Feeding competition in Japanese macaques in Yakushima: effects of intergroup hostility and group size

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2016

Abstract

Among the factors determining fitness of group-living animals across a wide range of species, feeding competition is the most prevalent. Intragroup scramble competition and intergroup contest competition are group-size-dependent, and their combination could cause variations in fitness across group sizes. Most studies have shown feeding and reproductive disadvantages in larger groups, suggesting that costs of intragroup scramble competition outweigh benefits of intergroup contest competition. Despite the presumed benefits of group living, the importance of intergroup feeding competition remains unclear. Japanese macaques (*Macaca fuscata yakui*) in Yakushima Island, Japan, are ideal subjects to study intergroup feeding competition. The island has two long-term research sites (coastal and highland forests), where macaques are genetically identical, but subjected to different levels of intergroup feeding competition. The objective of the present study is to reveal the costs and benefits of group living in Japanese macaques in Yakushima Island, Japan, from the perspective of feeding competition. Behavioral data were collected from three groups (larger coastal group, smaller coastal group, and highland group) in the coastal and highland forests of Yakushima, and vegetation survey and nutritional analysis of the food items were conducted for measuring the food conditions and estimating energy budgets of the macaques, respectively. Intergroup relationships were hostile when food patches were worth defending and easy to defend. In the coastal forest characterized by intense intergroup conflict, the smaller subordinate group increased the number of co-feeding individuals in response to location-specific risk of intergroup encounters. Feeding duration in one patch, frequency of visual scanning, and number of co-feeding adult males did not depend on such risk even in the coastal forest. The highland group did not modify food patch use based on such risk. Additionally, I found differences in feeding behaviors between two different-sized groups in the coastal forest. The larger group had a bigger home range and spent more time feeding, especially on mature leaves, suggesting more intense intragroup scramble competition. Although the number of visited patches and inter-patch distance did not differ between the two groups, the smaller group traveled longer distances and spent more time traveling, suggesting greater costs of intergroup contest competition. However, such group-size-related variation in feeding behavior was not translated into energy budgets of the macaques. The present study revealed ecological basis and behavioral mechanisms underlying intergroup feeding competition. The results of the present study emphasize the necessity of long-term research for assessing critically fitness consequences of intergroup feeding competition.

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This study was conducted under the supervision of Dr. G. Hanya. I am very grateful to him for his continuous support and encouragement. I appreciate Drs. T. Yumoto, M. A. Huffman, I. Matsuda, and Y. Tsuji for their valuable comments on my manuscripts.

I would like to thank the members of the Department of Ecology and Social Behavior in Primate Research Institute and the Laboratory of Human Evolution Studies in Kyoto University for giving me insightful comments and suggestions during my five years of study.

I would like to express my gratitude to Drs. N. Agetsuma, R. Tsujino, and H. Takafumi for working collaboratively, Drs. H. Sugiura, M. Suzuki, and A. Sawada for their warm support in the field, Dr. K. Kinoshita for her help in measuring urinary C-peptide, Mr. T. Saito for his help in identifying plant species, Ms. Y. Shima for helping with food sample collection, Dr. S. Mochizuki for helping with the GPS data analysis, and Drs. N. Nakagawa, E. Inoue, and N. Kazahari for their comments improving my study.

I thank the Yakushima Forest Ecosystem Conservation Center and Kagoshima Prefectural Government for their permission to conduct behavioral data collection in Yakushima. This study was supported financially by the Cooperation Research Program of Wildlife Research Center, Kyoto University, Daiko Foundation Scholarship, Grant-in-Aid for Scientific Research (B) from the Japan Society for the Promotion of Science (No. 23370099 to Dr. N. Nakagawa), and Grant-in-Aid for JSPS Research Fellow from the Japan Society for the Promotion of Science (No. 16J01208 to YK).

Chapter 1

General Introduction

Group living provides benefits such as resource defense (advantages in intergroup feeding competition) [Wrangham, 1980], predation avoidance [Hamilton, 1971; Sorato et al., 2012], and efficient resource detection [Struhsaker, 1981] and entails costs such as intragroup feeding competition [Janson & van Schaik, 1988; Janson & Goldsmith, 1995], parasite and disease transmission [Altizer et al., 2003; Sanderson et al., 2014], and infanticide [Crockett & Janson, 2000]. Among these factors determining fitness of animals, feeding competition is prevalent across a wide range of primate species [Chapman et al., 2012]. In particular, intragroup scramble competition and intergroup contest competition are group-size-dependent, and their combination could cause variation in fitness across group sizes [Koenig, 2002]. Socio-ecological models formulate the relationships among food conditions, feeding competition, and fitness consequence [van Schaik, 1989; Sterck et al., 1997; Koenig & Borries, 2009], and the ecological constraints model proposes mechanisms where costs of intragroup feeding competition determine group size [Chapman & Chapman, 2000]. By testing these models, previous studies have provided empirical evidence of different competitive regime depending on group size. Most studies demonstrated feeding and reproductive disadvantages of larger groups because of greater costs of intragroup feeding competition [Janson & Goldsmith, 1995; Koenig, 2002; Majolo et al., 2008]. Despite presumed benefits of group living, the importance of intergroup feeding competition remains unclear.

Japanese macaques *(Macaca fuscata yakui)* in the coastal and highland forests of Yakushima Island, Japan, are ideal subjects to investigate intergroup feeding competition. The island has two long-term research sites where macaques are genetically identical but are subjected to different intensity of intergroup conflict [Hayaishi & Kawamoto, 2006; Hanya et al., 2008]. In the coastal forest, larger dominant groups had higher birth rates than did smaller subordinate groups [Suzuki et al., 1998; Takahata et al., 1998; Sugiura et al., 2000]. By contrast, birth rates did not depend on group size in the highland forest [Hanya et al., 2008]. This different pattern of birth rates is assumed to be caused by higher fruit production (better habitat quality), higher group density, and more frequent aggression between groups in the coastal forest [Yoshihiro et al., 1999; Hanya et al., 2004; Hanya et al., 2008]. However, food patch characteristics and behavioral patterns of macaques under different levels of intergroup conflict have not been clarified. Thus, comparing food conditions and food patch use between the two sites can help to understand the ecological basis and behavioral mechanisms of intergroup feeding competition. Additionally, the positive relationship between group size and birth rate in Japanese macaques of the coastal forest is in contrast to the general trend in primates [Majolo et al., 2008]; however, it remains unclear how group size affects the behavior and energy balance of these macaques. Revealing mechanisms of group-size effects on reproductive success in macaques of the coastal forest will contribute to understanding costs and benefits of group living.

The objective of the present study is to reveal costs and benefits of group living in Japanese macaques in Yakushima Island from the perspective of feeding competition. In Chapter 2, I aim to reveal patch characteristics underlying the difference in intergroup hostility in macaques in the coastal and highland forests and their direct effect on food patch use, and also an indirect effect via intergroup hostility. Using vegetation and behavioral data from macaques in three groups, I compare food patch characteristics and food patch use between the two sites. Additionally, to test whether macaques modify food patch use in response to location-specific risk of intergroup encounters, I investigate the effects of location of food patches on food patch use in the two sites. Based on the results, I discuss food conditions facilitating intergroup feeding competition and behavioral patterns of macaques to cope with location-specific risk of intergroup encounters.

In Chapter 3, I aim to reveal effects of group size on feeding behavior including food patch use in macaques in the coastal forest. I test predictions of the ecological constraints model [Chapman & Chapman, 2000] by using behavioral data from two different-sized groups of macaques. Based on the results, I discuss costs and benefits of feeding competition depending on group size from the viewpoint of feeding behavior and propose a possible mechanism of group-size effects on birth rates in the coastal forest.

In Chapter 4, I aim to reveal energetic consequences of the differences in feeding behavior between the two groups (the results of Chapter 3). Using behavioral data from macaques in the two groups and nutritional composition of food items, I compare ingestion rates, energetic/nutritional content of diet, energy budgets (intake, expenditure, and balance), and C-peptide levels between the two groups. Based on the results, I examine whether behavioral measures of feeding competition are translated into fitness consequences and discuss the possible mechanism of group-size effects on birth rates, proposed in Chapter 3. In the general discussion, I examine the implications of the present study for socio-ecological models and discuss the necessity of long-term research for understanding the importance of intergroup feeding competition.

Chapter 2

Relationship between Patch Characteristics, Intergroup Hostility, and Food Patch Use in Japanese Macaques (*Macaca fuscata yakui*): Comparisons between Two Local Populations that Differ in the Intensity of Intergroup Feeding Competition

2-1 Abstract

Ecological basis of intergroup feeding competition remains unclear despite its theoretical importance as the benefit of group living. Japanese macaques (*Macaca fuscata yakui*) in the coastal and highland forests of Yakushima, Japan, are ideal subjects because they are genetically identical but are subjected to different levels of intergroup feeding competition. I aimed to reveal food conditions underlying the difference in intergroup hostility between the two sites and their direct effect on food patch use, and also an indirect effect via intergroup hostility. I conducted vegetation survey and behavioral data collection from three macaque groups via focal animal sampling. I compared patch characteristics and food patch use between the two sites, and investigated whether food patch use depended on location-specific risk of intergroup encounters. Food patches in the coastal forest were sparser but of higher-quality and larger than those in the highland forest. Consequently, macaques in the coastal forest had a longer duration of feeding in one food patch and stayed with a larger number of co-feeding individuals than those in the highland forest. Additionally, macaques in the coastal forest, not in the highland forest, increased the number of co-feeding individuals in the border of their home range, which could detect other groups quickly and reduce the probability of being injured due to intergroup aggression. The present study revealed ecological basis of intergroup feeding competition and

highlights the importance of intergroup relationships as a social factor affecting food patch use by animals.

2-2 Introduction

Intergroup feeding competition has been discussed as one of the evolutionary drivers of group living [Alexander, 1974; Wrangham, 1980]. Through intergroup interaction, dominant groups can obtain better feeding and reproductive success than subordinate groups [van Schaik, 1989; Koenig, 2002]. The socio-ecological model predicts that groups compete over food patches that are high-quality, clumped in space, and large enough to accommodate all group members [van Schaik, 1989; Sterck et al., 1997]. These patches are worth defending owing to higher energetic return as well as easy to defend [Whitten, 1988; Barton & Whiten, 1994; Saito, 1996]. Empirical studies provided mixed support for the theoretical prediction regarding patch characteristics facilitating intergroup feeding competition: Harris [2006] supported the prediction while Koenig [2000] suggested that food abundance was more important as the determinant than patch characteristics. While Brown [2013] summarized food conditions facilitating intergroup aggression based on the literature of non-human primates, evaluating such food conditions quantitatively by focusing on within-species variation would be useful for understanding ecological basis of intergroup feeding competition [Nakagawa, 2008; Chapman & Rothman, 2009].

Since ecological characteristics of food patches should be key variables to determine intergroup relationships, patch characteristics may not only affect food patch use directly but also indirectly through intergroup relationships. Although social factors within a group (e.g., dominance rank and number of co-feeding individuals) have been studied intensively [Hanya, 2009; Kazahari et al., 2013], effects of intergroup relationships on food patch use remain unclear because of the difficulty in measuring immediate consequences of intergroup encounters. As an alternative means of investigating the effects of intergroup relationships, it is useful to compare food patch use between areas with different levels of risk of intergroup encounters (e.g., the border of the home range vs. the interior) [Gibson & Koenig, 2012]. Most animals avoid intergroup conflicts to minimize costs such as injury or death and energy consumption [Mech, 1994; Marler et al., 1995; Wilson & Wrangham, 2003; Crofoot & Wrangham, 2010]. Specifically, animals use the border of the home range or overlap zones with neighboring groups less frequently than the interior [Samson & Huot 2001; Mech & Harper, 2002; Kelly, 2005; Wrangham et al., 2007; Gibson & Koenig, 2012]. This pattern is also influenced by heterogeneity of the risk within the border or overlap zones [Wilson et al., 2007; Müller & Manser, 2007; Gibson & Koenig, 2012]. Additionally, animals change behavior within areas with high risk of intergroup encounters. They advertise their presence by using auditory and/or olfactory signals [Waser, 1976; Wilson et al., 2007; Müller & Manser, 2007] and perform visual monitoring frequently [MacIntosh & Sicotte, 2009]. They also increase spatial cohesion of the group [Benadi et al., 2008] or the number of adult males in the party [Wilson et al., 2007], which could lead to effective defense of their home range [Wilson et al., 2007; Benadi et al., 2008] or collective vigilance [Pulliam, 1973; Isbell & Young, 1993]. Therefore, revealing variation in food patch use depending on locations of food patches should contribute to understanding how animals use food patches efficiently under intergroup feeding competition.

Japanese macaques (*Macaca fuscata yakui*) in the coastal and highland forests of Yakushima Island, Japan, are ideal subjects to study food patch use from the viewpoint of intergroup feeding competition. Macaques in the two sites are genetically identical [Hayaishi & Kawamoto, 2006] but are subjected to different intensity of intergroup feeding competition [Hanya et al., 2008]. Home range overlap was greater and intergroup aggressive encounters occurred more frequently in the coastal forest than in the highland forest [Maruhashi et al., 1998; Hanya et al., 2003; Hanya et al., 2008]. In the coastal forest, larger dominant groups had higher birth rates than did smaller subordinate groups [Suzuki et al., 1998; Takahata et al., 1998; Sugiura et al., 2000]. By contrast, intergroup dominance relationships were unclear, and birth rates did not depend on group size in the highland forest [Hanya et al., 2008]. These differences are assumed to be caused by higher fruit production in the coastal forest [Hanya et al., 2004; Hanya, 2014]; however, ecological basis of the difference in the intensity of intergroup feeding competition has not been clarified.

I aimed to reveal food patch characteristics underlying the difference in intergroup relationships between the coastal and highland groups of Japanese macaques in Yakushima and their direct effect on food patch use, and also an indirect effect via intergroup relationships. I tested two hypotheses about (1) effects of food patch characteristics on intergroup hostility and food patch use and (2) effects of intergroup relationships on food patch use. First, I hypothesized that food patches in the coastal forest would be more worth defending and easier to defend than those in the highland forest because intergroup relationships were hostile in the coastal forest but not in the highland forest [Hanya et al., 2008]. I compared food patch characteristics and food patch use between the two sites. Following the predictions of the socio-ecological models [van Schaik, 1989], I predicted that food patches in the coastal forest would be sparser but of higher-quality and larger enough to accommodate all group members than those in the highland forest. Thus, macaques in the coastal forest would have longer durations of feeding in one patch and stay with a larger number of co-feeding individuals than those in the highland forest. Next, I hypothesized that macaques in the coastal forest would modify food patch use in response to location-specific risk of intergroup encounters but those in the highland forest would not. I investigated effects of locations of food patches within their home ranges on food patch use. I made three predictions regarding the macaques in the coastal forest. First, macaques would have a shorter duration of feeding in one patch in the border with dominant groups, but not with subordinate groups, than in the interior. This prediction was derived from the hypothesis that a high risk of intergroup aggression could prevent animals from using the border of the home range [Kelly, 2005]. Second, macaques would exhibit visual scanning more frequently in the border with dominant groups, but not with subordinate groups, than in the interior. Macaques may depend on visual cues to detect other groups [MacIntosh & Sicotte, 2009] because they do not exhibit territorial advertisement such as loud call [Wich & Nunn, 2002] and scent marking behavior, to the best of my knowledge. Thirdly, macaques would increase the number of co-feeding individuals, especially co-feeding adult males, in the border with dominant groups, but not with subordinate groups, than in the interior. In the coastal forest, the relative group size determined the outcome of intergroup encounters [Sugiura et al., 2000], and adult males played active roles in intergroup encounters [Majolo et al., 2005]. In contrast to the coastal forest, I predicted that duration of feeding in one patch and the number of co-feeding individuals would not depend on locations of food patches in the highland forest because of the lower risk of intergroup encounters.

2-3 Methods

2-3-1 Study sites and groups

I conducted this study in coastal (0–350 m a.s.l.) and highland (1000–1200 m a.s.l.)

areas in Yakushima Island (30°N, 130°E), Japan. The coastal area was in primary and secondary warm temperate evergreen broad-leaved forest [Agetsuma, 1995a; Tsujino & Yumoto, 2007]. The highland area was in the transitional forest between warm and cool temperate forest, including coniferous forest [Hanya, 2004a]. Effects of predation pressure on behavior were eliminated owing to the absence of predators in both sites [Yamagiwa & Hill, 1998; Hanya et al., 2008].

