1 Comparison of Feeding Behavior between Two Different-Sized Groups of Japanese

2 Macaques (*Macaca fuscata yakui*)

3

4 Yosuke Kurihara, Goro Hanya

5

6 Primate Research Institute, Kyoto University, Inuyama, Japan

7

8 Correspondence to: Y. Kurihara, Primate Research Institute, Kyoto University, Kanrin

9 41-2, Inuyama, Aichi, 484-8506 Japan. E-mail: kurihara.yosuke.35s@st.kyoto-u.ac.jp

10 Tel: +81-568-63-0545, Fax: +81-568-63-056

11

12 Short title: Feeding competition in Japanese macaques

ABSTRACT

Group-living animals face intragroup scramble and intergroup contest competitions. Many studies have shown that larger groups bear the costs of intragroup scramble competition, which negatively affects the reproductive success of females. Unlike most primate species, Japanese macaques in the Yakushima coastal forest show increased reproductive success with group size. However, it remains unclear how group size affects the behavior of macaques. The present study examined the effects of group size on the feeding behavior of Japanese macaques in the Yakushima coastal forest. We investigated 9–13 adult females from two different-sized groups via focal animal sampling during October 2012–August 2013. We compared the feeding behavior, including patch use, between the two groups. The larger group had a larger home range and spent more time feeding, especially on mature leaves. This suggests that intragroup feeding competition should be more intense in the larger group than in the smaller group. The feeding of mature leaves might enable the larger group to increase the number of co-feeding individuals. Contrary to the predictions that the larger group travels longer distances and spends more time moving, the smaller group traveled longer distances and spent more time moving, although the number of visited patches did not differ between the two groups. The immediate consequences of the loss of intergroup encounters could accumulate as daily travel costs, considering that group size is associated with intergroup dominance and that intergroup aggressive encounters occur frequently in the Yakushima coastal forest. This suggests that the smaller group has increased travel costs as a result of intergroup contest competition, which leads to decline in reproductive success.

Key words: feeding competition; ecological constraints model; patch use; group size; *Macaca fuscata yakui*

INTRODUCTION

Group living has benefits such as resource defense (advantage in intergroup feeding competition) [Wrangham, 1980], predator avoidance [Hamilton, 1971], and efficient resource detection [Struhsaker, 1981], and includes costs such as intragroup feeding competition [Janson & van Schaik, 1988] and disease transmission [Sanderson et al., 2014]. Feeding competition has been considered the most important factor affecting the fitness of group-living animals [Chapman et al., 2012]. Animals in groups face two types of group-size-dependent feeding competition: intragroup scramble competition and intergroup contest competition.

Intragroup scramble competition occurs when animals use the same food patches, thereby reducing the amount of food intake per capita for all members of the group [Janson & van Schaik, 1988; Koenig, 2002]. Its intensity increases with group size because larger groups need more food resources. The ecological constraints model [Chapman & Chapman, 2000] predicts that the larger groups are required to visit more food patches, which forces them to have larger home ranges, to travel longer distances and to spend more time feeding and moving. Two mechanisms are assumed to explain the need for more patches. One is patch depletion: a larger number of animals leads to faster depletion of food resources [Chapman & Chapman, 2000]. The other is spatial compression (termed "funneling"): larger groups will fill in a food patch more quickly because the patch can accommodate a limited number of animals. Therefore, animals in larger groups will leave the patch earlier and move further to the next patch than those in smaller groups because they will be pushed forward by succeeding animals [Isbell, 2012].

The costs of intragroup scramble competition could influence the fitness of group-living animals [Koenig, 2002]. Most of the studies have demonstrated

63   disadvantages of larger groups: the costs of intragroup scramble competition negatively

64   affect the net energy gain / reproductive success [van Schaik et al., 1983; van

65   Noordwijk & van Schaik, 1999; Borries et al., 2008; Zhao et al., 2011]. Meta-analysis

66   on the relationship between group size and behavior and demography [Majolo et al.,

67   2008] also support the predictions of the ecological constraints model. This study

68   concludes that, in most primate species, the costs of intragroup feeding competition

69   balanced or outweighed the benefits of intergroup feeding competition which lead to

70   higher net energy gain / reproductive success in large-sized, dominant groups than in

71   small-sized, subordinate groups through intergroup encounters [Janson & van Schaik,

72   1988; Koenig, 2002]. However, several studies have revealed different patterns of

73   relationships between net energy gain / reproductive success and group size [Cheney &

74   Seyfarth, 1987; Robinson, 1988; Koenig, 2000; Takahata et al., 2006]. In particular, it

75   remains untested the predictions of the ecological constraints model and unclear how

76   group size affects behavior when the net energy gain / reproductive success increases

77   with group size.

78   Among Japanese macaques (*Macaca fuscata yakui*) of the Yakushima coastal

79   forest, larger groups have higher birth rates than smaller groups [Suzuki et al., 1998;

80   Takahata et al., 1998]. Since group density is high (4.8 groups/km^2) [Yoshihiro et al.,

81   1999] and the home range is worth defending against other groups [Maruhashi et al.,

82   1998], aggressive intergroup encounters occur frequently [Saito et al., 1998; Sugiura et

83   al., 2000; Hanya et al., 2008]. The outcome of intergroup encounter is determined by the

84   relative group size: larger groups are dominant over smaller groups [Sugiura et al.,

85   2000]. Based on these results, previous studies have suggested that larger groups, which

86   have advantages in intergroup encounters, achieve higher reproductive success [Suzuki

87   et al., 1998; Takahata et al., 1998]. Japanese macaques in the Yakushima coastal forest

88   are ideal subjects to investigate the relationships between group size and feeding

89   competition because the effects of predation pressure on group size can be ignored

90   owing to the absence of predators in this region [Yamagiwa & Hill, 1998]. Majolo et al.

91   [2009] clarified that a larger group had a larger home range, traveled longer distances,

92   and spent more time moving than did a smaller group. These results supported the

93   predictions of the ecological constraints model, and showed that intragroup scramble

94   competition was more intense in the larger group. However, more detailed study is

95   needed to elucidate the mechanisms whereby, in contrast to most primate species,

96   reproductive success declines as group size decreases. It is necessary to investigate

97   feeding behavior thoroughly, including food patch use, which is the assumption of the

98   ecological constraints model. This investigation should be conducted under controlling

99   habitat quality, to avoid obscuring the effects of group size on feeding behavior [Majolo

100 et al., 2009].

101   The objective of this study was to reveal effects of group size on feeding

102 behavior including food patch use of Japanese macaques in the Yakushima coastal forest.

103 We compared behavioral proxies of intragroup scramble competition such as home

104 range size, travel distance, activity budget, and the number of visited patches between

105 two different-sized groups. Following the ecological constraints model, we predicted

106 that the larger group will have a larger home range, travel longer distances, spend more

107 time feeding and moving, and visit more patches than the smaller group. Additionally,

108 dietary composition and diversity were compared between the two groups. We predict

109 that the animals in the larger group will consume less-preferred and/or lower-quality

110 foods and increase dietary diversity due to intense intragroup scramble competition

111 [Steenbeek & van Schaik, 2001; Gogarten et al., 2014]. We also compared four

112 characteristics of patch use: patch residency time, patch size, the number of co-feeding

113 individuals, and inter-patch distance. According to the ecological constraints model, we

114 predicted that patch residency time will be shorter and the number of co-feeding

115 individuals will be larger in the larger group than in the smaller group. Patch size and

116 inter-patch distance will not differ between the two groups due to the similarity of

117 habitat environment. In addition, we examined two assumptions underlying the

118 ecological constraints model. First, to examine patch depletion, we compared feeding

119 rate between the two groups and examined the relationship between feeding rate and

120 patch residency time. If the patch depletion occurs more frequently in the larger group,

121 feeding rate in the larger group is expected to be lower than that in the smaller group,

122 which leads to shorter patch residency time. Second, to examine funneling, we

123 compared proportions of patches within which the maximum number of animals

124 outweighs the number of feeding sites between the two groups, and tested whether

125 patch residency time was shortened in such patches. If funneling occurs more frequently

126 in the larger group, animals in the group fill in feeding sites in the patch more frequently,

127 which leads to shorter patch residency time.

