TITLE:

Comparison of feeding behavior between two different-sized groups of Japanese macaques (*Macaca fuscata yakui*).

AUTHOR(S):

Kurihara, Yosuke; Hanya, Goro

CITATION:

Kurihara, Yosuke ...[et al]. Comparison of feeding behavior between two different-sized groups of Japanese macaques (*Macaca fuscata yakui*).. American journal of primatology 2015, 77(9): 986-1000

ISSUE DATE:

2015-09

URL:

<http://hdl.handle.net/2433/202032>

RIGHT:

This is the peer reviewed version of the following article: Kurihara, Y. and Hanya, G. (2015), Comparison of feeding behavior between two different-sized groups of Japanese macaques (*Macaca fuscata yakui*). Am. J. Primatol., 77: 986–1000, which has been published in final form at <http://dx.doi.org/10.1002/ajp.22429>. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.; The full-text file will be made open to the public on 13 MAY 2016 in accordance with publisher's 'Terms and Conditions for Self-Archiving'; 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.

Yosuke Kurihara, Goro Hanya 1

- 1 Comparison of Feeding Behavior between Two Different-Sized Groups of Japanese
- 2 Macaques (*Macaca fuscata yakui*)
- 3
- 4 Yosuke Kurihara, Goro Hanya
- 5
- 6 Primate Research Institute, Kyoto University, Inuyama, Japan
- 7
- 8 Correspondence to: Y. Kurihara, Primate Research Institute, Kyoto University, Kanrin
- 9 41-2, Inuyama, Aichi, 484-8506 Japan. E-mail: kurihara.yosuke.35s@st.kyoto-u.ac.jp
- 10 Tel: +81-568-63-0545, Fax: +81-568-63-056
- 11
- 12 Short title: Feeding competition in Japanese macaques

ABSTRACT

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

Key words: feeding competition; ecological constraints model; patch use; group size;

Macaca fuscata yakui

38 INTRODUCTION

39 Group living has benefits such as resource defense (advantage in intergroup feeding
40 competition) [Wrangham, 1980], predator avoidance [Hamilton, 1971], and efficient
41 resource detection [Struhsaker, 1981], and includes costs such as intragroup feeding
42 competition [Janson & van Schaik, 1988] and disease transmission [Sanderson et al.,
43 2014]. Feeding competition has been considered the most important factor affecting the
44 fitness of group-living animals [Chapman et al., 2012]. Animals in groups face two
45 types of group-size-dependent feeding competition: intragroup scramble competition
46 and intergroup contest competition.

47 Intragroup scramble competition occurs when animals use the same food
48 patches, thereby reducing the amount of food intake per capita for all members of the
49 group [Janson & van Schaik, 1988; Koenig, 2002]. Its intensity increases with group
50 size because larger groups need more food resources. The ecological constraints model
51 [Chapman & Chapman, 2000] predicts that the larger groups are required to visit more
52 food patches, which forces them to have larger home ranges, to travel longer distances
53 and to spend more time feeding and moving. Two mechanisms are assumed to explain
54 the need for more patches. One is patch depletion: a larger number of animals leads to
55 faster depletion of food resources [Chapman & Chapman, 2000]. The other is spatial
56 compression (termed “funneling”): larger groups will fill in a food patch more quickly
57 because the patch can accommodate a limited number of animals. Therefore, animals in
58 larger groups will leave the patch earlier and move further to the next patch than those
59 in smaller groups because they will be pushed forward by succeeding animals [Isbell,
60 2012].

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

disadvantages of larger groups: the costs of intragroup scramble competition negatively affect the net energy gain / reproductive success [van Schaik et al., 1983; van Noordwijk & van Schaik, 1999; Borries et al., 2008; Zhao et al., 2011]. Meta-analysis on the relationship between group size and behavior and demography [Majolo et al., 2008] also support the predictions of the ecological constraints model. This study concludes that, in most primate species, the costs of intragroup feeding competition balanced or outweighed the benefits of intergroup feeding competition which lead to higher net energy gain / reproductive success in large-sized, dominant groups than in small-sized, subordinate groups through intergroup encounters [Janson & van Schaik, 1988; Koenig, 2002]. However, several studies have revealed different patterns of relationships between net energy gain / reproductive success and group size [Cheney & Seyfarth, 1987; Robinson, 1988; Koenig, 2000; Takahata et al., 2006]. In particular, it remains untested the predictions of the ecological constraints model and unclear how group size affects behavior when the net energy gain / reproductive success increases with group size.

Among Japanese macaques (*Macaca fuscata yakui*) of the Yakushima coastal forest, larger groups have higher birth rates than smaller groups [Suzuki et al., 1998; Takahata et al., 1998]. Since group density is high (4.8 groups/km²) [Yoshihiro et al., 1999] and the home range is worth defending against other groups [Maruhashi et al., 1998], aggressive intergroup encounters occur frequently [Saito et al., 1998; Sugiura et al., 2000; Hanya et al., 2008]. The outcome of intergroup encounter is determined by the relative group size: larger groups are dominant over smaller groups [Sugiura et al., 2000]. Based on these results, previous studies have suggested that larger groups, which have advantages in intergroup encounters, achieve higher reproductive success [Suzuki et al., 1998; Takahata et al., 1998]. Japanese macaques in the Yakushima coastal forest

are ideal subjects to investigate the relationships between group size and feeding competition because the effects of predation pressure on group size can be ignored owing to the absence of predators in this region [Yamagiwa & Hill, 1998]. Majolo et al. [2009] clarified that a larger group had a larger home range, traveled longer distances, and spent more time moving than did a smaller group. These results supported the predictions of the ecological constraints model, and showed that intragroup scramble competition was more intense in the larger group. However, more detailed study is needed to elucidate the mechanisms whereby, in contrast to most primate species, reproductive success declines as group size decreases. It is necessary to investigate feeding behavior thoroughly, including food patch use, which is the assumption of the ecological constraints model. This investigation should be conducted under controlling habitat quality, to avoid obscuring the effects of group size on feeding behavior [Majolo et al., 2009].

