1 Inter-annual variation in nut abundance is related to agonistic interactions of foraging

2 female Japanese macaques (*Macaca fuscata*)

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17

18 Abstract

19   The importance of dominance status to foraging and ultimately survival and or

20   reproductive success in wild primates is known; however, few studies have addressed

21   these variables simultaneously. We investigated foraging and social behaviour among 17

22   adult female Japanese macaques (*Macaca fuscata*) on Kinkazan Island, northern Japan,

23   from September to November in two consecutive years (2004 and 2005) to determine

24   whether inter-annual variation in food availability was related to variation in agonistic

25   interactions over food resources and the feeding behaviour of animals of different

26   dominance rank. We compared energy obtained with daily energy requirements and also

27   examined the effect of variation in feeding behaviour on female survival and

28   reproductive success. Fruiting conditions differed considerably between the two years:

29   of four nut-producing species, only *Torreya nucifera* nuts fruited in 2004, whereas all

30   four species, particularly *Fagus crenata*, produced nuts in abundance in 2005. The

31   abundance and average crown size of *T. nucifera* trees were smaller than those of *F.*

32   *crenata*, and there was a higher frequency of agonistic interactions during 2004, when

33   dominant, but not subordinate, individuals were able to satisfy daily energy

34   requirements from nut feeding alone through longer nut feeding bouts. In contrast, all

35   macaques, regardless of their dominance rank, were able to satisfy their energy

36   requirements by feeding on nuts in 2005. Subordinate macaques appeared to counter

37 their disadvantage in 2004 by moving and searching for food more and maintaining

38 larger inter-individual distances. Several lower-ranking females died during the

39 food-scarce season of 2004, and only one dominant female gave birth the following

40 birth season. In contrast, none of the adult females died during the food-scarce season of

41 2005, and 12 females gave birth the following birth season. These findings suggest that

42 an interaction between dominance rank and inter-annual variation in food availability

43 are related to macaque behaviour, survival and reproduction.

44 Key-words: dominance rank, energy intake, foraging success, fruiting, inter-annual

45

46   Introduction

47   A fundamental problem facing group-living animals is that individuals are unable to

48   avoid within-group competition completely (Tilson and Hamilton 1984). In social

49   mammals, the influence of within-group competition on foraging success can ultimately

50   affect population levels by affecting adult mortality (Cheney *et al*. 1988), birth rate

51   (Holekamp *et al*. 1996) and infant mortality (Borries *et al*. 1991). Agonistic interactions

52   often cause differences in resource acquisition among individuals (Sutherland 1996;

53   Robichard *et al*. 1996; Holand *et al*. 2004). Such interactions become more frequent

54   and/or more severe when food resources are concentrated, food patches are small and/or

55   inter-patch distances are long, resulting in the monopolization of food resources by

56   dominant animals (Vogel *et al*. 2007). For example, in tufted capuchins (*Cebus apella*),

57   white-faced capuchins (*C. capucinus*) and Hanuman langurs (*Semnopithecus entellus*),

58   foraging success among dominant individuals is greater than that of subordinates when

59   resources are more concentrated, but not when more dispersed resources are available

60   (Janson 1985; Koenig 2000; Vogel *et al*. 2007). Foraging success can ultimately affect

61   population parameters like adult mortality (Wrangham 1981; Cheney *et al*. 1988), birth

62   interval (Frank 1986), birth rate (Bulger and Hamilton 1987; Holekamp *et al*. 1996),

63   and infant mortality (Borries *et al*. 1991).

64   Nuts are the staple foods of many frugivorous mammals in temperate regions of

65 Japan, Fagaceae, Betulaceae and Ulmaceae (Koike 2010). The abundance, distribution

66 and size of nut food patches/feeding sites available to animals vary from year to year

67 (Suzuki *et al*. 2005). Thus, we can predict that the rate of agonistic interactions

68 displayed by group-living animals will also vary between years, as in tropical regions

69 (Barton 1993). For example, in years when nuts are available but are monopolizable,

70 dominant individuals would achieve greater foraging success through agonistic defence

71 of food resources, leading to lower mortality and higher birth rates. Conversely, to

72 compensate for potential energy shortages, subordinate individuals might increase their

73 foraging effort, e.g., by prolonging their total feeding time (van Schaik and van

74 Noordwijk 1985) and increasing inter-individual distances to avoid agonistic

75 interactions (van Noordwijk and van Schaik 1987).

76   We tested the importance of dominance status in foraging, survival and short-term

77 reproductive success among wild Japanese macaques (*Macaca fuscata*) on Kinkazan

78 Island in northern Japan. Several previous studies have addressed the relationships

79 between i) inter-annual variation in the availability of nuts (i.e., the distribution of

80 nut-producing patches, patch size and density of nuts) and ii) the frequency of agonistic

81 interactions (Barton and Whiten 1993; Saito 1996), i) and iii) foraging-related behaviour

82 and foraging success among dominant and subordinate animals (Iwamoto 1987), and ii)

83 and iii) (Foerster *et al*. 2011) but few studies have systematically addressed all three

84 variables simultaneously, as we do in the present study. In addition, few studies

85 addressing inter-annual variation in food availability on mortality and the reproductive

86 output of dominant and subordinate animals (Bercovich and Strum 1993), have

87 considered foraging behaviour. Japanese macaques are a group-living, matrilocal

88 primate species typified by a clear, linear dominance hierarchy among adult females

89 (Kawamura 1958). Between September and November, which corresponds to the

90 mating season (Fujita *et al*. 2004), the macaques of Kinkazan feed on four main species

91 of fallen nut: *Fagus crenata*, *Zelkova serrata*, *Carpinus* spp. (including *C. tshonoskii*

92 and *C. laxiflora*) and *Torreya nucifera* (Tsuji *et al*. 2006). As the nutritional content, unit

93 weight and feeding speed are all greater for these nuts than other food items, their

94 acquisition allows macaques to deposit fat (Nakagawa 1989; Tsuji *et al*. 2008), which is

95 important for female oestrus and conception (Takahashi 2002; Fujita *et al*. 2004) and for

96 over-winter survival (Muroyama *et al*. 2006). Nut production on Kinkazan varies

97 greatly from year to year (Tsuji 2010), and the food habits (Tsuji *et al*. 2006) and

98 ranging patterns (Tsuji and Takatsuki 2009) of Kinkazan macaques vary accordingly. A

99 lack of predators and low intergroup competition (Saito *et al*. 1998) control for these

100 potentially confounding variables, and we can readily evaluate nut availability because

101 the macaques on Kinkazan feed mainly on nuts that have fallen to the ground during

102 this season (Nakagawa 1989).

103   We examined inter-annual variation in the availability of nuts, the frequency of

104 agonistic interactions, foraging-related behaviour and foraging success among dominant

105 and subordinate animals, and mortality and the reproductive output of dominant and

106 subordinate animals. We compared these variables over 2 years (2004–2005) to test the

107 hypothesis that inter-annual variation in nut availability is linked to variation in

108 agonistic interactions over nuts. In 2004, only *T. nucifera* fruited, whereas all four

109 nut-bearing species fruited in 2005, with *F. crenata* being especially abundant (Tsuji

110 2010). As a result, the energy available from the nuts was extremely low in 2004, but

111 higher in 2005 than any other year between 2000 and 2006 (Tsuji 2010). Under these

112 conditions, we tested the following four predictions.

113 *Prediction 1*: Agonistic interactions related to feeding would be more frequent in 2004

114   than in 2005.

115 *Prediction 2*: Agonistic interactions in 2004 would be linked to differences in

116   foraging-related behaviour (e.g., activity budgets, length of feeding bouts,

117   inter-individual distances) among females of different dominance rank, but there

118   would be fewer differences in 2005.

119   *Prediction 3*: In 2004, agonistic interactions would lead to greater foraging success

120   among dominant female macaques; this difference would be smaller in 2005.

121   *Prediction 4*: Inter-annual variation in the foraging success of females of different

122   dominance rank would be reflected in differential mortality and/or birth rates

123   during the following birth season.

124   Figure 1 should appear here

125   Methods

126   *Study area*

127   Our study site was Kinkazan Island (141°35'E, 38°16'N), located 0.7 km off Oshika

128   Peninsula of northern Japan. The island is 5.1 km long and 3.7 km wide, with a total

129   area of 9.6 km^2. The highest peak is 445 m above sea level. The mean (± SD) daily

130   rainfall on the island did not differ significantly between 2004 and 2005 between

131   September and November (paired *t*-test, $t = 1.47$, df = 90, $p = 0.144$), which

132   corresponds to the mating season, and between December and February (paired *t*-test, *t*

133      $= 0.46$, df = 89, $p = 0.444$), which corresponds to the food-scarce season (data source:

134   Ishinomaki Weather Station; http//:www.data.kishou.go.jp; Fig. 1a). In contrast, while

135   the mean (± SD) temperature between September and November did not differ between

136   2004 and 2005 (paired *t*-test, *t* = 1.47, df = 90, *p* = 0.144), the mean temperature was

137   significantly different between December and February of the 2 years (paired *t*-test, *t* =

138   3.77, df = 89, *p* < 0.001; Fig. 1b).