128

129 **METHODS**

130 This study was conducted with permission from the Yakushima Forest Ecosystem

131 Conservation Center and Kagoshima Prefectural Government, complied with the ethical

132 guidelines for field research of non-human primates of the Kyoto University Primate

133 Research Institute and the legal requirements of Japan, and adhered to the American

134 Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

135

136 **Study Site and Groups**

137 We studied two groups (KwA and KwCE, hereafter referred to as larger and smaller

138 groups, respectively) of Japanese macaques living in the western coastal forest on

139 Yakushima Island (30°N, 130°E) during October 2012–April 2013.The study period

140 included mating season (mid-August–January) [Yamagiwa, 1985]. The study area was

141 covered with primary and secondary warm temperate evergreen broad-leaved forest,

142 mainly comprising Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae [Agetsuma,

143 1995; Tsujino et al., 2007]. Vegetation was essentially the same in the respective home

144 ranges of each of the two groups because they had partly overlapped home ranges in

145 similar altitudinal zones (ca. 0–350 m a.s.l.). The larger group had 30–35 individuals,

146 including 6–8 adult females (>6 yrs old), 3–6 adult males (>6 yrs old), 15–21 juveniles

147 (1–5 yrs old), and 1–6 infants (<1 yr old). The smaller group had 13–15 individuals,

148 including 4–5 adult females, 4–5 adult males, 2–5 juveniles, and 0–4 infants. The sizes

149 of the larger and smaller groups were larger and smaller than the mean group size of this

150 local population (16.9 individuals) [Yoshihiro et al., 1999], respectively. Neither group

151 exhibited sub-grouping ranging during the study period [Kurihara, unpublished data].

152 We confirmed that the larger group had advantages in intergroup encounters in

153 accordance with the previous study [Sugiura et al., 2000]: the larger group won two of

154 the four encounters, and the smaller group did not win any encounter (0/8) (larger

155 group: 0.020 times/h; smaller group: 0.067 times/h).

156

157 **Behavioral Data Collection**

158 We followed one or both of the two groups each day and changed the focal group at

159 least once every three days. We investigated all adult females in the two groups (9–13

160 individuals) via one-hour focal animal sampling. We changed the focal animal every

161 hour and selected the following one for which the observation time accumulated so far

162 was shortest. Total observation time was 333 h (larger group: 199 h, smaller group: 134

163   h). Via instantaneous recording, we recorded activities (feeding, moving, resting,

164   grooming and other) of the focal animal every minute. When the focal animal was

165   feeding, we recorded the onset and the end of feeding to the nearest second and feeding

166   items (species and part). We regarded the onset as the time when the focal animal puts

167   food into the mouth, and the end as the time when 20 seconds had passed without

168   manipulating the food. In addition, we recorded feeding rate: the number of food units

169   that the focal animal puts into the mouth per 10 seconds. A food unit was defined for

170   each feeding item (one fruit, one leaf, one cluster of fruits, etc.). The recording was

171   repeated as many times as possible while the focal animal was feeding. We defined a

172   food patch as one individual tree or liana in which the focal animal fed. In the present

173   study, terrestrial patches (fallen fruits / seeds or insects) could not be defined because

174   these foods were uniformly distributed on the ground. When the focal animal left a

175   patch and returned back without feeding in any other patches, we considered it as one

176   patch. If the focal animal fed in a patch, we also collected the following data: (1) time

177   when the focal animal entered into and departed from the patch, (2) time when other

178   individuals entered into and departed from the same patch in which the focal animal fed,

179   and (3) length of major and minor axes and height of the patch. By using GPS

180   (GARMIN 60CSx, GARMIN), we recorded locations of the focal animal every 30

181   seconds and food patches when the focal animal visited.

182

183   **Data Analysis**

184   *Home Range and Travel Distance*

185   We estimated home range size and calculated travel distance based on GPS data points

186   plotted every five minutes. Home range size was estimated by using fixed kernel

187   density method. The grid size was 10 m $\times$ 10 m, and the smoothing parameter h was

188   determined by an *ad hoc* technique because the calculation by the least square cross

189   validation method did not converge. We regarded 95% kernel area as overall home

190   range, and 50% kernel area as the core area. Travel distance was calculated as the sum

191   of linear distance among GPS points plotted consecutively.

192

193   *Diet*

194   Feeding items were categorized into eight types: fruits / seeds, mature leaves, young

195   leaves (including buds and shoots), flowers (including nectar and flower buds), animal

196   matter, fungi, other (pith, bark, water, soil, etc.), and unidentified. Furthermore,

197   fruits/seeds were categorized as fallen (focal animals fed on the ground) or not (on the

198   trees). In addition, foraging (searching for food such as fallen fruits / seeds or insects in

199   the litter on forest floor) was considered as a type of feeding as per Hill [1997]. The

200   feeding behaviors could not be categorized into one specific feeding item, because

201   discriminating whether macaques searched fallen fruits / seeds, insects, or other

202   items in the litter could not be determined, and the food-searching behavior did not

203   always result in actual feeding.

204   To evaluate the monthly diversity of food repertoire, we calculated the

205   Shannon-Wiener index *H*:

206    $$H = -\sum_i pi \ln pi$$

207   where, p_i is the proportion of time spent feeding on the item *i* among the total feeding

208   time. *H* increases with the diversity of food repertoire, and equals zero when one

209   specific feeding item accounts for 100% of the total feeding time.

210

211   *Comparison of Behavioral Proxies of Intragroup Scramble Competition*

212   We constructed generalized linear mixed models (GLMMs) to explain diet composition,

213   activity budget, travel distance, and the number of visited patches (Table I). The

214   distribution of travel distances was normalized by square root transformation. In the diet

215   composition model, group (larger or smaller) was included as fixed effect and

216   observation date as random effect. To explain feeding on young leaves, we used

217   generalized linear model (GLM) because GLMM did not converge. In the remaining

218   models, group, copulatory behavior and dietary composition were included as fixed

219   effect, and observation date or identities of the focal animals as random effect. It has

220   already been established that diet composition and copulatory behavior affect the

221   overall feeding patterns of animals [Agetsuma, 1995; Matsubara & Sprague, 2004]. The

222   proportions of time spent feeding on fruits / seeds and animal matter were included as

223   factors of diet composition, because seasonal variation in diet could be considered on

224   the basis of these two types of foods. The proportion of time spent feeding on mature

225   leaves, young leaves, flowers, and time spent foraging were correlated with that on

226   fruits / seeds (Spearman's rank order correlation: mature leaves: $\rho = -0.71$, $p < 0.001$;

227   young leaves: $\rho = -0.42$, $p < 0.001$; flowers: $\rho = -0.39$, $p < 0.001$; foraging: $\rho = -0.46$,

228    $p < 0.001$), and the proportion of time spent feeding on fungi were correlated with that

229   on animal matter (fungi: $\rho = 0.56$, $p < 0.001$). As a factor of copulatory behavior,

230   whether male-female mounting series involving the focal animal was observed (1) or

231   not (0) during a one-hour session was included in the models on travel distance and the

232   number of visited patches, and number of one-hour sessions during which the mounting

233   series was observed in a day was included in the model for activity budget.