The objective of this study was to reveal effects of group size on feeding behavior including food patch use of Japanese macaques in the Yakushima coastal forest. We compared behavioral proxies of intragroup scramble competition such as home range size, travel distance, activity budget, and the number of visited patches between two different-sized groups. Following the ecological constraints model, we predicted that the larger group will have a larger home range, travel longer distances, spend more time feeding and moving, and visit more patches than the smaller group. Additionally, dietary composition and diversity were compared between the two groups. We predict that the animals in the larger group will consume less-preferred and/or lower-quality foods and increase dietary diversity due to intense intragroup scramble competition [Steenbeek & van Schaik, 2001; Gogarten et al., 2014]. We also compared four characteristics of patch use: patch residency time, patch size, the number of co-feeding

individuals, and inter-patch distance. According to the ecological constraints model, we predicted that patch residency time will be shorter and the number of co-feeding individuals will be larger in the larger group than in the smaller group. Patch size and inter-patch distance will not differ between the two groups due to the similarity of habitat environment. In addition, we examined two assumptions underlying the ecological constraints model. First, to examine patch depletion, we compared feeding rate between the two groups and examined the relationship between feeding rate and patch residency time. If the patch depletion occurs more frequently in the larger group, feeding rate in the larger group is expected to be lower than that in the smaller group, which leads to shorter patch residency time. Second, to examine funneling, we compared proportions of patches within which the maximum number of animals outweighs the number of feeding sites between the two groups, and tested whether patch residency time was shortened in such patches. If funneling occurs more frequently in the larger group, animals in the group fill in feeding sites in the patch more frequently, which leads to shorter patch residency time.

METHODS

This study was conducted with permission from the Yakushima Forest Ecosystem Conservation Center and Kagoshima Prefectural Government, complied with the ethical guidelines for field research of non-human primates of the Kyoto University Primate Research Institute and the legal requirements of Japan, and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Study Site and Groups

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

groups, respectively) of Japanese macaques living in the western coastal forest on Yakushima Island (30°N, 130°E) during October 2012–April 2013. The study period included mating season (mid-August–January) [Yamagiwa, 1985]. The study area was covered with primary and secondary warm temperate evergreen broad-leaved forest, mainly comprising Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae [Agetsuma, 1995; Tsujino et al., 2007]. Vegetation was essentially the same in the respective home ranges of each of the two groups because they had partly overlapped home ranges in similar altitudinal zones (ca. 0–350 m a.s.l.). The larger group had 30–35 individuals, including 6–8 adult females (>6 yrs old), 3–6 adult males (>6 yrs old), 15–21 juveniles (1–5 yrs old), and 1–6 infants (<1 yr old). The smaller group had 13–15 individuals, including 4–5 adult females, 4–5 adult males, 2–5 juveniles, and 0–4 infants. The sizes of the larger and smaller groups were larger and smaller than the mean group size of this local population (16.9 individuals) [Yoshihiro et al., 1999], respectively. Neither group exhibited sub-grouping ranging during the study period [Kurihara, unpublished data]. We confirmed that the larger group had advantages in intergroup encounters in accordance with the previous study [Sugiura et al., 2000]: the larger group won two of the four encounters, and the smaller group did not win any encounter (0/8) (larger group: 0.020 times/h; smaller group: 0.067 times/h).

Behavioral Data Collection

We followed one or both of the two groups each day and changed the focal group at least once every three days. We investigated all adult females in the two groups (9–13 individuals) via one-hour focal animal sampling. We changed the focal animal every hour and selected the following one for which the observation time accumulated so far was shortest. Total observation time was 333 h (larger group: 199 h, smaller group: 134

h). Via instantaneous recording, we recorded activities (feeding, moving, resting, grooming and other) of the focal animal every minute. When the focal animal was feeding, we recorded the onset and the end of feeding to the nearest second and feeding items (species and part). We regarded the onset as the time when the focal animal puts food into the mouth, and the end as the time when 20 seconds had passed without manipulating the food. In addition, we recorded feeding rate: the number of food units that the focal animal puts into the mouth per 10 seconds. A food unit was defined for each feeding item (one fruit, one leaf, one cluster of fruits, etc.). The recording was repeated as many times as possible while the focal animal was feeding. We defined a food patch as one individual tree or liana in which the focal animal fed. In the present study, terrestrial patches (fallen fruits / seeds or insects) could not be defined because these foods were uniformly distributed on the ground. When the focal animal left a patch and returned back without feeding in any other patches, we considered it as one patch. If the focal animal fed in a patch, we also collected the following data: (1) time when the focal animal entered into and departed from the patch, (2) time when other individuals entered into and departed from the same patch in which the focal animal fed, and (3) length of major and minor axes and height of the patch. By using GPS (GARMIN 60CSx, GARMIN), we recorded locations of the focal animal every 30 seconds and food patches when the focal animal visited.

Data Analysis

Home Range and Travel Distance

We estimated home range size and calculated travel distance based on GPS data points plotted every five minutes. Home range size was estimated by using fixed kernel density method. The grid size was 10 m × 10 m, and the smoothing parameter h was

determined by an *ad hoc* technique because the calculation by the least square cross validation method did not converge. We regarded 95% kernel area as overall home range, and 50% kernel area as the core area. Travel distance was calculated as the sum of linear distance among GPS points plotted consecutively.

Diet

Feeding items were categorized into eight types: fruits / seeds, mature leaves, young leaves (including buds and shoots), flowers (including nectar and flower buds), animal matter, fungi, other (pith, bark, water, soil, etc.), and unidentified. Furthermore, fruits/seeds were categorized as fallen (focal animals fed on the ground) or not (on the trees). In addition, foraging (searching for food such as fallen fruits / seeds or insects in the litter on forest floor) was considered as a type of feeding as per Hill [1997]. The feeding behaviors could not be categorized into one specific feeding item, because discriminating whether macaques searched fallen fruits / seeds, insects, or other items in the litter could not be determined, and the food-searching behavior did not always result in actual feeding.