139

140   *Study animals and dominance rank*

141   Six troops of wild Japanese macaque live on Kinkazan (Izawa 2009). We studied

142   Troop A, which lives in the north-western part of the island (Tsuji and Takatsuki 2009).

143   Troop A have been habituated to observation at close proximity (< 10 m) since 1982.

144   During the study period, the troop size varied from 29 to 39 individuals, including 2–5

145   adult males (> 5 y), 14–17 adult females (> 5 y), 8–9 juveniles (1–5 y) and 1–12 infants

146   (< 1 y). Data on the maternal kinship and dominance ranks of 17 adult females was

147   available prior to the study (Table I, see also Tsuji 2007). We confirmed the dominance

148   hierarchy using a matrix based on submissive behaviours observed during *ad libitum*

149   sampling (see Lehner 1979), giving 4 high-ranking (*H*), 6 middle-ranking (*M*), and 7

150   low-ranking (*L*) females (Table I). Landau's index of linearity (*h*) for the adult females

151   was 0.926, reflecting an almost linear hierarchy (Lehner 1979). Japanese macaques are

152   seasonal breeders, and females on Kinkazan mate mainly from October to November

153   and give birth mainly between April and June (Fujita *et al*. 2004). From 1982 to 1995,

154   no female gave birth the year after a surviving infant was born (Izawa 2009). Thus, we

155   assumed that all females without an infant during the mating season could potentially

156   conceive (Fujita *et al*. 2004). Based on this, nine females had the potential to conceive

157   in 2004 ($H = 2$, $M = 3$, and $L = 4$) and 13 in 2005 ($H = 3$, $M = 4$, and $L = 6$; Table I).

158   *Data collection*

159   We observed A-troop from late September to late November in both years (41 d in 2004

160   and 36 d in 2005). Total data collection time was 578 hrs (304 hrs in 2004 and 274 hrs

161   in 2005). We followed the troop (17 females in 2004 and 14 females in 2005) from

162   dawn to dusk, during which time we conducted focal animal observations as follows: in

163   the morning we searched for females for whom we had less behavioural data than other

164   females. Once we found an appropriate female we started a focal sample. When we lost

165   the female during the sampling or we had obtained 6 hr of focal data, we terminated the

166   given focal sample, and searched for the next candidate females and started a new focal

167   sample after an interval of several minutes. We followed one to three adult females daily,

168   conducting a total of 146 focal samples during the study (72 focal samples in 2004 and

169   74 focal samples in 2005) (Table I). Mean length of a focal sample was 257 ± 70

170   minutes ($N = 146$). We ensured that we sampled all females during both the morning

171   (6:00–12:00) and afternoon (12:00–18:00) on different days (Table I). We did not follow

172 females in oestrus, who we identified by facial redness and/or consortship with adult

173 males (Fujita *et al*. 2004), to eliminate the effect of this physiological status on foraging

174 behaviour (Matsubara and Sprague 2004). Table I shows total sampling time for each

175 female. Our methodology adhered to Japanese legal requirements.

176 *Activity and food habits*

177   We recorded the behavioural state of the focal animal every minute using

178 instantaneous sampling. We classified activity into five categories: 1) feeding (including

179 picking up, processing and chewing at one location), 2) moving (including quadrupedal

180 walking, searching for food and running), 3) resting (including standing, sitting, lying

181 without motion), 4) social grooming and 5) others (including drinking, fighting and

182 alarm calling). If the animals were feeding at a given sampling point, we recorded the

183 number of food items consumed (e.g., one leaf, one entire fruit and nut, or a single bite

184 of bark). We categorised food items as 1) nuts (including *F. crenata*, *T. nucifera*, *Z.*

185 *serrata*, *Carpinus* spp. and others), 2) fruits/seeds (except for nuts), 3) leaves, 4) other

186 woody plant materials (including buds, bark, sap and gum), 5) herbaceous plants, 6)

187 fungi, 7) animal materials and 8) others (including soil and unidentified materials). As

188 the macaques fed on herbaceous plants with great rapidity, such plants were difficult to

189 identify. The females rarely discarded any part of the feeding unit. When the focal

190 female fed on a given food item at locations where observation conditions were poor

191 (e.g., within a tree crown or on a cliff), we recorded only the food item(s) and the

192 number of instantaneous sampling points to determine the duration of the feeding

193 episode. We defined the proportion of instantaneous sampling points for consuming

194 food item *i* relative to all sampling points associated with feeding as the "feeding time

195 percentage for food item *i*".

196 *Nut-feeding bout, size of feeding trees and number of neighbouring macaques*

197 For each nut feeding bout on the ground, we recorded the onset (when the focal

198 female ingested the first nut) and end of nut feeding (when the focal female left the

199 feeding tree). We also visually estimated the crown diameters of feeding trees in 1-m

200 intervals, from which we calculated the size of ground area (obtained by $\text{diameter}^2 \times \pi$)

201 beneath the feeding tree (m^2). Finally, we recorded the number of adult females within 3

202 m of the focal animal every 5 min to provide an indication of inter-individual distances.

203 Three metres has been shown to be the minimum distance tolerated by Japanese

204 macaques before agonistic interactions become more common while foraging (Saito

205 1996).

206 *Nut availability*

207 To evaluate the availability of edible nuts on the ground from the four different

208   species in the feeding patches for 2004 and 2005, we positioned 0.5×0.5-m quadrats at

209   ground level under randomly selected nut-producing trees ($N = 36$ for each species), and

210   estimated the number of nuts (#/m^2) from these quadrats. To calculate temporal changes,

211   we repeated this procedure every 2 to 3 weeks (2004: five times, 2005: six times), using

212   different trees each time. In 2004 only *T. nucifera* produced fruit so sampling was

213   limited to this species, while in 2005 all four species fruited and were sampled.

214   *Agonistic interactions*

215   We recorded agonistic behaviour on a continuous basis. We recorded only agonistic

216   interactions directed by the focal female toward other individuals, not those received by

217   the focal female, to simplify the analyses. Following previous studies (Barton 1993;

218   Saito 1996), we recorded both overt (e.g., attack) and subtle (e.g., displacement and

219   threat) agonistic interactions.

220   *Estimation of foraging success*

221   a) Estimation of metabolizable energy intake (MEI)

222   During the study period, we collected almost all food items consumed by the study

223   subjects (72 of 80 food items). Of these, we reported the nutritional characteristics of 37

224   items elsewhere (Tsuji *et al.* 2007; Tsuji and Takatsuki 2008). We report the nutritional

225   characteristics of the remaining 35 food items here. We dried each food item and

226   weighed it according to its feeding unit (g) ($N = 5$). Then we milled and analysed the

227   item for crude proteins (*%CP*, obtained by C.N. coder), neutral detergent fibre (*%NDF*,

228   obtained from the remnants left after neutral detergent boiling), crude lipids (*%CL*,

229   determined in a Soxhlet tube) and crude ash (*%CA*, obtained from the ignition loss)

230   (Tsuji *et al.* 2008). We measured the nutritional contents in duplicate and took the mean

231   of the results. We calculated the gross energy content of food item i (e_i, kcal/g) using the

232   following formula (Maynard *et al.* 1979):

233    $$e_i = 0.0415 \times (100 - [\%CP_i + \%CL_i + \%CA_i]) + 0.0565 \times \%CP_i + 0.0940 \times \%CL_i$$

234   We calculated the rate of consumption of different food items as the dry weight

235   consumed/min, and the rate of energy intake (EIS) by multiplying this number by the

236   gross energy content/g of that food item.

237   We estimated the amount of energy intake (kcal) for a focal female during an focal

238   sample, which provides a good indicator of foraging success, by combining behavioural

239   data from the subjects and EIS for each food item, as employed by Iwamoto (1982),

240   Nakagawa (1989) and Tsuji *et al.* (2008). First, we calculated the gross energy intake

241   (GEI) for a focal female during a focal sample (kcal), using the following formula:

242    $$GEI_i = \sum_{i=1}^{n} EIS_i \times FT_i \,,$$

243   where FT_i represents the number of instantaneous sampling points for consuming food

244   item i. To estimate the energy intake from food item i when observation conditions were

245   poor, we used the average EIS for the given food item (Nakagawa 1989; Tsuji *et al.*

246   2008). Then we multiplied the apparent energy digestibility for a given wild food item

247   (55%, Nakagawa 1989; Tsuji *et al.* 2008) by GEI to estimate the digestible energy

248   intake. Finally, we calculated metabolizable energy intake (MEI, kcal) during the focal

249   sample by subtracting the energy lost in urine (estimated as 4% of GEI, Nagy and

250   Milton 1979) from the digestible energy intake.

251
$$MEI_i = \left(\sum_{i=1}^{n} EIS_i \times FT_i \right) \times 0.51$$

252   b) Estimation of energy requirements (ER) during focal samples

253   We estimated daily energy requirements according to Nakagawa (1989): a non-nursing

254   adult female (8 kg in body weight) requires 517.9 kcal during one whole day in autumn

255   (600 min). This gave us the energy required per minute, and we calculated the energy

256   requirement during the focal sample i (ER$_i$) (kcal) using the following formula:

257
$$\begin{aligned} ER_i &= \left(\frac{517.9}{600} \right) \times OT_i , \\ &= 0.863 \times OT_i \end{aligned}$$

258   where OT_i represents the duration of the focal sample i. When MEI$_i$ was inferior to ER$_i$,

259   we considered the focal female to be experiencing an energy shortage.

