1 Food type and the number of feeding sites in a tree affect aggression during

2 feeding in wild Japanese macaques

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10 Running title: Factors affecting aggression during feeding

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26 **Abstract**   It is important to understand the effects of ecological factors on

27 aggression during feeding in order to link habitat characteristics to competitive

28 regime and social relationships.   Multiple habitat characteristics are likely to

29 affect aggression, but few studies have examined the effect of multiple factors on

30 within-group competition simultaneously.   I examined the effect of eight factors

31 on aggression during feeding in wild Japanese macaques living in a coniferous

32 forest in Yakushima: density of the tree species, feeding time, number of feeding

33 sites within a feeding tree, number of co-feeding animals, within-tree macaque

34 density, food type, rank and sex of the focal animal.   When macaques co-fed

35 with other individuals, food type, the number of feeding sites and their

36 interactions significantly influenced aggression.   Aggression increased when

37 macaques ate fruits/seeds when compared to other foods and as the number of

38 feeding sites decreased.   Primate socioecological models highlight the

39 importance of clumped distribution of food patches as a correlate of within-group

40 contest.   However, this study indicated that primatologists need to pay attention

41 to the factors related to the current feeding tree (food type and feeding tree size

42 with respect to monopolizability) in addition to the distribution of food in the entire

43 home range.

44 **Keywords** aggression; co-feeding; food distribution; monopolizability;

45 Yakushima

46

47 **Introduction**

48 Patterns of aggression in defense of food resources during feeding affect

49 competitive regimes (Janson 1985), which in turn affect female social

50 relationships (van Schaik and van Hooff 1983; van Schaik 1989).   Animals

51　make decision on whether to defend a food patch or not based on the

52　distribution of available food resources (Pruetz and Isbell 2000; van Schaik

53　1989).　Most primate socioecological models predict that a clumped food

54　distribution and the monopolizability of a food patch enhance contest

55　competition (Sterck *et al.* 1997).　Furthermore, high-quality patches of

56　intermediate size relative to group size can also lead to within-group contest

57　competition (Koenig 2002; van Schaik and van Noordwijk 1988).　However,

58　conceptualizing the 'distribution' of food resources is problematic, and it remains

59　unclear at which level food distribution affects the likelihood of aggression

60　among wild primates (Isbell and Young 2002).

61　　　　In order to reveal a biologically meaningful scale of food distribution, it

62　may be useful to clarify the area within which foods can be monopolized by one

63　individual.　Wittig and Boesch (2003) categorized the foods of female

64　chimpanzees into monopolizable foods, such as meat, nuts cracked by stone

65　hammers, water holes, and ant eggs and non-monopolizable foods and showed

66　that chimpanzees exhibited more aggression when eating monopolizable foods.

67　However, this kind of qualitative categorization is not always applicable to other

68　species.　Vogel and Janson (2007) defined the area of one feeding site within a

69　feeding tree as 200 m^3 (a sphere with a radius of 3.63 m), based on the

70　maximum number of animals which can occupy a food patch of a given size, and

71　showed that the total number of available feeding sites was negatively correlated

72　with the frequency of agonistic interactions in capuchin monkeys.　Furthermore,

73　experimentation illustrated that food monopolization by captive rhesus

74　macaques depended upon inter-food distances (Chancellor and Isbell 2008;

75　Mathy and Isbell 2001).　Captive rhesus and long-tailed macaques were able to

76 monopolize foods within a distance of 1 m (Mathy and Isbell 2001; Schaub 1995).

77 Similarly, wild Japanese macaques in Yakushima exhibited aggression only

78 when inter-individual distances were less than 1 m (Furuichi 1983).

79 The availability of alternative resources (e.g. feeding sites, other

80 feeding trees) may also affect the likelihood of aggression (Saito 1996; Vogel

81 and Janson 2007). For example, when only a few alternative feeding

82 sites/trees are available, animals must increase the time allotted to searching for

83 an alternative food source if displaced, and thus they are more likely to exhibit

84 aggression in defense of such resources. Food size affects the likelihood of

85 aggression in captive macaques positively, either because vulnerability to

86 aggression increases due to long processing time or because large foods are

87 more attractive to other individuals (Chancellor and Isbell 2008; Mathy and Isbell

88 2001). The number of co-feeding animals also affects the occurrence of

89 aggression positively (Robbins 2008).

90 In summary, monopolizability, availability of alternative resources

91 (either inside or out of the feeding tree), feeding time, food quality, and the

92 number of co-feeders have been suggested to affect aggression. Among

93 primate studies, only Vogel and Janson (2007) have investigated all of these

94 factors simultaneously, in their case for capuchin monkeys. Robbins (2008)

95 also analyzed multiple factors for mountain gorillas, including number of

96 co-feeders, tree size and feeding time, but did not study the effect of other

97 feeding trees and food quality and did not investigate tree size with respect to

98 monopolizability. Mitchell *et al*. (1991) suggested that the difference in

99 aggression frequency between two *Saimiri* species was due to ecological factors

100 (e.g. tree size); however, they did not analyze this quantitatively. Current

101   knowledge of the relative importance of ecological factors that might affect

102   aggression is clearly limited.   Primate socioecological models hold that food

103   conditions determine a competitive regime, at least partly by way of aggression

104   during feeding, but this assumption has rarely been tested and more work is

105   needed to reveal the critical characteristics of food resources which influence

106   within-group aggression during feeding (Isbell and Young 2002).