To evaluate the monthly diversity of food repertoire, we calculated the Shannon-Wiener index H :

$$H = -\sum_i p_i \ln p_i$$

where, p_i is the proportion of time spent feeding on the item i among the total feeding time. H increases with the diversity of food repertoire, and equals zero when one specific feeding item accounts for 100% of the total feeding time.

Comparison of Behavioral Proxies of Intragroup Scramble Competition

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

activity budget, travel distance, and the number of visited patches (Table I). The distribution of travel distances was normalized by square root transformation. In the diet composition model, group (larger or smaller) was included as fixed effect and observation date as random effect. To explain feeding on young leaves, we used generalized linear model (GLM) because GLMM did not converge. In the remaining models, group, copulatory behavior and dietary composition were included as fixed effect, and observation date or identities of the focal animals as random effect. It has already been established that diet composition and copulatory behavior affect the overall feeding patterns of animals [Agetsuma, 1995; Matsubara & Sprague, 2004]. The proportions of time spent feeding on fruits / seeds and animal matter were included as factors of diet composition, because seasonal variation in diet could be considered on the basis of these two types of foods. The proportion of time spent feeding on mature leaves, young leaves, flowers, and time spent foraging were correlated with that on fruits / seeds (Spearman's rank order correlation: mature leaves: $\rho = -0.71$, $p < 0.001$; young leaves: $\rho = -0.42$, $p < 0.001$; flowers: $\rho = -0.39$, $p < 0.001$; foraging: $\rho = -0.46$, $p < 0.001$), and the proportion of time spent feeding on fungi were correlated with that on animal matter (fungi: $\rho = 0.56$, $p < 0.001$). As a factor of copulatory behavior, whether male-female mounting series involving the focal animal was observed (1) or not (0) during a one-hour session was included in the models on travel distance and the number of visited patches, and number of one-hour sessions during which the mounting series was observed in a day was included in the model for activity budget.

To examine the effects of “group” on each dependent variable, we compared the models with and without the factor “group” using ANOVA (likelihood ratio test). If $P < 0.05$ was obtained, “group” was regarded as a factor significantly affecting the goodness-of-fit of the models. To examine the difference in the diversity of food

repertoire, the Shannon-Wiener index H of the two groups was compared using Wilcoxon rank-sum test.

Patch Use

To investigate how group size affected the general characteristics of patch use, we compared patch residency time, patch size, number of co-feeding individuals, and inter-patch distance between the two groups. Patch residency time was calculated as the feeding time of the focal animal in a patch to the nearest seconds. When entrance or departure time into / from the patch by the focal animal could not be recorded, the data on patch residency time for the patch was discarded. Patch size was calculated as the volume of an elliptic cylinder (major axis*minor axis*height* π) [Kazahari & Agetsuma, 2010]. The number of co-feeding individuals was calculated as the average number of other individuals (except infants) within the same patch during the focal animal's residency [Hanya, 2009]. If, during a stay for two minutes, three individuals stayed with the focal animal for the first 90 seconds and two individuals for the last 30 seconds, the number of co-feeding individuals in the patch was regarded as 2.75. Inter-patch distance was calculated as linear distance between patches that the focal animal visited consecutively. We constructed GLMMs to explain patch residency time, patch size, and number of co-feeding individuals (Table I). The distributions of patch residency time and patch size were normalized by log transformation. The number of co-feeding individuals was rounded up and transformed to integers to treat as Zero-inflated Poisson distribution. In the model for patch residency time, group, patch size, number of co-feeding individuals, and food category (fruits / seeds, mature leaves, young leaves, and other) were included as fixed effect, and the identities of the focal animal as random effect. In the model for patch size, group and food category were included as fixed

effect, and the identities of the focal animal as random effect. In the model for number of co-feeding individuals, group, patch size, and food category were included as fixed effect, and the identities of the focal animal as random effect. It has already been established that (1) patch residency time is influenced by patch size and number of co-feeding individuals, (2) number of co-feeding individuals is influenced by patch size, and (3) the three characteristics of patch use are influenced by food category [Kazahari & Agetsuma, 2008; Hanya, 2009; Potts et al., 2011]. Likelihood ratio tests were conducted to examine the effects of group on patch residency time and patch size. For the effects of group on number of co-feeding individuals, we examined the significance of “group” in the model because the likelihood ratio test could not be conducted. In addition, inter-patch distance was compared between the two groups using Wilcoxon rank-sum test.

To test whether patch depletion occurred more frequently in the larger group, we compared feeding rate between the two groups and examined correlation between feeding rate and patch residency time. This analysis was conducted for each feeding item separately to minimize effects of patch characteristics [Kazahari et al., 2013]. We selected 12 main feeding items that accounted for 56% (290/516) of all visited patches in the larger group and 43% (163/380) in the smaller group. Feeding rate was averaged for each patch, and compared using Wilcoxon rank-sum test. The correlation between feeding rate and patch residency time was tested using Spearman’s rank order correlation. Ideally, we should have examined time-series variations in feeding rate in the patch [Kazahari & Agetsuma, 2008], but it was difficult to collect sufficient data for conducting such an analysis. Although this comparison may be preliminary, group differences in feeding rate could be detected sufficiently.

We tested whether funneling effect shortened patch residency time more

frequently in the larger group. First, we examined the relationships between the maximum number of animals and the number of feeding sites in a patch. The number of feeding sites was calculated by dividing the patch size by 4.18 m^3 (the volume of a sphere with a radius of 1 m, a monopolizable area for one individual) [Hanya, 2009]. We defined a *filled patch* as when the maximum number of animals outweighed the number of feeding sites in the patch. The proportion of the filled patches among all visited patches was compared between the two groups by Fisher's exact test. Second, we examined whether patch residency time was shortened at the filled patches. We constructed GLMM on patch residency time for each group (Table I). The distribution of patch residency time was normalized by log transformation. Whether the patch was filled or not, food category (fruits / seeds, mature leaves, young leaves, and other), and dominance rank of the focal animal were included as fixed effect, the identities of the focal animal as random effect, and patch size as offset term. Dominance rank was determined by the normalized David's scores calculated on the basis of aggressive interaction [de Vries et al., 2006]. A likelihood ratio test was conducted to examine effects of filling patches on patch residency time.