260   *Population parameters*

261   During the birth season (from April to June) of 2005 and 2006, we recorded all births

262   and the presence of each adult female. We assumed that females who had disappeared

263   during our observations in the two seasons had died. For each dominance rank, we

264   calculated a modified birth rate and adult mortality (Fujita *et al*. 2004):

265   Modified birth rate = [# of females that delivered]

266   / [# of adult females with no infant < 1 y]×100

267   Adult mortality = [# of females disappeared]

268   / [# of adult females in last May]×100

269   *Statistical analyses*

270   We employed the Kruskal-Wallis tests and post hoc Steel-Dwass tests to test the

271   temporal change in nut availability. We employed the Mann-Whitney U tests to test the

272   difference in the average crown size of nut producing trees between 2004 and 2005. For

273   these analyses we set significant levels at 5%.

274   We constructed generalised linear mixed models (GLMMs) to examine the effects

275   of year, dominance rank and their interaction on 1) the frequency of agonistic

276   interactions, 2) the mean length of nut-feeding bouts in the focal sample, 3) time spent

277   on a given activity (represented by the number of instantaneous scan samples), 4)

278   number of neighbouring macaques and 5) MEI. We treated a single focal sample as a

279   unit of data. We conducted the statistical tests using the glmmML, lme4, MASS and aod

280   packages in the statistical software package R.2.9.1 (R Development Core Team, Vienna,

281   Austria). We included the identity of each individual as a random effect in our models

282   (Bolker *et al*. 2008). We analysed the main effects of year and rank and their interaction

283   on nut feeding and eating other food items separately. In order to eliminate the effect of

284   difference in focal sample lengths on the given dependent variables, we added an offset

285   term to the model for each analysis, except for the length of nut-feeding bouts, which

286   are independent of focal sample length (Table II). We selected the best models using the

287   "stepAIC" function in the MASS package in the statistical software package R.2.9.1 (R

288   Development Core Team, Vienna, Austria). We omitted seven focal samples where we

289   achieved less than 2 hrs of observation from the analyses.

290   Tables I and II should appear here

291   Results

292   *Food habits in autumn*

293   We obtained 19817 instantaneous scan samples (13859 in 2004 and 5958 in 2005) over

294   146 focal samples (Appendix 1). The females ate 60 different food items (excluding

295   unidentified insects and soil) in 2004 and fed mainly on fruits and seeds other than nuts

296   (5987 scans, 43.2% of all feeding time). Of the available nuts, the females spent more

297   time feeding on *T. nucifera* than any other nut variety (1109 scans, 8.0% of all feeding

298   time and 64.1% of total feeding time for all nuts; Appendix 1). Herbaceous plants (4060

299   scans, 29.3%) were also important food items in 2004. Conversely, in 2005, focal

300   females consumed 47 different food items, but fed mainly on nuts (3592 scans, 60.3%

301   of all feeding time). Of the nuts, the percentage of *F. crenata* consumed was the largest

302   (2872 scans, 48.2% of all feeding time and 79.9% of total feeding time for nuts)

303   (Appendix 1). The contributions of fruits and seeds other than nuts (1144 scans, 19.2%)

304   and herbaceous plants (560 scans, 9.4%) was lower in 2005.

305

306   *Description of nut-producing trees*

307   In 2004, 93 of the 128 nut-producing trees used by macaques were of the species *T.*

308   *nucifera*. The next most commonly used species was *Quercus serrata* ($N = 31$). The

309   mean $\pm$ SD nut tree size was 40 ± 28 m^2 (34 ± 20 m^2 for *T. nucifera*). In contrast, 220 of

310   the 294 nut-producing trees used by the macaques in 2005 were *F. crenata*. In addition,

311   macaques fed on the nuts of *T. nucifera* ($N = 28$), *Q. serrata* ($N = 17$), *Carpinus* spp. (N

312    $= 13$) and *Z. serrata* ($N = 9$). The average crown size of nut-producing trees was

313   significantly smaller in 2004 than in 2005 (Mann-Whitney *U*- test: all trees: $U = 10895$,

314    $N_1 = 128$, $N_2 = 294$, $p < 0.001$).

315

316   *Nut availability*

317   The density of *T. nucifera* nuts beneath the crowns of the trees examined peaked at

318     $20/m^2$ in September 2004, and decreased dramatically to almost zero in early December.

319   The temporal difference in nut availability was statistically significant (Kruskal-Wallis

320   test: $H = 12.5$, df = 4, $p = 0.013$), though multiple comparisons did not show any

321   significant differences among sampling times (Steel-Dwass tests, $p > 0.05$). In 2005, the

322   nut density under the crowns of *F. crenata*, *Z. serrata* and *Carpinus* spp. increased until

323   November, with densities maintained at over $50/m^2$ even in early December. All species

324   exhibited statistically significant temporal changes in 2005 (Kruskal-Wallis tests: *F.*

325   *crenata*: $H = 17.8$, df = 5, $p = 0.003$; *T. nucifera*: $H = 14.1$, df = 5, $p = 0.015$; *Z. serrata*:

326     $H = 11.7$, df = 5, $p = 0.039$; *Carpinus* spp.: $H = 13.3$, df = 5, $p = 0.021$), although

327   multiple comparisons did not show any significant differences among sampling times

328   (Steel-Dwass tests, $p > 0.05$) except for *F. crenata*, in which number of nuts on the

329   ground in early November was significantly greater than that in early December

330   (Steel-Dwass test, $p < 0.05$).

331

332   *Agonistic interactions (Prediction 1)*

333   We observed a total of 257 agonistic interactions during the study period. The mean (±

334   SD) frequency of agonistic interactions initiated by the focal animals (times/sampling

335   hour) was significantly greater in 2004 (0.68 ± 0.78, $N = 17$) than in 2005 (0.22 ± 0.27,

336    $N = 14$; paired t-test, $t = 2.62$, df $= 13$, $p = 0.021$). Agonistic interactions occurred more

337   frequently during feeding (both nut feeding and other feeding) in 2004, whereas they

338   occurred more frequently during resting and grooming in 2005 (Table IIIa). Selected

339   models showed that year affected the occurrence of agonistic interactions during all

340   activities with the exception of resting (i.e., the frequencies of agonistic interactions

341   were greater in 2004; Table IIIa). The frequency of agonistic interactions was greater

342   during resting in 2005 than in 2004 (Table IIIa). Moreover, rank showed a negative

343   association with the frequency of aggressive behaviour during feeding and moving

344   (Table IIIa). Finally, we found an interaction between rank and year for feeding on other

345   food items, showing that dominance status affected the frequency of agonistic

346   interactions during feeding in 2004, but not in 2005 (Table IIIa).

347   Table III should appear here

348   *Foraging-related behaviour (Prediction 2)*

349   The frequencies of total feeding, feeding on other items and moving all decreased from

350   2004 to 2005, whereas resting and grooming both increased from 2004 to 2005 (Table

351   IIIb). Furthermore, rank showed a negative association with total feeding ($H > M > L$).

352 Our models showed an interaction between rank and year for nut feeding, moving and

353 resting such that rank was negatively correlated with nut feeding in 2004 ($H > M > L$),

354 but this effect was not clear in 2005 ($H > M = L$; Table IIIb). Subordinates spent longer

355 moving and resting than dominants ($H < M < L$) in 2004 during the nut shortage,

356 whereas this relationship was not apparent in 2005 ($H = M = L$), when many nuts were

357 available (Table IIIb).

358 Year had a positive effect on the number of neighbours within 3 m of a focal

359 female during moving and resting (2005 > 2004; Table IIIc). Rank showed a negative

360 association with the number of neighbours a focal female had while moving ($H > M >$

361 L). Finally, an interaction between rank and year affected the number of neighbours a

362 focal female had during feeding (on both nuts and other items) and grooming. During

363 feeding, rank showed a negative association with the number of neighbours in 2004 (H

364 $> M > L$); however, there was no clear relationship in 2005 ($H > M < L$; Table IIIc).