107   In this study, I examine the occurrence of aggression during feeding in

108   wild Japanese macaques with respect to six factors that describe the

109   characteristics of food patches: density of conspecific food trees, feeding time,

110   food type, number of feeding sites per tree, number of co-feeding animals, and

111   within-tree macaque density.   In addition to these external (ecological) variables,

112   I also examined animal rank and age of focal animal in order to elucidate the

113   possible effect of social factors.   I test the following predictions regarding the

114   influence of these factors on rate of aggression during feeding.   No specific

115   predictions was made concerning the effect of age.

116   1) Density of alternative conspecific food trees: I predicted that the frequency of

117   aggression would increase with lower density of the food tree species.   When

118   eating low-density food items, macaques are predicted to defend the food tree

119   against competitors because there are no alternative conspecific food trees

120   available.   I examined the density of only conspecific food trees because each

121   food species has its own particular nutritional properties, and thus macaques

122   may selectively eat each species accordingly.   Although the nutritional property

123   varies even within species, between-species variations are larger than

124   within-species variations (Chapman *et al.* 2003).   In addition, in the study forest,

125   food tree density is generally very high throughout the year (ca. 4000 trees/ha)

126   when all food species are combined (Hanya 2004a).   Therefore, it seems

127   unlikely that the total availability of food trees affects the likelihood of aggression.

128   2) Feeding time: I predicted that the frequency of aggression would increase with

129   longer feeding time.

130   3) Food type: I predicted that the frequency of aggression would increase when

131   eating fruits/seeds.   Macaques in this forest prefer fruits and seeds over leaves

132   and flowers (Hanya 2004b).   This preference is likely to relate to the higher

133   nutritional quality of fruits and seeds when compared to other foods (Iwamoto

134   1982) and the digestive system of Japanese macaques, which is better at

135   digesting non-structural rather than structural carbohydrates (Hanya 2004b).

136   Japanese macaques eat mostly mature leaves rather than young leaves in this

137   forest (Hanya 2004b).

138   4) Number of feeding sites in a tree: I predicted that the frequency of aggression

139   would increase as the number of feeding sites decreased.   When the number of

140   monopolizable feeding sites is small, few other feeding sites are available within

141   a feeding tree, and macaques must defend them against other group members.

142   I also predicted an interaction between the number of feeding sites in a tree and

143   the availability of alternative conspecific food trees, with the effect of the number

144   of feeding sites increasing when the availability of conspecific feeding tree is low.

145   5) Number of co-feeding animals: I predicted that the frequency of aggression

146   would increase with more co-feeding animals.

147   6) Within-tree macaque density: I predicted that the frequency of aggression

148   would increase with increased within-tree macaque density.   The number of

149   co-feeding animals is influenced by the number of available feeding sites,

150   creating a confounding relationship between the number of feeding sites and

151   aggression.   For example, in terms of macaque density, a tree with 4 feeding

152   sites and 2 animals is the same as one with 8 feeding sites with 4 animals.   In

153   order to reveal which is the most significant factor among number of co-feeding

154   animals, number of feeding sites, or within-tree macaque density, I examined all

155   of these factors.

156   7) Rank: Higher-ranked individuals are predicted to be involved in aggression in

157   order to confirm and strengthen their dominance (Chancellor and Isbell 2008).

158

159   **Methods**

160   Study site, subjects, and periods

161   I conducted the study in a coniferous forest of Yakushima (Hanya *et al.* 2004).

162   The study group of Japanese macaques (*Macaca fuscata*), HR group, contained

163   24-27 individuals, including 7-9 adult females, 6-7 adult males, 7-10 juveniles

164   and 2 infants.   I identified all individuals in the study group using natural

165   markings, such as facial characteristics, loss of fingers, etc.   There was a linear

166   dominance hierarchy among group females (Hanya *et al.* 2008).   I observed the

167   behavior of 7 adult females in the group from April 2000 to March 2001 (on 107

168   days) and 5 adult females from October 2003 to January 2004 (on 39 days).

169   Each of the 5 focal animals in the second study period was also observed in the

170   first study period.   Two focal females in the first study period were lactating.

171   Other females were not followed because they were less habituated to observer

172   presence.

173

174   Term definition

175   I defined the following four terms:

176 *Feeding bout*: A feeding bout occurred from the point that a focal animal began

177 manipulating the food item until either leaving the tree or after 20 seconds had

178 passed since last moving in the feeding tree or manipulating the food item.

179 *Aggression*: Aggression included attacks, both overt and subtle threats

180 (open-mouth display and beating branches, ground, etc.) and chases.   Subtle

181 acts of avoidance were not included in the definition of 'aggression' for several

182 reasons.   First, I was interested in assessing only the active defense of feeding

183 trees.   Second, 'avoidance' and 'aggression' are two different behavioral tactics,

184 used by subordinates and dominants, respectively, and it may not be appropriate

185 to lump them together.   Third, avoidance may simply represent an animal

186 leaving the patch for other reasons, such as satiation, whereas aggression is an

187 overt and directed behavior that does not easily remain unnoticed.   Fourth,

188 avoidance is difficult to detect or record: when eating in large trees, it is difficult

189 to collect data on avoidance that are not biased with respect to tree size.

190 Finally, avoidance may occur at various spatial scales, and it is impossible to

191 record all of them.

192 *Co-feeding animals*: I defined co-feeding animals as those either in or in contact

193 with the tree in which the focal animal was feeding.   Though this definition

194 potentially included animals that were not feeding in the tree, in practice it was

195 impossible to determine the behavior of all of the non-focal animals.

196 Regardless, the definition remains meaningful since each individual sharing

197 space with a focal animal in a feeding tree constituted a potential competitor.

198 *Feeding site and monopolizable area*: I defined feeding site with respect to

199 monopolizability.   There are two possible ways to define monopolizable area.