234   To examine the effects of "group" on each dependent variable, we compared

235   the models with and without the factor "group" using ANOVA (likelihood ratio test). If

236    $P < 0.05$ was obtained, "group" was regarded as a factor significantly affecting the

237   goodness-of-fit of the models. To examine the difference in the diversity of food

238 repertoire, the Shannon-Wiener index *H* of the two groups was compared using

239 Wilcoxon rank-sum test.

240

241 *Patch Use*

242 To investigate how group size affected the general characteristics of patch use, we

243 compared patch residency time, patch size, number of co-feeding individuals, and

244 inter-patch distance between the two groups. Patch residency time was calculated as the

245 feeding time of the focal animal in a patch to the nearest seconds. When entrance or

246 departure time into / from the patch by the focal animal could not be recorded, the data

247 on patch residency time for the patch was discarded. Patch size was calculated as the

248 volume of an elliptic cylinder (major axis*minor axis*height*π) [Kazahari & Agetsuma,

249 2010]. The number of co-feeding individuals was calculated as the average number of

250 other individuals (except infants) within the same patch during the focal animal's

251 residency [Hanya, 2009]. If, during a stay for two minutes, three individuals stayed with

252 the focal animal for the first 90 seconds and two individuals for the last 30 seconds, the

253 number of co-feeding individuals in the patch was regarded as 2.75. Inter-patch distance

254 was calculated as linear distance between patches that the focal animal visited

255 consecutively. We constructed GLMMs to explain patch residency time, patch size, and

256 number of co-feeding individuals (Table I). The distributions of patch residency time

257 and patch size were normalized by log transformation. The number of co-feeding

258 individuals was rounded up and transformed to integers to treat as Zero-inflated Poisson

259 distribution. In the model for patch residency time, group, patch size, number of

260 co-feeding individuals, and food category (fruits / seeds, mature leaves, young leaves,

261 and other) were included as fixed effect, and the identities of the focal animal as random

262 effect. In the model for patch size, group and food category were included as fixed

263   effect, and the identities of the focal animal as random effect. In the model for number

264   of co-feeding individuals, group, patch size, and food category were included as fixed

265   effect, and the identities of the focal animal as random effect. It has already been

266   established that (1) patch residency time is influenced by patch size and number of

267   co-feeding individuals, (2) number of co-feeding individuals is influenced by patch size,

268   and (3) the three characteristics of patch use are influenced by food category [Kazahari

269   & Agetsuma, 2008; Hanya, 2009; Potts et al., 2011]. Likelihood ratio tests were

270   conducted to examine the effects of group on patch residency time and patch size. For

271   the effects of group on number of co-feeding individuals, we examined the significance

272   of "group" in the model because the likelihood ratio test could not be conducted. In

273   addition, inter-patch distance was compared between the two groups using Wilcoxon

274   rank-sum test.

275   To test whether patch depletion occurred more frequently in the larger group,

276   we compared feeding rate between the two groups and examined correlation between

277   feeding rate and patch residency time. This analysis was conducted for each feeding

278   item separately to minimize effects of patch characteristics [Kazahari et al., 2013]. We

279   selected 12 main feeding items that accounted for 56% (290/516) of all visited patches

280   in the larger group and 43% (163/380) in the smaller group. Feeding rate was averaged

281   for each patch, and compared using Wilcoxon rank-sum test. The correlation between

282   feeding rate and patch residency time was tested using Spearman's rank order

283   correlation. Ideally, we should have examined time-series variations in feeding rate in

284   the patch [Kazahari & Agetsuma, 2008], but it was difficult to collect sufficient data for

285   conducting such an analysis. Although this comparison may be preliminary, group

286   differences in feeding rate could be detected sufficiently.

287   We tested whether funneling effect shortened patch residency time more

288 frequently in the larger group. First, we examined the relationships between the

289 maximum number of animals and the number of feeding sites in a patch. The number of

290 feeding sites was calculated by dividing the patch size by 4.18 m^3 (the volume of a

291 sphere with a radius of 1 m, a monopolizable area for one individual) [Hanya, 2009].

292 We defined a *filled patch* as when the maximum number of animals outweighed the

293 number of feeding sites in the patch. The proportion of the filled patches among all

294 visited patches was compared between the two groups by Fisher's exact test. Second,

295 we examined whether patch residency time was shortened at the filled patches. We

296 constructed GLMM on patch residency time for each group (Table I). The distribution

297 of patch residency time was normalized by log transformation. Whether the patch was

298 filled or not, food category (fruits / seeds, mature leaves, young leaves, and other), and

299 dominance rank of the focal animal were included as fixed effect, the identities of the

300 focal animal as random effect, and patch size as offset term. Dominance rank was

301 determined by the normalized David's scores calculated on the basis of aggressive

302 interaction [de Vries et al., 2006]. A likelihood ratio test was conducted to examine

303 effects of filling patches on patch residency time.

304   We used the *adehabitat* package for estimating home range and the *lme4* and

305 *glmmADMB* package for GLMM in R 3.0.1.We calculated travel distance and

306 inter-patch distance and visualized the home ranges by QGIS 2.0.1.All statistical tests,

307 except the likelihood ratio test, were two-tailed, and alpha level was set at < 0.05.

308

309 **RESULTS**

310 *Comparison of Behavioral Proxies of Intragroup Scramble Competition*

311 The larger group had a larger home range (Figure 1, larger group: 38.9 ha, smaller

312 group: 34.8 ha) and spent more time feeding than did the smaller group (Tables II, III),

313   although the two groups had the same core areas in size (9.4 ha).

314   Dietary composition was different but dietary diversity did not differ between

315   the two groups. The larger group spent less time feeding on fruits / seeds and young

316   leaves and more time feeding on mature leaves and foraging than did the smaller group

317   (Tables II, III). In particular, fallen fruits / seeds feeding time accounted for a larger

318   proportion of the total fruits / seeds feeding time in the larger group than in the smaller

319   group (Table III, larger group: 29.1% ± 36.2%; smaller group: 15.7% ± 28.5%;

320   likelihood ratio test: $df = 1$, $\chi^2 = 59.18$, $p < 0.001$). There were no differences in feeding

321   time on flowers, animal matter, and fungi (Tables II, III). Further, the monthly diversity

322   of food repertoire did not differ between the two groups (H: larger group: 2.43 ± 0.23,

323   smaller group: 2.40 ± 0.42; Wilcoxon rank-sum test: $W = 18$, $p = 0.58$). Over the study

324   period, 33 species and 57 items were common among the two groups (Appendix I,

325   larger group: 45 species, 83 items; smaller group: 47 species, 84 items). In a month, the

326   common repertoire accounted for 61.7% ± 11.7% of species and 56.7% ± 10.8% of

327   items in the larger group, and 66.7% ± 11.6% and 63.6% ± 12.6% in the smaller group,

328   respectively.

329   Contrary to the predictions, the smaller group spent more time moving (Tables

330   II, III) and traveled longer distances than did the larger group (Table III, larger group:

331   188 ± 72 m/h, smaller group: 219 ± 116 m/h; likelihood ratio test: $df = 1$, $\chi^2 = 7.67$,

332    $p < 0.01$). In addition, there were no differences in the number of visited patches (Table

333   III, larger group: 2.8 ± 2.3/h, smaller group: 3.0 ± 2.5/h; likelihood ratio test: $df = 1$,

334    $\chi^2 = 1.08$, $p = 0.30$).

335

336   *Patch Use*

337   The number of co-feeding individuals was larger in the larger group than in the smaller

338 group, although patch residency time, patch size, and inter-patch distance did not differ

339 between the two groups (Table III; patch residency time: larger group: 407.3 ± 544.5

340 sec., smaller group: 350.7 ± 520.0 sec.; likelihood ratio test: $df = 1$, $\chi^2 = 0.07$, $p = 0.79$;

341 patch size: larger group: 148.3 ± 211.1 m^3, smaller group: 137.6 ± 214.8 m^3; likelihood

342 ratio test: $df = 1$, $\chi^2 = 3.58$, $p = 0.06$; number of co-feeding individuals: larger group:

343 0.91 ± 1.68 individuals, smaller group: 0.40 ± 0.99 individuals; GLMM: Estimate ± SE

344 = -0.62 ± 0.10, $z = -6.48$, $p < 0.001$; inter-patch distance: larger group: 25.6 ± 33.0 m,

345 smaller group: 28.3 ± 35.0 m; Wilcoxon rank-sum test: $W = 17791$, $p = 0.25$).