365 Similarly, rank was negatively related to the number of neighbours while grooming in

366 2004 ($H > M > L$); however, this effect was not apparent in 2005 ($H = M <$ L; Table

367 IIIc).

368 Year, rank and their interaction in our models all affected the length of feeding

369 bouts on nuts, on other food items and on all food items. Rank showed a negative

370   association with nut feeding in 2004 ($H > M > L$) but not in 2005 ($H = M = L$; Table

371   IV).

372

373   *Foraging success (Prediction 3)*

374   We found clear differences in the association between MEI and rank in 2004 (Fig. 2,

375   Table IV). Most of the dominant individuals obtained enough energy from nuts to

376   exceed their estimated ER (Fig. 2a); they generally obtained less energy from other food

377   items than did subordinates (Fig. 2b). Furthermore, the MEI from all food items was

378   greater for dominant than for subordinate individuals (Fig. 2c). These differences in

379   MEI among females of different rank disappeared in 2005, when all females were able

380   to satisfy most of their ER by consuming nuts. We found no difference in MEI between

381   individuals of different rank in 2005 (Fig. 2, Table IV).

382   Table IV should appear here

383   *Survival and reproduction (Prediction 4)*

384   Three adult females (two middle-ranking and one low-ranking) died during the winter

385   of 2004 (mortality: 0% [0/4] for *H*, 33% [2/6] for *M* and 14% [1/7] for *L*), whereas no

386   adult females died during the winter of 2005 (Table I). However, the mortality of adult

387   females, as a group, did not significantly vary between 2004 and 2005 ([3/17] vs [0/14];

388   Fisher's exact test, $p = 0.251$).

389

390   Only one high-ranking female gave birth in the spring of 2005 (modified birth rate: 50%

391   [1/2] for *H*, 0% [0/3] for *M* and 0% [0/4] for *L*). In contrast, 12 females gave birth in the

392   spring of 2006 (modified birth rate: 100% [4/4] for *H*, 75% [3/4] for *M* and 83% [5/6]

393   for *L*; Table I). One of the high-ranking females with a surviving infant born in 2005

394   (*Kr*) also gave birth in 2006. The difference in birth rate between 2004 and 2005 was

395   close to significant ([1/9] vs [12/14]; Fisher's exact test, $p = 0.060$).

396   Figure 2 should appear here

397

398   **Discussion**

399   The frequency of agonistic interactions during each activity, with the exception of

400   resting, was greater in 2004 than in 2005, and decreased with dominance during feeding

401   (both on nuts and other food items) and moving in 2004 but not in 2005. Thus, our

402   results support Prediction 1. We found an interaction between year and dominance rank

403   during "other feeding" in 2004, when dominant females frequently initiated agonistic

404   interactions, however we did not find this same interaction during 2005 season . This

405   finding reflected differences in the main food items in the two years: food items other

406 than nuts consumed during the autumn of 2004 mainly consisted of fruits and seeds. In

407 2005, competition for such food items decreased because the macaques spent

408 significantly more time feeding on nuts, the availability of which was markedly higher

409 than in 2004, particularly those of *F. crenata*.

410 Engaging in aggressive interactions is disadvantageous for subordinate individuals,

411 because in addition to losing the opportunity to access quality food resources such as

412 nuts, they run the risk of physical injury (Sutherland 1996). In the present study,

413 low-ranking individuals were unable to remain at feeding trees for long periods in 2004,

414 possibly because of the increased risk of agonistic interactions. Among long-tailed

415 macaques (*Macaca fascicularis*) subordinate individuals tend to increase their foraging

416 effort when faced with food restrictions, e.g., they prolong total feeding time (van

417 Schaik and van Noordwijk 1985) and increase their inter-individual distances (van

418 Noordwijk and van Schaik 1987). In the current study, subordinate individuals engaged

419 in longer periods of moving (perhaps thereby increasing the amount of time available

420 for searching for food on the ground) and appeared to avoid getting within close

421 proximity to neighbouring macaques by increasing their inter-individual distances and

422 often feeding alone. Therefore, it seems that low-ranking macaques in our study

423 modified their foraging tactics in response to inter-annual variation in the food

424 environment. These findings support Prediction 2.

425   In 2004, the MEI from nuts available to subordinate individuals was much lower

426 than that available to dominant females, due to differences in the length of nut-feeding

427 bouts exhibited by the different dominance ranks. Previous studies have shown that the

428 amount of time spent at feeding patches is important to an animal's foraging success

429 (Janson 1985; van Noordwijk and van Schaik 1987), and our results support these

430 findings. In the present study, subordinate individuals were able to increase their MEI

431 by resorting to other food items and, in this way, some were able to obtain sufficient

432 total energy. Such foraging tactics only occurred over the short term because *T. nucifera*

433 nuts were not available in 2004 beyond late November, after which subordinate

434 individuals fed on non-nut foods. As a consequence, the MEI after late November could

435 not satisfy the ER of these individuals. From December to February, which corresponds

436 to the food-scarce season, Japanese macaques expend body fat accumulated during the

437 previous season (Muroyama *et al*. 2006), and it is possible that subordinate individuals

438 were unable to deposit adequate amounts of body fat after late November, 2004. A food

439 shortage at this time could thus cause more serious long-term consequences for

440 lower-ranking individuals. The fact that two mid-ranking adults and one low-ranking

441 adult died during the food-scarce season of 2004, and only one female gave birth the

442   next birth season, supports this hypothesis. However, nut production in 2005 was much

443   greater (Tsuji 2010) and the macaques were able to feed on nuts until the following

444   April (Tsuji personal observation). The MEI did not differ among females of different

445   dominance rank in 2005. Nutritional conditions during the food-scarce season of 2005

446   were therefore the same regardless of the dominance rank of focal females. The fact that

447   none of the females died during the food-scarce season of 2005, and 12 females gave

448   birth in the spring of 2006 supports this notion.

449   The physical conditions of temperature and rainfall often affect population

450   parameters (Pavelka *et al*. 2003); however, these conditions did not play a role in the

451   results of the present study because both daily rainfall and temperature during the

452   mating season (September to November) and following the food-scarce season

453   (December to February of the next year) were similar in 2004 and 2005, with the

454   exception of the temperature during the food-scarce season. The fact that no females

455   died during the food-scarce season of 2005, when the temperature was lower (that is,

456   more severe for the macaques) than that in 2004, further suggests that physical

457   conditions were not a factor in the present study. Our results therefore support

458   Predictions 3 and 4, although the findings for Prediction 4 are inconclusive owing to the

459   small sample size. The large annual variation in birth rate and mortality on the island

460   reported by Izawa (2009) may be partially explained by the yearly variation in nut

461   availability and consequent variation in feeding behaviour of animals in different

462   dominance rank. However, a longer-term study of population parameters needs to be

463   undertaken to confirm this hypothesis.

464   In conclusion, a great deal of evidence indicates that yearly changes in food

465   availability can affect the physical condition of animals, in terms of energy intake

466   (Knott 1998, Curran and Leighton 2000), body weight (Feldhamer *et al*. 1989), oestrus

467   patterns (Takahashi 2002) and birth rate/infant mortality (Eiler *et al*. 1989). The present

468   study tested the hypothesis that inter-annual variation in the food environment indirectly

469   influences primate nutritional conditions through modification of their foraging

470   behaviour. We also demonstrated that such variation in food supply differentially

471   affected animals according to dominance rank; subordinate females faced serious food

472   shortages during a year of low nut availability. In addition, the behavioural variation

473   was reflected in survival and reproduction, although these results should be treated with

474   caution due to small sample size and short-term measures of reproduction.Because

475   yearly changes in food availability, especially nut fruiting, are common in temperate

476   regions (Suzuki *et al*. 2005), yearly changes in staple food production may thereby

477   ultimately affect the population dynamics of animals.

478

485

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609

610   Figure legends

611   Figure 1. Mean daily rainfall a) and temperature b) from September to November

612   (mating season, left) and from December to February (food-scarce season, right) in

613   2004 and 2005. Data source: Ishinomaki Weather Station.

614   (http//:www.data.kishou.go.jp). *p*-values were obtained from paired *t*-tests for

615   yearly comparisons (see text).

616   Figure 2. Metabolizable energy intake (MEI, kcal) from a) nuts, b) other food items and

617   c) all foods during the study periods, 2004 (left) and 2005 (right). ●: high-ranking

618   (*H*); ●: middle-ranking (*M*); and ○: low-ranking (*L*). Energy shortage is

619   highlighted in grey (for details, see Methods).