200 One is simply to defined the monopolizable area as being within 1 m of a focal

201   animal, based on a previous study of this population (Furuichi 1983).   Furuichi

202   roughly categorized observed inter-individual distance as 1 m, 3 m, and 5+ m

203   and showed that aggression during feeding occurred only when the

204   inter-individual distance was less than 1 m.   Thus he regarded the area within 1

205   m as monopolizable, and one feeding site constitutes 4.18 m^3 – the volume of a

206   sphere with a radius of 1 m.   The second method, employed by Vogel and

207   Janson (2007) yields a similar result.   This method plots the maximum number

208   of feeding animals in a tree against a given crown volume, and draws a line such

209   that most points lie below it.   The inverse of the resulting slope gives a minimum

210   volume per feeding animal.   This procedure gives a minimum monopolizable

211   area for Japanese macaques of radius 1.48 m (Fig. 1).

212

213   Behavioral observation

214   I conducted 1 hour focal samples on 7 adult female macaques between 07:00

215   and 17:00 for a total of 142 days.   When changing between subjects, I selected

216   the animal with the fewest hours of observation up until that point in an attempt

217   to equalize the total observation time for each animal.   The observation time for

218   each individual was not biased by time of day.   The mean (±SD) total

219   observation time per focal animal was 70±22 hours.   The dataset is comprised

220   of 310 hours of 94 days of focal observation in the first study period and 193

221   hours of 48 days in the second study period.

222   While focal animals were feeding in a tree, I recorded the onset and

223   end of feeding bouts, the occurrence of aggression involving focal animals (both

224   given and received), the diameter at breast height (DBH) of the tree, the number

225   of co-feeding animals when the focal animal entered the feeding tree (excluding

226   dependent infants), and all entries into and exits out of the feeding tree by other

227   animals.   I used data from 181 feeding bouts (mean±SD per individual:

228   25.8±10.1) in which feeding lasted for more than five minutes and there was at

229   least one co-feeding animal.   The number of feeding bouts was not biased to

230   particular individuals (the range for the number of feeding bouts per individual

231   was 10-39).   No focal animal was in estrous during the observation, so it was

232   unlikely that occurrences of aggression related to mating behavior.

233

234   Vegetation and phenology

235   To assess the density of available food trees, I set a 0.25 ha

236   vegetational plot within the home range of the group to include both ridges and

237   valleys.   This plot is smaller than the recommended plot size, which is 5% of the

238   home range: 2.7 km^2*5%=13.5 ha (National Research Council 1981).   However,

239   this plot size was too large to be feasible.   Tree species diversity in temperate

240   forests is much lower than that in tropical forests (Takyu *et al.* 2005), and species

241   composition, basal area and primary production in this plot do not vary

242   considerably from other plots in the same altitudinal zone in Yakushima (Aiba *et*

243   *al.* 2007).   Seasonal variations in fruit availability in this plot clearly explained

244   the variations in diet and activity budget of this group (Hanya 2004a, b).

245   Therefore, I regarded this plot as being representative of the home range.

246   I recorded the species and DBH of all trees >5 cm DBH.   For 30% of

247   the area of the plot, I recorded the crown height, as well as the largest and

248   smallest width of the crown.   To sample smaller trees (i.e. <5 cm DBH), I

249   divided the plot into one hundred 5 x 10 m subplots and randomly selected 10

250   subplots.   In these selected subplots, I recorded the DBH and the species of all

251   trees taller than 1 m (all macaque feeding trees were more than 1 m in height).

252   Density of trees (N/ha) was calculated as (Number of trees of DBH>5 cm in the

253   0.25 ha plot)/0.25+ (Number of tree of DBH<5cm in the 0.025 ha subplot)/0.025,

254   for each species.

255   I conducted monthly phenological surveys during the entire study

256   period to examine the fruit production of all marked trees (N=705, including the

257   small trees in 0.025 ha subplots).   There was a high degree of synchrony in fruit

258   production within species (Hanya 2005).   The number of fruiting tree per

259   hectare in any given month was calculated as: (Number of fruiting trees of

260   DBH>5 cm in the 0.25 ha plot)/0.25+ (Number of fruiting trees of DBH<5cm in

261   the 0.025 ha subplot)/0.025, for each species.

262

263   Data analysis

264   I calculated or defined the eight independent variables as follows:

265   (1) *Density of available conspecific food trees* (tree density, hereafter): For fruit

266   and seed foods, which constitute 50% of the arboreal feeding time (Hanya

267   2004b), I calculated the density of available trees using the phenological data.

268   Since the number of fruiting trees differed among months, I used the number of

269   fruiting trees in that month for the analysis.   For flower foods (17%),

270   phenological data were not available, so I regarded all of the trees in which

271   fruiting was observed in the following months of the year as available flower-food

272   trees.   For leafy foods, I regarded all trees of the food species in question

273   available.

274   (2) *Feeding time*: Duration of the feeding bout (min).

275   (3) *Food type*: Binary categorization: fruit/seed or other.

276 (4) N*umber of available feeding sites within a feeding tree* (#feeding site): I

277 calculated the number of available feeding sites within a feeding tree by dividing

278 the crown volume by 4.18 m^3 and rounding down (Vogel and Janson 2007).