346   Both patch depletion and funneling, the assumptions of the ecological

347 constraints model, did not occur more frequently in the larger group. First, we find

348 neither significant difference in feeding rate between the two groups nor significant

349 correlation between feeding rate and patch residency time for each group for all of the

350 12 main feeding items (Appendix II). Second, the proportions of filled patches among

351 all visited patches did not differ between the two groups (larger group: 23/494, smaller

352 group: 23/362; Fisher's exact test: $p = 0.29$). Contrary to the prediction, patch residency

353 time was longer in the filled patches than in the non-filled patches in both of the two

354 groups (Table IV, likelihood ratio test: larger group: $df = 1$, $\chi^2 = 50.19$, $p < 0.001$;

355 smaller group: $df = 1$, $\chi^2 = 52.20$, $p < 0.001$). We also checked the following definitions

356 of the number of feeding sites in a patch: (1) dividing an elliptic cylinder by 113 m^3 (the

357 volume of a sphere with a radius of 3 m), (2) dividing an ellipsoid ((4/3)*major

358 axis*minor axis*crown length*π) by 4.18 m^3, and (3) dividing an ellipsoid by 113 m^3.

359 Since we were able to obtain the same results based on all of these definitions, only the

360 results based on the initial definition are shown.

361

362 **DISCUSSION**

363   *Consistency with the Ecological Constraints Model*

364   In the present study, the larger group had a larger home range and spent more time

365   feeding than did the smaller group, in accordance with the predictions of the ecological

366   constraints model and the results of previous studies [Chapman & Chapman, 2000;

367   Majolo et al., 2009; etc.]. This suggests that intragroup scramble competition was more

368   intense in the larger group than in the smaller group.

369   To mitigate the costs of intragroup scramble competition, macaques in the

370   larger group changed dietary composition but did not increase dietary diversity. The

371   larger group spent more time feeding on mature leaves. Mature leaves are less

372   contestable because they are more abundant and less preferred than fruits / seeds and

373   young leaves [Agetsuma, 1995; Harris & Chapman, 2007; Hanya, 2009]. Among

374   Thomas's langurs (*Presbytis thomasi*), larger groups are also known to increase feeding

375   on less-preferred foods [Steenbeek & van Schaik, 2001]. In terms of patch use,

376   mature-leaf feeding positively influenced the number of co-feeding individuals (shown

377   in the model in Table III). Less-contestable foods enable animals to remain with many

378   individuals in a patch [Iwamoto, 1982; Agetsuma, 1995; Hanya, 2009]. Therefore, the

379   mature-leaf feeding might lead to maintaining spatial cohesion as a group. In addition,

380   the larger group spent more time feeding on fallen fruits / seeds and foraging (searching

381   for food in forest litter). Such terrestrial feeding might prolong the total feeding time in

382   the larger group, considering that there were no group differences in residency time on

383   the patch (tree or liana). Animals could save energy by increasing foraging on the

384   ground, given that terrestrial travel was less energetically costly than arboreal travel

385   [Janson, 1988; Hirsch et al., 2013]. In addition, dietary diversity did not differ between

386   the two groups. This contradicted the previous study, which suggested that larger groups

387   increased dietary diversity to deal with intense intragroup scramble competition

388   [Gogarten et al., 2014]. It is necessary to investigate energetic / nutritional intake of

389   animals in order to clarify whether this dietary strategy influences the fitness of animals.

390

391   *Inconsistency with the Ecological Constraints Model: Number of Visited Patches and*

392   *Patch Use*

393   One of the discrepancies between the results of our study and the ecological constraints

394   model is related to the number of visited patches and patch use. The ecological

395   constraints model predicted that larger groups stayed for shorter duration in one patch

396   and visited a larger number of patches [Chapman & Chapman, 2000]; however, patch

397   residency time and the number of visited patches were not different between the two

398   groups in the present study. There are two possible explanations for this.

399   First, patch depletion did not occur more frequently in the larger group. In our

400   study, we found no difference in feeding rate between the two groups and no correlation

401   between feeding rate and patch residency time for each group for all of the main feeding

402   items. This was consistent with previous studies demonstrating that increasing the

403   number of co-feeding individuals did not decrease feeding rate and that patch depletion

404   did not occur [Kazahari & Agetsuma, 2008; Tombak et al., 2012]. Furthermore,

405   Kazahari et al. [2013] demonstrated that the characteristics of the food items were

406   associated with the relationships between feeding-group size and feeding rate. For

407   example, feeding rate increased with feeding-group size in a patch where within-patch

408   food density was high. In our study, considering that the larger group depended more on

409   mature leaves, patch depletion will be unlikely to occur in the larger group because

410   mature leaves are superabundant within a patch. Thorough examination on the

411   time-series variations in feeding rate in combination with the characteristics of the food

412   items are required to elucidate this mechanism further in the Japanese macaques of

413   Yakushima.

414   Second, funneling did not occur in both of the two groups. The proportions of

415   filled patches did not differ between the two groups although it varied according to the

416   definitions (larger group: 4.7%–83.8%, smaller group: 6.4%–86.1%). Furthermore, in

417   contrast to the prediction, filling in patches did not shorten but prolonged patch

418   residency time. This could be explained by the result of a previous study that the

419   number of co-feeding individuals positively affected patch residency time in Japanese

420   macaques of Kinkazan Island [Kazahari & Agetsuma, 2008]. By staying with many

421   group members, macaques can be less dependent on following the group movement and

422   visually monitoring group members to maintain spatial cohesion [Kazahari & Agetsuma,

423   2010; Kazahari, 2014]. These results of funneling effect were robust regardless of the

424   definitions of feeding sites. Therefore, it is unlikely that feeding space in a patch

425   constrains patch residency time in Japanese macaques in Yakushima. Whether funneling

426   works as the mechanism of increasing the number of patches will depend on the

427   cost-benefit balance of group foraging, determined by the combinations of habitat

428   environment (patch size, presence of neighboring groups, etc.) and group size of a

429   population or species.

430

431   *Inconsistency with the Ecological Constraints Model: Travel Behavior*

432   The other discrepancy was travel behavior. In the present study, the smaller group

433   traveled longer distances and spent more time moving than did the larger group,

434   contrary to the predictions of the ecological constraints model. The intergroup

435   differences in travel distance and moving time were detected in our study even if other

436   factors such as dietary composition and mating behavior were controlled. There are two

437   possibilities to explain this. First, patch characteristics such as patch size, density, and

438 distribution could influence the moving behavior of animals [Maruhashi et al., 1998;

439 Cords, 2012; Dunn et al., 2012]. When the relative group size was related to intergroup

440 dominance, smaller-sized, subordinate groups may be obliged to use lower-quality

441 home range than larger-sized, dominant groups [Cheney & Seyfarth, 1987; Harris,

442 2006; Scarry, 2013]. In this case, smaller groups are expected to travel longer distances

443 in order to find high-quality food resources that have not been used by larger groups

444 [Robinson, 1988; Koenig, 2002]. In our study, we controlled vegetation differences in

445 the home ranges by selecting two neighboring groups as subjects. The two groups had

446 partly overlapped home ranges in the same altitudinal zones, and inter-patch distance

447 and patch size were not different between the two groups. Therefore, it is unlikely that

448 the heterogeneity of vegetation causes the differences in moving behavior between the

449 two groups.

450   Second, disadvantages in intergroup encounters could lead to great travel

451 costs of subordinate groups. After losing intergroup encounters, defeated groups were

452 forced to travel longer distances for a longer time than victorious groups [Srikosamatara,

453 1987; Crofoot, 2013]. In addition, defeated groups were forced to change travel

454 direction, which may cause inefficient and extended travel routes [Srikosamatara, 1987].

455 The frequency of intergroup encounters in the Yakushima coastal forest was as high

456 (0.067 times/h: smaller group in this study; 0.039 times/h: [Sugiura et al., 2000]) as

457 those in the study sites of the previous studies which showed losing encounters led to

458 longer travel distances (0.033 times/h [Crofoot, 2007; 2013]; 0.086 times/h

459 [Srikosamatara, 1987], given that the observation time during daytime was 10 h per

460 day). Considering that the intergroup encounters were aggressive in all of the study sites,

461 the immediate consequences of the loss of intergroup encounters could accumulate as

462 daily travel costs in the smaller group in Yakushima.