Fig. 1

a) Rainfall

b) Temperature

Fig. 2

2004

2005

a) Nuts

High-ranking
Middle-ranking
Low-ranking
Energy shortage

b) Other food items

c) All foods

Metabolizable energy intake (kcal)

Length of focal sample (min)
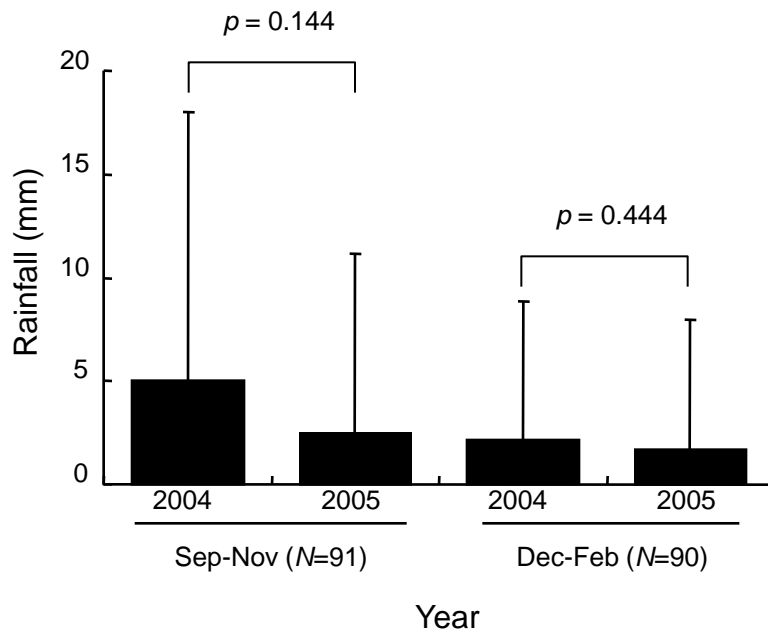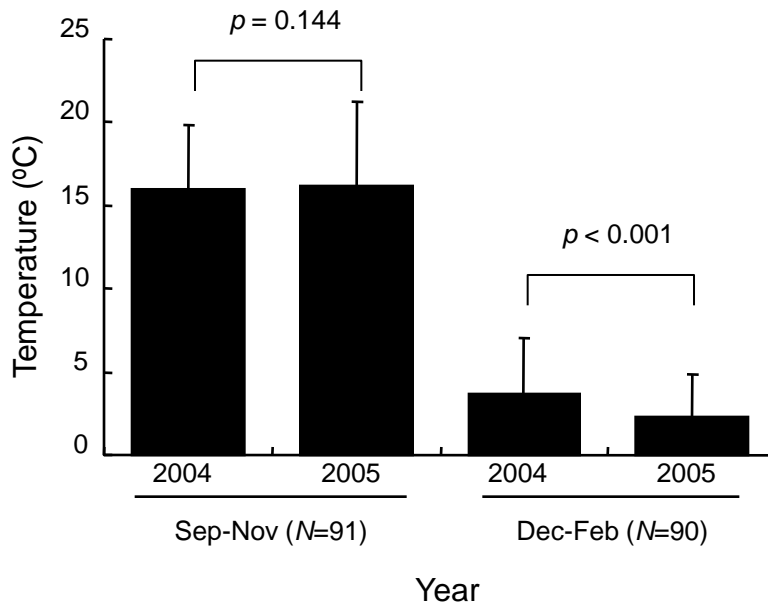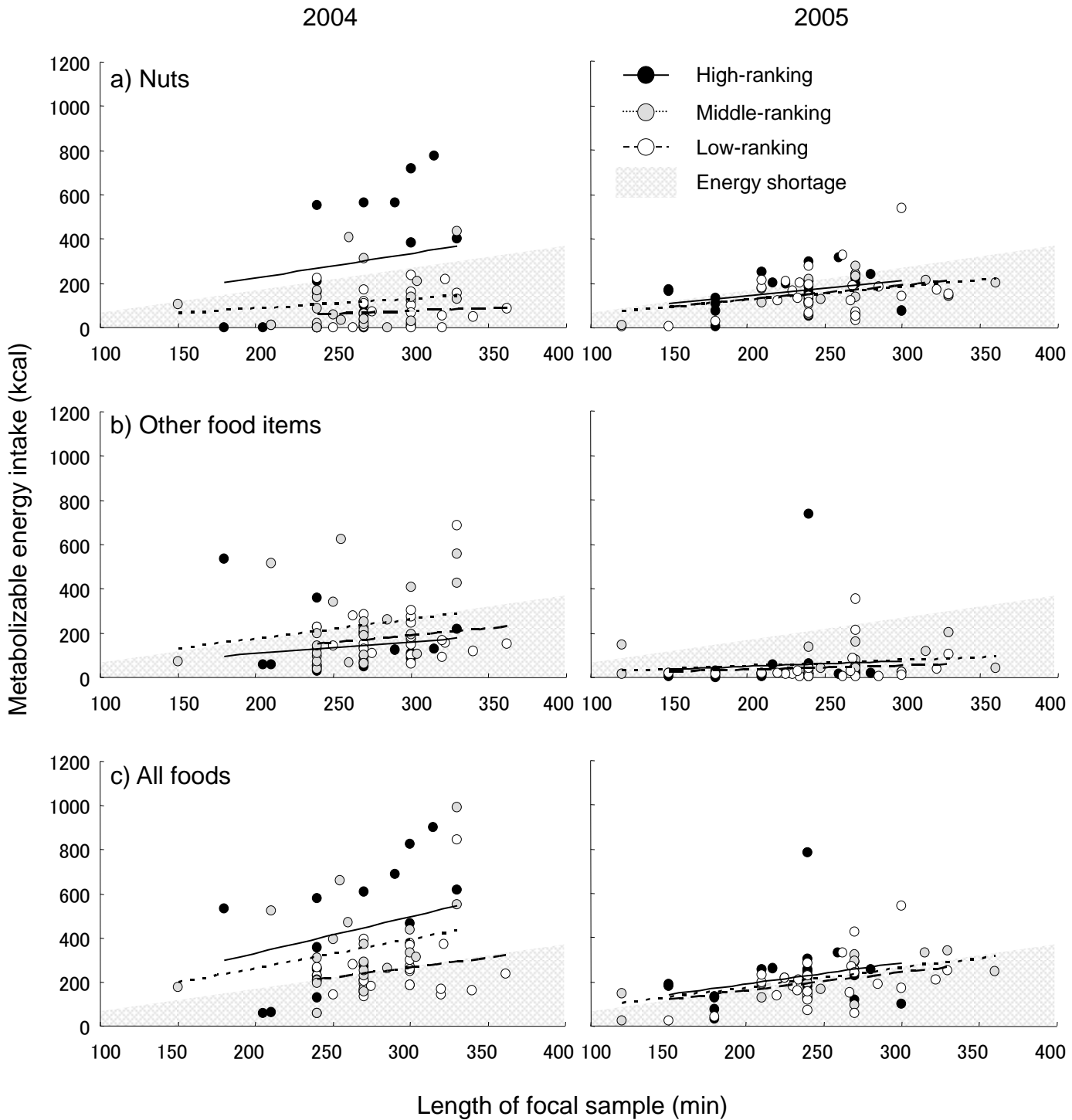
Table I. Details of the study subjects

ID	Rank[a]	Class	Age[b]	2004				2005			
				# Focal sample	Time (min)	Infant < 1y	Death / reproduced	# Focal sample	Time (min)	Infant < 1y	Death / reproduced
At	1	*H*	18	4 (2, 2)	952 (567, 385)	N	—	6 (3, 3)	1394 (744, 650)	N	R
Ar	2	*H*	6	4 (2, 2)	987 (505, 482)	Y	R	5 (1, 4)	1006 (233, 773)	Y	R
Kr	3	*H*	16	5 (2, 3)	1275 (478, 797)	N	—	7 (4, 3)	1426 (789, 637)	N	R
								1	*97*		
Rr	4	*H*	6	4 (2, 2)	1095 (565, 530)	Y	—	6 (1, 5)	1485 (298, 1187)	N	R
Be	5	*M*	19	4 (1, 3)	1081 (300, 781)	Y	—	4 (1, 3)	896 (247, 649)	N	R
								1	*110*		
Sf	6	*M*	17	5 (2, 3)	1260 (476, 784)	N	D	—	—	—	—
Ib	7	*M*	10	4 (2, 2)	1058 (541, 517)	N	—	6 (3, 3)	1088 (814, 274)	N	R
								2	*100*		
Kk	8	*M*	14	4 (2, 2)	1069 (454, 615)	N	—	6 (5, 1)	1434 (1157, 277)	N	—
Ku	9	*M*	11	4 (2, 2)	1038 (498, 540)	Y	—	5 (2, 3)	1115 (485, 630)	N	R
Hn	10	*M*	19	2 (1, 1)	245 (93, 152)	Y	D	—	—	—	—
				1	*93*						
Fr	11	*L*	17	5 (2, 3)	1342 (501, 841)	Y	—	5 (2, 3)	967 (315, 652)	N	R
								1	*32*		
Fp	12	*L*	8	6 (4, 2)	981(612, 369)	Y	—	6 (4, 2)	1453 (910, 543)	N	R
				3	*143*						
Fk	13	*L*	6	5 (3, 2)	1152 (618, 363)	N	—	6 (3, 3)	999 (530, 469)	N	R
				1	*35*			*2*	*81*		
Op	14	*L*	8	4 (2, 2)	1113 (575, 538)	N	—	5 (4, 1)	1208 (935, 273)	N	R
Hr	15	*L*	13	3 (1, 2)	902 (247, 655)	N	—	3 (1, 2)	703 (237, 466)	N	—
Mr	16	*L*	20	4 (2, 2)	1128 (508, 620)	N	D	—	—	—	—
Ml	17	*L*	11	5 (2, 3)	1334 (511, 823)	Y	—	5 (1, 4)	1224 (228, 996)	N	R

Ar is *At*'s daughter. *Rr* is *Kr*'s daughter. *Be*, *Sf*, and *Ib* are sisters. *Fk* and *Fp* are *Fr*'s daughters. *Mr* and *Ml* are sisters.