279 For example, if the estimated crown volume was 6 m^3, the number of available

280 feeding sites was 1.   I estimated the crown height and crown area of a feeding

281 tree from its basal area ($\pi*(DBH/2)^2$)) using the following regression equation

282 derived from the vegetational data:

283 Log (crown height; m)=log (basal area, cm^2)*0.269+0.691

284 Log(crown area, m^2)=log(basal area, cm^2)*0.505-0.064

285 whereas

286 Crown area=π* largest width of the crown/2*smallest width/2

287 I used 127 trees to calculate this equation.   It should be noted that this

288 procedure inevitably causes error in the estimation of crown volume when

289 compared to direct measurement.   However, the error in the estimation of the

290 number of feeding sites is small because the value is rounded.   Finally, I

291 calculated crown volume as:

292 Crown volume= 1/3*crown area*crown height (m^3) (Janson 1988).

293 (5) N*umber of co-feeding animals* (#co-feed): The number of co-feeding animals

294 was the average number of animals staying within the same tree throughout the

295 feeding bout of the focal individual.   For example, if the number of co-feeding

296 animals was 1 for the first minute, and 2 for the second minute, then the average

297 number of co-feeding animals in the bout was 1.5.   I used this value in the

298 analysis, regardless of when aggression occurred during that feeding bout.

299 (6) Within-tree macaque density (macaque density): #Co-feed divided by

300 #feeding site.

301   (7) Rank: Rank of the focal animal: 1 (highest) to 9 (lowest).   Rank was

302   determined using submissive behaviors such as grimace and silent supplanting

303   (see Hanya et al 2008 for details).   Dominance relationships were linear in this

304   group (Hanya *et al.* 2008).

305   (8) Age: Since exact age was unknown because habituation started only a few

306   months age of this study, age of the focal animal was categorized as adult or

307   adolescent, from external characteristics following Maruhashi (1982).

308

309   Models

310   I ran a series of generalized linear models (GLM), assuming Poisson

311   distribution, to examine the number of aggression events occurring during

312   feeding bouts.   I used the above eight factors as fixed factors.   Number of

313   aggression events in each feeding bout (range=0, 1, 2, or 3, mean=0.23,

314   variance=0.30) was not significantly different from Poisson distribution (χ^2=13.0,

315   *P*=0.11).   A positive coefficient means that aggression is more likely to occur

316   with an increase in the independent variable.   I selected the best-fit model with

317   the smallest AIC (Akaike's Information Criterion), as follows.   First I conducted

318   single-factor analyses, then I conducted all combinations of two-factor analyses,

319   three-factor analyses, etc, only if any of the models including a larger number of

320   independent factors had a lower AIC than all of the models with smaller number

321   of factors.   I examined all combinations of two-way interaction terms.   The

322   number of explanatory variables (*K*) was large relative to the sample size

323   (*N*=181), i.e. *N*/*K* < 40.   Therefore, a correction factor ($2K(K+1)/(N-K-1)$) was

324   added to the AIC scores (Burnham and Anderson 2002).   I did not examine

325   macaque density simultaneously with either #feeding sites or #co-feed in the

326 same model because the former was calculated from the latter.   I excluded

327 feeding trees without co-feeding animals from the model because there was no

328 opportunity for aggression to occur.   Collinearity (correlations between

329 independent factors) was not severe in this dataset: the maximum variance

330 inflation factor (VIF) was smaller (2.63) than the cut-off value (5) recommended

331 in Neter *et al.* (2004).

332   I log transformed all independent variables except food type and age

333 before conducting the GLM.   I set the alpha level at 0.05.   I used R 2.8.1. (©

334 The R Foundation for Statistical Computing) for statistical analysis.

335

336 **Results**

337 During feeding bouts which lasted more than 5 minutes with co-feeding animals,

338 the frequency of aggression was 0.92 times/feeding hour (45/48.6), or once

339 every 1 hour and 5 minutes.   The average duration of a feeding bout was only

340 16.1 minutes, and thus I observed aggression in 18% of the feeding bouts

341 (33/181).   I summarize statistics of independent factors and crown volume in

342 Table I.

343   Macaques exhibited aggression more often when they ate fruit/seeds

344 than when eating other foods, and when the number of feeding sites was small.

345 In the best-fit model, the number of aggressions was predicted to increase with

346 small #feeding sites and when macaques ate fruits/seeds (Table II, Fig. 2).   In a

347 tree with one feeding site, when aggression was most likely to occur, the

348 expected count of aggression per feeding bout was 0.68 when macaques were

349 eating fruits/seeds and 0.21 when macaques were eating other foods.   In a tree

350 with 45 feeding sites, which was the median value, the expected count of

351   aggression per feeding bout was 0.051 when macaques were eating fruits/seeds

352   and 0.21 when macaques were eating other foods.   The model with the

353   second-smallest AIC only used #feeding sites.   The difference in AIC between

354   the best and second best-fit models was 2.4.   The addition of other factors to

355   the best-fit model increased AIC by at least 2, and the effect of the added factors

356   was not significant in any model, meaning that the effect of food type and

357   #feeding sites on aggression was fairly robust.   In the model that included both

358   tree density and #feeding sites, only #feeding site was significant, and the AIC

359   was larger than the best-fit model by 10.1.

360   The effect of the number of feeding sites was apparent only when

361   macaques were eating fruits and seeds.   Number of feeding sites was

362   significantly smaller for fruits/seeds than other foods (t=3.07, P=0.0025).

363   However, the effect of food type was not merely a by-product of the large

364   number of feeding sites for non-fruit/seed food trees.   When I analyzed only

365   fruit/seed feeding, the effect of the number of feeding sites on occurrences of

366   aggression was significantly negative (z=3.90, P<0.0001).   When I analyzed

367   only other food feeding, the effect of the number of feeding sites was not

368   significant (z=0.017, P =0.98).   Therefore, when macaques ate fruit and seeds

369   in small feeding trees, aggression increased.