I studied two groups in the coastal forest (KwA and KwCE groups, defined as a larger coastal group and a smaller coastal group, respectively, based on the mean group size in the forest [21.7 individuals: Hanya et al., 2004]) from February to October 2013 and one group in the highland forest (HR group, hereafter, referred as to a highland group) from April 2000 to March 2001 and from October 2003 to January 2004. The larger coastal group had 30–33 individuals, including 6–7 adult females (> 6 years old), 2–5 adult males (> 6 years old), 15–21 juveniles (1-5 years old), and 1–6 infants (< 1 year old). The smaller coastal group had 8–13 individuals, including 1–4 adult females, 2–4 adult males, 2–5 juveniles, and 0–3 infants. The highland group had 24–27 individuals, including 7–9 adult females, 6–7 adult males, 7–10 juveniles, and 2 infants. The size of this group was larger than the mean group size in the highland forest (15.8 individuals) [Hanya et al., 2004]. The difference in the study year between the two sites will not significantly affect the results of the present study because fruit production is consistently higher in the coastal forest than in the highland forest, regardless of year [Hanya et al., 2004].

2-3-2 Behavioral data collection

I investigated all adult females in the two coastal groups (7–11 individuals) and 5–7 adult females in the highland group. All females in the three groups were individually identified. Total observation time for the coastal and highland groups was 383 hr (larger coastal group: 221 hr, smaller coastal group: 162 hr) and 546 hr, respectively. The protocol of behavioral observation was common to all the three groups, unless otherwise noted. I conducted behavioral data collection via 1-hr focal animal sampling. I changed the focal animal every hour, distributing the 1-hr duration sampling evenly throughout the day. I selected the next one for which the observation time accumulated so far was shortest. I recorded the onset and end of a feeding bout to the nearest second and food items (species and part) eaten by the focal animal. The onset was defined as the time when the focal animal put food into the mouth, and the end as the time when 20 sec had passed without manipulating the food. A food item was categorized into four types: fruits/seeds, mature leaves, young leaves (including buds and shoots), and others. A food patch was defined as one individual tree in which the focal animal fed. Macaques mainly fed in trees (coastal groups: mean 66% of total feeding time [Kurihara, unpublished data]; highland group: 71% [Hanya, 2004a]). Terrestrial patches (e.g., fallen fruits/seeds and insects) could not be defined because of uniform distribution of these foods on the ground. When the focal animal left a patch and returned back without feeding in any other patches, I considered it as one patch. If the focal animal fed in a patch, I also collected the following data: (1) time when other animals entered into and departed from the same patch in which the focal animal fed; (2) the size of the patch (length of major and minor axes and height of crown in the coastal forest; diameter at breast height (DBH) in the highland forest). Additionally, in the coastal forest, I recorded visual scanning during the focal animal's patch residency via one-zero sampling at one-minute intervals. Visual scanning was defined as turning horizontally the head for more than 3 sec [Suzuki & Sugiura, 2011]. By using a handy–type GPS device (GARMIN 60CSx, GARMIN, USA), I recorded locations of the focal animal (every five minutes in the coastal forest; every one hour in the highland forest) and food patches in which the focal animal fed.

2-3-3 Vegetation survey

I conducted vegetation survey in the coastal forest during 2002–2003 and in the highland forest in 1999. In the coastal forest, I set a plot of 2.4 ha and recorded the species, DBH, and height of all trees with ≥ 5 cm DBH. In a subplot of 0.2125 ha within the plot, I recorded the species and height of all trees with ≥ 1 m height. These plots were set outside of the home ranges of the study groups (100 m north from the northern end of the home range of the smaller group; Figure 2-1) in the same altitudinal zones. In the highland forest, I set a plot of 0.75 ha within the home range of the highland group and recorded the species and DBH of all trees with ≥ 5 cm DBH. In a subplot of 0.075 ha within the plot, I recorded all trees with ≥ 1 m height. Although the plot size was small (0.3% of the home range size), these plots can be regarded as representative of the home range [Hanya, 2009].

2-3-4 Data analysis

2-3-4-1 Comparison of patch characteristics and food patch use between the coastal and highland forest

Using vegetation data, I calculated patch density as number of potentially available trees of main foods per hectare. Main food was defined as a food item which accounted for >1% of the total feeding time during the study period in each site (mean value of the two groups was used for the coastal forest) [Hanya, 2004b]. For fruits/seeds and flowers, I excluded patches whose sizes were smaller than the minimum size of the patch that I actually observed feeding by the macaques. For other foods, I regarded all trees, including small trees with ≥ 1 m height and DBH < 5 cm, as potentially available.

Using behavioral data, I calculated duration of feeding in one patch, patch size, the number of co-feeding individuals, patch quality, and the proportion of patches that can accommodate all group members. Duration of feeding in one patch was calculated as the total duration of feeding bouts during the focal animal's patch residency. I omitted data from the analysis when I was unable to observe the entrance into or departure from the patch by the focal animal or when the focal animal left the patch by being aggressed by other animals. Patch size was calculated as the volume of an elliptic cone ((1/3) × (major axis of crown/2) × (minor axis/2) × height × π). For the highland forest, crown area ((major axis of crown/2) × (minor axis/2) × π) and height were calculated from basal area (π × (DBH)^2) using the regression equations derived from the vegetation data [see Hanya, 2009 for the detail]. The number of co-feeding individuals was calculated as the average number of other individuals (except infants) within the same patch [Hanya, 2009]. Duration of feeding in one patch, patch size, and the number of co-feeding individuals were compared between the two sites using Brunner-Munzel test. Patch quality was calculated as the proportion of fruit/seed patches in all patches visited. Fruits/seeds are more preferred and nutritious than other foods for the macaques [Iwamoto, 1982; Agetsuma, 1995a; Hanya, 2009]. Patch quality was compared between the two sites using Fisher's exact test. Patches that can accommodate all group members were defined as when the number of available feeding sites in a patch outweighed mean group size of each population (21.7 in the coastal forest, 15.8 in the highland forest [Hanya et al., 2004]). The number of available feeding sites in a patch was calculated by dividing patch size by 4.18 m^3 (the volume of a sphere with a radius of 1 m, monopolizable space for one individual) and rounding down [Hanya, 2009]. As an exception, when the number of available feeding sites was <1, I regarded it as 1. The proportion of patches that can accommodate all group members was compared between each coastal group and highland group using Fisher's exact test with Bonferroni correction ($\alpha = 0.05/2 = 0.025$).

2-3-4-2 Home range estimation and area categorization

I estimated home range based on GPS data (larger coastal group: 2773 points, smaller coastal group: 1993 points, highland group: 891 points) by using the fixed kernel density method [Worton, 1989]. The raster size was 10 m × 10 m, and the smoothing parameter h was determined by an *ad hoc* technique. I defined 95% kernel area as overall home range, 50 m buffer inside from the outline of the home range as the border, and the remaining area within the home range as the interior. Categorization of the border and interior was based on previous studies where an intergroup encounter was defined to occur when two groups approached within 50 m [Saito et al., 1998; Sugiura et al., 2000]. To consider the heterogeneity of the risk within the border for the two coastal groups, I further divided the border into four parts (north, south, east and west) by using the centroid of the home range as the center point and categorized them into three types: border with dominant groups, subordinate groups, and the sea (no neighboring groups). Intergroup dominance relationships were determined based on the outcome of intergroup encounters [Sugiura et al., 2000]. The larger coastal group was bordered with subordinate groups in the north and east and with a dominant group in the south during February-April 2013, and was bordered with a subordinate group in the east and with dominant groups in the north and south during May-October 2013. The smaller coastal group was surrounded with dominant groups except in the west throughout the study period. The two coastal groups were not bordered with any groups in the west (on the side of the sea). In the highland forest, I was unable to consider the heterogeneity of the risk within the border because of insufficient data on intergroup encounters [Hanya et al., 2008].

2-3-4-3 Effects of locations of food patches on food patch use

To examine whether macaques modify food patch use in response to location-specific risk of intergroup encounters, I constructed generalized linear mixed models (GLMMs) to explain duration of feeding in one patch and the number of co-feeding individuals for each three groups and to explain the frequency of visual scanning and the number of co-feeding adult males for each two coastal groups. Owing to difficulty in behavioral data collection, I was unable to investigate the frequency of visual scanning and the number of co-feeding adult males in the highland forest. Frequency of visual scanning was calculated as the proportion of its occurrence in the total number of one-zero sampling points during a focal animal's patch residency. I excluded data when I was unable to record details owing to the limited visibility. The number of co-feeding adult males was calculated as the average number of adult males within the same patch in the same way as the number of co-feeding individuals. Duration of feeding in one patch was log-transformed to achieve normality, and the number of co-feeding individuals was rounded up to treat as a Zero-inflated Poisson distribution [Kurihara & Hanya, 2015]. I included "locations of food patches" as a fixed effect and the identity of the focal animal as a random effect in all models (Table 2-1). Food patches were categorized according to the category of areas within the home range. Food patches in the border with the sea were excluded from the analysis. Additionally, to control confounding factors, I included patch size, the number of co-feeding individuals, and food type as fixed effects in the models (Table 2-1). I examined the significance of "locations of food patches" ($p < 0.05$ or not) in the full model. I used the *adehabitat* package for estimating home ranges, *nlme*, *glmmML*, and *glmmADMB* packages for GLMMs in R 3.0.1 [R Core Team, 2013]. I visualized GPS data by using QGIS 2.6.1.

2-4 Results

Patch density in the coastal forest was lower than that in the highland forest (main food: 11 species in the coastal forest; 9 species in the highland forest, Table 2-2). Patch quality was higher in the coastal forest than in the highland forest (Table 2-2). Patch size was larger in the coastal forest than in the highland forest (Table 2-2). Similarly, the number of available feeding sites in a patch was larger in the coastal forest than in the highland forest (Table 2-2). Proportion of food patches that can accommodate all group members was higher in the coastal forest than in the highland forest (Table 2-2). Consequently, macaques in the coastal forest had a longer duration of feeding in one patch and stayed with a larger number of individuals than those in the highland forest (Table 2-2).

The number of co-feeding individuals increased in the border of the home range for the smaller coastal group but not for the larger coastal group (Figure 2-1, Table 2-3). However, for the two coastal groups, the number of co-feeding adult males did not depend on locations of food patches (Table 2-3). Additionally, duration of feeding in one patch and the frequency of visual scanning did not depend on locations of food patches (Table 2-3). For the highland group, duration of feeding in one patch and the number of co-feeding individuals did not depend on locations of food patches (Table 2-3).

2-5 Discussion

2-5-1 Inter-site differences in patch characteristics and food patch use

As I hypothesized, food patches in the coastal forest were more worth defending and easier to defend than those in the highland forest. Macaques in the coastal forest used sparser but higher-quality and larger patches than those in the highland forest. Moreover, food patches in the coastal forest were more likely to accommodate all group members than those in the highland forest. As a result, macaques in the coastal forest had longer durations of feeding in one patch and stayed with a larger number of co-feeding individuals than those in the highland forest. In contrast, macaques in the highland group mainly fed alone in a low-quality small patch. Therefore, patch characteristics in the coastal forest fit the food condition under which intergroup feeding competition was presumed to occur [van Schaik, 1989; Sterck et al., 1997].

High value of defending home ranges should also facilitate intergroup feeding competition in the Yakushima coastal forest. Food patches in Kinkazan Island (a habitat of Japanese macaques in a cool temperate forest) were sparsest and largest, followed in order by those in the Yakushima coastal forest and in the Yakushima highland forest [Maruhashi et al., 1998; Hanya, 2014; present study]; however, intergroup relationships were not hostile in Kinkazan, which was similar to the Yakushima highland forest but different from the Yakushima coastal forest. Intergroup aggression occurred 11.1% of intergroup encounters (7/63) in Kinkazan, 0% (0/4) in the Yakushima highland forest, and 46.4% (70/151) in the Yakushima coastal forest [Sugiura et al., 2000; Hanya et al., 2008]. This may be because home ranges in Kinkazan were less worth defending than those in the Yakushima coastal forest owing to less abundance of food per unit area [Maruhashi et al., 1998]. This situation is different from the Yakushima highland forest, where food patches were less worth defending and more difficult to defend. Therefore, macaques in Kinkazan do not compete with other groups owing to low value of defending home ranges, although they used food patches that were worth defending and easy to defend. While Koenig [2000] demonstrated that intergroup feeding competition intensified during the food-scarce season in Hanuman langurs, the results of the present study suggest that limited food abundance could moderate intergroup feeding competition via lowering the value of defending home ranges.

Based on the assumption of socio-ecological models that all group members participate in intergroup aggression [Wrangham, 1980], I concluded that intergroup hostility in Japanese macaques was linked to food conditions in the Yakushima coastal forest. Contrary to such assumption, the recent study on vervet monkeys (*Chlorocebus aethiops pygerythrus*) have revealed that the frequency of individual participation in intergroup aggression depends on individual status (i.e., rank within a group and the presence of an infant) and amounts of support by group members [Arseneau-Robar et al., 2017]. However, this study also showed that better food condition stimulated intergroup aggression. Therefore, the conclusion of the present study still holds regardless of which mechanism works. Investigating the proximate mechanisms of escalating intergroup aggression can further clarify the link between food conditions and intergroup hostility in Japanese macaques in Yakushima.

2-5-2 Effects of locations of food patches on food patch use

As I predicted, the number of co-feeding individuals increased along the border of the home range of the smaller coastal group, and duration of feeding in one patch and the number of co-feeding individuals did not depend on locations of food patches for the highland group. These results suggest that macaques in the coastal forest, unlike those in the highland forest, could modify food patch use in response to the location-specific risk of intergroup encounters. However, the hypothesis of the present study was not fully supported because the number of co-feeding individuals did not depend on locations of food patches for the larger coastal group, and the duration of feeding in one patch, the frequency of visual scanning, and the number of co-feeding adult males did not depend on locations of food patches for the larger and smaller coastal groups.

Contrary to the prediction, duration of feeding in one patch did not depend on locations of food patches for macaques in the coastal and highland forests. Similarly, duration of feeding in one patch did not differ between core and overlapped areas in Verreaux's sifakas (*Propithecus verreauxi*) [Benadi et al., 2008]. These results imply that the under-use of the border zones may not necessarily shorten duration of feeding in one patch there. Macaques in the coastal forest were forced to leave a food patch when they encountered dominant groups [Kurihara, unpublished data]. However, intergroup aggression is rarely fatal, unlike chimpanzees [Wilson & Wrangham, 2003] and humans [Kelly, 2005]. Therefore, it could be too costly to avoid intergroup encounters at the expense of energetic returns from feeding in a patch for such medium-risk species [*sensu* Wrangham et al., 2007] as Japanese macaques in the coastal forest and Verreaux's sifakas [Benadi et al., 2008].

Contrary to the prediction, macaques in the coastal forest did not increase the frequency of visual scanning along the border of their home range. This result was in accord with the previous study on blue monkeys [Gaynor & Cords, 2012], but was in contrast to that on black and white colobus [MacIntosh & Sicotte, 2009]. Primates may increase visual scanning in response to a location-specific risk only where intergroup encounters occur frequently. Black and white colobus encountered other groups at 0.10 times/hr [Sicotte & MacIntosh, 2004], twice more frequently than did Japanese macaques in the study site of the present study (0.04 times/hr [Sugiura et al., 2000]) and blue monkeys (0.05 times/hr, given that the observation time was 10 hr/day [Cords, 2002]). Considering the trade-off between feeding and visual monitoring in Japanese macaques in another study site [Kazahari & Agetsuma, 2010], intergroup encounters may be too infrequent to perform ordinary preemptive vigilance even for macaques in the coastal forest [Suzuki & Sugiura, 2011]. Alternatively, it is possible that adult females depend on vigilance and/or reaction toward extra-group conspecifics by other group members [Lima & Zollner 1996; Pays et al., 2007]. To test this possibility, it is necessary to investigate age/sex differences in the frequency of vigilance and the synchrony of vigilance among co-feeding individuals in a patch in more detail.