We used the *adehabitat* package for estimating home range and the *lme4* and *glmmADMB* package for GLMM in R 3.0.1. We calculated travel distance and inter-patch distance and visualized the home ranges by QGIS 2.0.1. All statistical tests, except the likelihood ratio test, were two-tailed, and alpha level was set at < 0.05 .

RESULTS

Comparison of Behavioral Proxies of Intragroup Scramble Competition

The larger group had a larger home range (Figure 1, larger group: 38.9 ha, smaller group: 34.8 ha) and spent more time feeding than did the smaller group (Tables II, III),

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

Dietary composition was different but dietary diversity did not differ between the two groups. The larger group spent less time feeding on fruits / seeds and young leaves and more time feeding on mature leaves and foraging than did the smaller group (Tables II, III). In particular, fallen fruits / seeds feeding time accounted for a larger proportion of the total fruits / seeds feeding time in the larger group than in the smaller group (Table III, larger group: $29.1\% \pm 36.2\%$; smaller group: $15.7\% \pm 28.5\%$; likelihood ratio test: $df = 1$, $\chi^2 = 59.18$, $p < 0.001$). There were no differences in feeding time on flowers, animal matter, and fungi (Tables II, III). Further, the monthly diversity of food repertoire did not differ between the two groups (H : larger group: 2.43 ± 0.23 , smaller group: 2.40 ± 0.42 ; Wilcoxon rank-sum test: $W = 18$, $p = 0.58$). Over the study period, 33 species and 57 items were common among the two groups (Appendix I, larger group: 45 species, 83 items; smaller group: 47 species, 84 items). In a month, the common repertoire accounted for $61.7\% \pm 11.7\%$ of species and $56.7\% \pm 10.8\%$ of items in the larger group, and $66.7\% \pm 11.6\%$ and $63.6\% \pm 12.6\%$ in the smaller group, respectively.

Contrary to the predictions, the smaller group spent more time moving (Tables II, III) and traveled longer distances than did the larger group (Table III, larger group: 188 ± 72 m/h, smaller group: 219 ± 116 m/h; likelihood ratio test: $df = 1$, $\chi^2 = 7.67$, $p < 0.01$). In addition, there were no differences in the number of visited patches (Table III, larger group: 2.8 ± 2.3 /h, smaller group: 3.0 ± 2.5 /h; likelihood ratio test: $df = 1$, $\chi^2 = 1.08$, $p = 0.30$).

Patch Use

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

group, although patch residency time, patch size, and inter-patch distance did not differ between the two groups (Table III; patch residency time: larger group: 407.3 ± 544.5 sec., smaller group: 350.7 ± 520.0 sec.; likelihood ratio test: $df = 1$, $\chi^2 = 0.07$, $p = 0.79$; patch size: larger group: $148.3 \pm 211.1 \text{ m}^3$, smaller group: $137.6 \pm 214.8 \text{ m}^3$; likelihood ratio test: $df = 1$, $\chi^2 = 3.58$, $p = 0.06$; number of co-feeding individuals: larger group: 0.91 ± 1.68 individuals, smaller group: 0.40 ± 0.99 individuals; GLMM: Estimate $\pm$ SE = -0.62 ± 0.10 , $z = -6.48$, $p < 0.001$; inter-patch distance: larger group: 25.6 ± 33.0 m, smaller group: 28.3 ± 35.0 m; Wilcoxon rank-sum test: $W = 17791$, $p = 0.25$).

Both patch depletion and funneling, the assumptions of the ecological constraints model, did not occur more frequently in the larger group. First, we find neither significant difference in feeding rate between the two groups nor significant correlation between feeding rate and patch residency time for each group for all of the 12 main feeding items (Appendix II). Second, the proportions of filled patches among all visited patches did not differ between the two groups (larger group: 23/494, smaller group: 23/362; Fisher's exact test: $p = 0.29$). Contrary to the prediction, patch residency time was longer in the filled patches than in the non-filled patches in both of the two groups (Table IV, likelihood ratio test: larger group: $df = 1$, $\chi^2 = 50.19$, $p < 0.001$; smaller group: $df = 1$, $\chi^2 = 52.20$, $p < 0.001$). We also checked the following definitions of the number of feeding sites in a patch: (1) dividing an elliptic cylinder by 113 m^3 (the volume of a sphere with a radius of 3 m), (2) dividing an ellipsoid $((4/3) \times \text{major axis} \times \text{minor axis} \times \text{crown length} \times \pi)$ by 4.18 m^3 , and (3) dividing an ellipsoid by 113 m^3 . Since we were able to obtain the same results based on all of these definitions, only the results based on the initial definition are shown.

DISCUSSION

Consistency with the Ecological Constraints Model

In the present study, the larger group had a larger home range and spent more time feeding than did the smaller group, in accordance with the predictions of the ecological constraints model and the results of previous studies [Chapman & Chapman, 2000; Majolo et al., 2009; etc.]. This suggests that intragroup scramble competition was more intense in the larger group than in the smaller group.