370

371   **Discussion**

372   This study showed that aggression by Japanese macaques in a coniferous

373   forest on Yakushima increased when the number of feeding sites was small and

374   when macaques were feeding on high-quality foods.   However, the number of

375   feeding sites did not affect the frequency of aggression when macaques were

376   feeding on low-quality foods, such as leaves and flowers.   A number of previous

377   studies have identified factors influencing aggression during feeding including

378   monopolizability, availability of alternative resources (either inside or out of the

379   feeding tree), feeding time, food quality, and the number of co-feeders (see

380   Introduction); however, the results of this study indicate the relative importance

381   of these two among the ecological and social factors.

382   It is easy to imagine how the density of feeding trees might affect the

383   occurrence of aggression: when the density of the feeding tree is high, individual

384   macaques can forage in different trees, and thus avoid conflict.   For example,

385   Saito (1996) showed that among wild Japanese macaques in Kinkazan,

386   aggression over food occurred only with respect to low-density food species

387   because alternative food patches were seldom available, forcing group members

388   to forage in the same patch.   Such a mechanism would affect the likelihood of

389   aggression indirectly via the number of co-feeding animals.   Therefore, when

390   the number of co-feeding animals is examined simultaneously, as in this study,

391   the effect of tree density of trees is not apparent.   The number of feeding trees

392   and the number of feeding sites within the tree represent different measures of

393   alternative feeding locations.   Macaques in the present study seemed to

394   respond only to the latter, which is perhaps a more cogent factor influencing an

395   individual's behavior.

396   In terms of food type, aggression was more likely to occur when feeding

397   on fruits and/or seeds, as predicted.   Because the number of feeding sites in

398   fruit/seed feeding trees was smaller than that of other food trees, there remained

399   a possibility that the effect of food type was only a by-product of the number of

400   feeding sites.   However, the number of feeding sites did not affect aggression

401   when only low-quality foods were analyzed.   It is not clear whether limited

402   distribution or high nutritional quality is the cause of frequent aggression during

403   fruit/seed eating.   However, because tree density did not affect aggression, high

404   nutritional quality seems to be more important.

405   The number of feeding sites within a feeding tree affected the

406   occurrence of aggression while foraging on fruits and seeds.   When only a few

407   feeding sites existed within a fruit/seed feeding tree, macaques defended the

408   feeding site against other members.   These results are in accordance with

409   Vogel and Janson (2007), who showed that agonism in capuchin monkeys

410   increases when fewer feeding sites are available.   The authors based these

411   conclusions on the result that number of feeding sites was negatively related to

412   aggression.   The average number of feeding sites was much larger for

413   Japanese macaques (56, Table I) than for capuchins (2.15=429 m^3 crown

414   volume/200 m^3 per one feeding site).   However, the data in this study included

415   considerable number of small trees having only one or two feeding sites (21 and

416   6 among 181 feeding trees, respectively).   These trees in Yakushima were

417   small enough to provoke aggression when there were multiple co-feeding

418   animals.

419   Vogel and Janson (2007) defined monopolizable areas as 200 m^3, a

420   sphere with a radius of 3.63 m, which was much larger than our definition based

421   on a radius of 1 m.   Because macaques are larger than capuchins, we would

422   expect the opposite.   This is not because of the different definitions of

423   monopolizable areas, because using the same definition of monopolizable area

424   for Japanese macaques gives 1.48 m.   Definitions aside, macaques and

425   capuchins may tolerate different levels of proximity to other individuals during

426   feeding.   Because of the smaller feeding tree size for Japanese macaques

427   (mean+SD: 172+13 m^3) than for capuchins (429$\pm$24 m^3; Vogel and Janson,

428   2007), macaques would need to exhibit greater levels of tolerance in order to

429   keep the frequency of aggression (and thus injury or time costs) at the same

430   level as capuchins.   Another possibility is that the food distribution within a

431   feeding patch is different within a feeding patch in Costa Rica (Vogel and

432   Janson's (2007) study site) and Yakushima.   Further investigations are required

433   to understand this difference in monopolizable area between the two species.

434   For example, the monopolizable area could be compared directly for the two

435   species using a feeding experiment, giving attractive foods at two places at

436   varying distances.   If the average size of feeding tree affects the tolerance

437   levels, it would be useful to compare different populations of the same species

438   having different sizes of feeding trees.

439   Possible limitations to the analysis presented here include (1) small R^2

440   value, (2) other possible factors affecting aggression and (3) small sample size.

441   (1) *Small R^2 value*: The value of R^2 was small (0.072), indicating that although

442   the model was highly significant, it only explained a small portion of the

443   occurrence of aggression.   Thus, knowing the food type being eaten and the

444   number of available feeding sites was still unlikely to help one predict when

445   aggression will occur.   The most likely reason for this is the overall low

446   frequency of aggression, which occurred in only 18% of the feeding bouts.

447   Aggression was a rare behavior, and macaques often did not exhibit aggression

448   under the circumstances when the likelihood of aggression increased (e.g.

449   feeding on fruits and seeds in small trees).   The model was highly significant,

450   thus perhaps these factors really do account for much of the actual variation in

451   aggression in spite of the low R^2 value.   The results of this study still have

452   values because they can point out the importance of food type and number of

453   feeding sites on the occurrence of aggression, which would be useful

454   information for future studies of aggressive behavior.

455   (2) *Other possible factors affecting aggression*: Other food characteristics that

456   could not be incorporated in the model, such as patch depletion time (Isbell and

457   Young 2002), satiation level (Janson and Vogel 2006), and fruit abundance

458   within the fruiting tree, might also affect the occurrence of aggression.   Patch

459   depletion time does not seem to affect this population because macaques often

460   leave patches before feeding speed decreases (Hanya, unpublished data).

