

Inter-annual variation in nut abundance is related to agonistic interactions of foraging
female Japanese macaques (*Macaca fuscata*)

Yamato Tsuji^{1,2*} and Seiki Takatsuki^{3,4}

¹School of Agriculture and Life Sciences, University of Tokyo, 1-1-1, Yayoi, Bunkyo-ku,
Tokyo, 113-8657, Japan

²Primate Research Institute, Kyoto University, 41-2, Kanrin, Inuyama, Aichi, 484-8506,
Japan

³University Museum, University of Tokyo, 7-3-1, Hongo, Bunkyo-ku, Tokyo, 113-0033,
Japan

⁴Department of Veterinary Medicine, Azabu University, 1-17-71, Fuchinobe, Chuo-ku,
Sagamihara, Kanagawa, 252-5201, Japan

*Corresponding author

Address: 41-2, Kanrin, Inuyama, Aichi 484-8506, Japan

E-mail: ytsuji@pri.kyoto-u.ac.jp

Tel / Fax: +81-568-63-0539

Abstract

The importance of dominance status to foraging and ultimately survival and or reproductive success in wild primates is known; however, few studies have addressed these variables simultaneously. We investigated foraging and social behaviour among 17 adult female Japanese macaques (*Macaca fuscata*) on Kinkazan Island, northern Japan, from September to November in two consecutive years (2004 and 2005) to determine whether inter-annual variation in food availability was related to variation in agonistic interactions over food resources and the feeding behaviour of animals of different dominance rank. We compared energy obtained with daily energy requirements and also examined the effect of variation in feeding behaviour on female survival and reproductive success. Fruiting conditions differed considerably between the two years: of four nut-producing species, only *Torreya nucifera* nuts fruited in 2004, whereas all four species, particularly *Fagus crenata*, produced nuts in abundance in 2005. The abundance and average crown size of *T. nucifera* trees were smaller than those of *F. crenata*, and there was a higher frequency of agonistic interactions during 2004, when dominant, but not subordinate, individuals were able to satisfy daily energy requirements from nut feeding alone through longer nut feeding bouts. In contrast, all macaques, regardless of their dominance rank, were able to satisfy their energy requirements by feeding on nuts in 2005. Subordinate macaques appeared to counter

their disadvantage in 2004 by moving and searching for food more and maintaining larger inter-individual distances. Several lower-ranking females died during the food-scarce season of 2004, and only one dominant female gave birth the following birth season. In contrast, none of the adult females died during the food-scarce season of 2005, and 12 females gave birth the following birth season. These findings suggest that an interaction between dominance rank and inter-annual variation in food availability are related to macaque behaviour, survival and reproduction.

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

46 Introduction

47 A fundamental problem facing group-living animals is that individuals are unable to
48 avoid within-group competition completely (Tilson and Hamilton 1984). In social
49 mammals, the influence of within-group competition on foraging success can ultimately
50 affect population levels by affecting adult mortality (Cheney *et al.* 1988), birth rate
51 (Holekamp *et al.* 1996) and infant mortality (Borries *et al.* 1991). Agonistic interactions
52 often cause differences in resource acquisition among individuals (Sutherland 1996;
53 Robichard *et al.* 1996; Holand *et al.* 2004). Such interactions become more frequent
54 and/or more severe when food resources are concentrated, food patches are small and/or
55 inter-patch distances are long, resulting in the monopolization of food resources by
56 dominant animals (Vogel *et al.* 2007). For example, in tufted capuchins (*Cebus apella*),
57 white-faced capuchins (*C. capucinus*) and Hanuman langurs (*Semnopithecus entellus*),
58 foraging success among dominant individuals is greater than that of subordinates when
59 resources are more concentrated, but not when more dispersed resources are available
60 (Janson 1985; Koenig 2000; Vogel *et al.* 2007). Foraging success can ultimately affect
61 population parameters like adult mortality (Wrangham 1981; Cheney *et al.* 1988), birth
62 interval (Frank 1986), birth rate (Bulger and Hamilton 1987; Holekamp *et al.* 1996),
63 and infant mortality (Borries *et al.* 1991).

Nuts are the staple foods of many frugivorous mammals in temperate regions of Japan, Fagaceae, Betulaceae and Ulmaceae (Koike 2010). The abundance, distribution and size of nut food patches/feeding sites available to animals vary from year to year (Suzuki *et al.* 2005). Thus, we can predict that the rate of agonistic interactions displayed by group-living animals will also vary between years, as in tropical regions (Barton 1993). For example, in years when nuts are available but are monopolizable, dominant individuals would achieve greater foraging success through agonistic defence of food resources, leading to lower mortality and higher birth rates. Conversely, to compensate for potential energy shortages, subordinate individuals might increase their foraging effort, e.g., by prolonging their total feeding time (van Schaik and van Noordwijk 1985) and increasing inter-individual distances to avoid agonistic interactions (van Noordwijk and van Schaik 1987).