The number of co-feeding individuals increased in the border of the home range of the smaller coastal group, but not in the border of the larger coastal and highland groups, which partly supported the prediction. However, contrary to the prediction, macaques in the coastal forest did not increase co-feeding with adult males along the border. This suggests that co-feeding with a larger number of individuals may be sufficient to reduce the location-specific risk without selectively co-feeding with adult males, unlike chimpanzees characterized by escalated aggression between groups [Wilson et al., 2007]. This result can be interpreted in two ways. First, macaques can reduce the possibility of being injury or death due to physical fighting by being in proximity with a larger number of group members [Wilson & Wrangham, 2003]. It was reported that lone animals were injured or killed by receiving coalitionary aggression even in species forming cohesive groups [Mech, 1994; Gros-Louis et al., 2003; Shimada et al., 2009]. Second, macaques can detect other groups more quickly and avoid intergroup encounters involving physical fighting because more eyes and ears become available to scan the surroundings [Beauchamp, 2015]. Although the frequency of visual scanning of each individual did not depend on locations of food patches as shown above, collective vigilance may function as a consequence of increase in the number of co-feeding individuals [Pulliam, 1973; Isbell & Young, 1993; Pays et al., 2007]. In the coastal forest characterized by frequent intergroup encounters and hostile intergroup relationships, smaller groups especially would be required to minimize the location-specific risk of intergroup encounters because of their subordinate position [Sugiura et al., 2000].

2-5-3 Implications for mechanisms of feeding competition in primates

Intergroup relationships were hostile when food patches were worth defending and easy to defend (i.e., sparse but high-quality and large) and the value of defending home ranges (food abundance per unit area) was high. Such food patch characteristics enabled the macaques in the coastal forest to gain such benefits as longer durations of feeding in one patch and a larger number of co-feeding individuals. The results of the present study supported predictions of socio-ecological models formulating ecological basis of intergroup feeding competition [van Schaik, 1989; Sterck et al., 1997]. Additionally, patch characteristics affected food patch use indirectly via intergroup relationships. Unlike the highland group with a low risk of intergroup encounters, the smaller subordinate group in the coastal forest increased the number of co-feeding individuals in response to the location-specific risk of the encounters. While this behavioral pattern could reduce the potential costs of the encounters, it could increase the level of intragroup contest competition [Hanya, 2009], which would likely alter the energy intake rate [Kazahari et al., 2013]. Future studies should examine the relative impact of intragroup and intergroup feeding competition to food patch use for understanding behavioral mechanisms of feeding competition.

The results of the present study may be preliminary owing to the limited research effort (e.g., number of study groups). It remains unclear whether the absence of the effects of locations of food patches on food patch use was due to the low risk of intergroup encounters in the highland forest or the dominance of the highland group. Since even intergroup encounters rarely occur in the highland forest, it will be reasonable to conclude that the results of the present study can be applied to other groups in the highland forest regardless of intergroup dominance. To make this conclusion more valid, it is necessary to investigate multiple groups in the highland group. Additionally, although the present study focused on inter-site difference in intergroup hostility, the frequency of intergroup aggression could fluctuate within each site. Identifying factors facilitating intergroup aggression within each site by using a larger dataset will contribute to better understanding of ecological basis of intergroup feeding competition. Even with these limitation, considering that home range overlap has been reported extensively in many species [Pearce et al., 2013; Willems et al., 2013], the present study emphasizes the importance of intergroup relationships as a social factor affecting food patch use by animals.

Chapter 3

Comparison of Feeding Behavior between Two Different-Sized Groups of Japanese Macaques (*Macaca fuscata yakui*)

3-1 Abstract

Group-living animals face intragroup scramble and intergroup contest competition. 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 overall. The present study examined the effects of group size on the feeding behavior of Japanese macaques in the Yakushima coastal forest. I investigated 10–13 adult females from two different-sized groups using focal animal sampling during October 2012–April 2013. I 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.

3-2 Introduction

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

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

The costs of intragroup scramble competition could influence the fitness of group-living animals [Koenig, 2002]. Most of the studies have demonstrated disadvantages of larger groups: the costs of intragroup scramble competition negatively affect the net energy gain and/or 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, 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 balances or outweighs the benefits of intergroup feeding competition which leads to higher net energy gain and/or reproductive success in larger-sized, dominant groups than in smaller-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 and/or reproductive success and group size [Cheney & Seyfarth, 1987; Robinson, 1988; Koenig, 2000; Takahata et al., 2006]. In particular, the predictions of the ecological constraints model remain untested and it is unclear how group size affects behavior when the net energy gain and/or reproductive success increase with group size.

Among Japanese macaques (*Macaca fuscata yakui*) of the Yakushima coastal forest, larger groups have higher birth rates than smaller ones [Suzuki et al., 1998; Takahata et al., 1998]. Also since group density is high (4.8 groups/km^2) [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 relative group size: larger groups are dominant over smaller ones [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 [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 controlled 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. I 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, I 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. I 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]. I 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, I 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, I examined two assumptions underlying the ecological constraints model. First, to examine patch depletion, I 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, I 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.

3-3 Methods

3-3-1 Study site and groups

I studied two groups (KwA and KwCE, hereafter referred to as a larger group and a smaller group, respectively) of Japanese macaques living in the western coastal forest on Yakushima Island (30°N, 130°E) from October 2012 to April 2013. The study period included the 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, 1995a; Tsujino & Yumoto, 2007]. Habitat quality was regarded as similar 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 years old), 3–6 adult males (>6 years old), 15–21 juveniles (1–5 years old), and 1–6 infants (<1 year 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-group ranging during the study period [Kurihara, unpublished data]. I 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 (0/8) (larger group: 0.020 times/h; smaller group: 0.067 times/h).

3-3-2 Behavioral data collection

I followed one or both of the two groups each day and changed the focal group at least once every three days. I investigated all adult females in the two groups (9–13 individuals) with one-hour focal animal sampling. I changed the focal animal every hour, distributing the 1-hr duration sampling evenly throughout the day. I selected the next 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). Using instantaneous recording, I recorded activities (feeding, moving, resting, grooming and other (e.g., aggressive interaction, copulatory behavior)) of the focal animal every minute. When the focal animal was feeding, I recorded the onset and the end of feeding to the nearest second and feeding items (species and part). I 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, I 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. I 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, I considered it as one patch. If the focal animal fed in a patch, I 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), I recorded locations of the focal animal every 30 seconds and the food patches it visited.

3-3-3 Data analysis

3-3-3-1 Home range and travel distance

I estimated home range size and calculated travel distance based on GPS data points plotted every five minutes. Home range size was estimated by using the fixed kernel density method [Worton, 1989]. Grid size was operationally set as 10 m × 10 m, and the smoothing parameter h was determined by an *ad hoc* technique because calculation by the least square cross validation method did not converge. I 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 distances between GPS points plotted consecutively.

3-3-3-2 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 for 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 the food repertoire, I calculated the Shannon-Wiener index H:

$$H = -\sum_{i} pi \ln pi$$

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.

3-3-3-3 Comparison of behavioral proxies of intragroup scramble competition

I constructed generalized linear mixed models (GLMMs) to explain diet composition, activity budget, travel distance, and the number of visited patches (Table 3-1). The distribution of travel distances was normalized by square root transformation. In the diet composition model, group (larger or smaller) was included as a fixed effect and observation date as random effect. To explain feeding on young leaves, I used a generalized linear model (GLM) because GLMM did not converge. In the remaining models, group, copulatory behavior and dietary composition were included as fixed effects, and observation date or identities of the focal animals as random effects. In order to perform robust analysis with limited amount of data, I included “diet composition” and “copulatory behavior” as explanatory variables in the models to control for seasonal variation in diet rather than dividing the data by season. Activity budgets, travel distance, and the number of visited patches depend on seasonal variation in diet [Agetsuma, 1995a; 1995b; Agetsuma & Nakagawa, 1998; Tsuji, 2010]. In the present study, 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: $\rho = 0.56$, $p < 0.001$). Additionally, copulatory behavior affects the overall feeding patterns of animals [Matsubara & Sprague, 2004]. 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 a 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, I 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 the food repertoire, the Shannon-Wiener index H of the two groups was compared using Wilcoxon rank-sum test.

3-3-3-4 Patch use

To investigate how group size affected the general characteristics of patch use, I 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 second. 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/2)*(minor axis/2)*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 the linear distance between patches that the focal animal visited consecutively. I constructed GLMMs to explain patch residency time, patch size, and number of co-feeding individuals (Table 3-1). 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 effects, 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 were included 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) patch residency time, patch size, and the number of co-feeding individuals 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, I 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, I 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]. I 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 (Table 3-6). 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, I 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.

I tested whether funneling effect shortened patch residency time more frequently in the larger group. First, I 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]. I 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, I examined whether patch residency time was shortened at the filled patches. I constructed GLMM on patch residency time for each group (Table 3-1). 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.

I used the *adehabitat* package for estimating home range and the *lme4* and *glmmADMB* package for GLMM in R 3.0.1 [R Core Team, 2013]. I 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.

3-4 Results

3-4-1 Comparison of behavioral proxies of intragroup scramble competition

The larger group had a larger home range (Figure 3-1, larger group: 38.9 ha, smaller group: 34.8 ha) and spent more time feeding than did the smaller group (Tables 3-2 and 3-3), although the two groups' core areas were the same 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 3-2 and 3-3). 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 3-3, larger group: 29.1% ± 36.2%; smaller group: 15.7% ± 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 3-2 and 3-3). 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 (Table 3-5, larger group: 45 species, 83 items; smaller group: 47 species, 84 items). In a month, the common repertoire accounted for 61.7% ± 11.7% of species and 56.7% ± 10.8% of items in the larger group, and 66.7% ± 11.6% and 63.6% ± 12.6% in the smaller group, respectively.

Contrary to the predictions, the smaller group spent more time moving (Tables 3-2 and 3-3) and traveled longer distances than did the larger group (Table 3-3, 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 3-3, larger group: 2.8 ± 2.3/h, smaller group: 3.0 ± 2.5/h; likelihood ratio test: $df = 1, \chi^2 = 1.08, p = 0.30$).

3-4-2 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 3-3; 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 ± 211.1 m^3, smaller group: 137.6 ± 214.8 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 ± 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, I 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 food items (Table 3-6). 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 3-4, likelihood ratio test: larger group: $df = 1, \chi^2 = 50.19, p < 0.001$; smaller group: $df = 1, \chi^2 = 52.20, p < 0.001$). I 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)*(major axis/2)*(minor axis/2)*crown length*π) by 4.18 m^3, and (3) dividing an ellipsoid by

113 m^3. Since I was able to obtain the same results based on all of these definitions, only the results based on the initial definition are shown.

3-5 Discussion

3-5-1 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 [e.g., Chapman & Chapman, 2000; Majolo et al., 2009]. 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, 1995a; 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 3-3). Less-contestable foods enable animals to remain together with many individuals in a patch [Iwamoto, 1982; Agetsuma, 1995b; Hanya, 2009]. Therefore, 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 in 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 and nutritional intake of animals in order to clarify whether this dietary strategy influences the fitness of animals.

3-5-2 Inconsistency with the ecological constraints model: number of visited patches and patch use

One of the discrepancies between the results of the present 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 a 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 the present study, I 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 the present 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 of the time-series variations in feeding rate in combination with the characteristics of the food items is required to elucidate this mechanism further in the Japanese macaques of Yakushima.

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

3-5-3 Inconsistency with the ecological constraints model: travel behavior

The other discrepancy was travel behavior. In the present study, the smaller group traveled longer distances and spent more time moving than did the larger group, contrary to the predictions of the ecological constraints model. The intergroup differences in travel distance and moving time were detected in the present study even if other factors such as dietary composition and mating behavior were controlled for. There are two 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 a 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 the present study, I controlled differences in habitat quality of 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. It is unlikely that the difference in habitat quality causes the differences in moving behavior between the two groups detected here. It is still possible that fine-scale vegetation heterogeneity affect the moving behavior despite similar habitat quality. To make our results more valid, it will be necessary to conduct vegetation survey in details sufficient for capturing fine-scale vegetation heterogeneity.

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 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 the present 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. [2009] was similar to the average size of the neighboring groups (17.6), while the size of the smaller group in the present study (13–15) was half the average size of the neighboring groups (32.1). Under the circumstance in Majolo et al. [2009], 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. [2009] was larger than that of the smaller group (13–15) in the present study and that of the group (14) that actually showed the lower birth rate in Takahata et al. [1998]. Therefore, only when the group size was below that threshold value and was smaller than the sizes of the neighboring groups, did animals in the group have increased travel costs, as a result of intergroup competition.

3-5-4 Implications for group-size effects on reproductive success 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 the positive correlation between group size and reproductive success. Unlike most primate species, birth rate increases with group size in Japanese macaques of the Yakushima coastal forest. Previous studies of this population [Suzuki et al., 1998; Takahata et al., 1998] 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, dominant groups have higher-quality home ranges, which brings adult females better energetic and nutritional conditions and a higher birth rate. Although intragroup scramble competition has not been investigated extensively, the present study showed that the larger group had the costs of intragroup scramble competition, as has been reported in many of other primate species [e.g., van Noordwijk & van Schaik, 1999; Borries et al., 2008; Majolo et al., 2008]. In addition, the results of the present study were unique in proposing behavioral mechanism driving the positive correlation between group size and reproductive success, and suggesting that smaller groups incur the cost of intergroup contest competition from energy expenditure: smaller-sized, subordinate groups are required to travel longer distances and/or for a longer time, worsening the energetic and nutritional conditions of adult females, which lowers the birth rate. Travel behavior is energetically costly [Tucker, 1970; Dunn et al., 2013] and could affect energy balance, and in turn, reproductive success of adult females [Emery Thompson et al., 2012; McCabe et al., 2013]. To test how the costs and benefits of each group translate into differences in reproductive success, the energy balance of the animals must be quantified: not only energy intake but also energy expenditure of animals in different-sized groups should be considered to better understand the mechanisms of group-size effects on feeding behavior and reproductive success.

Chapter 4

Comparison of Energy Balance between Two Different-Sized Groups of Japanese Macaques (*Macaca fuscata yakui*)

4-1 Abstract

Quantifying energy balance is essential for testing socio-ecological models. To reveal costs and benefits of group living in Japanese macaques from the perspective of feeding competition, I previously compared feeding behavior between two different-sized groups of macaques (larger group: 30–35 individuals; smaller group: 13–15 individuals) in the coastal forest of Yakushima, Japan [Kurihara & Hanya, 2015]. The results suggested that the larger group exhibited greater feeding effort because of intragroup scramble competition and that the smaller group suffered from higher travel costs owing to intergroup contest competition. However, it remained unclear whether the behavioral differences affected their energy budgets. The present study examined energetic consequences of the different feeding behaviors in the two groups. Using behavioral data from 10–13 adult females and nutritional composition of food items, I compared ingestion rates, energetic/nutritional content of diet, energy budgets, and C-peptide levels between the two groups. Ingestion rates and energetic content of diet did not differ between the two groups. Despite the higher feeding effort of the larger group, energy intake did not differ between the two groups. Energy expenditure did not differ between the two groups because higher travel costs were negated by lower feeding effort in the smaller group. Consequently, the energy balance and C-peptide levels did not differ between the two groups. The present study demonstrated that the behavioral measures of feeding competition were not translated into their energetic condition; moreover, the findings of the present study re-emphasize the importance of measuring

energy balance as the outcome of feeding behavior.

4-2 Introduction

Examining costs and benefits of group living helps us understand why animals form a group, which is a central topic in primate behavioral ecology [Wrangham, 1980; Sterck et al., 1997; Chapman & Chapman, 2000]. Group-living animals have benefits such as resource defense and predation avoidance [Wrangham, 1980; Hamilton, 1971], and costs such as intragroup feeding competition and susceptibility to parasite infection and disease [Janson & van Schaik, 1988; Sanderson et al., 2014]. Among these, feeding competition has been recognized as one of the most basic factors determining the fitness of animals [Chapman et al., 2012]. The socio-ecological model predicts that feeding competition among conspecifics leads to variation in reproductive success through energy balance [Sterck et al., 1997; Koenig & Borries, 2009].