D: died during the winter (December to May in the next year), R: reproduced the following spring (April to June in the next year). *H*: high-ranking, *M*: middle-ranking, and *L*: low-ranking.

[a] from Tsuji (2007), [b] Age at April in 2004.

Numbers and times of focal samples within parentheses indicate those collected in morning (left) and afternoon (right).

Numbers and times of focal samples within italics indicate those excluded from the analyses.

Table II. Dependent variables, independent variables, offset, error distributions and link functions used in the GLMM analysis.

Prediction	Dependent variables	Independent variables	Offset	Error distribution	Link function
1	# agonistic interaction	Year, Rank, Year × Rank	log(time of focal sample)	Poisson	log
2	# instantaneous sampling points	Year, Rank, Year × Rank	log(time of focal sample)	Negative binomial	log
2	# neighbouring macaques	Year, Rank, Year × Rank	log(# scan sampling)	Negative binomial	log
2	Length of nut feeding bouts (sec)	Year, Rank, Year × Rank	—	Gaussian	identity
3	Energy intake during the focal sample (kcal)	Year, Rank, Year × Rank	log(time of focal sample)	Gaussian	identity

Table III. Factors affecting agonistic interactions, activity budgets and number of neighbouring macaques revealed by the GLMM analysis using year, rank, and their interaction as independent variables (139 focal samples).

Dependent variables.	Independent variables	Type of activity					
		Feeding (nuts)	Feeding (other than nuts)	Feeding (all)	Moving	Resting	Grooming
		Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
a) # agonistic interactions	Intercept	0.296 ± 0.824 (z = 0.36, p = 0.720)	1.912 ± 1.437 (z = 1.33, p = 0.183)	0.746 ± 0.551 (z = 1.35, p = 0.176)	-0.847 ± 0.668 (z = -1.27, p = 0.205)	-7.352 ± 1.182 (z = -6.22, p < 0.001)	-3.766 ± 0.755 (z = -4.99, p < 0.001)
	Year	-1.883 ± 0.383 (z = -4.92, p < 0.001)	-2.081 ± 0.960 (z = -2.17, p = 0.030)	-2.033 ± 0.253 (z = -8.04, p < 0.001)	-1.384 ± 0.246 (z = -5.64, p < 0.001)	0.385 ± 0.646 (z = 0.60, p = 0.551)	-1.113 ± 0.416 (z = -2.68, p = 0.007)
		(2004 > 2005)	(2004 > 2005)	(2004 > 2005)	(2004 > 2005)	(2004 < 2005)	(2004 > 2005)
	Rank	-1.319 ± 0.345 (z = -3.82, p < 0.001)	-1.780 ± 0.913 (z = -1.95, p = 0.051)	-1.507 ± 0.245 (z = -6.16, p < 0.001)	-1.107 ± 0.292 (z = -3.79, p < 0.001)	—	—
	Year × Rank	—	-0.254 ± 0.722 (z = -0.35, p = 0.724)	—	—	—	—
		(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H = M = L$)	(2004: $H = M = L$)
		(2005: $H > M > L$)	(2005: $H = M = L$)	(2005: $H > M > L$)	(2005: $H > M > L$)	(2005: $H = M = L$)	(2005: $H = M = L$)
b) # instantaneous scan samples	Intercept	-1.720 ± 0.249 (z = -6.91, p < 0.001)	0.795 ± 0.193 (z = 4.12, p < 0.001)	0.064 ± 0.159 (z = 0.41, p = 0.685)	-0.370 ± 0.128 (z = -2.88, p = 0.004)	-6.012 ± 0.495 (z = -1.22, p = 1.000)	-2.655 ± 0.331 (z = -8.01, p < 0.001)
	Year	—	-1.784 ± 0.126 (z = -1.42, p = 1.000)	-0.599 ± 0.080 (z = -7.44, p < 0.001)	-0.654 ± 0.103 (z = -6.34, p < 0.001)	2.431 ± 0.315 (z = 7.72, p < 0.001)	0.616 ± 0.185 (z = 3.32, p < 0.001)
		(2004 = 2005)	(2004 > 2005)	(2004 > 2005)	(2004 > 2005)	(2004 < 2005)	(2004 < 2005)
	Rank	-0.779 ± 0.169 (z = -4.60, p < 0.001)	—	-0.131 ± 0.047 (z = -2.77, p = 0.006)	—	0.792 ± 0.201 (z = 3.94, p < 0.001)	—
	Year × Rank	0.398 ± 0.087 (z = 4.59, p < 0.001)	—	—	0.028 ± 0.030 (z = 0.91, p = 0.361)	-0.416 ± 0.126 (z = -3.31, p < 0.001)	—
		(2004: $H > M > L$)	(2004: $H = M = L$)	(2004: $H > M > L$)	(2004: $H < M < L$)	(2004: $H < M < L$)	(2004: $H = M = L$)
		(2005: $H > M = L$)	(2005: $H = M = L$)	(2005: $H > M > L$)	(2005: $H = M = L$)	(2005: $H = M = L$)	(2005: $H = M = L$)
c) # neighbouring macaques	Intercept	0.134 ± 0.209 (z = 0.64, p = 0.523)	0.102 ± 0.191 (z = 0.53, p = 0.593)	-0.002 ± 0.101 (z = -0.02, p = 0.985)	-0.782 ± 0.251 (z = -3.12, p = 0.002)	-1.278 ± 0.326 (z = -3.92, p < 0.001)	0.675 ± NA (z = NA, p = NA)
	Year	—	—	—	0.405 ± 0.108 (z = 3.74, p < 0.001)	0.678 ± 0.178 (z = 3.81, p < 0.001)	—
		(2004 = 2005)	(2004 = 2005)	(2004 = 2005)	(2004 < 2005)	(2004 < 2005)	(2004 = 2005)
	Rank	-1.190 ± 0.181 (z = -6.56, p < 0.001)	-0.387 ± 0.170 (z = -2.28, p = 0.023)	-0.627 ± 0.073 (z = -8.63, p = 1.000)	-0.259 ± 0.070 (z = -3.72, p < 0.001)	—	-0.272 ± NA (z = NA, p = NA)
	Year × Rank	0.548 ± 0.087 (z = 6.30, p < 0.001)	0.003 ± 0.067 (z = 0.05, p = 0.964)	0.284 ± 0.042 (z = 6.74, p < 0.001)	—	—	0.117 ± 0.033 (z = 3.61, p < 0.001)
		(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H = M = L$)	(2004: $H > M > L$)
		(2005: $H > M < L$)	(2005: $H > M < L$)	(2005: $H > M < L$)	(2005: $H > M > L$)	(2005: $H = M = L$)	(2005: $H = M < L$)

Comparison of results among year / ranks are shown in parenthesis.

Table IV. Factors affecting length of nut-feeding bouts and metabolizable energy intake revealed by GLMM analysis using year, rank, and their interaction as independent variables.

Independent variables	Length of nut feeding bouts ($N = 584$)	Metabolizable energy intake		
		Nuts	Other than nuts	All foods
	Estimate ± SE	Estimate ± SE	Estimate ± SE	Estimate ± SE
Intercept	978.63 ± 203.56 (t = 4.81, $p < 0.001$)	492.83 ± 102.85 (t = 4.79, $p < 0.001$)	248.50 ± 97.24 (t = 2.56, $p = 0.012$)	747.45 ± 125.53 (t = 5.95, $p < 0.001$)
Year	-236.03 ± 115.36 (t = -2.05, $p = 0.041$)	-179.76 ± 44.83 (t = -2.64, $p < 0.001$)	-93.51 ± 58.58 (t = -1.60, $p = 0.112$)	-260.90 ± 77.00 (t = -3.39, $p = 0.001$)
	(2004 > 2005)	(2004 > 2005)	(2004 > 2005)	(2004 > 2005)
Rank	-252.73 ± 89.93 (t = -2.81, $p = 0.005$)	-166.68 ± 63.09 (t = -4.01, $p = 0.009$)	34.37 ± 42.43 (t = 0.81, $p = 0.419$)	-147.37 ± 54.71 (t = -2.69, $p = 0.009$)
Year × Rank	110.86 ± 51.16 (t = 2.17, $p = 0.030$)	88.15 ± 27.77 (t = 3.17, $p = 0.002$)	-21.28 ± 25.85 (t = -0.82, $p = 0.412$)	68.58 ± 33.89 (t = 2.02, $p = 0.045$)
	(2004: $H > M > L$)	(2004: $H > M > L$)	(2004: $H < M > L$)	(2004: $H > M > L$)
	(2005: $H = M = L$)	(2005: $H = M = L$)	(2005: $H = M = L$)	(2005: $H = M = L$)

Comparison of results among year/ranks are shown in parenthesis. H: high-ranking females; M: middle-ranking females; and L: low-ranking females.

