TITLE:

Effects of food type and number of feeding sites in a tree on aggression during feeding in wild *Macaca fuscata*

AUTHOR(S):

Hanya, Goro

CITATION:

Hanya, Goro. Effects of food type and number of feeding sites in a tree on aggression during feeding in wild *Macaca fuscata*. *International Journal of Primatology* 2009, 30(4): 569-581

ISSUE DATE:

2009-08

URL:

<http://hdl.handle.net/2433/87309>

RIGHT:

© Springer Science + Business Media, LLC 2009.; この論文は著者最終稿です。内容が印刷版と異なることがありますので、引用の際には出版社版をご確認ご利用ください。This is the Accepted Author Manuscript. Please cite only the published version.

Hanya

Factors affecting aggression during feeding

1 Food type and the number of feeding sites in a tree affect aggression during
2 feeding in wild Japanese macaques
3
4 Goro Hanya
5
6 G. Hanya: Primate Research Institute, Kyoto University, Kanrin 41-2, Inuyama,
7 Aichi, 484-8506 Japan. E-mail: hanya@pri.kyoto-u.ac.jp, Tel: +81-568-63-0542,
8 Fax: +81-568-63-0564

9
10 Running title: Factors affecting aggression during feeding

11
12 Date of acceptance: June 26, 2009
13
14
15
16
17
18
19
20
21
22
23
24
25

Hanya
Factors affecting aggression during feeding

Abstract It is important to understand the effects of ecological factors on aggression during feeding in order to link habitat characteristics to competitive regime and social relationships. Multiple habitat characteristics are likely to affect aggression, but few studies have examined the effect of multiple factors on within-group competition simultaneously. I examined the effect of eight factors on aggression during feeding in wild Japanese macaques living in a coniferous forest in Yakushima: density of the tree species, feeding time, number of feeding sites within a feeding tree, number of co-feeding animals, within-tree macaque density, food type, rank and sex of the focal animal. When macaques co-fed with other individuals, food type, the number of feeding sites and their interactions significantly influenced aggression. Aggression increased when macaques ate fruits/seeds when compared to other foods and as the number of feeding sites decreased. Primate socioecological models highlight the importance of clumped distribution of food patches as a correlate of within-group contest. However, this study indicated that primatologists need to pay attention to the factors related to the current feeding tree (food type and feeding tree size with respect to monopolizability) in addition to the distribution of food in the entire home range.

Keywords aggression; co-feeding; food distribution; monopolizability; Yakushima

Introduction

Patterns of aggression in defense of food resources during feeding affect competitive regimes (Janson 1985), which in turn affect female social relationships (van Schaik and van Hooff 1983; van Schaik 1989). Animals

Hanya
Factors affecting aggression during feeding

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

Hanya Factors affecting aggression during feeding

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

Hanya
Factors affecting aggression during feeding

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)

Hanya Factors affecting aggression during feeding

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

Hanya Factors affecting aggression during feeding

aggression. For example, in terms of macaque density, a tree with 4 feeding sites and 2 animals is the same as one with 8 feeding sites with 4 animals. In order to reveal which is the most significant factor among number of co-feeding animals, number of feeding sites, or within-tree macaque density, I examined all of these factors.

7) Rank: Higher-ranked individuals are predicted to be involved in aggression in order to confirm and strengthen their dominance (Chancellor and Isbell 2008).

Methods

Study site, subjects, and periods

I conducted the study in a coniferous forest of Yakushima (Hanya *et al.* 2004). The study group of Japanese macaques (*Macaca fuscata*), HR group, contained 24-27 individuals, including 7-9 adult females, 6-7 adult males, 7-10 juveniles and 2 infants. I identified all individuals in the study group using natural markings, such as facial characteristics, loss of fingers, etc. There was a linear dominance hierarchy among group females (Hanya *et al.* 2008). I observed the behavior of 7 adult females in the group from April 2000 to March 2001 (on 107 days) and 5 adult females from October 2003 to January 2004 (on 39 days). Each of the 5 focal animals in the second study period was also observed in the first study period. Two focal females in the first study period were lactating. Other females were not followed because they were less habituated to observer presence.

Term definition

I defined the following four terms:

Hanya

Factors affecting aggression during feeding

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

Hanya

Factors affecting aggression during feeding

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 ($\pm$ 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

Hanya

Factors affecting aggression during feeding

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: $2.7 \text{ km}^2 \times 5\% = 13.5 \text{ ha}$ (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

Hanya

Factors affecting aggression during feeding

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.

Hanya

Factors affecting aggression during feeding

276 (4) *Number 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 m³ and rounding down (Vogel and Janson 2007).
 279 For example, if the estimated crown volume was 6 m³, 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 ($\pi \cdot (\text{DBH}/2)^2$) using the following regression equation
 282 derived from the vegetational data:
 283 $\text{Log (crown height; m)} = \text{log (basal area, cm}^2\text{)} \cdot 0.269 + 0.691$
 284 $\text{Log(crown area, m}^2\text{)} = \text{log(basal area, cm}^2\text{)} \cdot 0.505 - 0.064$
 285 whereas
 286 $\text{Crown area} = \pi \cdot \text{largest width of the crown}/2 \cdot \text{smallest width}/2$
 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 $\text{Crown volume} = 1/3 \cdot \text{crown area} \cdot \text{crown height (m}^3\text{)}$ (Janson 1988).
 293 (5) *Number 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.