Group-living species face two types of group-size-dependent feeding competition: intragroup feeding competition and intergroup feeding competition, and their combination could cause variation in the fitness between groups of different sizes [Koenig, 2002]. Intragroup scramble competition equally reduces the feeding success of all group members because members share limited food resources. Its intensity increases with group size. Intergroup contest competition results in greater feeding success of dominant groups than that of subordinate groups through intergroup interactions. Intergroup dominance relationships are usually determined by group size [Wrangham, 1980; Cheney & Seyfarth, 1987; Sugiura et al., 2000], although there are exceptions [e.g., Crofoot et al., 2008]. In most primates, larger groups experience feeding disadvantages, suggesting the costs of intragroup scramble competition outweighs the benefits of intergroup contest competition [Majolo et al., 2008]. To cope with reduced foraging efficiency, larger groups increased foraging efforts by increasing home range size, feeding time, traveling time, travel distance, number of food patches, and diversity of their food repertoire [van Schaik et al., 1983; Janson & Goldsmith, 1995; Chapman & Chapman, 2000; Snaith & Chapman, 2008; Fan et al., 2015]. Nevertheless, as a general trend in primates, female fecundity decreases with increasing group size [Majolo et al., 2008].

Behavioral measures of feeding competition do not necessarily explain variation in energy balance and/or reproductive success [Gogarten et al., 2014; Grueter et al., 2016]. However, few studies have investigated fitness consequences of feeding competition [e.g., Stacey, 1986; Janson, 1988; Koenig, 2000; Tsuji & Takatsuki, 2012; Roberts & Cords, 2013; Potts et al., 2015]. To test the socio-ecological model rigorously, it is necessary to investigate whether feeding competition influences fitness measures while controlling confounding factors such as habitat quality and infanticide risk [Koenig & Borries, 2009].

Japanese macaques (*Macaca fuscata yakui*) in the coastal forest of Yakushima Island, Japan, are characterized by hostile intergroup relationships and frequent intergroup encounters [Saito et al., 1998; Sugiura et al., 2000; Hanya, 2014]. The outcome of these encounters depends on group size: larger groups are dominant over smaller groups [Sugiura et al., 2000]. To understand the effects of group size on feeding behavior under conditions of intense intergroup conflict, I compared the feeding behavior of two different-sized groups of macaques in the Yakushima coastal forest, as described in Kurihara & Hanya [2015]. The larger group had a bigger home range and spent more time feeding, especially on mature leaves, than did the smaller group, which suggested that intragroup scramble competition was more intense in the larger group. On the other hand, inconsistent with the general tendency found among primates

[Majolo et al., 2008], the smaller group traveled longer distances and spent more time traveling than did the larger group. This finding implies that the smaller group is forced to travel further because of displacement by the larger group, owing to disadvantages of intergroup feeding competition [see Crofoot, 2013]. However, it remains unknown whether the differences in feeding behavior between the two groups caused differences in their energy budgets. Further examination of the fitness consequences of feeding behavior will aid in elucidating the costs and benefits of group living.

The goal of the present study was to reveal the costs and benefits of group living in Japanese macaques in the Yakushima coastal forest from the perspective of feeding competition. For this purpose, I investigated the energetic consequences of differences in feeding behavior between the two different-sized groups that I observed in the previous study [Kurihara & Hanya, 2015]. I compared ingestion rates (dry weight intake per second), energetic/nutritional content of diet, and energy budgets (intake, expenditure, and balance) between the two groups. I predicted that ingestion rates would not differ between the two groups because, for the 12 main food items, feeding rates (number of food units ingested per second) did not differ between the two groups in Kurihara & Hanya [2015]. I predicted that the larger group would have a diet with lower energy concentration than that of the smaller group. The larger group spent more time feeding on mature leaves and less on fruits/seeds than did the smaller group in Kurihara & Hanya [2015]. Mature leaves typically contain more protein and fiber but less non-structural carbohydrate, lipid, and energy than fruits/seeds [Nakagawa et al., 1996; Lambert & Rothman, 2015]. Despite the lower feeding efficiency of the larger group, energy intake should not differ between the two groups because the larger group spent more time feeding than did the smaller group in Kurihara & Hanya [2015]. Given that travel behavior is energetically costly [Tucker, 1970; Dunn et al., 2013], I predicted that the smaller group would expend more energy than the larger group. The smaller group spent more time traveling and traveled longer distances than did the larger group in Kurihara & Hanya [2015]. Therefore, I predicted that the larger group would have a more positive energy balance than the smaller group. In addition to the conventional estimation method using behavioral data of macaques and nutritional composition of food items, I measured urinary C-peptide as a biomarker of energy balance [Sherry & Ellison, 2007; Girard-Buttoz et al., 2011]. Urinary C-peptide levels reflect the amount of insulin secreted in the body and becomes higher as the energy balance becomes more positive [Zavaroni et al., 1987; Girard-Buttoz et al., 2011]. I compared C-peptide concentrations between the two groups, although it was preliminary due to the limited number of urine samples. I predicted that the larger group would have higher C-peptide levels than the smaller group. Finally, I discuss the results of the present study in light of the relationship between group size and birth rate that was previously reported in the study population [Suzuki et al., 1998; Takahata et al., 1998].

4-3 Methods

4-3-1 Study site and groups

This study was conducted in the western coastal forest of Yakushima Island (30°N, 130°E), Japan. The study area was located in a primary and secondary warm temperate evergreen broad-leaved forest [Agetsuma, 1995a; Tsujino & Yumoto, 2007]. I studied two groups (KwA and KwCE, hereafter, referred to as a larger group and a smaller group, respectively) of Japanese macaques from October 2012 to April 2013. The larger group had 30–35 individuals, including 6–8 adult females (> 6 years old), 3–6 adult males (> 6 years old), 15–21 juveniles (1–5 years old), and 1–6 infants (<1 year 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 larger group was dominant over the smaller group [Kurihara & Hanya, 2015] in accordance with the general tendency in the study population [Sugiura et al., 2000]. Habitat quality of the home range of these two study groups were regarded as similar because their home ranges overlapped partially (20.1% and 22.4% of the home ranges of the larger and smaller groups, respectively), were within the same altitudinal zones (Figure 4-1), and the inter-patch distance and patch size did not differ between the two groups [Kurihara & Hanya, 2015].

4-3-2 Behavioral data collection

I followed one or both of the two groups each day and changed the focal group at least once every three days. I investigated all adult females in the two groups (10–13 individuals) via 1-hr focal animal sampling. I changed the focal animal every hour, distributing the 1-hr duration sampling evenly throughout the day. I selected the next 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; 4.2 ± 1.4 hours per female per month). I recorded activity (feeding, traveling, resting, grooming, being groomed, and other) of the focal animal every minute via instantaneous recording. When the focal animal was feeding, I recorded the onset and the end of a feeding bout to the nearest second and food items (species, part, and maturity of fruits and leaves). I regarded the onset as the time when the focal animal put food into the mouth, and the end as the time when 20 sec had passed without manipulating the food. Feeding rate was recorded as the number of food units that the focal animal put into the mouth per 10 sec. A food unit was operationally defined for each food item (e.g., one fruit, one leaf, a portion of leaf). I repeatedly recorded feeding rate as many times as possible during a feeding bout. By using a global positioning system (GPS, Garmin 60CSx, Garmin, USA), I recorded locations of the focal animal every 30 sec.

4-3-3 Food sample collection

For nutritional analysis, I collected as many samples of the food fed on by focal animals, as possible. This included all food items that accounted for >5% of the total monthly feeding time in each group. Sample collection was conducted outside of areas registered as a World Heritage Site and 2.5–3 km from the home ranges of the study groups (Figure 4-1) due to environmental resource use restrictions in this protected area. I took the samples directly from trees/lianas that were similar in phenophase to those that the focal animals fed on. I chose multiple trees/lianas to minimize effects of variation in nutritional content among individual trees/lianas [Chapman et al., 2003]. I kept all samples at -20°C in a freezer at the Yakushima field station of Kyoto University (a facility equipped with a laboratory, Figure 4-1) until they were brought to the Primate Research Institute (PRI), Kyoto University, for nutritional analysis.

4-3-4 Nutritional analysis

I conducted nutritional analysis of the food samples at PRI. I processed the samples in the same manner as the focal animals did (i.e., removed the portion that was not ingested by the focal animals). I dried the samples at 40°C for 24 h using a vacuum incubator and weighed them to obtain dry weight per food unit (unit dry weight, g/unit). Then I milled them and measured its nutritional content (Table 4-3). The crude ash (CA) content was determined through combustion. The crude lipid (CL) content was measured by the Soxhlet method with a diethyl-ether solvent [Soxhlet, 1879]. The neutral detergent fiber (NDF) was measured by boiling residues from the CL measurement in an NDF solution for 1 hr, following the method described by van Soest et al. [1991]. The crude protein (CP) content was determined as 6.25 times the total nitrogen content, where I measured total nitrogen following the Kjeldahl method [Conklin-Brittain et al., 1999]. Total non-structural carbohydrates (TNC) were calculated as follows [Rothman et al., 2012]:

$$\%TNC = 100 - (\%CA + \%CL + \%NDF + \%CP)$$

Data on unit dry weight were available for 55 out of 90 food items of the larger group (85.9% of the total feeding time) and 63 out of 94 food items of the smaller group (79.1% of the total feeding time). Data on nutritional content were available for 40 out of 90 food items of the larger group (77.5% of the total feeding time) and 46 out of 94 food items of the smaller group (76.0% of the total feeding time). A portion of the data on unit dry weight has already been published in Hanya et al. [2014].

4-3-5 Urine sample collection and urinary C-peptide analysis

I collected 56 urine samples from adult females opportunistically during behavioral observation. Urine samples were pipetted off the road or other substrate (e.g. fallen leaves, rocks) with disposable transfer pipettes and 2 ml microtubes. I did not collect urine samples contaminated with feces. Urine samples were transported on ice packs during behavioral observation and kept under -20 °C in a freezer at the Yakushima field station of Kyoto University until they were brought to PRI. All samples were stored under -20 °C in PRI.

I analyzed urinary C-peptide using a commercial C-peptide ELISA kit (10-1136-01, Mercodia AB, Uppsala, Sweden). All C-peptide concentrations were corrected by creatinine (Cr) concentrations for adjusting urinary concentrations [Taussky, 1954] and expressed as pmol C-peptide/mg Cr. Urine samples with Cr concentrations <0.1 mg/ml were excluded to avoid overinflating the estimation of

C-peptide concentrations. I was able to quantify 46 urine samples (3.5 ± 1.3 samples per adult female). A parallelism test was conducted to assess the validity of the kit by using urine samples diluted by kit-specific EIA buffer. The slope calculated from the serially diluted samples was not significantly different from that of the standard curve (ANOVA, $p = 0.71$). The intra- and inter-assay coefficients of variation were 3.6% and 23.7%. The sensitivity of the assay was 15 pmol/l.

4-3-6 Data analysis

4-3-6-1 Average ingestion rate

Ingestion rate (g/sec), total amount of dry weight ingested by the focal animal per second, was calculated as the product of unit dry weight (g/unit) and average feeding rate (unit/sec) for each food item for each focal animal. Then, an average ingestion rate was calculated as the mean ingestion rate of primary foods. Primary food was defined as a food item that accounted for >5% of the total dry weight of food ingested for each focal animal for each month.

4-3-6-2 Average energetic/nutritional content of diet

Average energetic content of diet (kcal/g) was calculated as mean available energy content of primary foods for each focal animal for each month. Similarly, average nutritional content of diet (percentage of CL, CP, TNC, and NDF in a gram of dry weight) were calculated for each focal animal for each month. The available energy content of a food item *i* (kcal/g) was calculated using the modified formula of previous studies [Nakagawa, 1989; Tsuji & Takatsuki, 2012]:

$$\text{available energy content}_{\text{i}} = (9 \times \%CL_i + 4 \times \%CP_i + 4 \times \%TNC_i) \times (\text{digestibility}_{\text{i}} - \text{energy lost in urine}) / 100$$

I assigned physiological fuel values to each nutrient (CL: 9 kcal/g, CP: 4 kcal/g, TNC: 4

kcal/g) [National Research Council, 2003]. The energy lost in urine was regarded as 4% [Nagy & Milton, 1979]. I used digestibility *i* (%), which was linearly correlated with the NDF content of a food item *i* [Iwamoto, 1988; Nakagawa et al., 1996]. According to Sawada et al. [2011], who studied the relationships between digestibility and NDF content in captive Japanese macaques, apparent digestibility of dry matter (aD DM) decreased with increases in the NDF content of a food item: mean aD DM was 83.2% when the NDF content was 13.6%, and the mean aD DM was 56.9% when the NDF content was 37.5%. By using these data in Sawada et al. [2011], I obtained the following regression equation:

$$\mathrm{digestibility}_{\mathrm{i}} = -1.10 \times \% NDF_i + 98.15$$

When data on unit dry weight or energetic/nutritional content of a given food item were not available, I assigned the mean value for the same food category (e.g., mature leaves and flowers).

4-3-6-3 Estimation of energy intake

For each month, I estimated the daily energy intake for each focal animal. This was determined by multiplying the monthly energy intake rate (energy intake/observation time) by the monthly mean day length. The monthly energy intake was calculated as the sum of digestible energy ($DE_{i,j}$, expressed in kcal) obtained from a food item *i* during a feeding bout *j*.

$$DE_{i,j} = \sum_{i,j} \left(\mathrm{available\ energy\ content}_{\mathrm{i}} \times \mathrm{unit\ dry\ weight}_{\mathrm{i}} \times \mathrm{average\ feeding\ rate}_{\mathrm{i,j}} \times \mathrm{feeding\ time}_{\mathrm{i,j}} \right)$$

When data on feeding rate during a given feeding bout was not available, I assigned the mean value for the same food item recorded for the same animal during other feeding bouts. When such data was also unavailable, I assigned the mean value for the same food item recorded for other animals in the same group [Nakagawa, 1997]. The day length was calculated by using data on daily sunrise and sunset times (Ephemeris Computation Office Public Relations Center: http://eco.mtk.nao.ac.jp/koyomi/), which was averaged for each month. I assumed that macaques were active during daytime.

4-3-6-4 Estimation of energy expenditure

For each month, I estimated the daily energy expenditure for each focal animal. This was determined as the sum of energy expended during daytime and at night. Energy expended during daytime was calculated by multiplying the monthly energy expenditure rate (energy expenditure/observation time) by the monthly mean day length. Monthly energy expenditure was calculated as the sum of energy expended for each activity i (A_i) [Key & Ross, 1999]. For sleeping, resting, feeding, grooming, and other activities, A_i was estimated as follows:

$$A_i = \sum_i \left(D_i \times \mathrm{Basal\ Metabolic\ Rate} \times T_i / 60 / 24 \right)$$

D_i is a constant, indicating physical activity level for activity i ($D_{sleep} = 1.00$, $D_{rest} = 1.25$, $D_{feed} = 1.38$, $D_{groom} = 2.35$, D_{other} (mean of D_{rest}, D_{feed}, and D_{groom}) = 1.66; [Leonard & Robertson, 1997]), and T_i is time spent (in minutes) on activity i. The activity "being groomed" was included in "resting". Basal metabolic rate (BMR) was calculated from body mass W (kg) using the following formula [Kleiber, 1961]:

$$BMR = 70 \times W^{0.75}$$

Body mass was considered to be 5.3 kg, the mean value of adult females in the study population [Fooden & Aimi, 2005]. Energy expenditure for traveling (A_{travel}) was calculated from body mass W (g), travel distance R (km), and travel time T (h) by the following formula [Taylor et al., 1970]:

$$A_{travel} = 0.041 \times W^{0.60} \times R + 0.029 \times W^{0.75} \times T$$

Travel distance was calculated as the sum of linear distances between GPS points plotted every five minutes consecutively by using QGIS (version 2.0.1) [Kurihara & Hanya, 2015]. In the present study, I estimated only BMR and the energy expended for physical activity. Additionally, the energy used for climbing was not considered because I did not collect the relevant data. Energy expenditure during night is the energy expended for sleeping (A_{sleep}) for the entire duration of the night (24 h minus the day length). I assumed that macaques slept through the entire duration of the night.