Appendix 1. Time spent feeding, and nutritional compositions (mean ± SD) of the foods eaten by Japanese macaques in Kinkazan during the study period

No	Food items	Family	Part eaten	Feeding time percentage 2004 (N = 13859)	2005 (N = 5958)	FUW (g)	Nutritional compositions (% dry matter) (mean ± SD) %NDF	%CP	%CL	%CA	GE (kcal·g⁻¹)	Reference[a]
	Woody plants											
1	*Akebia trifoliata*	Lardizabalaceae	leaf	—	0.02	0.048 ± 0.015	38.21 ± 1.17	12.70 ± 1.13	2.99 ± 0.75	5.62 ± 0.63	4.51	A
2	*Aralia elata*	Araliaceae	sap	—	0.03							
3	*Benthamidia japonica*	Cornaceae	fruit	—	2.79	1.011 ± 0.419	43.36 ± 1.32	3.77 ± 0.44	4.01 ± 0.13	0.79 ± 0.33	4.39	A
4	*Benthamidia japonica*	Cornaceae	leaf	0.01	—	0.083 ± 0.064	36.63 ± 1.62	17.94 ± 0.42	3.87 ± 0.61	5.52 ± 1.36	4.39	A
5	*Benthamidia japonica*	Cornaceae	bud	0.35	—	0.013 ± 0.003	42.16 ± 1.03	9.41 ± 0.28	0.68 ± 0.96	2.74 ± 0.52	4.21	A
6	*Berberis thumbergii*	Berberidaceae	fruit	0.12	0.02	0.016 ± 0.007	37.70 ± 0.54	11.69 ± 1.04	2.87 ± 0.13	0.66 ± 0.03	4.45	A
7	*Berberis thumbergii*	Berberidaceae	leaf	0.48	1.34	0.007 ± 0.004	58.08 ± 2.79	9.56 ± 0.00	0.43 ± 0.85	2.34 ± 0.35	4.22	C
8	*Berchemia racemosa*	Rhamnaceae	fruit	—	0.32	0.005 ± 0.003	57.50 ± 0.23	18.94 ± 0.09	3.28 ± 0.49	1.54 ± 0.37	4.54	A
9	*Callicarpa japonica*	Vervenaceae	leaf	0.01	—	0.045 ± 0.017	80.52 ± 1.53	12.36 ± 0.46	2.92 ± 0.38	3.18 ± 0.03	4.36	C
10	*Carpinus* spp.	Betulaceae	nut	—	0.97	0.012 ± 0.004	57.47 ± 2.16	16.23 ± 0.03	12.39 ± 1.42	2.95 ± 0.31	4.92	A
11	*Castanea crenata*	Fagaceae	nut	0.24	1.76	1.683 ± 0.430	25.46 ± 9.12	8.76 ± 0.34	5.29 ± 1.57	0.66 ± 0.11	4.53	C
12	*Celtis sinensis*	Ulmaceae	leaf	0.02	—	0.165 ± 0.079	40.63 ± 0.11	11.95 ± 0.93	2.82 ± 0.43	6.10 ± 0.12	4.22	A
13	*Diospyros kaki*	Ebenaceae	fruit	—	0.07	2.769 ± 3.747	23.93 ± 0.38	2.11 ± 0.14	2.77 ± 3.75	1.51 ± 0.11	4.26	B
14	*Eunymus fortunei*	Celastraceae	leaf	0.01	—	0.017 ± 0.003	49.21 ± 0.53	8.56 ± 0.39	2.00 ± 0.03	12.27 ± 0.20	3.87	A
15	*Fagus crenata*	Fagaceae	nut	—	48.20	0.123 ± 0.021	31.70 ± 1.45	18.66 ± 2.15	49.66 ± 3.08	1.32 ± 0.02	7.04	A
16	*Fraxinus lanuginosa*	Oleaceae	seed	—	0.25	0.017 ± 0.004	48.88 ± 1.23	7.60 ± 0.53	17.01 ± 0.34	0.39 ± 0.08	5.14	A
17	*Ilex macropoda*	Aquifoliaceae	fruit	—	0.02	0.037 ± 0.008	24.63 ± 0.19	2.71 ± 0.02	3.09 ± 0.60	0.00 ± 0.00	4.35	A
18	*Leucothoe grayana* var. *venosa*	Ericaceae	flower bud	0.01	—							
19	*Leucothoe grayana* var. *venosa*	Ericaceae	fruit	—	0.03	0.007 ± 0.002	68.75 ± 4.15	5.99 ± 1.29	3.06 ± 0.05	7.27 ± 0.47	4.49	C
20	*Lonicera japonica*	Caprifoliaceae	fruit	0.06	—	0.030 ± 0.008	33.44 ± 0.19	5.87 ± 0.10	2.44 ± 0.04	1.22 ± 0.21	4.32	A
21	*Lonicera japonica*	Caprifoliaceae	leaf	1.54	—	0.036 ± 0.030	48.06 ± 0.22	11.21 ± 0.19	2.27 ± 0.11	4.42 ± 0.62	4.25	A
22	*Magnolia obovata*	Magnoliaceae	fruit, seed	0.04	0.12	0.118 ± 0.030	65.87 ± 1.54	6.59 ± 0.18	23.03 ± 0.40	0.37 ± 0.21	5.44	C
23	*Malus tchonoskii*	Rosaceae	fruit	0.06	0.35	3.290 ± 0.057	49.61 ± 0.17	1.37 ± 0.10	3.29 ± 0.06	1.35 ± 0.15	4.29	B
24	*Pourthiaea villosa*	Rosaceae	fruit	—	0.94	0.050 ± 0.015	56.04 ± 0.11	8.54 ± 0.60	2.54 ± 0.28	1.16 ± 0.11	4.36	A
25	*Prunus* ×yedoensis	Rosaceae	gum	—	0.07							
26	*Quercus acuta*	Fagaceae	nut	0.02	—	3.800 ± 1.047	33.31 ± 1.08	3.90 ± 0.08	3.80 ± 1.05	1.32 ± 0.03	4.35	B
27	*Quercus crispula*	Fagaceae	nut	0.03	—	1.901 ± 0.001	34.33 ± 1.68	6.19 ± 0.17	3.65 ± 0.44	0.87 ± 1.02	4.40	A
28	*Quercus myrsinaefolia*	Fagaceae	nut	0.09	—							
29	*Quercus serrata*	Fagaceae	nut	4.05	3.16	0.727 ± 0.211	45.97 ± 4.47	4.51 ± 0.20	1.46 ± 0.50	1.59 ± 0.22	4.23	C
30	*Rosa multiflora*	Rosaceae	leaf	0.25	—	0.014 ± 0.008	65.51 ± 2.37	22.50 ± 0.66	2.33 ± 0.12	0.50 ± 0.18	4.42	A
31	*Rosa multiflora*	Rosaceae	fruit	6.11	1.64	0.031 ± 0.008	47.81 ± 0.01	9.41 ± 0.51	5.17 ± 0.23	1.14 ± 0.21	4.52	C
32	*Rubus microphyllus*	Rosaceae	leaf	2.56	2.72	0.014 ± 0.006	54.14 ± 0.12	14.62 ± 0.41	2.30 ± 0.25	2.79 ± 0.11	4.37	A
33	*Rubus palmatus*	Rosaceae	leaf	0.01	—	0.049 ± 0.020	57.98 ± 2.20	11.93 ± 1.05	5.34 ± 0.20	5.63 ± 1.10	4.38	C
34	*Schisandra nigra*	Schisandraceae	fruit	0.01	1.24	0.127 ± 0.038	30.31 ± 1.66	7.54 ± 0.20	14.65 ± 0.16	0.53 ± 0.60	5.01	C
35	*Sorbus japonica*	Rosaceae	fruit	0.04	0.10	2.567 ± 0.152	68.94 ± 0.27	3.46 ± 0.27	2.90 ± 0.09	1.15 ± 0.13	4.31	B
36	*Stephanandra incisa*	Rosaceae	leaf	—	0.05	0.011 ± 0.003	63.41 ± 0.18	15.06 ± 0.00	2.48 ± 0.45	3.53 ± 0.52	4.36	A
37	*Swida macrophylla*	Cornaceae	fruit	1.10	1.53	0.036 ± 0.008	68.37 ± 3.32	6.52 ± 1.54	12.62 ± 2.17	1.63 ± 0.27	4.84	C
38	*Symplocos chinensis*	Symplocaceae	leaf	0.03	—	0.064 ± 0.016	45.11 ± 2.16	12.56 ± 0.09	1.98 ± 0.29	2.76 ± 1.96	4.33	A
39	*Taxas euspidata*	Taxaceae	fruit	—	0.20	0.074 ± 0.013	46.99 ± 0.43	6.87 ± 1.11	23.58 ± 1.41	2.26 ± 0.08	5.40	A
40	*Torreya nucifera*	Taxaceae	nut	7.95	3.64	0.627 ± 0.181	46.89 ± 0.70	13.25 ± 0.52	43.02 ± 0.08	0.72 ± 0.09	6.74	C
41	*Viburnum dilatatum*	Caprifoliaceae	fruit	2.63	5.34	0.005 ± 0.005	49.81 ± 2.98	4.85 ± 0.74	9.60 ± 0.33	1.77 ± 0.10	4.65	C
42	*Viscum album*	Loranthaceae	fruit	1.15	—	0.041 ± 0.005	20.82 ± 1.18	8.56 ± 0.89	6.58 ± 0.02	0.63 ± 0.89	4.60	A
43	*Vitis flexuosa*	Vitaceae	fruit	0.01	1.31	0.034 ± 0.009	47.09 ± 2.43	8.75 ± 0.23	8.56 ± 0.16	0.55 ± 0.03	4.71	A
44	*Zanthoxylum piperitum*	Rutaceae	bark	—	0.02	0.023 ± 0.011	75.98 ± 0.88	14.39 ± 2.27	0.42 ± 0.59	1.85 ± 0.33	4.31	A
45	*Zanthoxylum piperitum*	Rutaceae	fruit, seed	0.06	1.21	0.020 ± 0.008	72.88 ± 3.47	5.77 ± 0.31	7.81 ± 0.04	14.56 ± 3.14	4.09	C
46	*Zanthoxylum piperitum*	Rutaceae	leaf	0.04	0.20	0.020 ± 0.008	62.77 ± 1.39	14.14 ± 0.16	2.20 ± 0.07	3.80 ± 0.09	4.32	C
47	*Zanthoxylum schinifolium*	Rutaceae	leaf	0.02	—							
48	*Zelkova serrata*	Ulmaceae	nut	—	2.52	0.013 ± 0.004	59.91 ± 0.78	13.44 ± 0.05	19.02 ± 0.53	8.19 ± 0.20	5.03	A
49	*Sasa* sp.	Gramineae	leaf	—	0.02	0.025 ± 0.009	60.33 ± 0.38	15.59 ± 0.04	2.37 ± 0.81	5.41 ± 0.46	4.28	A
	Herbaceous plants											
50	*Boehmeria biloba*	Urticaceae	seed	0.06	—	0.361 ± 0.107	45.18 ± 2.28	10.34 ± 0.22	14.46 ± 0.01	5.40 ± 1.59	4.84	A
51	*Boehmeria longispica*	Urticaceae	seed	0.05	—	0.668 ± 0.195	45.35 ± 2.04	14.83 ± 0.76	14.28 ± 1.85	2.51 ± 0.12	5.02	A
52	*Boehmeria spicata*	Urticaceae	seed	0.08	0.02							
53	*Clematis apiifolia*	Ranunculaceae	seed	0.53	—	0.005 ± 0.001	66.26 ± 0.72	16.29 ± 0.51	5.47 ± 0.26	1.07 ± 0.52	4.64	A
54	*Dioscorea japonica*	Dioscoreaceae	leaf	0.09	—	0.088 ± 0.066	38.50 ± 2.88	15.91 ± 0.04	5.28 ± 0.40	3.45 ± 1.88	4.52	C
55	*Eragrostis curvula*	Gramineae	leaf	3.33	—	0.032 ± 0.017	65.88 ± 2.84	10.76 ± 0.32	1.50 ± 0.02	3.37 ± 1.68	4.25	A