463   The results of our study on travel behavior also differed from those of Majolo

464   et al. [2009], which indicated that the larger group traveled longer distances and spent

465   more time moving, among Japanese macaques in the Yakushima coastal forest. This

466   would be explained by the difference in the relative and absolute sizes of the subject

467   groups. First, the size of the smaller group (18) in Majolo et al. was similar to the

468   average size of the neighboring groups (17.6), while the size of the smaller group in our

469   study (13–15) was half the average size of the neighboring groups (32.1). Under the

470   circumstance in Majolo et al., the smaller group might not be required to travel long

471   distances and/or for a long time as a consequence of losing encounters. Second,

472   Takahata et al. [1998] demonstrated that birth rate decreased further when group size

473   was less than 14 in the Yakushima coastal forest. The size of the smaller group (18) in

474   Majolo et al. was larger than that of the smaller group (13–15) in our study and that of

475   the group (14) that actually showed the lower birth rate in Takahata et al. Therefore,

476   only when the group size was below that threshold value and was smaller than the sizes

477   of the neighboring groups, animals in the group would have increased travel costs as a

478   result of intergroup competition.

479

480   *Implications of Population Dynamics in the Yakushima Coastal Forest*

481   This study revealed how feeding competition works in Japanese macaques in the

482   Yakushima coastal forest, which helps in understanding the behavioral mechanisms

483   underlying positive correlation between group size and reproductive success. Unlike

484   most primate species, birth rate increases with group size in the Yakushima coastal

485   forest. Previous studies in this population [Suzuki et al., 1998; Takahata et al., 1998]

486   have focused on the benefits of larger groups and costs of smaller groups through

487   intergroup contest competition from the point of view of energy intake: larger-sized,

488   dominant groups have higher-quality home ranges, which brings adult females better

489   energetic / nutritional conditions and higher birth rate. Although intragroup scramble

490   competition has not been investigated extensively, our study showed that the larger

491   group had the costs of intragroup scramble competition, as has been reported in many of

492   other primate species [e.g., Majolo et al., 2008]. In addition, our results were unique in

493   proposing behavioral mechanism causing positive correlation between group size and

494   reproductive success and suggesting that smaller groups have the costs of intergroup

495   contest competition from the point of view of energy expenditure: smaller-sized,

496   subordinate groups are required to travel long distances and/or for a long time, which

497   worsens energetic / nutritional conditions of adult females and lowers birth rate. Travel

498   behavior is energetically costly [Tucker, 1970; Dunn et al., 2013] and could affect

499   energy balance, and in turn, reproductive success of adult females [Emery Thompson et

500   al., 2012; McCabe et al., 2013]. To test how the costs and benefits of each group

501   translate into the differences in reproductive success, the energy balance of the animals

502   must be quantified: not only energy intake but also energy expenditure of animals in

503   different-sized groups should be considered to understand the mechanisms of group-size

504   effects on feeding behavior and reproductive success.

505 **ACKNOWLEDGMENTS**

REFERENCES

Agetsuma N. 1995. Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). International Journal of Primatology 15:595-609.

Borries C, Larney E, Lu A, Ossi K, Koenig A. 2008. Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. Behavioral Ecology 19:1186-1191.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates; the importance of travel costs. In: Boinski S, Garber PA, editors. On the Move: How and Why Animals Travel in Groups. Chicago: University of Chicago Press. p 24-42.

Chapman CA, Rothman JM, Lambert JE. 2012. Food as a Selective Force in Primates. In: Mitani J, Call J, Kappeler P, Palombit R, Silk J, editors. The Evolution of Primate Societies. Chicago: University of Chicago Press. p 149-168.

Cheney D, Seyfarth RM. 1987. The influence of intergroup competition on the survival and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology 21:375-386.

Cords M. 2012. The 30-Year Blues: What We Know and Don't Know About Life History, Group Size, and Group Fission of Blue Monkeys in the Kakamega Forest, Kenya. In: Kappeler PM, Watts DP, editors. Long-Term Field Studies of Primates. Springer. p 289-311.

Crofoot MC. 2007. Mating and feeding competition in white-faced capuchins (*Cebus capucinus*): the importance of short-and long-term strategies. Behaviour 144:1473-1496.

Crofoot MC. 2013. The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors. American Journal of Physical Anthropology 152:79-85.

541   de Vries H, Stevens JMG, Vervaecke H. 2006. Measuring and testing the steepness of

542   dominance hierarchies. Animal Behaviour 71:585-592.

543   Dunn JC, Asensio N, Arroyo‐Rodríguez V, Schnitzer S, Cristóbal‐Azkarate J. 2012.

544   The ranging costs of a fallback food: liana consumption supplements diet but increases

545   foraging effort in howler monkeys. Biotropica 44:705-714.

546   Dunn JC, Cristóbal-Azkarate J, Schulte-Herbrüggen B, Chavira R, Veà JJ. 2013. Travel

547   Time Predicts Fecal Glucocorticoid Levels in Free-Ranging Howlers (*Alouatta*

548   *palliata*). International Journal of Primatology 34:246-259.

549   Emery Thompson M, Muller MN, Wrangham RW. 2012. The energetics of lactation and

550   the return to fecundity in wild chimpanzees. Behavioral Ecology 23:1234-1241.

551   Gogarten JF, Bonnell TR, Brown LM., et al. 2014. Increasing group size alters behavior

552   of a folivorous primate. International Journal of Primatology 35:590-608.

553   Hanya G. 2009. Effects of food type and number of feeding sites in a tree on aggression

554   during feeding in wild *Macaca fuscata*. International Journal of Primatology

555   30:569-581.

556   Hanya G, Matsubara M, Hayaishi S., et al. 2008. Food conditions, competitive regime,

557   and female social relationships in Japanese macaques: within-population variation on

558   Yakushima. Primates 49:116-25.

559   Harris TR. 2006. Between-group contest competition for food in a highly folivorous

560   population of black and white colobus monkeys (*Colobus guereza*). Behavioral

561   Ecology and Sociobiology 61:317-329.

562   Harris TR, Chapman CA. 2007. Variation in diet and ranging of black and white colobus

563   monkeys in Kibale National Park, Uganda. Primates 48: 208-221.

564   Hill DA. 1997. Seasonal variation in the feeding behavior and diet of Japanese

565   macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. American Journal

566   of Primatology 43: 305-320.

567   Hirsch BT, Tujague MP, Di Blanco YE, Di Bitetti MS, Janson CH. 2013. Comparing

568   capuchins and coatis: causes and consequences of differing movement ecology in two

569   sympatric mammals. Animal Behaviour 86:331-338.

570   Isbell LA. 2012. Re-evaluating the ecological constraints model with red colobus

571   monkeys (*Procolobus rufomitratus tephrosceles*). Behaviour 149:493-529.

572   Iwamoto T. 1982. Food and nutritional condition of free ranging Japanese monkeys on

573   Koshima Islet during winter. Primates 23:153-170.

574   Janson CH. 1988. Food competition in brown capuchin monkeys (*Cebus apella*):

575   quantitative effects of group size and tree productivity. Behaviour 105:53-76.

576   Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food

577   competition: methods. Behaviour 105:165-186.

578   Kazahari N. 2014. Maintaining social cohesion is a more important determinant of

579   patch residence time than maximizing food intake rate in a group-living primate,

580   Japanese macaque (*Macaca fuscata*). Primates 55:179-184.

581   Kazahari N, Agetsuma N. 2008. Social factors enhancing foraging success of a wild

582   group of Japanese macaques (*Macaca fuscata*) in a patchy food environment.

583   Behaviour 145:843-860.

584   Kazahari N, Agetsuma N. 2010. Mechanisms determining relationships between feeding

585   group size and foraging success in food patch use by Japanese macaques (*Macaca

586   fuscata*). Behaviour 147:1481-1500.

587   Kazahari N, Agetsuma N, Tsuji Y. 2013. The relationships between feeding-group size

588   and feeding rate vary from positive to negative with characteristics of food items in

589   wild Japanese macaques (*Macaca fuscata*). Behaviour 150:175-197.

590   Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females

591   (*Semnopithecus entellus*). Behavioral Ecology and Sociobiology 48:93-109.

592   Koenig A. 2002. Competition for resources and its behavioral consequences among

593   female primates. International Journal of Primatology 23:759-783.