4-3-6-5 Statistical procedure

I constructed nine generalized estimating equations (GEEs) to explain the following variables: (1) average ingestion rate, (2) average energetic content of diet, (3) average CL content, (4) average CP content, (5) average TNC content, (6) average NDF content, (7) energy intake, (8) energy expenditure, and (9) energy balance (energy intake minus expenditure). The unit of analysis was data per focal animal per month. The GEE is an extension of the generalized linear model (GLM) [Zuur et al., 2009]. A benefit of using the GEE was that correlation structure of a dependent variable can be incorporated in the model, thereby considering temporal autocorrelation of monthly data. In the present study, I set the correlation structure as AR1 to account for temporal autocorrelation of data points in each model [Zuur et al., 2009; Gogarten et al., 2014]. As for C-peptide levels, I used a generalized linear mixed model (GLMM) without incorporating the correlation structure because of missing data for some months. C-peptide levels were averaged for each focal animal for each month. The distribution of energy intake, average CL content of diet, C-peptide levels were normalized by log transformation. I included group (larger group or smaller group) and season (fruit/seed season or leaf season) as fixed effects and the identity of the focal animal as a random effect in all models. “Season” was included to account for seasonal variation in diet [Agetsuma, 1995]. The study period was categorized into the fruit/seed season (October–December) and leaf season (January–April) based on monthly data for dry weight intake for the two groups (Figure 4-2). Effects of dominance rank of adult females within a group were not considered in the present study because birth rates did not depend on dominance rank in the study population according to Takahata et al. [1998]. I examined the significance of "group" ($p < 0.05$ or not) in the full model. I used *geeglm* function in the *geepack* package for GEE and *lme* function in the *nlme* package for GLMM in R 3.0.1 [R Core Team, 2013]. All statistical tests were two-tailed, and the significance level was set at $p < 0.05$.

4-4 Results

The larger group tended to obtain more energy than did the smaller group, especially during the fruit/seed season; however, energy intake did not statistically differ between the two groups (Tables 4-1 and 4-2). Average ingestion rate tended to be higher in the larger group than in the smaller group, but the difference was not statistically significant (Tables 4-1 and 4-2). Average energetic/nutritional content of diet did not differ between the two groups (Tables 4-1 and 4-2).

The smaller group tended to expend more energy than did the larger group; however, energy expenditure did not statistically differ between the two groups (Tables 4-1 and 4-2). The percentage of energy expended for each activity was 23.0% ± 7.9% for feeding, 15.0% ± 3.5% for traveling, 10.0% ± 4.1% for resting, 10.8% ± 7.7% for grooming, 0.1% ± 0.2% for other activities, and 41.1% ± 3.7% for sleeping in the larger group. The percentages were 19.6% ± 8.2% for feeding, 18.7% ± 3.9% for traveling, 9.6% ± 3.9% for resting, 11.9% ± 8.3% for grooming, 0.1% ± 0.3% for other activities, and 40.1% ± 4.2% for sleeping in the smaller group.

The larger group tended to have a more positive energy balance than did the smaller group, especially during the fruit/seed season; however, energy balance did not statistically differ between the two groups (Tables 4-1 and 4-2). Similarly, C-peptide levels did not differ between the two groups (Tables 4-1 and 4-2).

4-5 Discussion

4-5-1 Energy intake

The larger group tended to obtain more energy than did the smaller group; however, as I predicted, energy intake did not statistically differ between the two groups. The larger group exhibited a higher feeding efficiency and greater feeding effort; however, the differences were not large enough to cause a statistically significant difference in energy intake. The larger group tended to have higher ingestion rates than the smaller group, although the average energetic/nutritional content of diet did not differ. These results contradicted the previous study, which demonstrated that feeding rates for the 12 main food items did not differ between the two groups and that the larger group spent more time feeding on mature leaves than did the smaller group [Kurihara & Hanya, 2015]. This implies that the larger group selected food items upon which they were able to feed at a higher rate. Additionally, the typical characteristics of food categories [Nakagawa et al., 1996; Lambert & Rothman, 2015] may not be applicable to the study site in the present study, similar to recent studies demonstrating variation in energetic/nutritional content within a food category [Danish et al., 2006; Rothman et al., 2008]. To understand further the cause of the difference in feeding efficiency between the two groups, it would be useful to examine the possibility that animals modify food selection criteria depending on group size. This can be explored using a more extensive dataset for vegetation and the nutritional content of food items.

The larger group spent more time feeding than did the smaller group [Kurihara & Hanya, 2015], which did not lead to greater energy intake of the larger group. The results of the present study contrasted with previous studies that showed that larger groups increased feeding effort to compensate for reduced feeding efficiency [Stacey, 1986; Janson, 1988]. It remains unclear why the larger group exhibited higher feeding effort despite higher feeding efficiency. It is still possible that the greater energy intake of the larger group was critical for improving energy balance; however, to argue the biological significance of the statistically insignificant difference in the energy intake, it is necessary to accumulate information on what amount of surplus energy leads to successful birth. Alternatively, the smaller group might be required to shorten feeding time because of the forced traveling due to intergroup encounters [e.g., Crofoot, 2013]. More study might be necessary before concluding that feeding time is valid as a behavioral proxy of intragroup scramble competition.

4-5-2 Energy expenditure

The smaller group tended to expend more energy than did the larger group; however, energy expenditure did not statistically differ between the two groups, contrary to the prediction. In accordance with Stacey [1986], the difference between the two groups in energy expenditure was eliminated because the smaller group expended more energy for traveling but less for feeding than did the larger group. Within the range of size of study groups in the present study, macaques might be able to counterbalance travel costs with feeding effort [Dunbar, 1988]. In contrast, Wright et al. [2014] demonstrated that the longer travel time was translated into higher energy expenditures for low-ranking females in mountain gorillas (*Gorilla beringei beringei*). Although they obtained statistically significant results, the range of energy expenditure was smaller (ca. 135–

170 kcal/h) than that of energy intake (ca. 750–2500 kcal/h). Similarly, energy expenditure fluctuated within a narrower range compared to energy intake in other species (yellow baboon [*Papio cynocephalus*]: Stacey, 1986; crowned sifaka [*Propithecus coronatus*]: Pichon & Simmen, 2015) including the present study. These results suggest that the impact of energy expenditure on energy balance may be minimal regardless of whether energy expenditure fluctuates depending on activity and ranging patterns.

4-5-3 Linking feeding behavior, energy balance, and reproductive outcome

Contrary to the prediction, energy balance did not statistically differ between the two groups. Similarly, C-peptide levels did not differ, although this data was preliminary owing to the small sample size. As a result of the similarities in energy intake and expenditure, the two groups achieved similar levels of energy balance despite different patterns of feeding behavior. This was in accordance with the results of previous studies [Stacey, 1986; Janson, 1988]. Kurihara & Hanya [2015] proposed a possible consequence of different feeding behavior between the two groups, where greater travel costs could worsen the energetic condition of adult females in the smaller group; however, the results of the present study did not support this. A couple of studies [Kurihara & Hanya, 2015; present study] stress the importance of quantifying energy balance as the outcome of feeding behavior for scrutinizing the test of the socio-ecological model [Koenig & Borries, 2009].

Considering that the energetic status affects reproduction [Garcia et al., 2011], reproductive success would not differ between the two groups. The results of the present study contradicted declining birth rates in smaller groups that was previously reported in the study population [Suzuki et al., 1998; Takahata et al., 1998]. This was in spite of the size of the smaller group in the present study (10–13 individuals excluding infants) being comparable to the sizes of other Yakushima groups (7–14 individuals excluding infants) that showed low birth rates [Takahata et al., 1998]. There are two possible explanations for this inconsistency. First, high abundance of fruits could have mitigated the intensity of intergroup contest competition in the study year. The positive relationship between group size and birth rate was found only in poor-fruiting years [Noma, 1997; Suzuki et al., 1998]. The study year in the present study is unlikely to have been a poor-fruiting year, because dietary shift from fruits/seeds to mature leaves occurred in January (Figure 4-2), a month later than that reported for a poor-fruiting year [Hanya et al., 2004]. Second, better habitat quality could increase birth rates of larger groups in the study conducted by Suzuki et al. [1998]. Maruhashi [1982] reported that subordinate groups were forced to range in lower-quality habitats in the Yakushima coastal forest, although quantitative data were not provided. Unlike in the present study, habitat quality could have been a key factor mediating the positive relationships between group size and birth rate in the study by Suzuki et al. [1998].

The present study clarified the energetic consequences of the differences in feeding behavior between two different-sized groups of Japanese macaques in the Yakushima coastal forest. The differences in feeding behavior between the two groups that I observed in the previous study [Kurihara & Hanya, 2015] were not translated into differences in their energy budgets. The results of the present study are not conclusive because of the limited research efforts (i.e., number of study groups, length of study period, and observation time). To elucidate the complex mechanisms of group-size effects on reproductive success, continuous and long-term data collection is needed on various factors, including food availability and energetic condition of animals.

Chapter 5

General Discussion

5-1 Ecological factors facilitating intergroup feeding competition

The present study revealed food conditions facilitating intergroup feeding competition. Intergroup relationships were hostile when food patches were worth defending and easy to defend and the value of defending home ranges (food abundance per unit area) was high, supporting predictions of socio-ecological models (Chapter 2). The present study examined direct effects of food condition on intergroup hostility; however, population density could be a factor affecting intergroup hostility directly or a factor mediating the relationship between food condition and intergroup hostility. Other than the direct effects of food condition on intergroup hostility, there are three possible pathways determining intergroup hostility. First, higher population density promotes intergroup hostility by increasing the frequency of intergroup encounters (direct effect of population density: [Sugiura et al., 2000; Hutchinson & Waser, 2007]). Second, higher population density decreases food abundance per group or individual, leading to intergroup hostility (indirect effect of population density via food conditions: [Hixon et al., 2002]). Third, better food condition increases population density [Balcomb et al., 2000; Hanya et al., 2004], which promotes intergroup hostility as explained above (indirect effect of food conditions via population density). Cubaynes et al. [2014] investigated wolf behavior in two sites that were different in prey density (food condition) and wolf density, thereby revealing that social aggression was enhanced by prey availability not directly but indirectly via wolf density in the site with higher wolf density. To evaluate the relative importance of food condition and population density in Japanese macaques, it will be necessary to investigate how interannual fluctuation of the two factors affects the frequency of intergroup aggression in Yakushima.

5-2 Behavioral mechanisms of feeding competition

In the coastal forest characterized by intense intergroup conflict, the smaller group increased the number of co-feeding individuals in response to the location-specific risk of intergroup encounters. Feeding duration in one patch, the frequency of visual scanning, and the number of co-feeding adult males did not depend on such risk even in the coastal forest. The highland group did not modify food patch use depending on such risk. Additionally, I found differences in feeding behaviors between two different-sized groups of macaques in the coastal forest. The larger group had a bigger home range and spent more time feeding, especially on mature leaves, suggesting intense intragroup scramble competition. Mature-leaf feeding did not lead to longer duration of feeding in one patch but enabled macaques to stay with a larger number of co-feeding individuals in the larger group. The smaller group traveled longer distances and spent more time traveling despite the similarities of the number of visited patches and inter-patch distance between the two groups, suggesting greater costs of intergroup contest competition.

Variation in food patch use depending on the location-specific risk of intergroup encounters for the two coastal groups (Chapter 2) would be mutually linked to the differences in food patch use between the two groups (Chapter 3). Contrary to the prediction that macaques in the coastal forests would not feed sufficiently in food patches in areas with high risk of intergroup encounters, even the smaller coastal group was not forced to shorten feeding duration in one patch in such areas (Chapter 2). Intergroup hostility itself may not constrain feeding in a patch for Japanese macaques. This result may lead to the similarities of patch residency time between the larger and smaller coastal groups (Chapter 3). On the other hand, the number of co-feeding individuals did not depend on the location-specific risk in the larger coastal group (Chapter 2). Such variation may be masked by a larger number of co-feeding individuals in the larger coastal group (Chapter 3). The larger coastal group would not be required to increase the number of co-feeding individuals in the border with dominant groups because a sufficient number of group members would always be in the same food patch. The results of the present study proposed the importance of investigating effects of intra- and intergroup feeding competition on food patch use comprehensively, unlike socioecological studies previously demonstrating effects of the two types of feeding competition separately. Although immediate consequences of intergroup encounters are still difficult to measure, locations of food patches will be useful as a proxy for the risk of intergroup encounters.

Behavioral changes in areas with high risks of intergroup aggression have mainly been reported in species with advertisement behaviors such as loud calls and scent marking [howler monkeys: Kitchen, 2004; chimpanzees: Wilson et al., 2007; Verreaux's sifakas: Benadi et al., 2008]; however, the results of the present study suggest that animals can modify behavior depending on potential costs of intergroup aggression without such advertisement behaviors. It remains unclear whether coo calls function as vocalization for intergroup communication [Suzuki & Sugiura, 2011]. Even if macaques use coo calls to detect neighboring groups, coo calls would function differently from loud calls. Coo calls cannot be transmitted across long-distances [5–30 m: Okayasu, 1987; 50 m: Hanya et al., 2003] relative to the radius of a mean-sized home range in the Yakushima coastal forest [radius: 439.6 m (mean home range size: 60.7 ha), Takasaki, 1981; radius: 350.1 m (mean home range size: 38.5 ha), Hanya et al., 2006]. Therefore, the results of the present study warrant further study on border zone use by species without loud calls and scent marking behavior, which could contribute to a better understanding of the roles of advertisement behaviors in intergroup spacing.

5-3 Fitness consequences of intergroup feeding competition

Although the present study revealed variation in feeding behavior depending on group size, such variation was not translated into energy budgets. The size of the smaller group in the present study was similar to the minimum size reported in the Yakushima coastal forest (7–46 individuals) [Hanya et al., 2004] and sizes of groups (7–14 individuals) that showed lower birth rates in Takahata et al [1998]. Nevertheless, the results of the present study indicated that the smaller group did not always suffer from the costs of intergroup feeding competition, as demonstrated by the positive relationship between group size and birth rate found only in poor-fruiting years [Suzuki et al., 1998]. This finding was in accordance with previous studies showing that primates maintained similar levels of energy balance regardless of group size [Stacey, 1986; Janson, 1988].

Previous studies suggest that intergroup feeding competition is at best, of second importance as a selective force of group living [Alexander, 1974; Janson, 1985; van Schaik, 1989]. To the best of my knowledge, only Koenig [2000] succeeded in revealing the relationships between group size and physical condition of animals, where intergroup feeding competition intensified during a specific season. Based on his study, it is necessary to capture group-size-related variation in feeding behavior and fitness measures during the limited period when intergroup feeding competition predominates depending on food condition and population density. Therefore, long-term study is indispensable for the critical assessment of intergroup feeding competition, and few studies are still available to discuss the importance of intergroup feeding competition as a benefit of group living. This warrants further examination of food availability, population density, and nutritional conditions of macaques in the Yakushima coastal forest over a long-term basis.

5-4 Future perspectives

To make the results of the present study more valid, it is necessary to conduct long-term research on a larger number of groups in the Yakushima coastal forest. Revealing mechanisms of population dynamics of Japanese macaques in the Yakushima coastal forest could contribute to assessing intergroup feeding competition more critically. It is ideal but not practical to continue labor-intensive research, such as detailed behavioral observation that was conducted in the present study, over the long-term basis. Therefore, establishment of a research system is needed to monitor food availability, population dynamics, and nutritional and health conditions of macaques by using time- and labor-saving methods [Chapman et al., 2015]. A population census has been conducted every summer since 1998 to monitor group size and composition [Sugiura et al., unpublished data]. Additionally, fruit production and vegetation heterogeneity should be assessed as measures of food availability affecting population dynamics [Hanya et al., 2004; Potts et al., 2009], and fecal sample collection enables the measurement of nutritional and health conditions of macaques [MacIntosh et al., 2010; Maestripieri & Georgiev, 2015; Schaebs et al., 2016]. In particular, fecal thyroid has been established as a non-invasive biomarker of energy intake [Schaebs et al., 2016]. This method could eliminate the difficulty in collecting a sufficient number and volume of urine samples for C-peptide analysis in the wild. Since energy balance depends on energy intake (Chapter 4), monitoring energy intake of macaques non-invasively will be useful. By accumulating these data, it is possible to investigate whether and how relationships between group size, nutritional/health condition of macaques, and reproductive success can vary depending on food availability and population density. It is a rare opportunity to assess the importance of intergroup feeding competition as a selective force of group living from ecological and social points of view.