461   Although Janson and Vogel (2006) proposed a procedure to estimate satiation

462   level by the time since ingestion and amount of ingestion, it was not applicable to

463   this study because data on previous feeding were not available.

464   (3) *Small sample size*: Considering the low frequency of aggression, the sample

465   size (*N*=181 feeding bouts) was not large.   Therefore, it is possible that the

466   effect of other significant factors was not detected due to the small sample size.

467   However, the effects of food type and number of feeding sites can be considered

468   the largest because the effects were clear even in this small sample size.

469   In conclusion, the present study indicates that both food type and the

470   number of feeding sites within a feeding tree affect the occurrence of aggression.

471   Japanese macaques are more likely to engage in conflict when they forage on

472   'high-quality' (in terms of energy content and limited availability) fruit/seeds and

473   when alternative food resources (feeding sites) are not available within the

474   feeding tree.   Primate socioecological models have highlighted the importance

475   of clumped distribution of food patches as a correlate of within-group contest

476   (Isbell and Young 2002; Sterck *et al.* 1997).   However, this study indicated that

477   primatologists need to pay attention to the factors related to the current feeding

478   tree (food type and feeding tree size with respect to monopolizability) in addition

479   to the distribution of food in the entire home range.

480

481 **Acknowledgements**

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References

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497   Aiba, S., Hanya G., Tsujino R., Takyu M., Seino T., Kimura K. & Kitayama K.

498   (2007). Comparative study of additive basal area of conifers in forest

499   ecosystems along elevational gradients. *Ecological Research*, 22, 439-450.

500   Burnham, K. P. & Anderson D. R. (2002). *Model Selection and Multi-model*

501   *Inference. 2nd Edition*. Springer, New York.

502   Chancellor, R. L. & Isbell L. A. (2008). Punishment and competition over food in

503   captive rhesus macaques, *Macaca mulatta. Animal Behaviour*, 75,

504   1939-1947.

505   Chapman, C. A., Chapman L. J., Rode K. D., Hauck E. M. & McDowell L. R.

506   (2003). Variation in the nutritional value of primate foods: Among trees, time

507   periods, and areas. *International Journal of Primatology*, 24, 317-333.

508   Furuichi, T. (1983). Interindividual distance and influence of dominance on

509   feeding in a natural Japanese macaque troop. *Primates*, 24, 445-455.

510   Hanya, G. (2004a). Seasonal variations in the activity budget of Japanese

511   macaques in the coniferous forest of Yakushima: Effects of food and

512   temperature. *American Journal of Primatology*, 63, 165-177.

513   Hanya, G. (2004b). Diet of a Japanese macaque troop in the coniferous forest of

514   Yakushima. *International Journal of Primatology*, 25, 55-71.

515   Hanya, G., Yoshihiro S., Zamma K., Matsubara H., Ohtake M., Kubo R., Noma N.,

516   Agetsuma N. & Takahata Y. (2004). Environmental determinants of the

517   altitudinal variations in relative group densities of Japanese macaques on

518   Yakushima. *Ecological Research*, 19, 485-493.

519   Hanya, G. (2005). Comparisons of dispersal success between the species

520   fruiting prior to and those at the peak of migrant frugivore abundance. *Plant*

521   *Ecology*, 181, 167-177.

522   Hanya, G., Matsubara M., Hayaishi S., Zamma K., Yoshihiro S., Kanaoka M. M.,

523   Sugaya S., Kiyono M., Nagai M., Tsuriya Y., Hayakawa S., Suzuki M., Yokota

524   T., Kondo D. & Takahata Y. (2008). Food conditions, competitive regime, and

525   female social relationships in Japanese macaques: within-population

526   variation on Yakushima. *Primates*, 49, 116-125.

527   Isbell, L. A. & Young T. P. (2002). Ecological models of female social

528   relationships in primates: Similarities, disparities, and some directions for

529   future clarity. *Behaviour*, 139, 177-202.

530   Iwamoto, T. (1982). Food and nutritional condition of free ranging Japanese

531   monkeys on Koshima Islet during winter *Primates*, 23, 153-170.

532   Janson, C. (1985). Aggressive competition and individual food consumption in

533   wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and*

534   *Sociobiology*, 18, 125-138.

535   Janson, C. & Vogel E. (2006). Hunger and aggression in capuchin monkeys In G.

536   Hohmann, M. Robbins & C. Boesch (eds), *Feeding Ecology in Apes and*

537   *Other Primates: Ecological, Physical and Behavioral Aspects* (pp. 285-312).

538   New York: Cambridge Univ Press.

539   Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus*

540   *apella*): quantitative effects of group size and tree productivity. *Behaviour*,

541   105, 53-76.

542   Koenig, A. (2002). Competition for resources and its behavioral consequences

543   among female primates. *International Journal of Primatology*, 23, 759-783.

544   Maruhashi, T. (1982). An ecological study of troop fissions of Japanese monkeys

545   (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates*, 23, 317-337.

546 Mathy, J. W. & Isbell L. A. (2001). The relative importance of size of food and

547   interfood distance in eliciting aggression in captive rhesus macaques

548   (*Macaca mulatta*). *Folia Primatologica*, 72, 268-277.

549 Mitchell, C. L., Boinski S. & van Schaik C. P. (1991). Competitive regimes and

550   female bonding in 2 species of squirrel monkeys (*Saimiri oerstedi* and *S.