594   Majolo B, de Bortoli Vizioli A, Schino G. 2008. Costs and benefits of group living in

595   primates: group size effects on behaviour and demography. Animal Behaviour

596   76:1235-1247.

597   Majolo B, Knapp L, Hardie S., et al. 2009. Analysing the effects of group size and food

598   competition on Japanese macaque social relationships. Behaviour 146:113-137.

599   Maruhashi T, Saito C, Agetsuma N. 1998. Home range structure and inter-group

600   competition for land of Japanese macaques in evergreen and deciduous forests.

601   Primates 39:291-301.

602   Matsubara M, Sprague DS. 2004. Mating tactics in response to costs incurred by mating

603   with multiple males in wild female Japanese macaques. International Journal of

604   Primatology 25:901-917.

605   McCabe GM, Fernandez D, Ehardt CL. 2013. Ecology of reproduction in Sanje

606   mangabeys (*Cercocebus sanjei*): dietary strategies and energetic condition during a

607   high fruit period. American Journal of Primatology 75:1196-208.

608   Potts KB, Watts DP, Wrangham RW. 2011. Comparative feeding ecology of two

609   communities of chimpanzees (*Pan troglodytes*) in Kibale National Park,

610   Uganda. International Journal of Primatology 32: 669-690.

611   Robinson JG. 1988. Group size in wedge-capped capuchin monkeys *Cebus olivaceus*

612   and the reproductive success of males and females. Behavioral Ecology and

613   Sociobiology 23:187-197.

614   Saito C, Sato S, Suzuki S., et al. 1998. Aggressive intergroup encounters in two

615   populations of Japanese macaques (*Macaca fuscata*). Primates 39:303-312.

616 Sanderson CE, Jobbins SE, Alexander KA. 2014. With Allee effects, life for the social

617   carnivore is complicated. Population Ecology 56:417-425.

618 Scarry CJ. 2013. Between-group contest competition among tufted capuchin monkeys,

619   *Sapajus nigritus*, and the role of male resource defence. Animal Behaviour

620   85:931-939.

621 Srikosamatara S. 1987. Group size in wedge-capped capuchin monkeys (*Cebus*

622   *olivanceus*): vulnerability to predators, intragroup and intergroup feeding competition

623   [dissertation]. Gainesville: University of Florida. 126p.

624 Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs

625   (*Presbytis thomasi*): the folivore paradox revisited. Behavioral Ecology and

626   Sociobiology 49:100-110.

627 Sugiura H, Saito C, Sato S., et al. 2000. Variation in intergroup encounters in two

628   populations of Japanese macaques. International Journal of Primatology 21:519-535.

629 Suzuki S, Noma N, Izawa K. 1998. Inter-annual variation of reproductive parameters

630   and fruit availability in two populations of Japanese macaques. Primates 39:313-324.

631 Takahata Y, Koyama N, Ichino S, Miyamoto N, Nakamichi M. 2006. Influence of group

632   size on reproductive success of female ring-tailed lemurs: distinguishing between

633   IGFC and PFC hypotheses. Primates 47:383-387.

634 Takahata Y, Suzuki S, Agetsuma N., et al. 1998. Reproduction of wild Japanese

635   macaque females of Yakushima and Kinkazan Islands: a preliminary report. Primates

636   39:339-349.

637 Tombak KJ, Reid AJ, Chapman CA., et al. 2012. Patch depletion behavior differs

638   between sympatric folivorous primates. Primates 53:57-64.

639 Tsujino R, Yumoto T. 2007. Spatial distribution patterns of trees at different life stages

640   in a warm temperate forest. Journal of Plant Research 120:687-695.

641 Tucker VA. 1970. Energetic cost of locomotion in animals. Comparative Biochemistry

642 and Physiology 34:841-846.

643 van Noordwijk MA, van Schaik CP. 1999. The effects of dominance rank and group size

644 on female lifetime reproductive success in wild long-tailed macaques, *Macaca*

645 *fascicularis*. Primates 40:105-130.

646 van Schaik CP, van Noordwijk MA, de Boer RJ, den Tonkelaar I. 1983. The effect of

647 group size on time budgets and social behaviour in wild long-tailed macaques

648 (*Macaca fascicularis*). Behavioral Ecology and Sociobiology 13:173-181.

649 Wrangham RW. 1980. An ecological model of female-bonded primate groups.

650 Behaviour 75:262-300.

651 Yamagiwa J. 1985. Socio-sexual factors of troop fission in wild Japanese monkeys

652 (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates 26: 105-120.

653 Yamagiwa J, Hill DA. 1998. Intraspecific variation in the social organization of

654 Japanese macaques: past and present scope of field studies in natural habitats. Primates

655 39:257-273.

656 Yoshihiro S, Ohtake M, Matsubara H., et al. 1999. Vertical distribution of wild

657 Yakushima macaques (*Macaca fuscata yakui*) in the western area of Yakushima Island,

658 Japan: preliminary report. Primates 40:409-415.

659 Zhao D, Li B, Watanabe K. 2011. Impact of group size on female reproductive success

660 of free-ranging *Rhinopithecus roxellana* in the Qinling Mountains, China. Folia

661 Primatologica 82:1-12.

662 **FIGURE LEGENDS**

663 Figure 1. Home ranges of the larger and smaller groups (scale: 1/25,000). Doubled lines

664 indicate a road running through the study area.

Table I. Summary of Variables in the GLMMs				
Response variable	Unit of analysis	Explanatory variable	Error distribution	Offset term
Diet composition	Day	Group	Binomial	-
		Observation date (random)		
Activity budget	Day	Group	Binomial	-
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Observation date (random)		
Travel distance	Hour	Group	Gaussian	Observation time
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Animal ID (random)		
Number of visited patches	Hour	Group	Poisson	Feeding and moving times
		Copulation		
		Fruits / seeds feeding time		
		Animal matter feeding time		
		Animal ID (random)		
Patch residency time	Patch	Group	Gaussian	-
		Patch size		
		Number of co-feeding individuals		
		Food category		
		Animal ID (random)		
Patch size	Patch	Group	Gaussian	-
		Food category		
		Animal ID (random)		
Number of co-feeding individuals	Patch	Group	Zero-inflated Poisson	-
		Patch size		
		Food category		
		Animal ID (random)		
Patch residency time	Patch	Filled patch or not	Gaussian	Patch size
		Dominance rank		
		Food category		
		Animal ID (random)		

665

666

| Tabel II. Summary of Activity Budget and Dietary Composition of the Larger and Smaller Groups ||||
Activity	Diet	Larger group	Smaller group	Statistics
Feeding		45.1 ± 13.4	37.9 ± 14.0	$df = 1, \chi^2 = 9.13, p < 0.01$
	Fruits / seeds	37.2 ± 31.1	47.4 ± 38.3	$df = 1, \chi^2 = 2102, p < 0.001$
	Mature leaves	20.3 ± 23.0	16.7 ± 24.0	$df = 1, \chi^2 = 209.54, p < 0.001$
	Young leaves[a]	10.6 ± 20.2	14.6 ± 25.9	$df = 1, \chi^2 = 2668, p < 0.001$
	Flowers	1.5 ± 6.1	1.5 ± 4.5	$df = 1, \chi^2 = 0.0012, p = 0.97$
	Animal matter	1.0 ± 3.5	0.4 ± 1.9	$df = 1, \chi^2 = 0.13, p = 0.13$
	Fungi	0.3 ± 0.9	1.2 ± 3.8	$df = 1, \chi^2 = 0.20, p = 0.65$
	Other	3.2 ± 6.9	1.8 ± 4.2	-
	Unidentified	5.5 ± 7.7	5.7 ± 8.9	-
	Foraging	20.5 ± 17.9	10.5 ± 13.4	$df = 1, \chi^2 = 864.14, p < 0.001$
Moving		16.4 ± 4.8	22.0 ± 6.0	$df = 1, \chi^2 = 22.96, p < 0.001$
Resting		19.2 ± 9.6	16.3 ± 9.4	-
Grooming		19.2 ± 10.8	23.6 ± 14.2	-
Other		0.1 ± 0.3	0.2 ± 0.5	-
Mean percentage of time spent for each activity in a day ± SD is shown.				
a, the result of the likelihood ratio test for GLM is shown.				

