdita	flower			1	0.36
	leaf	1	1.52		
Pternandra galeata	fruit	1	1.52	2	0.72
	leaf			2	0.72
Spatholobus cf. macropterus	leaf			1	0.36
Vitex pinnata	fruit			1	0.36
Xylosma sumatrana	flower			5	1.81
Ziziphus bornensis	fruit	1	1.52		
unkown	flower	6	9.09	16	5.78
	fruit	2	3.03	4	1.44
	leaf	2	3.03	1	0.36
Total		66		277	

Table 3. Means, standard deviations (SD) and posterior credibility intervals (PCI) of the CtSEM model.

Parameter	Mean number of pig-tailed			Mean number of long-tailed			Amount of *Cayratia trifolia* fruits		
	mean	SD	PCI [2.5%, 97.5%]	mean	SD	PCI [2.5%, 97.5%]	mean	SD	PCI [2.5%, 97.5%]
T_0 mean	0.408	0.253	-0.089, 0.911	0.313	0.251	-0.199, 0.783	0.270	0.262	-0.230, 0.805
Manifest means	-0.021	0.129	-0.277, 0.233	-0.030	0.078	-0.192, 0.188	-0.011	0.100	-0.211, 0.184
Drift Parameters									
Mean number of pig-tailed		–		0.984	0.367	0.356, 1.802 *	0.557	0.446	-0.264, 1.486
Mean number of long-tailed	0.753	0.281	0.272, 1.373 *		–		0.101	0.215	-0.309, 0.527
Amount of *Cayratia trifolia* fruits	1.560	0.653	0.131, 2.710 *	0.850	0.148	0.581, 1.167 *		–	
Effect of time dependent parameters									
Rainfall	0.008	0.054	-0.098, 0.115	-0.022	0.049	-0.119, 0.075	0.020	0.053	-0.084, 0.124
Water level	-0.179	0.052	-0.282, -0.077 *	-0.110	0.049	-0.205, -0.011 *	-0.174	0.053	-0.278, -0.071 *
Effect of time independent parameters									
River width	-0.466	0.257	-0.971, 0.045	-0.155	0.259	-0.638, 0.365	-0.225	0.258	-0.779, 0.245

Asterisks (*) indicate that zero does not falls within the PCIs, i.e., positive or negative effects are indicated.
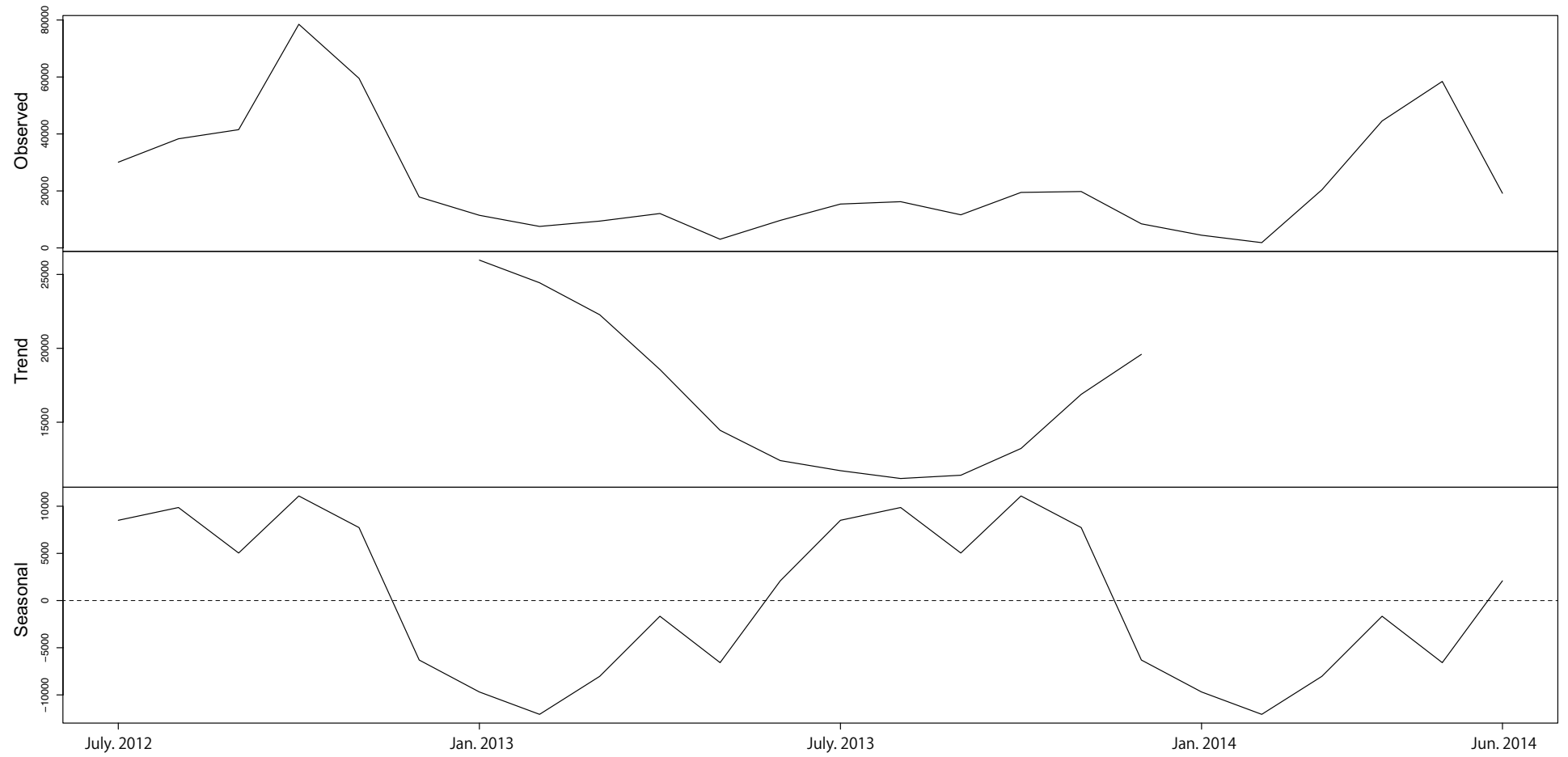
Fig. 1

Fig. 2a

Fig. 2b