To mitigate the costs of intragroup scramble competition, macaques in the larger group changed dietary composition but did not increase dietary diversity. The larger group spent more time feeding on mature leaves. Mature leaves are less contestable because they are more abundant and less preferred than fruits / seeds and young leaves [Agetsuma, 1995; Harris & Chapman, 2007; Hanya, 2009]. Among Thomas's langurs (*Presbytis thomasi*), larger groups are also known to increase feeding on less-preferred foods [Steenbeek & van Schaik, 2001]. In terms of patch use, mature-leaf feeding positively influenced the number of co-feeding individuals (shown in the model in Table III). Less-contestable foods enable animals to remain with many individuals in a patch [Iwamoto, 1982; Agetsuma, 1995; Hanya, 2009]. Therefore, the mature-leaf feeding might lead to maintaining spatial cohesion as a group. In addition, the larger group spent more time feeding on fallen fruits / seeds and foraging (searching for food in forest litter). Such terrestrial feeding might prolong the total feeding time in the larger group, considering that there were no group differences in residency time on the patch (tree or liana). Animals could save energy by increasing foraging on the ground, given that terrestrial travel was less energetically costly than arboreal travel [Janson, 1988; Hirsch et al., 2013]. In addition, dietary diversity did not differ between the two groups. This contradicted the previous study, which suggested that larger groups increased dietary diversity to deal with intense intragroup scramble competition

[Gogarten et al., 2014]. It is necessary to investigate energetic / nutritional intake of animals in order to clarify whether this dietary strategy influences the fitness of animals.

Inconsistency with the Ecological Constraints Model: Number of Visited Patches and Patch Use

One of the discrepancies between the results of our study and the ecological constraints model is related to the number of visited patches and patch use. The ecological constraints model predicted that larger groups stayed for shorter duration in one patch and visited a larger number of patches [Chapman & Chapman, 2000]; however, patch residency time and the number of visited patches were not different between the two groups in the present study. There are two possible explanations for this.

First, patch depletion did not occur more frequently in the larger group. In our study, we found no difference in feeding rate between the two groups and no correlation between feeding rate and patch residency time for each group for all of the main feeding items. This was consistent with previous studies demonstrating that increasing the number of co-feeding individuals did not decrease feeding rate and that patch depletion did not occur [Kazahari & Agetsuma, 2008; Tombak et al., 2012]. Furthermore, Kazahari et al. [2013] demonstrated that the characteristics of the food items were associated with the relationships between feeding-group size and feeding rate. For example, feeding rate increased with feeding-group size in a patch where within-patch food density was high. In our study, considering that the larger group depended more on mature leaves, patch depletion will be unlikely to occur in the larger group because mature leaves are superabundant within a patch. Thorough examination on the time-series variations in feeding rate in combination with the characteristics of the food items are required to elucidate this mechanism further in the Japanese macaques of

413 Yakushima.

414 Second, funneling did not occur in both of the two groups. The proportions of
415 filled patches did not differ between the two groups although it varied according to the
416 definitions (larger group: 4.7%–83.8%, smaller group: 6.4%–86.1%). Furthermore, in
417 contrast to the prediction, filling in patches did not shorten but prolonged patch
418 residency time. This could be explained by the result of a previous study that the
419 number of co-feeding individuals positively affected patch residency time in Japanese
420 macaques of Kinkazan Island [Kazahari & Agetsuma, 2008]. By staying with many
421 group members, macaques can be less dependent on following the group movement and
422 visually monitoring group members to maintain spatial cohesion [Kazahari & Agetsuma,
423 2010; Kazahari, 2014]. These results of funneling effect were robust regardless of the
424 definitions of feeding sites. Therefore, it is unlikely that feeding space in a patch
425 constrains patch residency time in Japanese macaques in Yakushima. Whether funneling
426 works as the mechanism of increasing the number of patches will depend on the
427 cost-benefit balance of group foraging, determined by the combinations of habitat
428 environment (patch size, presence of neighboring groups, etc.) and group size of a
429 population or species.

430

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

432 The other discrepancy was travel behavior. In the present study, the smaller group
433 traveled longer distances and spent more time moving than did the larger group,
434 contrary to the predictions of the ecological constraints model. The intergroup
435 differences in travel distance and moving time were detected in our study even if other
436 factors such as dietary composition and mating behavior were controlled. There are two
437 possibilities to explain this. First, patch characteristics such as patch size, density, and

distribution could influence the moving behavior of animals [Maruhashi et al., 1998; Cords, 2012; Dunn et al., 2012]. When the relative group size was related to intergroup dominance, smaller-sized, subordinate groups may be obliged to use lower-quality home range than larger-sized, dominant groups [Cheney & Seyfarth, 1987; Harris, 2006; Scarry, 2013]. In this case, smaller groups are expected to travel longer distances in order to find high-quality food resources that have not been used by larger groups [Robinson, 1988; Koenig, 2002]. In our study, we controlled vegetation differences in the home ranges by selecting two neighboring groups as subjects. The two groups had partly overlapped home ranges in the same altitudinal zones, and inter-patch distance and patch size were not different between the two groups. Therefore, it is unlikely that the heterogeneity of vegetation causes the differences in moving behavior between the two groups.

Second, disadvantages in intergroup encounters could lead to great travel costs of subordinate groups. After losing intergroup encounters, defeated groups were forced to travel longer distances for a longer time than victorious groups [Srikosamatara, 1987; Crofoot, 2013]. In addition, defeated groups were forced to change travel direction, which may cause inefficient and extended travel routes [Srikosamatara, 1987]. The frequency of intergroup encounters in the Yakushima coastal forest was as high (0.067 times/h: smaller group in this study; 0.039 times/h: [Sugiura et al., 2000]) as those in the study sites of the previous studies which showed losing encounters led to longer travel distances (0.033 times/h [Crofoot, 2007; 2013]; 0.086 times/h [Srikosamatara, 1987], given that the observation time during daytime was 10 h per day). Considering that the intergroup encounters were aggressive in all of the study sites, the immediate consequences of the loss of intergroup encounters could accumulate as daily travel costs in the smaller group in Yakushima.