667

Table III. Best-fit Models for Dietary Composition, Activity Budget, Number of Visited Patches, Travel Distance, and Patch Use

Item	Response variable	Explanatory variable	Estimate	SE	z	P
Dietary composition	Fruits / seeds	(Intercept)	-1.50	0.29	-5.19	< 0.001
		Group_Smaller	1.28	0.03	43.52	< 0.001
	Mature leaves	(Intercept)	-2.74	0.48	-5.76	< 0.001
		Group_Smaller	-2.01	0.16	-12.28	< 0.001
	Young leaves[a]	(Intercept)	-1.88	0.01	-354.62	< 0.001
		Group_Smaller	0.42	0.01	51.97	< 0.001
	Flowers	(Intercept)	-14.16	1.40	-10.09	< 0.001
	Animal matter	(Intercept)	-8.67	0.41	-20.95	< 0.001
	Fungi	(Intercept)	-15.22	1.83	-8.31	< 0.001
	Foraging	(Intercept)	-1.95	0.19	-10.31	< 0.001
		Group_Smaller	-0.91	0.03	-29.65	< 0.001
	Fallen fruits / seeds	(Intercept)	-4.74	0.45	-10.49	< 0.001
		Group_Smaller	-0.72	0.10	7.42	< 0.001
Activity budget	Feeding time	(Intercept)	0.10	0.11	0.95	0.34
		Group_Smaller	-0.31	0.10	-3.03	0.002
		Copulation	-0.03	0.11	-0.32	0.75
		Fruits / seeds feeding	-0.007	0.002	-3.59	< 0.001
		Animal matter feeding	-0.03	0.02	-1.36	0.17
	Moving time	(Intercept)	-1.64	0.07	-22.23	< 0.001
		Group_Smaller	0.38	0.08	4.98	< 0.001
		Copulation	-0.08	0.08	-0.91	0.37
		Fruits / seeds feeding	-0.0004	0.001	-0.30	0.77
		Animal matter feeding	-0.01	0.01	-0.80	0.42
Number of visited patches	Number of visited patches	(Intercept)	-2.79	0.06	-45.34	< 0.001
		Copulation	-0.05	0.16	-0.29	0.77
		Fruits / seeds feeding	0.0047	0.0009	5.31	< 0.001
		Animal matter feeding	-0.01	0.01	-1.59	0.11
Number of co-feeding individuals	Number of co-feeding individuals	(Intercept)	0.36	0.15	2.46	0.01
		Group_Smaller	-0.61	0.22	-2.76	0.006
		Patch size	0.001	0.0001	10.21	< 0.001
		Food category_mature leaves	0.24	0.11	2.23	0.03
		Food category_young leaves	0.07	0.13	0.55	0.58
		Food category_other	-0.46	0.22	-2.1	0.04

Item	Response variable	Explanatory variable	Estimate	SE	t	
Travel distance	Travel distance	(Intercept)	9.18	0.30	30.40	
		Group_Smaller	1.06	0.40	2.65	
		Copulation	-0.14	0.81	-0.18	
		Fruits / seeds feeding	0.01	0.01	1.86	
		Animal matter feeding	0.06	0.03	1.74	
Patch residency time	Patch residency time	(Intercept)	4.80	0.07	70.60	
		Patch size	0.00	0.00	6.18	
		Number of co-feeding individuals	0.26	0.03	8.27	
		Food category_mature leaves	0.29	0.10	2.75	
		Food category_young leaves	0.29	0.12	2.44	
		Food category_other	-0.26	0.14	-1.85	
Patch size	Patch size	(Intercept)	4.14	0.10	42.65	
		Food category_mature leaves	-0.52	0.12	-4.34	
		Food category_young leaves	0.55	0.14	4.06	
		Food category_other	0.17	0.16	1.05	

a, the result of GLM is shown.

668

669

Table IV. Best-fit Models for Funneling			
a. Larger group	Estimate	SE	t
(Intercept)	1.24	0.21	5.91
Filled_yes	2.12	0.29	7.21
Dominance rank	-0.42	0.30	-1.39
Food category_mature leaves	0.64	0.15	4.21
Food category_young leaves	-0.16	0.20	-0.80
Food category_other	-0.60	0.21	-2.87
b. Smaller group	Estimate	SE	t
(Intercept)	0.92	0.30	3.10
Filled_yes	2.07	0.28	7.46
Dominance rank	0.10	0.43	3.88
Food category_mature leaves	0.78	0.20	-1.61
Food category_young leaves	0.08	0.18	0.45
Food category_other	-0.42	0.26	0.23