Hanya

Factors affecting aggression during feeding

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 ($\chi^2=13.0$,
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

Hanya

Factors affecting aggression during feeding

same model because the former was calculated from the latter. I excluded feeding trees without co-feeding animals from the model because there was no opportunity for aggression to occur. Collinearity (correlations between independent factors) was not severe in this dataset: the maximum variance inflation factor (VIF) was smaller (2.63) than the cut-off value (5) recommended in Neter *et al.* (2004).

I log transformed all independent variables except food type and age before conducting the GLM. I set the alpha level at 0.05. I used R 2.8.1. (© The R Foundation for Statistical Computing) for statistical analysis.

Results

During feeding bouts which lasted more than 5 minutes with co-feeding animals, the frequency of aggression was 0.92 times/feeding hour (45/48.6), or once every 1 hour and 5 minutes. The average duration of a feeding bout was only 16.1 minutes, and thus I observed aggression in 18% of the feeding bouts (33/181). I summarize statistics of independent factors and crown volume in Table I.

Macaques exhibited aggression more often when they ate fruit/seeds than when eating other foods, and when the number of feeding sites was small. In the best-fit model, the number of aggressions was predicted to increase with small #feeding sites and when macaques ate fruits/seeds (Table II, Fig. 2). In a tree with one feeding site, when aggression was most likely to occur, the expected count of aggression per feeding bout was 0.68 when macaques were eating fruits/seeds and 0.21 when macaques were eating other foods. In a tree with 45 feeding sites, which was the median value, the expected count of

Hanya

Factors affecting aggression during feeding

aggression per feeding bout was 0.051 when macaques were eating fruits/seeds and 0.21 when macaques were eating other foods. The model with the second-smallest AIC only used #feeding sites. The difference in AIC between the best and second best-fit models was 2.4. The addition of other factors to the best-fit model increased AIC by at least 2, and the effect of the added factors was not significant in any model, meaning that the effect of food type and #feeding sites on aggression was fairly robust. In the model that included both tree density and #feeding sites, only #feeding site was significant, and the AIC was larger than the best-fit model by 10.1.

The effect of the number of feeding sites was apparent only when macaques were eating fruits and seeds. Number of feeding sites was significantly smaller for fruits/seeds than other foods ($t=3.07$, $P=0.0025$). However, the effect of food type was not merely a by-product of the large number of feeding sites for non-fruit/seed food trees. When I analyzed only fruit/seed feeding, the effect of the number of feeding sites on occurrences of aggression was significantly negative ($z=3.90$, $P<0.0001$). When I analyzed only other food feeding, the effect of the number of feeding sites was not significant ($z=0.017$, $P=0.98$). Therefore, when macaques ate fruit and seeds in small feeding trees, aggression increased.

Discussion

This study showed that aggression by Japanese macaques in a coniferous forest on Yakushima increased when the number of feeding sites was small and when macaques were feeding on high-quality foods. However, the number of feeding sites did not affect the frequency of aggression when macaques were

Hanya

Factors affecting aggression during feeding

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

Hanya

Factors affecting aggression during feeding

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 ($2.15 \pm 429 \text{ m}^3$ 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

Hanya

Factors affecting aggression during feeding

426 feeding. Because of the smaller feeding tree size for Japanese macaques
427 (mean±SD: 172±13 m³) than for capuchins (429±24 m³; 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

Hanya
Factors affecting aggression during feeding

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

Hanya Factors affecting aggression during feeding

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

Hanya
Factors affecting aggression during feeding481 **Acknowledgements**

482 I would like to thank my friends and colleagues in Yakushima for their hospitality
483 and help. The Yakushima Forest Environment Conservation Center gave me
484 permission to conduct the research. The Sarugoya Committee and Field
485 Research Center of the Primate Research Institute, Kyoto University (KUPRI;
486 presently, Wildlife Research Center) offered me excellent facilities. Dr. N.
487 Nakagawa, A. MacIntosh, reviewers and the editor of this journal and the staff at
488 the KUPRI gave me helpful suggestions. This study was financed in part by the
489 Cooperation Research Program of KUPRI, the MEXT Grant-in-Aid for JSPS
490 Fellows, for the 21st Century COE Program (A2) and for the Global COE
491 Program "Formation of a Strategic Base for Biodiversity and Evolutionary
492 Research: from Genome to Ecosystem". The research complied with protocols
493 approved by the guidelines for field research of non-human primates of KUPRI
494 and adhered to the legal requirements of Japan.

495

Hanya
Factors affecting aggression during feeding

496 **References**

- 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*

Hanya
Factors affecting aggression during feeding

- 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., Tsuruya 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.

Hanya
Factors affecting aggression during feeding

- 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 oerstedii* 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 Pruett, 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.

Hanya
Factors affecting aggression during feeding

- 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 Tai National Park. *International*
587 *Journal of Primatology*, 24, 847-867.
- 588
- 589
- 590

Hanya Factors affecting aggression during feeding

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.

604

Hanya

Factors affecting aggression during feeding

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 site)	0.08	0.22	0	2
Crown volume (m ³)*	229	243	0.03	1139

605 *: Not included in the GLM

Hanya

Factors affecting aggression during feeding

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

Independent factors	Coefficient	SE	<i>P</i>
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.
Positive coefficient means aggression is more likely to occur with increasing independent variables.

606

607

(a) Fruit/seed, aggression absent

(b) Fruit/seed, aggression present

(c) Other food, aggression absent

(d) Other food, aggression present