The results of our study on travel behavior also differed from those of Majolo et al. [2009], which indicated that the larger group traveled longer distances and spent more time moving, among Japanese macaques in the Yakushima coastal forest. This would be explained by the difference in the relative and absolute sizes of the subject groups. First, the size of the smaller group (18) in Majolo et al. was similar to the average size of the neighboring groups (17.6), while the size of the smaller group in our study (13–15) was half the average size of the neighboring groups (32.1). Under the circumstance in Majolo et al., the smaller group might not be required to travel long distances and/or for a long time as a consequence of losing encounters. Second, Takahata et al. [1998] demonstrated that birth rate decreased further when group size was less than 14 in the Yakushima coastal forest. The size of the smaller group (18) in Majolo et al. was larger than that of the smaller group (13–15) in our study and that of the group (14) that actually showed the lower birth rate in Takahata et al. Therefore, only when the group size was below that threshold value and was smaller than the sizes of the neighboring groups, animals in the group would have increased travel costs as a result of intergroup competition.

Implications of Population Dynamics in the Yakushima Coastal Forest

This study revealed how feeding competition works in Japanese macaques in the Yakushima coastal forest, which helps in understanding the behavioral mechanisms underlying positive correlation between group size and reproductive success. Unlike most primate species, birth rate increases with group size in the Yakushima coastal forest. Previous studies in this population [Suzuki et al., 1998; Takahata et al., 1998] have focused on the benefits of larger groups and costs of smaller groups through intergroup contest competition from the point of view of energy intake: larger-sized,

488 dominant groups have higher-quality home ranges, which brings adult females better
489 energetic / nutritional conditions and higher birth rate. Although intragroup scramble
490 competition has not been investigated extensively, our study showed that the larger
491 group had the costs of intragroup scramble competition, as has been reported in many of
492 other primate species [e.g., Majolo et al., 2008]. In addition, our results were unique in
493 proposing behavioral mechanism causing positive correlation between group size and
494 reproductive success and suggesting that smaller groups have the costs of intergroup
495 contest competition from the point of view of energy expenditure: smaller-sized,
496 subordinate groups are required to travel long distances and/or for a long time, which
497 worsens energetic / nutritional conditions of adult females and lowers birth rate. Travel
498 behavior is energetically costly [Tucker, 1970; Dunn et al., 2013] and could affect
499 energy balance, and in turn, reproductive success of adult females [Emery Thompson et
500 al., 2012; McCabe et al., 2013]. To test how the costs and benefits of each group
501 translate into the differences in reproductive success, the energy balance of the animals
502 must be quantified: not only energy intake but also energy expenditure of animals in
503 different-sized groups should be considered to understand the mechanisms of group-size
504 effects on feeding behavior and reproductive success.

505 **ACKNOWLEDGMENTS**

506 We thank the Yakushima Forest Ecosystem Conservation Center and Kagoshima
507 Prefectural Government for their permission to conduct behavioral data collection in
508 Yakushima. We would like to express our gratitude to Drs. H. Sugiura, M. Suzuki and A.
509 Sawada for their warm support in the field, Mr. T. Saito for his help in identifying plant
510 species and Dr. S. Mochizuki for helping GPS data analysis. We are grateful to the
511 members of the Department of Ecology and Social Behavior in Primate Research
512 Institute and the Laboratory of Human Evolution Studies in Kyoto University forgiving
513 us insightful comments and suggestions. This study was supported financially by the
514 Cooperation Research Program of Wildlife Research Center, Kyoto University, and
515 Grant-in-Aid for Scientific Research (B) (No. 23370099) to Naofumi Nakagawa.

REFERENCES

- Agetsuma N. 1995. Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*).
International Journal of Primatology 15:595-609.
- Borries C, Larney E, Lu A, Ossi K, Koenig A. 2008. Costs of group size: lower
developmental and reproductive rates in larger groups of leaf monkeys. Behavioral
Ecology 19:1186-1191.
- Chapman CA, Chapman LJ. 2000. Determinants of group size in primates; the
importance of travel costs. In: Boinski S, Garber PA, editors. On the Move: How and
Why Animals Travel in Groups. Chicago: University of Chicago Press. p 24-42.
- Chapman CA, Rothman JM, Lambert JE. 2012. Food as a Selective Force in Primates.
In: Mitani J, Call J, Kappeler P, Palombit R, Silk J, editors. The Evolution of Primate
Societies. Chicago: University of Chicago Press. p 149-168.
- Cheney D, Seyfarth RM. 1987. The influence of intergroup competition on the survival
and reproduction of female vervet monkeys. Behavioral Ecology and Sociobiology
21:375-386.
- Cords M. 2012. The 30-Year Blues: What We Know and Don't Know About Life
History, Group Size, and Group Fission of Blue Monkeys in the Kakamega Forest,
Kenya. In: Kappeler PM, Watts DP, editors. Long-Term Field Studies of Primates.
Springer. p 289-311.
- Crofoot MC. 2007. Mating and feeding competition in white-faced capuchins (*Cebus
capucinus*): the importance of short-and long-term strategies. Behaviour
144:1473-1496.
- Crofoot MC. 2013. The cost of defeat: Capuchin groups travel further, faster and later
after losing conflicts with neighbors. American Journal of Physical Anthropology
152:79-85.