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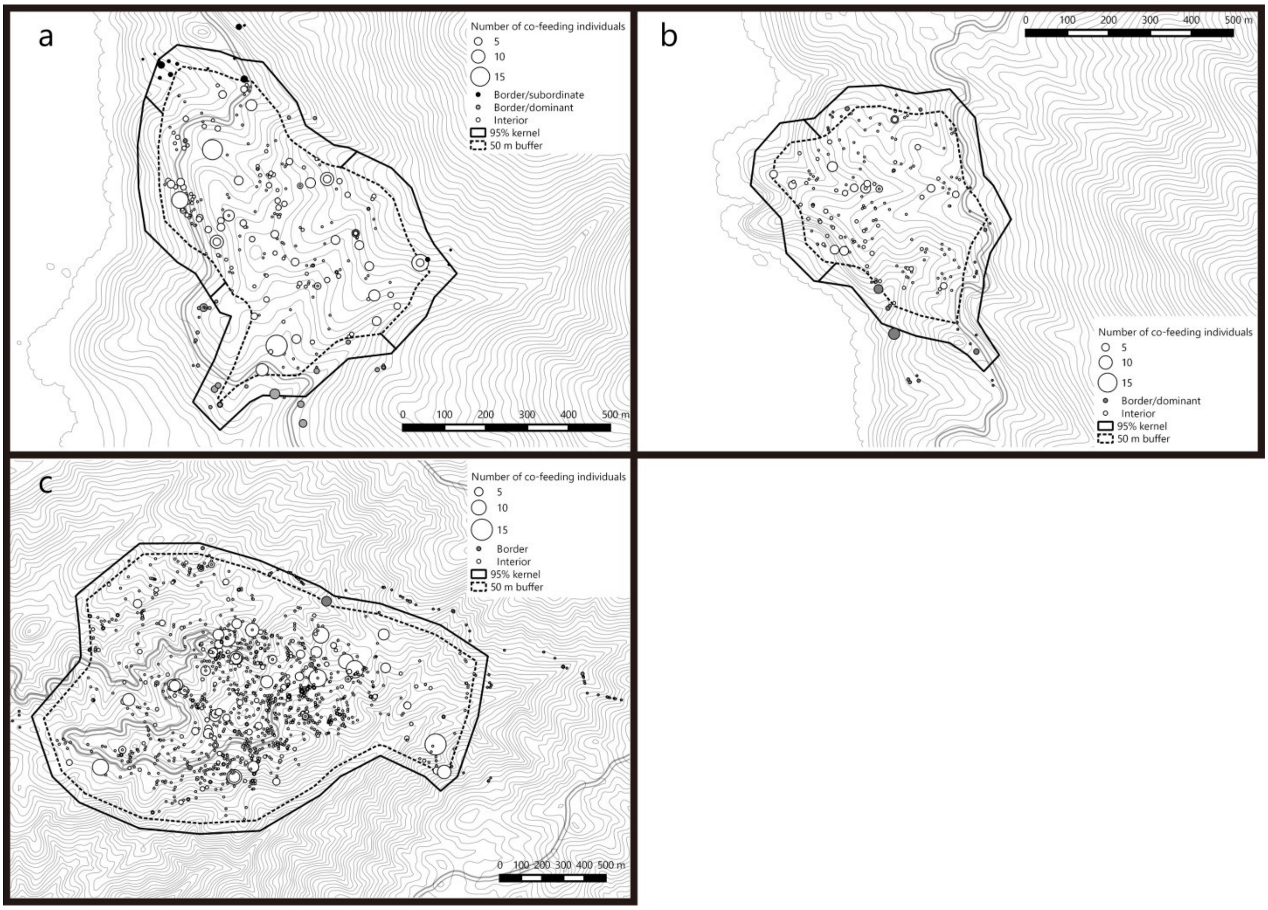

Figure 2-1 Variation in the number of co-feeding individuals depending on locations of food patches.

(a) the larger coastal group, (b) smaller coastal group, and (c) highland group. Solid and dotted lines indicate overall home range (95% kernel) and 50 m buffer inside from the outline of the overall home range, respectively. The size of each point corresponds to the number of co-feeding individuals. For (a) and (b), black: food patches along the border with subordinate groups, dark grey: those in the border with dominant groups, white: those in the interior. For (c), dark grey: food patches on the border, white: those in the interior. The contour line is set at 10 m intervals, and double lines indicate the road.

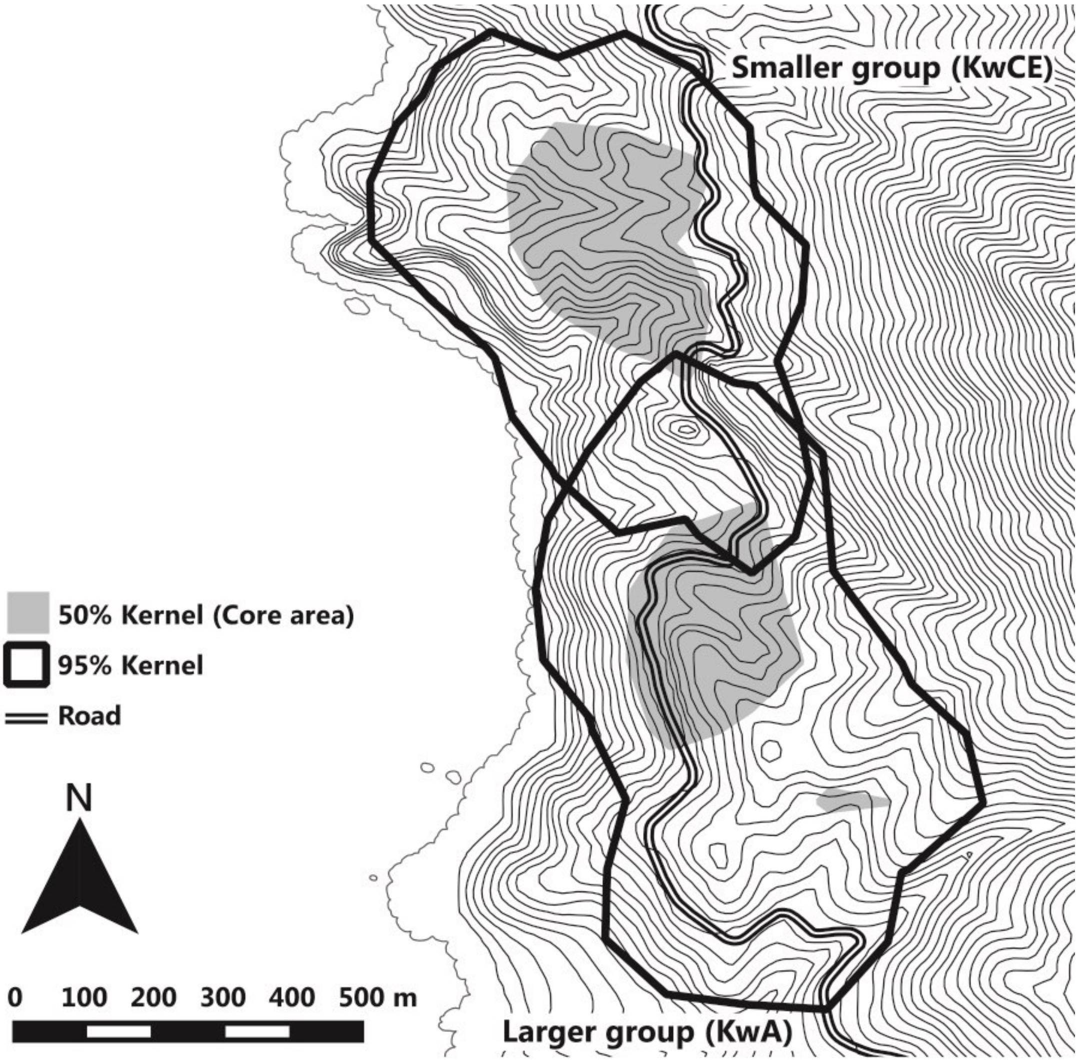

Figure 3-1 Home ranges of the larger and smaller groups.

Doubled lines indicate a road running through the study area. The contour line is set at 10 m intervals (scale: 1/25,000).

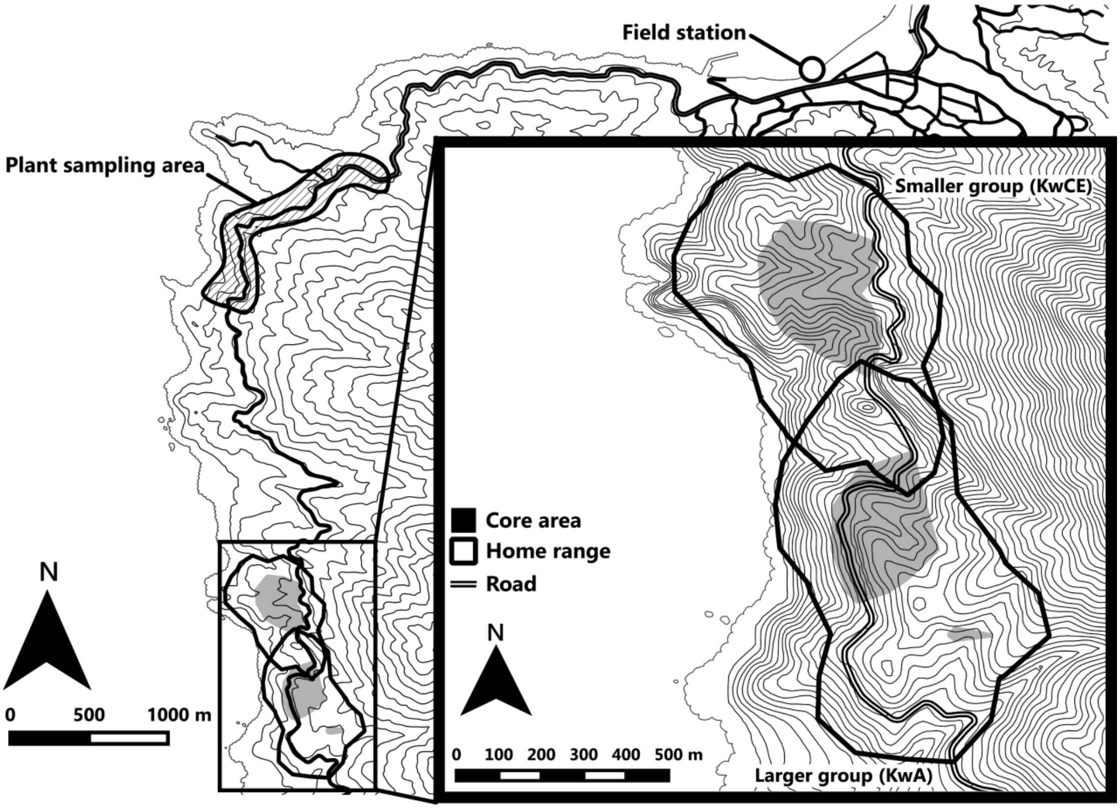

Figure 4-1 Map of the study site.

Home ranges of the larger and smaller groups, the area where plant sampling was undertaken, and the location of the field station are shown. The contour line is set at 50 m intervals on the wide map and 10 m on the detailed map.

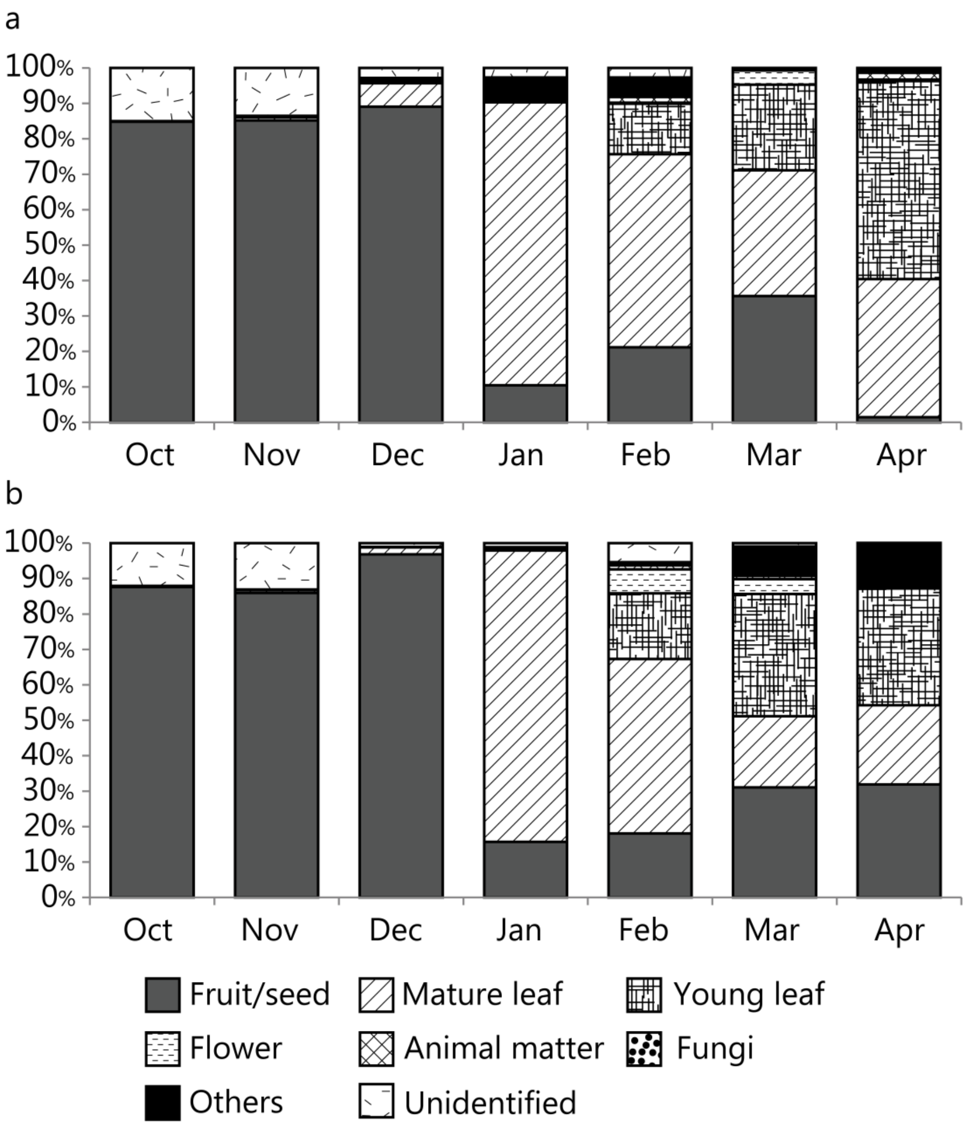

Figure 4-2 Seasonal variation in the diet composition.

(a) larger group, (b) smaller group. The mean monthly percentage of dry weight for each food category ingested by the focal animals in the total dry weight intake is shown.

Table 2-1 Summary of variables in the generalized linear mixed models

Group	Response variable	Explanatory variable	Error distribution
Coast & Highland	Duration of feeding in one patch	Location	Gaussian
		Patch size	
		Number of co-feeding individuals	
		Food type	
		Focal Animal ID (random effect)	
Coast	Frequency of visual scanning	Location	Binomial
		Number of co-feeding individuals	
		Focal Animal ID (random effect)	
Coast & Highland	Number of co-feeding individuals	Location	Zero-inflated Poisson
		Patch size	
		Food type	
		Focal Animal ID (random effect)	
Coast	Number of co-feeding adult males	Location	Zero-inflated Poisson
		Number of co-feeding individuals	
		Focal Animal ID (random effect)	

Table 2-2 Inter-site differences in food patch characteristics and food patch use

	Coastal forest	Highland forest	Statistics
Patch density (patches/ha)	998	9353	-
Patch quality (%)	51.2	41.7	Fisher's exact test: $p < 0.001$
(proportion of fruit/seed patches in all patches visited)			
Patch size (m^3)[a]	22.0	0.5	Brunner-Munzel Test: Brunner-Munzel Test Statistic = -40.1, df = 2867.2, $p < 0.001$
			$N_{\text{coastal group}} = 547$, $N_{\text{highland group}} = 2440$
Number of available feeding sites[a]	6 (larger group)	1	-
	3 (smaller group)		$N_{\text{larger coastal group}} = 316$, $N_{\text{smaller coastal group}} = 231$, $N_{\text{highland group}} = 2440$
Proportion of patches	20.1 (larger group)	11.9	Fisher's exact test:
that can accommodate all group members (%)	17.8 (smaller group)		larger coastal group vs. highland group: $p < 0.001$; smaller coastal group vs. highland group: $p < 0.001$
			$N_{\text{larger coastal group}} = 316$, $N_{\text{smaller coastal group}} = 231$, $N_{\text{highland group}} = 2440$
Duration of feeding in one patch (sec)[a]	232	70	Brunner-Munzel Test: Brunner-Munzel Test Statistic = -19.8, df = 901.7, $p < 0.001$
			$N_{\text{coastal group}} = 547$, $N_{\text{highland group}} = 2440$
Number of co-feeding individuals[a]	0.1	0	Brunner-Munzel Test: Brunner-Munzel Test Statistic = -16.6, df = 659.5, $p < 0.001$
			$N_{\text{coastal group}} = 547$, $N_{\text{highland group}} = 2440$

[a] The median is shown.