551   sciureus*). *Behavioral Ecology and Sociobiology*, 28, 55-60.

552 National Research Council (1981). *Techniques for the Study of Primate

553   Population Ecology*. National Academy Press, Washington, D.C.

554 Neter, J., Kutner M., Nachtsheim C. & Wasserman W. (2004). *Applied Linear

555   Regression Models. 5th edition*. McGraw-Hill/Irwin.

556 Pruetz, J. D. & Isbell L. A. (2000). Correlations of food distribution and patch size

557   with agonistic interactions in female vervets (*Chlorocebus aethiops*) and

558   patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral

559   Ecology and Sociobiology*, 49, 38-47.

560 Robbins, M. M. (2008). Feeding competition and agonistic relationships among

561   Bwindi *Gorilla beringei*. *International Journal of Primatology*, 29, 999-1018.

562 Saito, C. (1996). Dominance and feeding success in female Japanese

563   macaques, *Macaca fuscata*: Effects of food patch size and inter-patch

564   distance. *Animal Behaviour*, 51, 967-980.

565 Schaub, H. (1995). Dominance fades with distance: an experiment on food

566   competition in long-tailed macaques (*Macaca fascicularis*). *Journal of

567   Comparative Psychology*, 109, 196-202.

568 Sterck, E. H. M., Watts D. P. & van Schaik C. P. (1997). The evolution of female

569   social relationships in nonhuman primates. *Behavioral Ecology and

570   Sociobiology*, 41, 291-309.

571   Takyu, M., Kubota Y., Aiba S., Seino T. & Nishimura T. (2005). Pattern of

572   changes in species diversity, structure and dynamics of forest ecosystems

573   along latitudinal gradients in East Asia. *Ecological Research*, 20, 287-296.

574   van Schaik, C. P. & van Hooff J. A. R. A. M. (1983). On the ultimate causes of

575   primate social systems. *Behaviour*, 85, 91-117.

576   van Schaik, C. P. & van Noordwijk M. A. (1988). Scramble and contest in feeding

577   competition among female long-tailed macaques (*Macaca fascicularis*).

578   *Behaviour*, 105, 77-98.

579   van Schaik, C. P. (1989). The ecology of social relationships amongst female

580   primates. In V. Standen & R. A. Foley (eds), *Comparative Socioecology* (pp.

581   195-218). Oxford: Scientific Publications.

582   Vogel, E. R. & Janson C. H. (2007). Predicting the frequency of food-related

583   agonism in white-faced Capuchin monkeys (*Cebus capucinus*), using a novel

584   focal-tree method. *American Journal of Primatology*, 69, 533-550.

585   Wittig, R. M. & Boesch C. (2003). Food competition and linear dominance

586   hierarchy among female chimpanzees of the Taï National Park. *International*

587   *Journal of Primatology*, 24, 847-867.

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591   Legends to figures

592   Fig. 1.   Relationship between the crown area of the feeding tree and the

593   number of feeding animals in the tree.   The thick line is drawn such that

594   most points lie below the line, in order to assess the maximum number of

595   animals that can feed for a given size.   The dashed line is the one used

596   by Vogel and Janson for capuchins (Vogel and Janson 2007).   Because

597   the line for Japanese macaques is steeper than the one for capuchins,

598   more individuals can feed in a feeding tree of a given size for Japanese

599   macaques than for capuchins.

600   Fig. 2.   Number of feeding bouts with respect to number of feeding sites.   Note

601   that the x-axis is log-scale. (a) Fruit/seed, aggression absent.   (b)

602   fruit/seed, aggression present, (c) other foods, aggression absent and (d)

603   other foods, aggression present.

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Table I. Statistics of fixed effects of the generalized linear mixed model (GLMM)

Factor	Mean	SD	Min	Max
Density of available conspecific food trees (/ha)	184	686	1	3494
Feeding time (min)	16.7	13.3	6.03	60
#Feeding sites	56.3	58.4	2	274
#Co-feeding animals	4.23	3.36	1	16
Within-tree macaque density (#co-feeding animals/#feeding sit	0.08	0.22	0	2
Crown volume (m^3)*	229	243	0.03	1139

605   *: Not included in the GLM

Table II. Correlation coefficients in the best-fit generalized linear model on the number of aggression during feeding in trees.

Independent factors	Coefficient	SE	P
Food type (fruit/seed)	1.55	0.74	0.035
#Feeding sites	0.54	0.14	<0.0001
Interaction food type*#feeding sites	-0.54	0.22	0.014