No	Species	Family	Part	FUW	N		%NDF	%CP	%CA	%CL	GE	Source[a]
56	*Miscanthus sinensis*	Gramineae	seed	0.01	—	0.014 ±0.006	73.71 ±0.50	8.12 ±1.63	2.45 ±0.06	1.73 ±0.16	4.33	A
57	*Paederia scandens*	Rubiaceae	leaf	—	0.03							
58	*Perilla frutescens*	Labiatae	seed	30.67	1.56	0.004 ±0.003	74.60 ±1.31	17.18 ±1.63	13.75 ±0.06	1.66 ±0.06	5.36	C
59	*Smilax china*	Liliaceae	fruit	0.38	0.15	0.060 ±0.048	66.94 ±0.87	10.59 ±4.51	3.45 ±0.26	0.29 ±0.41	4.47	A
60	*Trifolium reoens*	Leguminosae	leaf	0.10	—	0.016 ±0.017	59.84 ±0.52	28.59 ±0.30	0.12 ±0.17	2.18 ±0.03	4.50	A
61	*Tubocapsicum anomalum*	Solanaceae	fruit	0.02	0.02	0.056 ±0.028	39.84 ±2.51	13.40 ±0.35	10.15 ±0.90	0.16 ±0.10	4.88	C
62	unidentified herbs		leaf	25.80	9.32	0.019 ±0.022	41.23 ±4.84	9.50 ±1.06	0.07 ±0.33	37.47 ±3.70	2.74	C
	Fungi											
63	Agaricales		-	0.69	1.54	1.318 ±1.619	65.46 ±3.56	7.82 ±0.30	1.31 ±0.19	1.24 ±0.18	4.45	C
64	Polyporales		-	3.20	0.50	0.359 ±0.143	47.78 ±0.14	19.30 ±0.02	5.60 ±0.33	6.80 ±0.10	4.28	C
	Animal materials											
65	Acrididae spp.		adult	1.09	1.64	0.138 ±0.116	76.74 ±0.86	65.19 ±0.82	1.81 ±0.23	1.43 ±0.34	5.16	C
66	Araneae		-	0.06	—	0.062 ±0.028	40.50 ±3.23	71.25 ±0.09	7.81 ±0.50	1.83 ±1.94	5.55	C
67	*Dorcus rubrofemoratus*		adult	0.01	—	0.062 ±0.028	40.50 ±3.23	71.25 ±0.09	7.81 ±0.50	1.83 ±1.94	5.55	C
68	gall on Fagus crenata leaves			2.69	—	0.012 ±0.005	85.96 ±0.03	3.08 ±0.15	2.04 ±0.09	2.69 ±0.01	4.19	A
69	Gastropoda (periwinkle)			0.06	—	0.459 ±0.592	32.00 ±0.85	53.12 ±3.98	7.15 ±0.13	8.29 ±0.20	6.31	A
70	Gastropoda (slug)		-	0.03	—	0.742 ±0.812	27.93 ±0.74	37.14 ±5.70	6.31 ±0.07	4.57 ±0.00	4.85	C
71	Gastropoda (snail)		-	0.01	—	0.742 ±0.812	27.93 ±0.74	37.14 ±5.70	6.31 ±0.07	4.57 ±0.00	4.85	C
72	Gryllidae spp.		adult	0.37	0.36	0.068 ±0.055	74.22 ±0.15	69.45 ±1.92	2.07 ±0.04	2.19 ±0.17	5.21	C
73	Lepidoptera sp.		adult	0.01	—	0.062 ±0.028	40.50 ±3.23	71.25 ±0.09	7.81 ±0.50	1.83 ±1.94	5.55	C
74	Mantodea spp.		egg	0.08	0.12	0.309 ±0.114	80.84 ±1.11	85.08 ±0.87	6.29 ±0.63	1.89 ±1.13	5.68	C
75	Pyralidae spp. in *Cirsium amplexifolium* stem		larva	0.53	0.40	0.034 ±0.010	19.43 ±0.27	24.01 ±1.75	50.66 ±0.00	0.43 ±0.29	7.15	C
76	Pyralidae spp. in *Senecio cannabifolius* stem		larva	0.07	0.08	0.034 ±0.010	19.43 ±0.27	24.01 ±1.75	50.66 ±0.00	0.43 ±0.29	7.15	C
77	*Rana tagoi*		adult	0.00	—	1.900 ±0.969	32.78 ±0.98	58.47 ±0.76	7.34 ±5.45	9.87 ±0.16	5.00	C
78	Tettigoniidae spp.		adult	0.06	0.15	0.138 ±0.116	76.74 ±0.86	65.19 ±0.82	1.81 ±0.23	1.43 ±0.34	5.16	C
79	unidentified insects		-	0.40	0.40	0.062 ±0.028	40.50 ±3.23	71.25 ±0.09	7.81 ±0.50	1.83 ±1.94	5.55	C
80	Soil			0.37	1.51							

%NDF: neutral detergent fibre content; *%CP*: crude protein content; *%CA*: crude ash content; *%CL*: crude lipid content; *GE:* gross energy. These were analysed at least twice and averaged.analysed at least twice and averaged.

FUW: feeding unit weight. *N*: total number of 1-min instantaneous scan samples for feeding.

a) A: this study, B: from Tsuji *et al.* (2007), and C: from Tsuji and Takatsuki (2008).