Table 2-3 Results of the generalized linear mixed models for duration of feeding in one patch, frequency of visual scanning, the number of co-feeding individuals, and the number of co-feeding adult males

Model	Group	Response variable	Explanatory variable	Estimate	SE	t or Z	p
1	Larger coastal	Duration of feeding in one patch	Intercept	4.95	0.11	44.62	0.00
		N = 300	Location_border with dominant groups	-0.27	0.19	-1.43	0.16
			Location_border with subordinate groups	0.31	0.26	1.17	0.24
			Patch size	0.00	0.00	3.59	0.00
			Number of co-feeding individuals	0.13	0.02	5.44	0.00
			Food type [fruits/seeds vs. mature leaves]	0.35	0.15	2.42	0.02
			Food type [fruits/seeds vs. young leaves]	0.52	0.16	3.25	0.00
			Food type [fruits/seeds vs. others]	-0.05	0.37	-0.13	0.89
2	Smaller coastal	Duration of feeding in one patch	Intercept	4.54	0.22	20.46	0.00
		N = 219	Location_border	-0.08	0.20	-0.39	0.70
			Patch size	0.01	0.00	4.93	0.00
			Number of co-feeding individuals	0.17	0.05	3.35	0.00
			Food type [fruits/seeds vs. mature leaves]	0.76	0.24	3.20	0.00
			Food type [fruits/seeds vs. young leaves]	0.45	0.20	2.28	0.02
			Food type [fruits/seeds vs. others]	0.53	0.33	1.58	0.12
3	Highland	Duration of feeding in one patch	Intercept	4.14	0.05	78.66	0.00
		N = 2210	Location_border	0.04	0.12	0.31	0.75
			Patch size	0.00	0.00	9.26	0.00
			Number of co-feeding individuals	0.25	0.03	9.68	0.00
			Food type [fruits/seeds vs. mature leaves]	-0.31	0.06	-5.36	0.00
			Food type [fruits/seeds vs. young leaves]	-0.10	0.13	-0.75	0.45
			Food type [fruits/seeds vs. others]	0.45	0.08	5.40	0.00
4	Larger coastal	Frequency of visual scanning	Intercept	-2.72	0.18	-15.39	0.00
		N = 180	Location_border with dominant groups	0.49	0.36	1.37	0.17
			Location_border with subordinate groups	-0.38	0.61	-0.63	0.53
			Number of co-feeding individuals	0.08	0.05	1.59	0.11
5	Smaller coastal	Frequency of visual scanning	Intercept	-2.59	0.20	-12.71	0.00
		N = 155	Location_border	0.06	0.34	0.16	0.87
			Number of co-feeding individuals	0.04	0.10	0.43	0.66

Table 2-3 (continued)

Model	Group	Response variable	Explanatory variable	Estimate	SE	t or Z	p
6	Larger coastal	Number of co-feeding individuals	Intercept	0.96	0.09	10.29	0.00
		N = 300	Location_border with dominant groups	-0.23	0.16	-1.43	0.15
			Location_border with subordinate groups	-0.48	0.28	-1.74	0.08
			Patch size	0.00	0.00	7.40	0.00
			Food type [fruits/seeds vs. mature leaves]	-0.33	0.13	-2.50	0.01
			Food type [fruits/seeds vs. young leaves]	-0.42	0.15	-2.75	0.01
			Food type [fruits/seeds vs. others]	0.09	0.31	0.30	0.77
7	**Smaller coastal**	**Number of co-feeding individuals**	Intercept	0.37	0.15	2.37	0.02
		N = 219	**Location_border**	0.93	0.29	3.23	0.00
			Patch size	0.00	0.00	4.79	0.00
			Food type [fruits/seeds vs. mature leaves]	-1.06	0.33	-3.16	0.00
			Food type [fruits/seeds vs. young leaves]	-1.02	0.28	-3.68	0.00
			Food type [fruits/seeds vs. others]	-2.17	0.64	-3.39	0.00
8	Highland	Number of co-feeding individuals	Intercept	0.42	0.12	3.54	0.00
		N = 2210	Location_border	-0.61	0.34	-1.81	0.07
			Patch size	0.00	0.00	13.56	0.00
			Food type [fruits/seeds vs. mature leaves]	-2.21	0.21	-10.75	0.00
			Food type [fruits/seeds vs. young leaves]	-2.24	0.48	-4.67	0.00
			Food type [fruits/seeds vs. others]	-1.01	0.13	-7.83	0.00
9	Larger coastal	Co-feeding with adult males	Intercept	-2.47	0.21	-11.84	0.00
		N = 300	Location_border with dominant groups	-0.40	0.60	-0.67	0.50
			Location_border with subordinate groups	-13.83	734.40	-0.02	0.98
			Number of co-feeding individuals	0.24	0.02	10.23	0.00
10	Smaller coastal	Co-feeding with adult males	Intercept	-3.38	0.35	-9.53	0.00
		N = 219	Location_border	-0.08	0.48	-0.16	0.87
			Number of co-feeding individuals	0.61	0.07	8.44	0.00

The model where effects of locations of food patches are statistically significant is shown in bold.

Table 3-1 Summary of variables in the generalized linear mixed models

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

Table 3-2 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[b]		0.1 ± 0.3	0.2 ± 0.5	-

Mean percentage of time spent for each activity in a day ± SD is shown ($N_{\text{larger group}} = 41$, $N_{\text{smaller group}} = 34$).

[a] The result of the likelihood ratio test for GLM is shown.

[b] aggressive interaction, copulatory behavior, etc.

Table 3-3 Best-fit models for dietary composition, activity budget, the number of visited patches, travel distance, and patch use

Item	Response variable	Explanatory variable	Estimate	SE	z	p
Dietary composition	Fruits / seeds	(Intercept)	-1.50	0.29	-5.19	< 0.001
		Group_Smaller	1.28	0.03	43.52	< 0.001
	Mature leaves	(Intercept)	-2.74	0.48	-5.76	< 0.001
		Group_Smaller	-2.01	0.16	-12.28	< 0.001
	Young leaves[a]	(Intercept)	-1.88	0.01	-354.62	< 0.001
		Group_Smaller	0.42	0.01	51.97	< 0.001
	Flowers	(Intercept)	-14.16	1.40	-10.09	< 0.001
	Animal matter	(Intercept)	-8.67	0.41	-20.95	< 0.001
	Fungi	(Intercept)	-15.22	1.83	-8.31	< 0.001
	Foraging	(Intercept)	-1.95	0.19	-10.31	< 0.001
		Group_Smaller	-0.91	0.03	-29.65	< 0.001
	Fallen fruits / seeds	(Intercept)	-4.74	0.45	-10.49	< 0.001
		Group_Smaller	-0.72	0.10	7.42	< 0.001
Activity budget	Feeding time	(Intercept)	0.10	0.11	0.95	0.34
		Group_Smaller	-0.31	0.10	-3.03	0.002
		Copulation	-0.03	0.11	-0.32	0.75
		Fruits / seeds feeding	-0.007	0.002	-3.59	< 0.001
		Animal matter feeding	-0.03	0.02	-1.36	0.17
	Moving time	(Intercept)	-1.64	0.07	-22.23	< 0.001
		Group_Smaller	0.38	0.08	4.98	< 0.001
		Copulation	-0.08	0.08	-0.91	0.37
		Fruits / seeds feeding	-0.0004	0.001	-0.30	0.77
		Animal matter feeding	-0.01	0.01	-0.80	0.42

[a] The result of GLM is shown.

Table 3-3 (continued)

Item	Response variable	Explanatory variable	Estimate	SE	z	p
Number of visited patches	Number of visited patches	(Intercept)	-2.79	0.06	-45.34	< 0.001
		Copulation	-0.05	0.16	-0.29	0.77
		Fruits / seeds feeding	0.0047	0.0009	5.31	< 0.001
		Animal matter feeding	-0.01	0.01	-1.59	0.11
Number of co-feeding individuals	Number of co-feeding individuals	(Intercept)	0.36	0.15	2.46	0.01
		Group_Smaller	-0.61	0.22	-2.76	0.006
		Patch size	0.001	0.0001	10.21	< 0.001
		Food category_mature leaves	0.24	0.11	2.23	0.03
		Food category_young leaves	0.07	0.13	0.55	0.58
		Food category_other	-0.46	0.22	-2.1	0.04

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

Table 3-4 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

Table 3-5 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	*Cinnamomum camphora*	Tree	Bud					L / S	L / S	L / S
2.50	3.66	Anacardiaceae	*Rhus succedanea*	Tree	Fruit	L / S	L / S	L / S				
1.75	3.66	Rubiaceae	*Psychotria serpens*	Liana	Mature leaf					L / S	L / S	L / S
2.28	3.63	Moraceae	*Ficus erecta*	Tree	Fruit		L / S	L / S		L / S	L / S	L / S
2.73	3.51	Lauraceae	*Litsea acuminata*	Tree	Fruit		L	L / S	L	L	L / S	
7.29	3.26	Rutaceae	*Zanthoxylum ailanthoides*	Tree	Seed	L	L / S	L / S				
1.43	3.04	Rubiaceae	*Morinda umbellata*	Liana	Fruit		L / S	L / S				
2.14	2.95	Moraceae	*Ficus wightiana*	Tree	Fruit	L / S	L		S	L		L
0.55	2.89	Fagaceae	*Lithocarpus edulis*	Tree	Fruit	L / S	L / S	L / S				
6.21	2.57	Moraceae	*Ficus wightiana*	Tree	Mature leaf			L	L / S	L / S	L	
3.62	2.37	Daphniphyllaceae	*Daphniphyllum teijimannii*	Tree	Mature leaf		L	L / S	L / S	L / S	L / S	L / S
1.54	2.35	Lauraceae	*Machilus thunbergii*	Tree	Shoot					L / S	L / S	L / S
1.51	2.19	Rubiaceae	*Morinda umbellata*	Liana	Mature leaf				L / S		L	
0.11	1.95	Theaceae	*Camellia japonica*	Tree	Nectar				L / S	L / S	L / S	L / S
2.78	1.92	Symplocaceae	*Symplocos lucida*	Tree	Mature leaf		L / S	L / S	L / S	L / S	L / S	L / S
3.51	1.66	Theaceae	*Eurya japonica*	Tree	Mature leaf				L	L	L / S	L / S
1.35	1.61	Theaceae	*Eurya emarginata*	Tree	Mature leaf	S				L / S	L / S	L
0.83	1.39	Rubiaceae	*Psychotria serpens*	Liana	Fruit	S	S	L	L / S	L		
0.49	1.29	Anacardiaceae	*Rhus succedanea*	Tree	Young leaf							L / S
0.67	1.27	Actinidaceae	*Actinidia rufa*	Liana	Fruit	L / S	L / S					
0.23	1.26	Fagaceae	*Quercus phillyraeoides*	Tree	Fruit	L / S	L / S	S				
1.73	1.25	Lauraceae	*Cinnamomum camphora*	Tree	Young leaf						L / S	L
1.45	1.23	Anacardiaceae	*Rhus succedanea*	Tree	Shoot							L / S
0.34	1.21	Myrsinaceae	*Ardisia sieboldii*	Tree	Fruit	S	L / S	S				
0.92	1.12	Aquifoliaceae	*Ilex integra*	Tree	Young leaf							L / S
0.36	1.01	Loranthaceae	*Taxillus yadoriki*	Liana	Fruit					S	L / S	S
1.57	0.95	Caprifoliaceae	*Lonicera affinis*	Liana	Shoot					L / S	L / S	L / S
1.90	0.85	Lauraceae	*Neolitsea sericea*	Tree	Fruit	L / S	L / S	L / S				
0.26	0.83	Moraceae	*Ficus pumila*	Liana	Fruit	L	L / S	S				
0.26	0.75	Sterculiaceae	*Firmiana plantanifolia*	Tree	Shoot							L / S

Table 3-5 (continued)

% 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.
0.29	0.28	Capparidaceae	*Crateava religiosa*	Tree	Mature leaf						L	L / S
0.68	0.27	Moraceae	*Ficus erecta*	Tree	Mature leaf		L / S	L / S				L
0.17	0.25	Caprifoliaceae	*Lonicera affinis*	Liana	Young leaf					L / S	L	
0.20	0.19	Caprifoliaceae	*Lonicera affinis*	Liana	Fruit	L / S	L / S					
0.27	0.19	Ericaceae	*Vaccinium bracteatum*	Tree	Fruit	L / S	L / S					
0.72	0.18	Theaceae	*Eurya japonica*	Tree	Fruit	L / S	L / S	L				
1.69	0.17	Lauraceae	*Cinnamomum camphora*	Tree	Fruit	L / S						
0.48	0.16	Theaceae	*Camellia japonica*	Tree	Mature leaf		L		L / S			
0.27	0.15	Araliaceae	*Schefflera octophylla*	Tree	Mature leaf				L / S	L	L	
0.33	0.13	Capparidaceae	*Crateava religiosa*	Tree	Young leaf					L	L / S	
3.17	0.13	Meliaceae	*Melia azendarach*	Tree	Seed			L	L / S	L / S	L	L / S
0.53	0.11	Fagaceae	*Quercus salicina*	Tree	Fruit		L / S					
2.03	0.00	Anacardiaceae	*Rhus succedanea*	Tree	Stalk			L	L	L	L	
1.24	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Fruit	L	L	L				
0.95	0.00	Lauraceae	*Neolitsea sericea*	Tree	Flower			L				
0.76	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Fruit		L	L	L	L	L	
0.62	0.00	Caprifoliaceae	*Lonicera affinis*	Liana	Mature leaf				L			
0.61	0.00	Moraceae	*Ficus erecta*	Tree	Stalk			L	L	L		
0.48	0.00	Moraceae	*Ficus wightiana*	Tree	Shoot							L
0.35	0.00	Aquifoliaceae	*Ilex rotunda*	Tree	Bud						L	
0.33	0.00	Fagaceae	*Quercus phillyraeoides*	Tree	Flower							L
0.21	0.00	Symplocaceae	*Symplocos prunifolia*	Tree	Mature leaf				L	L		
0.20	0.00	Euphorbiaceae	*Glochidion obovatum*	Tree	Fruit		L					
0.19	0.00	Polypodiaceae	*Pyrrosia lingua*	Epiphyte	Mature leaf				L	L		
0.19	0.00	Fagaceae	*Quercus salicina*	Tree	Mature leaf				L			
0.15	0.00	Moraceae	*Ficus microcarpa*	Tree	Fruit					L		
0.14	0.00	Aceraceae	*Acer morifolium*	Tree	Flower bud						L	
0.13	0.00	Rubiaceae	*Psychotria rubra*	Tree	Fruit		L	L				
0.12	0.00	Proteaceae	*Helicia cochinchinensis*	Tree	Mature leaf					L	L	
0.00	2.41	Fagaceae	*Lithocarpus edulis*	Tree	Bud							S

Table 3-5 (continued)

% 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.
0.00	1.09	Hamamelidaceae	*Distylium racemosum*	Tree	Gall							S
0.00	1.08	Euphorbiaceae	*Glochidion obovatum*	Tree	Young leaf						S	
0.00	1.06	Convolvulaceae	*Erycibe henryi*	Liana	Mature leaf				S			
0.00	1.06	Lauraceae	*Machilus thunbergii*	Tree	Fruit							S
0.00	1.05	Theaceae	*Ternstroemia gymnanthera*	Tree	Fruit	S	S	S	S	S		
0.00	0.88	Ebenaceae	*Diospyros japonica*	Tree	Fruit		S					
0.00	0.83	Vitaceae	*Parthenocissus tricuspidata*	Liana	Fruit	S						
0.00	0.70	Moraceae	*Ficus wightiana*	Tree	Young leaf							S
0.00	0.57	Anacardiaceae	*Rhus succedanea*	Tree	Mature leaf			S				
0.00	0.55	Rubiaceae	*Morinda umbellata*	Liana	Young leaf							S
0.00	0.52	Lauraceae	*Litsea acuminata*	Tree	Mature leaf					S	S	
0.00	0.50	Fagaceae	*Lithocarpus edulis*	Tree	Bark						S	
0.00	0.41	Aquifoliaceae	*Ilex integra*	Tree	Bud							S
0.00	0.38	Asteraceae	*Farfugium japonicum*	Herb	Mature leaf					S	S	
0.00	0.27	Gleicheniaceae	*Dicranopteris linearis*	Fern	Mature leaf					S		
0.00	0.23	Chloranthaceae	*Sarcandra glabra*	Tree	Pith					S		S
0.00	0.22	Asteraceae	*Cirsium spinosum*	Herb	Mature leaf					S		
0.00	0.21	Lauraceae	*Litsea japonica*	Tree	Fruit					S	S	
0.00	0.18	Vervenaceae	*Callicarpa dichotoma*	Tree	Fruit		S					
0.00	0.17	Moraceae	*Ficus erecta*	Tree	Bud					S		
0.00	0.14	Moraceae	*Ficus nipponica*	Liana	Fruit	S						
0.00	0.13	Theaceae	*Camellia japonica*	Tree	Fruit							S
0.00	0.12	Myrsinaceae	*Maesa tenera*	Tree	Mature leaf			S				
0.00	0.11	Primulaceae	*Lysimachia sikokiana*	Herb	Mature leaf						S	S

L / S indicates that the food was eaten by the larger and smaller groups in the month.