- 541 de Vries H, Stevens JMG, Vervaecke H. 2006. Measuring and testing the steepness of
- 542 dominance hierarchies. *Animal Behaviour* 71:585-592.
- 543 Dunn JC, Asensio N, Arroyo - Rodríguez V, Schnitzer S, Cristóbal - Azkarate J. 2012.
- 544 The ranging costs of a fallback food: liana consumption supplements diet but increases
- 545 foraging effort in howler monkeys. *Biotropica* 44:705-714.
- 546 Dunn JC, Cristóbal-Azkarate J, Schulte-Herbrüggen B, Chavira R, Veà JJ. 2013. Travel
- 547 Time Predicts Fecal Glucocorticoid Levels in Free-Ranging Howlers (*Alouatta*
- 548 *palliata*). *International Journal of Primatology* 34:246-259.
- 549 Emery Thompson M, Muller MN, Wrangham RW. 2012. The energetics of lactation and
- 550 the return to fecundity in wild chimpanzees. *Behavioral Ecology* 23:1234-1241.
- 551 Gogarten JF, Bonnell TR, Brown LM., et al. 2014. Increasing group size alters behavior
- 552 of a folivorous primate. *International Journal of Primatology* 35:590-608.
- 553 Hanya G. 2009. Effects of food type and number of feeding sites in a tree on aggression
- 554 during feeding in wild *Macaca fuscata*. *International Journal of Primatology*
- 555 30:569-581.
- 556 Hanya G, Matsubara M, Hayaishi S., et al. 2008. Food conditions, competitive regime,
- 557 and female social relationships in Japanese macaques: within-population variation on
- 558 Yakushima. *Primates* 49:116-25.
- 559 Harris TR. 2006. Between-group contest competition for food in a highly folivorous
- 560 population of black and white colobus monkeys (*Colobus guereza*). *Behavioral*
- 561 *Ecology and Sociobiology* 61:317-329.
- 562 Harris TR, Chapman CA. 2007. Variation in diet and ranging of black and white colobus
- 563 monkeys in Kibale National Park, Uganda. *Primates* 48: 208-221.
- 564 Hill DA. 1997. Seasonal variation in the feeding behavior and diet of Japanese
- 565 macaques (*Macaca fuscata yakui*) in lowland forest of Yakushima. *American Journal*

- 566 of Primatology 43: 305-320.
- 567 Hirsch BT, Tujague MP, Di Blanco YE, Di Bitetti MS, Janson CH. 2013. Comparing
568 capuchins and coatis: causes and consequences of differing movement ecology in two
569 sympatric mammals. *Animal Behaviour* 86:331-338.
- 570 Isbell LA. 2012. Re-evaluating the ecological constraints model with red colobus
571 monkeys (*Procolobus rufomitratus tephrosceles*). *Behaviour* 149:493-529.
- 572 Iwamoto T. 1982. Food and nutritional condition of free ranging Japanese monkeys on
573 Koshima Islet during winter. *Primates* 23:153-170.
- 574 Janson CH. 1988. Food competition in brown capuchin monkeys (*Cebus apella*):
575 quantitative effects of group size and tree productivity. *Behaviour* 105:53-76.
- 576 Janson CH, van Schaik CP. 1988. Recognizing the many faces of primate food
577 competition: methods. *Behaviour* 105:165-186.
- 578 Kazahari N. 2014. Maintaining social cohesion is a more important determinant of
579 patch residence time than maximizing food intake rate in a group-living primate,
580 Japanese macaque (*Macaca fuscata*). *Primates* 55:179-184.
- 581 Kazahari N, Agetsuma N. 2008. Social factors enhancing foraging success of a wild
582 group of Japanese macaques (*Macaca fuscata*) in a patchy food environment.
583 *Behaviour* 145:843-860.
- 584 Kazahari N, Agetsuma N. 2010. Mechanisms determining relationships between feeding
585 group size and foraging success in food patch use by Japanese macaques (*Macaca*
586 *fuscata*). *Behaviour* 147:1481-1500.
- 587 Kazahari N, Agetsuma N, Tsuji Y. 2013. The relationships between feeding-group size
588 and feeding rate vary from positive to negative with characteristics of food items in
589 wild Japanese macaques (*Macaca fuscata*). *Behaviour* 150:175-197.
- 590 Koenig A. 2000. Competitive regimes in forest-dwelling Hanuman langur females

- 591 (*Semnopithecus entellus*). Behavioral Ecology and Sociobiology 48:93-109.
- 592 Koenig A. 2002. Competition for resources and its behavioral consequences among
593 female primates. International Journal of Primatology 23:759-783.
- 594 Majolo B, de Bortoli Vizioli A, Schino G. 2008. Costs and benefits of group living in
595 primates: group size effects on behaviour and demography. Animal Behaviour
596 76:1235-1247.
- 597 Majolo B, Knapp L, Hardie S., et al. 2009. Analysing the effects of group size and food
598 competition on Japanese macaque social relationships. Behaviour 146:113-137.
- 599 Maruhashi T, Saito C, Agetsuma N. 1998. Home range structure and inter-group
600 competition for land of Japanese macaques in evergreen and deciduous forests.
601 Primates 39:291-301.
- 602 Matsubara M, Sprague DS. 2004. Mating tactics in response to costs incurred by mating
603 with multiple males in wild female Japanese macaques. International Journal of
604 Primatology 25:901-917.
- 605 McCabe GM, Fernandez D, Ehardt CL. 2013. Ecology of reproduction in Sanje
606 mangabeys (*Cercocebus sanjei*): dietary strategies and energetic condition during a
607 high fruit period. American Journal of Primatology 75:1196-208.
- 608 Potts KB, Watts DP, Wrangham RW. 2011. Comparative feeding ecology of two
609 communities of chimpanzees (*Pan troglodytes*) in Kibale National Park,
610 Uganda. International Journal of Primatology 32: 669-690.
- 611 Robinson JG. 1988. Group size in wedge-capped capuchin monkeys *Cebus olivaceus*
612 and the reproductive success of males and females. Behavioral Ecology and
613 Sociobiology 23:187-197.
- 614 Saito C, Sato S, Suzuki S., et al. 1998. Aggressive intergroup encounters in two
615 populations of Japanese macaques (*Macaca fuscata*). Primates 39:303-312.