df =177, P < 0.0001, R^2 =0.072, AIC=209.8

All independent variables except food category were log transformed, then z-standardized.
606 Positive coefficient means aggression is more likely to occur with increasing independent va
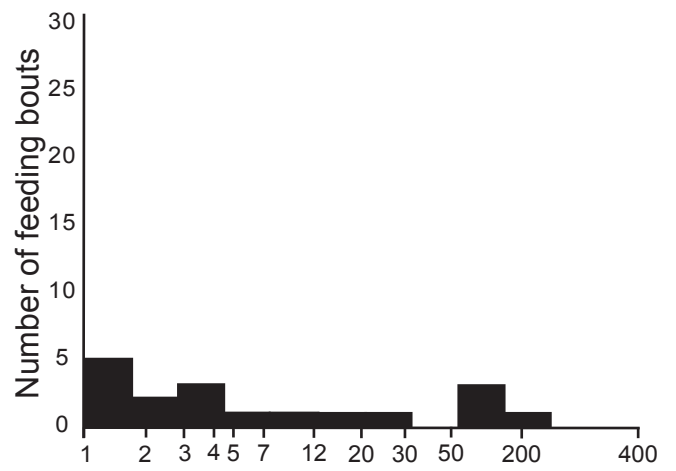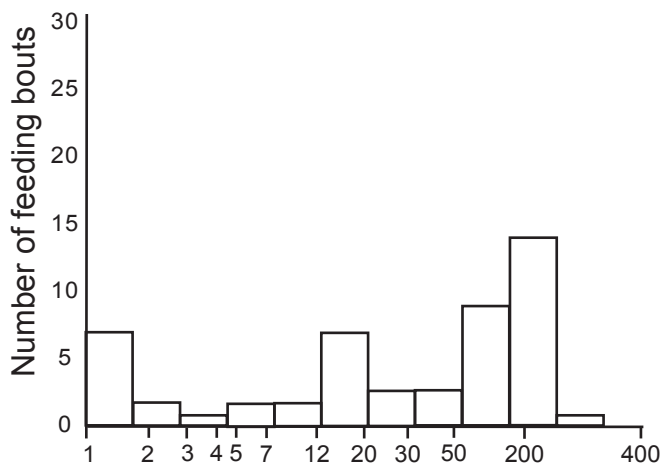
607
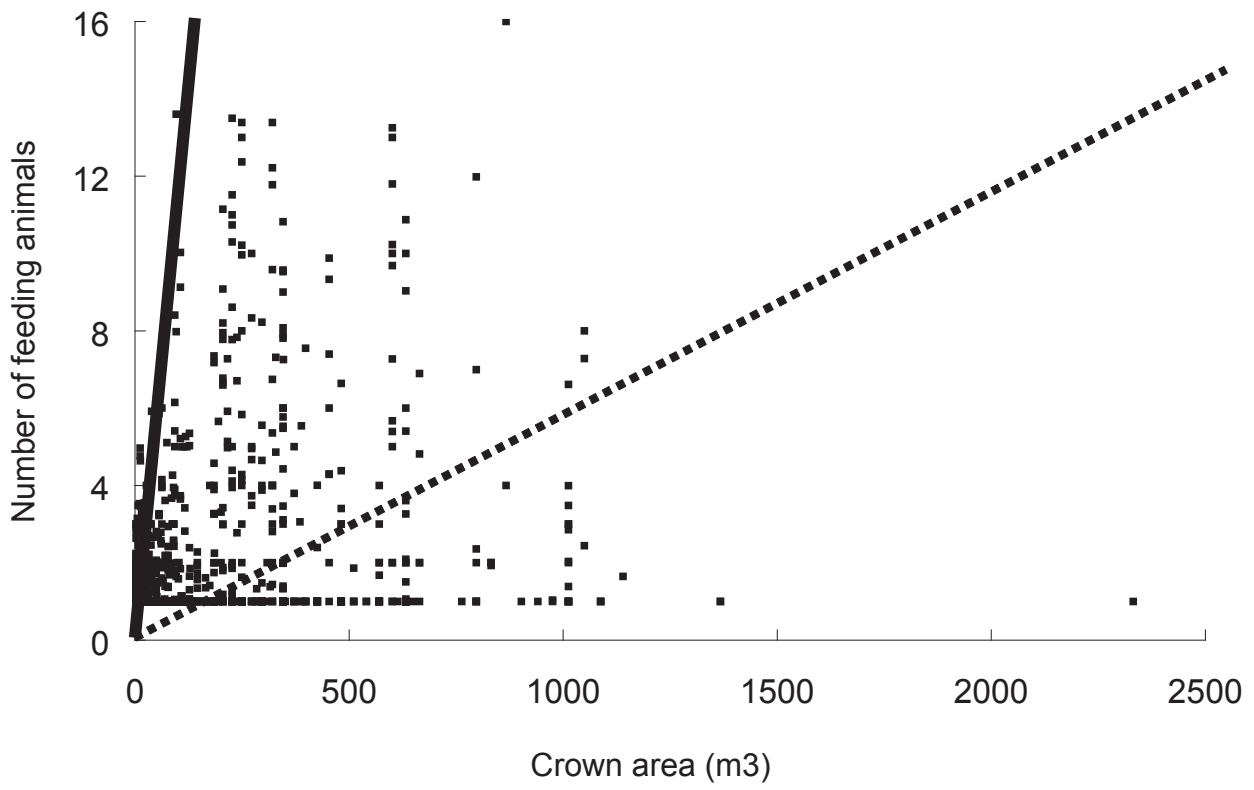
(a) Fruit/seed, aggression absent
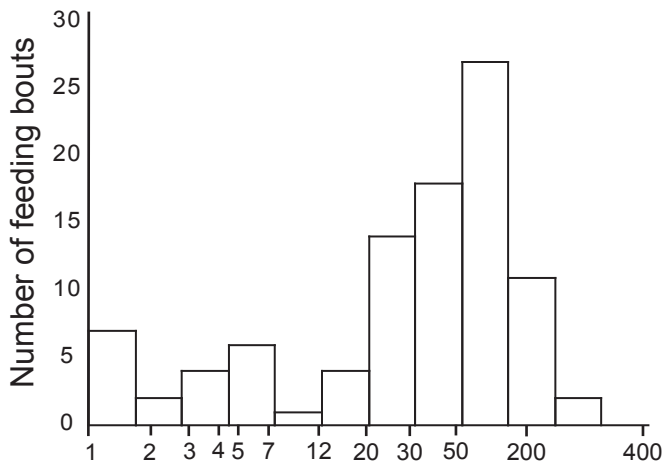
(b) Fruit/seed, aggression present

(c) Other food, aggression absent

(d) Other food, aggression present