L, Larger group; S, Smaller group.

Table 3-6 Comparison of feeding rate between the larger and smaller groups and correlation between feeding rate and patch residency time in the two groups

Species	Part	Feeding rate (unit/sec.)		Wilcoxon rank-sum test	Correlation with patch residency time[a]	
		Larger group	Smaller group		Larger group	Smaller group
Ficus wightiana	Fruit	0.48 ± 0.56	0.55 ± 0.16	$p = 0.7$ ($N_L = 5$, $N_S = 4$)	$p = 0.13$	$p = 0.75$
Litsea acuminata	Fruit	0.33 ± 0.16	0.29 ± 0.10	$p = 0.14$ ($N_L = 7$, $N_S = 7$)	$p = 0.09$	$p = 0.50$
Rhus succedanea	Fruit	0.51 ± 0.17	0.38 ± 0.12	$p = 0.06$ ($N_L = 10$, $N_S = 5$)	$p = 0.07$	$p = 1$
Rhus succedanea	Young leaf	0.30 ± 0.19	0.25 ± 0.23	$p = 0.3$ ($N_L = 5$, $N_S = 5$)	$p = 0.78$	$p = 0.33$
Daphniphyllum teijimannii	Mature leaf	0.13 ± 0.14	0.12 ± 0.05	$p = 0.38$ ($N_L = 5$, $N_S = 4$)	$p = 0.23$	$p = 0.33$
Ficus erecta	Fruit	0.36 ± 0.27	0.43 ± 0.27	$p = 0.36$ ($N_L = 13$, $N_S = 7$)	$p = 0.89$	$p = 0.24$
Zanthoxylum ailanthoides	Fruit	0.70 ± 0.21	0.72 ± 0.17	$p = 0.97$ ($N_L = 12$, $N_S = 7$)	$p = 0.59$	$p = 0.10$
Symplocos lucida	Mature leaf	0.17 ± 0.07	0.23 ± 0.14	$p = 0.35$ ($N_L = 9$, $N_S = 5$)	$p = 0.55$	$p = 0.95$
Cinnamomum japonicum	Young leaf	0.48 ± 0.10	0.49 ± 0.08	$p = 0.92$ ($N_L = 11$, $N_S = 5$)	$p = 0.17$	$p = 1$
Lithocarpus (Pasania) edulis	Fruit	0.16 ± 0.04	0.23 ± 0.15	$p = 0.63$ ($N_L = 5$, $N_S = 4$)	$p = 0.33$	$p = 0.92$
Neolitsea sericea	Fruit	0.77 ± 0.28	0.66 ± 0.10	$p = 0.31$ ($N_L =7$, $N_S = 4$)	$p = 0.50$	$p = 1$
Machilus thunbergii	Shoot	0.26 ± 0.17	0.32 ± 0.23	$p = 0.58$ ($N_L =5$, $N_S = 4$)	$p = 0.33$	$p = 0.92$

Mean feeding rate in a patch for each species is shown. N_L: larger group; N_S: smaller group

[a] The results of Spearman's rank order correlation test are shown.

Table 4-1 Summary of generalized estimating equations for ingestion rates, energetic/nutritional content of diet, and energy budget and a generalized linear mixed model for C-peptide levels

Response variable	Explanatory variable	Estimate	SE	t	p
Average ingestion rates	(Intercept)	0.07	0.01	106.65	< 0.001
(alpha = -0.03)	Group_Smaller	-0.01	0.01	3.71	0.05
	Season_Leaf	-0.03	0.01	36.85	< 0.001
Average enegetic content of diet	(Intercept)	1.66	0.05	1206.23	< 0.001
(alpha = -0.05)	Group_Smaller	-0.04	0.05	0.80	0.37
	Season_Leaf	-0.43	0.07	42.31	< 0.001
Average CL content of diet	(Intercept)	-2.09	0.08	618.91	< 0.001
(alpha = -0.05)	Group_Smaller	-0.13	0.07	3.74	0.05
	Season_Leaf	-0.86	0.11	58.81	< 0.001
Average CP content of diet	(Intercept)	0.07	0.00	426.80	< 0.001
(alpha = -0.03)	Group_Smaller	-0.01	0.00	2.50	0.11
	Season_Leaf	0.03	0.00	53.10	< 0.001
Average TNC content of diet	(Intercept)	0.36	0.02	479.84	< 0.001
(alpha = -0.09)	Group_Smaller	0.02	0.02	1.82	0.18
	Season_Leaf	-0.01	0.01	0.56	0.45
Average NDF content of diet	(Intercept)	0.37	0.01	1546.20	< 0.001
(alpha = 0.03)	Group_Smaller	0.00	0.01	0.00	0.96
	Season_Leaf	0.04	0.01	10.50	0.00
Energy intake	(Intercept)	6.74	0.11	3939.81	< 0.001
(alpha = -0.05)	Group_Smaller	-0.13	0.08	2.65	0.10
	Season_Leaf	-0.93	0.14	43.35	< 0.001
Energy expenditure	(Intercept)	320.47	2.25	20348.02	< 0.001
(alpha = 0.15)	Group_Smaller	4.45	2.52	3.10	0.08
	Season_Leaf	1.02	2.94	0.12	0.73
Energy balance	(Intercept)	802.60	206.69	15.08	< 0.001
(alpha = -0.08)	Group_Smaller	-122.68	137.23	0.80	0.37
	Season_Leaf	-664.07	180.99	13.46	< 0.001
C-peptide levels[a]	(Intercept)	1.65	0.36	4.56	< 0.001
	Group_Smaller	0.17	0.43	0.40	0.70
	Season_Leaf	-0.58	0.39	-1.49	0.16

The alpha is an estimated correlation parameter representing temporal autocorrelation between consecutive months.

[a] The result of GLMM is shown.

Table 4-2 Summary of ingestion rates, energetic/nutritional content of diet, energy budget, and C-peptide levels

Season	Group	Ingestion rate	Energetic content	TNC content	CP content	CL content
		g/sec	kcal/g	%	%	%
All	Larger group	0.06 ± 0.04	1.43 ± 0.36	35.98 ± 6.92	9.07 ± 2.88	9.66 ± 6.41
	Smaller group	0.04 ± 0.02	1.39 ± 0.29	38.16 ± 7.75	8.56 ± 2.81	8.14 ± 6.05
Fruit/seed	Larger group	0.08 ± 0.04	1.68 ± 0.26	35.96 ± 9.01	7.5 ± 2.06	14.25 ± 6.22
	Smaller group	0.06 ± 0.02	1.59 ± 0.27	39.28 ± 10.85	6.44 ± 1.07	11.75 ± 7.35
Leaf	Larger group	0.04 ± 0.03	1.22 ± 0.3	36 ± 4.5	10.47 ± 2.8	5.58 ± 2.84
	Smaller group	0.03 ± 0.01	1.21 ± 0.17	37.19 ± 3.45	10.42 ± 2.54	4.97 ± 1.08
Season	Group	NDF content	Energy intake	Energy expenditure	Energy balance	C-peptide levels
		%	kcal/day	kcal/day	kcal/day	pmol/mg Cr
All	Larger group	38.74 ± 5.6	767.65 ± 1039.65	320.62 ± 12.22	447.03 ± 1043.01	5.05 ± 4.20
	Smaller group	38.68 ± 5.15	648.62 ± 669.22	325.16 ± 16.18	323.47 ± 673.02	10.10 ± 15.63
Fruit/seed	Larger group	36.34 ± 4.75	1181.25 ± 1386.91	321.42 ± 12.97	859.83 ± 1393.41	7.96 ± 4.73
	Smaller group	37.1 ± 6.21	937.22 ± 852.54	322.52 ± 16.96	614.71 ± 855.35	8.12 ± 7.65
Leaf	Larger group	40.86 ± 5.52	400.01 ± 280.67	319.91 ± 11.72	80.1 ± 278.17	3.49 ± 3.03
	Smaller group	40.07 ± 3.67	396.1 ± 300.32	327.47 ± 15.64	68.63 ± 305.3	11.7 ± 20.8

Mean values for each individual for each month are shown.

Table 4-3 Nutritional composition of food items

Family	Species	Part	%CA	%CL	%NDF	%CP	%TNC	unit dry weight (g)
Fagaceae	*Lithocarpus edulis*	Bud	6.36	7.72	46.14	7.33	32.45	0.01
Lauraceae	*Cinnamomum camphora*	Bud	7.52	4.34	39.32	13.78	35.03	0.02
Actinidaceae	*Actinidia rufa*	Fruit	5.10	3.53	15.34	3.10	72.93	0.92
Anacardiaceae	*Rhus succedanea*	Fruit	0.62	46.99	48.49	2.12	1.78	0.04
Ebenaceae	*Diospyros japonica*	Fruit	4.07	0.28	46.64	2.58	46.43	1.72
Lauraceae	*Cinnamomum camphora*	Fruit	6.19	29.14	31.97	5.32	27.38	0.10
Lauraceae	*Neolitsea sericea*	Fruit	7.43	11.35	32.49	5.12	43.61	0.10
Lauraceae	*Machilus thunbergii*	Fruit	5.29	18.45	45.80	12.91	17.56	0.18
Lauraceae	*Litsea acuminata*	Fruit	4.02	29.22	30.08	14.11	22.58	0.05
Moraceae	*Ficus wightiana*	Fruit	7.78	4.43	45.10	6.93	35.77	0.09
Moraceae	*Ficus erecta*	Fruit	10.29	4.96	36.83	9.63	38.28	0.09
Moraceae	*Ficus pumila*	Fruit	14.16	5.57	31.49	4.13	44.64	1.15
Myrsinaceae	*Ardisia sieboldii*	Fruit	7.85	3.67	26.27	2.85	59.36	0.03
Rubiaceae	*Psychotria serpens*	Fruit	10.53	1.53	17.28	3.94	66.73	0.03
Rubiaceae	*Morinda umbellata*	Fruit	7.77	20.79	23.22	5.42	42.79	0.04
Rubiaceae	*Psychotria rubra*	Fruit	7.50	3.95	31.76	5.24	51.55	0.02
Theaceae	*Eurya japonica*	Fruit	3.96	2.57	20.73	2.10	70.64	0.01
Theaceae	*Ternstroemia gymnanthera*	Fruit	4.01	7.80	47.76	2.71	37.73	0.19
Anacardiaceae	*Rhus succedanea*	Mature leaf	7.32	1.72	36.31	9.14	45.51	0.04
Araliaceae	*Schefflera octophylla*	Mature leaf	7.56	11.00	30.83	10.53	40.09	0.27
Asteraceae	*Farfugium japonicum*	Mature leaf	12.79	1.56	37.61	9.61	38.44	0.14
Daphniphyllaceae	*Daphniphyllum teijimannii*	Mature leaf	6.46	3.33	45.73	7.49	37.00	0.11
Fagaceae	*Quercus salicina*	Mature leaf	4.98	4.52	64.95	10.33	15.22	0.18
Gleicheniaceae	*Dicranopteris linearis*	Mature leaf	8.53	1.75	44.29	10.04	35.39	0.32
Lauraceae	*Litsea acuminata*	Mature leaf	4.06	6.73	53.26	12.10	23.85	0.25
Moraceae	*Ficus wightiana*	Mature leaf	7.99	1.78	55.00	11.50	23.73	0.27
Moraceae	*Ficus erecta*	Mature leaf	12.38	2.61	42.22	14.85	27.94	0.17
Myrsinaceae	*Maesa tenera*	Mature leaf	6.87	2.54	41.03	14.74	34.82	0.12
Polypodiaceae	*Pyrrosia lingua*	Mature leaf	6.04	2.55	56.86	6.21	28.34	0.13
Primulaceae	*Lysimachia sikokiana*	Mature leaf	8.84	1.71	31.43	13.43	44.59	0.05
Proteaceae	*Helicia cochinchinensis*	Mature leaf	7.56	1.45	35.45	7.74	47.80	0.09
Rubiaceae	*Psychotria serpens*	Mature leaf	8.17	2.06	40.06	6.69	43.02	0.05
Rubiaceae	*Morinda umbellata*	Mature leaf	7.79	3.77	29.74	11.90	46.81	0.17
Symplocaceae	*Symplocos lucida*	Mature leaf	11.25	2.40	35.72	7.00	43.63	0.11
Symplocaceae	*Symplocos prunifolia*	Mature leaf	6.52	2.46	39.08	8.21	43.73	0.10
Theaceae	*Camellia japonica*	Mature leaf	6.27	1.25	42.12	6.51	43.86	0.31
Theaceae	*Eurya emarginata*	Mature leaf	8.13	1.85	35.88	8.07	46.08	0.02
Theaceae	*Eurya japonica*	Mature leaf	4.62	3.01	50.79	7.16	34.42	0.12
Anacardiaceae	*Rhus succedanea*	Seed	1.74	7.65	68.53	5.88	16.20	0.05
Fagaceae	*Quercus phillyraeoides*	Seed	1.50	1.36	26.00	3.17	67.97	0.49
Fagaceae	*Quercus salicina*	Seed	1.45	2.25	9.72	3.36	83.21	0.50
Fagaceae	*Lithocarpus edulis*	Seed	2.00	0.41	22.60	4.37	70.62	0.39
Lauraceae	*Machilus thunbergii*	Seed	1.25	5.88	36.23	6.24	50.40	0.05
Lauraceae	*Litsea acuminata*	Seed	3.32	12.63	21.19	12.01	50.86	0.00
Meliaceae	*Melia azendarach*	Seed	2.82	37.55	22.80	25.50	11.32	0.08
Rutaceae	*Zanthoxylum ailanthoides*	Seed	6.82	40.08	39.37	7.93	5.80	0.01
Anacardiaceae	*Rhus succedanea*	Shoot	7.91	5.04	37.51	28.16	21.38	0.08
Lauraceae	*Machilus thunbergii*	Shoot	4.46	2.75	59.68	8.66	24.45	0.02
Anacardiaceae	*Rhus succedanea*	Stalk	7.19	4.18	41.52	7.58	39.53	0.13
Anacardiaceae	*Rhus succedanea*	Young leaf	6.37	5.14	29.92	24.14	34.43	0.02
Euphorbiaceae	*Glochidion obovatum*	Young leaf	6.92	2.36	16.68	23.33	50.71	0.01
Lauraceae	*Cinnamomum camphora*	Young leaf	7.51	4.77	18.85	22.50	46.37	0.10

CA: crude ash, CL: crude lipid, NDF: neutral detergent fiber, CP: crude protein, TNC: total non-structural carbohydrate