- 616 Sanderson CE, Jobbins SE, Alexander KA. 2014. With Allee effects, life for the social
617 carnivore is complicated. *Population Ecology* 56:417-425.
- 618 Scarry CJ. 2013. Between-group contest competition among tufted capuchin monkeys,
619 *Sapajus nigritus*, and the role of male resource defence. *Animal Behaviour*
620 85:931-939.
- 621 Srikosamatara S. 1987. Group size in wedge-capped capuchin monkeys (*Cebus*
622 *olivanceus*): vulnerability to predators, intragroup and intergroup feeding competition
623 [dissertation]. Gainesville: University of Florida. 126p.
- 624 Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs
625 (*Presbytis thomasi*): the folivore paradox revisited. *Behavioral Ecology and*
626 *Sociobiology* 49:100-110.
- 627 Sugiura H, Saito C, Sato S., et al. 2000. Variation in intergroup encounters in two
628 populations of Japanese macaques. *International Journal of Primatology* 21:519-535.
- 629 Suzuki S, Noma N, Izawa K. 1998. Inter-annual variation of reproductive parameters
630 and fruit availability in two populations of Japanese macaques. *Primates* 39:313-324.
- 631 Takahata Y, Koyama N, Ichino S, Miyamoto N, Nakamichi M. 2006. Influence of group
632 size on reproductive success of female ring-tailed lemurs: distinguishing between
633 IGFC and PFC hypotheses. *Primates* 47:383-387.
- 634 Takahata Y, Suzuki S, Agetsuma N., et al. 1998. Reproduction of wild Japanese
635 macaque females of Yakushima and Kinkazan Islands: a preliminary report. *Primates*
636 39:339-349.
- 637 Tombak KJ, Reid AJ, Chapman CA., et al. 2012. Patch depletion behavior differs
638 between sympatric folivorous primates. *Primates* 53:57-64.
- 639 Tsujino R, Yumoto T. 2007. Spatial distribution patterns of trees at different life stages
640 in a warm temperate forest. *Journal of Plant Research* 120:687-695.

- 641 Tucker VA. 1970. Energetic cost of locomotion in animals. *Comparative Biochemistry*
642 *and Physiology* 34:841-846.
- 643 van Noordwijk MA, van Schaik CP. 1999. The effects of dominance rank and group size
644 on female lifetime reproductive success in wild long-tailed macaques, *Macaca*
645 *fascicularis*. *Primates* 40:105-130.
- 646 van Schaik CP, van Noordwijk MA, de Boer RJ, den Tonkelaar I. 1983. The effect of
647 group size on time budgets and social behaviour in wild long-tailed macaques
648 (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology* 13:173-181.
- 649 Wrangham RW. 1980. An ecological model of female-bonded primate groups.
650 *Behaviour* 75:262-300.
- 651 Yamagiwa J. 1985. Socio-sexual factors of troop fission in wild Japanese monkeys
652 (*Macaca fuscata yakui*) on Yakushima Island, Japan. *Primates* 26: 105-120.
- 653 Yamagiwa J, Hill DA. 1998. Intraspecific variation in the social organization of
654 Japanese macaques: past and present scope of field studies in natural habitats. *Primates*
655 39:257-273.
- 656 Yoshihiro S, Ohtake M, Matsubara H., et al. 1999. Vertical distribution of wild
657 Yakushima macaques (*Macaca fuscata yakui*) in the western area of Yakushima Island,
658 Japan: preliminary report. *Primates* 40:409-415.
- 659 Zhao D, Li B, Watanabe K. 2011. Impact of group size on female reproductive success
660 of free-ranging *Rhinopithecus roxellana* in the Qinling Mountains, China. *Folia*
661 *Primatologica* 82:1-12.

662 **FIGURE LEGENDS**

663 Figure 1. Home ranges of the larger and smaller groups (scale: 1/25,000). Doubled lines
664 indicate a road running through the study area.

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

665

666

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

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

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

Yosuke Kurihara, Goro Hanya 34

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

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

Appendix II. Comparison of Feeding Rate between the Larger and Smaller Groups and Correlation between Feeding Rate and Patch Residency Time in the Two Group							
Species	Part	Feeding rate (unit/sec.)		Wilcoxon rank-sum test	Correlation with patch residency time ^a		
		Larger group	Smaller group		Larger group	Smaller group	
<i>Ficus wightiana</i>	Fruit	0.48 ± 0.56	0.55 ± 0.16	$p = 0.7$	$p = 0.13$	$p = 0.75$	
<i>Litsea acuminata</i>	Fruit	0.33 ± 0.16	0.29 ± 0.10	$p = 0.14$	$p = 0.09$	$p = 0.50$	
<i>Rhus succedanea</i>	Fruit	0.51 ± 0.17	0.38 ± 0.12	$p = 0.06$	$p = 0.07$	$p = 1$	
<i>Rhus succedanea</i>	Young leaf	0.30 ± 0.19	0.25 ± 0.23	$p = 0.3$	$p = 0.78$	$p = 0.33$	
<i>Daphniphyllum teijimannii</i>	Mature leaf	0.13 ± 0.14	0.12 ± 0.05	$p = 0.38$	$p = 0.23$	$p = 0.33$	
<i>Ficus erecta</i>	Fruit	0.36 ± 0.27	0.43 ± 0.27	$p = 0.36$	$p = 0.89$	$p = 0.24$	
<i>Zanthoxylum ailanthoides</i>	Fruit	0.70 ± 0.21	0.72 ± 0.17	$p = 0.97$	$p = 0.59$	$p = 0.10$	
<i>Symplocos lucida</i>	Mature leaf	0.17 ± 0.07	0.23 ± 0.14	$p = 0.35$	$p = 0.55$	$p = 0.95$	
<i>Cinnamomum japonicum</i>	Young leaf	0.48 ± 0.10	0.49 ± 0.08	$p = 0.92$	$p = 0.17$	$p = 1$	
<i>Lithocarpus (Pasania) edulis</i>	Fruit	0.16 ± 0.04	0.23 ± 0.15	$p = 0.63$	$p = 0.33$	$p = 0.92$	
<i>Neolitsea sericea</i>	Fruit	0.77 ± 0.28	0.66 ± 0.10	$p = 0.31$	$p = 0.50$	$p = 1$	
<i>Machilus thunbergii</i>	Shoot	0.26 ± 0.17	0.32 ± 0.23	$p = 0.58$	$p = 0.33$	$p = 0.92$	
a, the results of Spearman's rank order correlation test are shown.							

672

673

Figure 1