670

% to the total feeding time in the larger group	% to the total feeding time in the smaller group	Family	Species	Life Form	Part	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
			Appendix I. Food Repertoire of the Larger and Smaller Groups									
5.15	5.49	Lauraceae	*Cinnamomum camphora*	Tree	Bud					L / S	L / S	L / S
2.50	3.66	Anacardiaceae	*Rhus succedanea*	Tree	Fruit	L / S	L / S	L / S				
1.75	3.66	Rubiaceae	*Psychotria serpens*	Liana	Mature leaf					L / S	L / S	L / S
2.28	3.63	Moraceae	*Ficus erecta*	Tree	Fruit			L / S	L / S			
2.73	3.51	Lauraceae	*Litsea acuminata*	Tree	Fruit		L	L / S	L	L	L / S	
7.29	3.26	Rutaceae	*Zanthoxylum ailanthoides*	Tree	Seed	L	L / S	L / S				
1.43	3.04	Rubiaceae	*Morinda umbellata*	Liana	Fruit		L / S	L / S				
2.14	2.95	Moraceae	*Ficus wightiana*	Liana	Fruit	L / S	L		S	L		L
0.55	2.89	Fagaceae	*Lithocarpus edulis*	Tree	Fruit	L / S	L / S	L / S				
6.21	2.57	Moraceae	*Ficus wightiana*	Liana	Mature leaf				L	L / S	L / S	L
3.62	2.37	Daphniphyllaceae	*Daphniphyllum teijimannii*	Tree	Mature leaf			L	L / S	L / S	L / S	L / S
1.54	2.35	Lauraceae	*Machilus thunbergii*	Tree	Shoot					L / S	L / S	L / S
1.51	2.19	Rubiaceae	*Morinda umbellata*	Liana	Mature leaf				L / S		L	
0.11	1.95	Theaceae	*Camellia japonica*	Tree	Nectar				L / S	L / S	L	L / S
2.78	1.92	Symplocaceae	*Symplocos lucida*	Tree	Mature leaf		L / S	L / S	L / S	L / S	L / S	L / S
3.51	1.66	Theaceae	*Eurya japonica*	Tree	Mature leaf				L	L	L / S	L / S
1.35	1.61	Theaceae	*Eurya emarginata*	Tree	Mature leaf	S				L / S	L / S	L
0.83	1.39	Rubiaceae	*Psychotria serpens*	Liana	Fruit	S	S	L	L / S	L		
0.49	1.29	Anacardiaceae	*Rhus succedanea*	Tree	Young leaf							L / S
0.67	1.27	Actinidaceae	*Actinidia rufa*	Liana	Fruit	L / S	L / S					
0.23	1.26	Fagaceae	*Quercus phillyraeoides*	Tree	Fruit	L / S	L / S	S				
1.73	1.25	Lauraceae	*Cinnamomum camphora*	Tree	Young leaf						L / S	L
1.45	1.23	Anacardiaceae	*Rhus succedanea*	Tree	Shoot							L / S
0.34	1.21	Myrsinaceae	*Ardisia sieboldii*	Tree	Fruit	S	L / S	S				
0.92	1.12	Aquifoliaceae	*Ilex integra*	Tree	Young leaf							L / S
0.36	1.01	Loranthaceae	*Taxillus yadoriki*	Liana	Fruit					S	L / S	S
1.57	0.95	Caprifoliaceae	*Lonicera affinis*	Liana	Shoot					L / S	L / S	L / S
1.90	0.85	Lauraceae	*Neolitsea sericea*	Tree	Fruit	L / S	L / S	L / S				
0.26	0.83	Moraceae	*Ficus pumila*	Liana	Fruit	L	L / S	S				
0.26	0.75	Sterculiaceae	*Firmiana plantanifolia*	Tree	Shoot							L / S
0.29	0.28	Capparidaceae	*Crateava religiosa*	Tree	Mature leaf						L	L / S
0.68	0.27	Moraceae	*Ficus erecta*	Tree	Mature leaf		L / S	L / S				L
0.17	0.25	Caprifoliaceae	*Lonicera affinis*	Liana	Young leaf					L / S	L	
0.20	0.19	Caprifoliaceae	*Lonicera affinis*	Liana	Fruit	L / S	L / S					
0.27	0.19	Ericaceae	*Vaccinium bracteatum*	Tree	Fruit	L / S	L / S					
0.72	0.18	Theaceae	*Eurya japonica*	Tree	Fruit	L / S	L / S	L				
1.69	0.17	Lauraceae	*Cinnamomum camphora*	Tree	Fruit	L / S						
0.48	0.16	Theaceae	*Camellia japonica*	Tree	Mature leaf		L		L / S			
0.27	0.15	Araliaceae	*Schefflera octophylla*	Tree	Mature leaf				L / S	L	L	
0.33	0.13	Capparidaceae	*Crateava religiosa*	Tree	Young leaf					L	L / S	
3.17	0.13	Meliaceae	*Melia azendarach*	Tree	Seed				L	L / S	L / S	L	L / S
0.53	0.11	Fagaceae	*Quercus salicina*	Tree	Fruit		L / S					
2.03	0.00	Anacardiaceae	*Rhus succedanea*	Tree	Stalk				L	L	L	L
1.24	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Fruit	L	L	L				
0.95	0.00	Lauraceae	*Neolitsea sericea*	Tree	Flower			L				
0.76	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Fruit		L	L	L	L	L	
0.62	0.00	Caprifoliaceae	*Lonicera affinis*	Liana	Mature leaf				L			
0.61	0.00	Moraceae	*Ficus erecta*	Tree	Stalk			L	L	L		
0.48	0.00	Moraceae	*Ficus wightiana*	Liana	Shoot							L
0.35	0.00	Aquifoliaceae	*Ilex rotunda*	Tree	Bud						L	
0.33	0.00	Fagaceae	*Quercus phillyraeoides*	Tree	Flower							L
0.21	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Mature leaf				L	L		
0.20	0.00	Euphorbiaceae	*Glochidion obovatum*	Tree	Fruit		L					
0.19	0.00	Polypodiaceae	*Pyrrosia lingua*	Epiphyte	Mature leaf				L	L		
0.19	0.00	Fagaceae	*Quercus salicina*	Tree	Mature leaf				L			
0.15	0.00	Moraceae	*Ficus microcarpa*	Liana	Fruit					L		
0.14	0.00	Aceraceae	*Acer morifolium*	Tree	Flower bud					L		
0.13	0.00	Rubiaceae	*Psychotria rubra*	Tree	Fruit		L	L				
0.12	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Mature leaf					L	L	
0.00	2.41	Fagaceae	*Lithocarpus edulis*	Tree	Bud							S
0.00	1.09	Hamamelidaceae	*Distylium racemosum*	Tree	Gall							S
0.00	1.08	Euphorbiaceae	*Glochidion obovatum*	Tree	Young leaf						S	
0.00	1.06	Convolvulaceae	*Erycibe henryi*	Liana	Mature leaf				S			
0.00	1.06	Lauraceae	*Machilus thunbergii*	Tree	Fruit							S
0.00	1.05	Theaceae	*Ternstroemia gymnanthera*	Tree	Fruit	S	S	S	S	S		
0.00	0.88	Ebenaceae	*Diospyros japonica*	Tree	Fruit		S					
0.00	0.83	Vitaceae	*Parthenocissus tricuspidata*	Liana	Fruit	S						
0.00	0.70	Moraceae	*Ficus wightiana*	Liana	Young leaf							S
0.00	0.57	Anacardiaceae	*Rhus succedanea*	Tree	Mature leaf			S				
0.00	0.55	Rubiaceae	*Morinda umbellata*	Liana	Young leaf							S
0.00	0.52	Lauraceae	*Litsea acuminata*	Tree	Mature leaf					S	S	
0.00	0.50	Fagaceae	*Lithocarpus edulis*	Tree	Bark						S	
0.00	0.41	Aquifoliaceae	*Ilex integra*	Tree	Bud							S
0.00	0.38	Asteraceae	*Farfugium japonicum*	Herb	Mature leaf					S	S	
0.00	0.27	Gleicheniaceae	*Dicranopteris linearis*	Fern	Mature leaf					S		
0.00	0.23	Chloranthaceae	*Sarcandra glabra*	Herb	Pith					S		S
0.00	0.22	Asteraceae	*Cirsium spinosum*	Herb	Mature leaf					S		
0.00	0.21	Lauraceae	*Litsea japonica*	Tree	Fruit					S	S	
0.00	0.18	Vervenaceae	*Callicarpa dichotoma*	Tree	Fruit		S					
0.00	0.17	Moraceae	*Ficus erecta*	Tree	Bud					S		
0.00	0.14	Moraceae	*Ficus nipponica*	Liana	Fruit	S						
0.00	0.13	Theaceae	*Camellia japonica*	Tree	Fruit							S
0.00	0.12	Myrsinaceae	*Maesa tenera*	Tree	Mature leaf			S				
0.00	0.11	Primulaceae	*Lysimachia sikokiana*	Herb	Mature leaf						S	S

L / S indicates that the food was eaten by the larger and smaller groups in the month.
L, Larger group; S, Smaller group.

Appendix II. Comparison of Feeding Rate between the Larger and Smaller Groups and Correlation between Feeding Rate and Patch Residency Time in the Two Group

Species	Part	Feeding rate (unit/sec.)		Wilcoxon rank-sum test	Correlation with patch residency time[a]			
		Larger group	Smaller group		Larger group	Smaller group		
Ficus wightiana	Fruit	0.48 ± 0.56	0.55 ± 0.16	$p = 0.7$	$p = 0.13$	$p = 0.75$		
Litsea acuminata	Fruit	0.33 ± 0.16	0.29 ± 0.10	$p = 0.14$	$p = 0.09$	$p = 0.50$		
Rhus succedanea	Fruit	0.51 ± 0.17	0.38 ± 0.12	$p = 0.06$	$p = 0.07$	$p = 1$		
Rhus succedanea	Young leaf	0.30 ± 0.19	0.25 ± 0.23	$p = 0.3$	$p = 0.78$	$p = 0.33$		
Daphniphyllum teijimannii	Mature leaf	0.13 ± 0.14	0.12 ± 0.05	$p = 0.38$	$p = 0.23$	$p = 0.33$		
Ficus erecta	Fruit	0.36 ± 0.27	0.43 ± 0.27	$p = 0.36$	$p = 0.89$	$p = 0.24$		
Zanthoxylum ailanthoides	Fruit	0.70 ± 0.21	0.72 ± 0.17	$p = 0.97$	$p = 0.59$	$p = 0.10$		
Symplocos lucida	Mature leaf	0.17 ± 0.07	0.23 ± 0.14	$p = 0.35$	$p = 0.55$	$p = 0.95$		
Cinnamomum japonicum	Young leaf	0.48 ± 0.10	0.49 ± 0.08	$p = 0.92$	$p = 0.17$	$p = 1$		
Lithocarpus (Pasania) edulis	Fruit	0.16 ± 0.04	0.23 ± 0.15	$p = 0.63$	$p = 0.33$	$p = 0.92$		
Neolitsea sericea	Fruit	0.77 ± 0.28	0.66 ± 0.10	$p = 0.31$	$p = 0.50$	$p = 1$		
Machilus thunbergii	Shoot	0.26 ± 0.17	0.32 ± 0.23	$p = 0.58$	$p = 0.33$	$p = 0.92$		

a, the results of Spearman's rank order correlation test are shown.

672

673

Figure 1