We tested the importance of dominance status in foraging, survival and short-term reproductive success among wild Japanese macaques (*Macaca fuscata*) on Kinkazan Island in northern Japan. Several previous studies have addressed the relationships between i) inter-annual variation in the availability of nuts (i.e., the distribution of nut-producing patches, patch size and density of nuts) and ii) the frequency of agonistic interactions (Barton and Whiten 1993; Saito 1996), i) and iii) foraging-related behaviour

and foraging success among dominant and subordinate animals (Iwamoto 1987), and ii) and iii) (Foerster *et al.* 2011) but few studies have systematically addressed all three variables simultaneously, as we do in the present study. In addition, few studies addressing inter-annual variation in food availability on mortality and the reproductive output of dominant and subordinate animals (Bercovich and Strum 1993), have considered foraging behaviour. Japanese macaques are a group-living, matrilineal primate species typified by a clear, linear dominance hierarchy among adult females (Kawamura 1958). Between September and November, which corresponds to the mating season (Fujita *et al.* 2004), the macaques of Kinkazan feed on four main species of fallen nut: *Fagus crenata*, *Zelkova serrata*, *Carpinus* spp. (including *C. tshonoskii* and *C. laxiflora*) and *Torreya nucifera* (Tsuji *et al.* 2006). As the nutritional content, unit weight and feeding speed are all greater for these nuts than other food items, their acquisition allows macaques to deposit fat (Nakagawa 1989; Tsuji *et al.* 2008), which is important for female oestrus and conception (Takahashi 2002; Fujita *et al.* 2004) and for over-winter survival (Muroyama *et al.* 2006). Nut production on Kinkazan varies greatly from year to year (Tsuji 2010), and the food habits (Tsuji *et al.* 2006) and ranging patterns (Tsuji and Takatsuki 2009) of Kinkazan macaques vary accordingly. A lack of predators and low intergroup competition (Saito *et al.* 1998) control for these

potentially confounding variables, and we can readily evaluate nut availability because the macaques on Kinkazan feed mainly on nuts that have fallen to the ground during this season (Nakagawa 1989).

We examined inter-annual variation in the availability of nuts, the frequency of agonistic interactions, foraging-related behaviour and foraging success among dominant and subordinate animals, and mortality and the reproductive output of dominant and subordinate animals. We compared these variables over 2 years (2004–2005) to test the hypothesis that inter-annual variation in nut availability is linked to variation in agonistic interactions over nuts. In 2004, only *T. nucifera* fruited, whereas all four nut-bearing species fruited in 2005, with *F. crenata* being especially abundant (Tsuji 2010). As a result, the energy available from the nuts was extremely low in 2004, but higher in 2005 than any other year between 2000 and 2006 (Tsuji 2010). Under these conditions, we tested the following four predictions.

Prediction 1: Agonistic interactions related to feeding would be more frequent in 2004 than in 2005.

Prediction 2: Agonistic interactions in 2004 would be linked to differences in foraging-related behaviour (e.g., activity budgets, length of feeding bouts, inter-individual distances) among females of different dominance rank, but there

would be fewer differences in 2005.

Prediction 3: In 2004, agonistic interactions would lead to greater foraging success among dominant female macaques; this difference would be smaller in 2005.

Prediction 4: Inter-annual variation in the foraging success of females of different dominance rank would be reflected in differential mortality and/or birth rates during the following birth season.

Figure 1 should appear here

Methods

Study area

Our study site was Kinkazan Island (141°35'E, 38°16'N), located 0.7 km off Oshika Peninsula of northern Japan. The island is 5.1 km long and 3.7 km wide, with a total area of 9.6 km². The highest peak is 445 m above sea level. The mean ($\pm$ SD) daily rainfall on the island did not differ significantly between 2004 and 2005 between September and November (paired *t*-test, $t = 1.47$, $df = 90$, $p = 0.144$), which corresponds to the mating season, and between December and February (paired *t*-test, $t = 0.46$, $df = 89$, $p = 0.444$), which corresponds to the food-scarce season (data source: Ishinomaki Weather Station; <http://www.data.kishou.go.jp>; Fig. 1a). In contrast, while the mean ($\pm$ SD) temperature between September and November did not differ between

2004 and 2005 (paired t -test, $t = 1.47$, $df = 90$, $p = 0.144$), the mean temperature was significantly different between December and February of the 2 years (paired t -test, $t = 3.77$, $df = 89$, $p < 0.001$; Fig. 1b).

Study animals and dominance rank

Six troops of wild Japanese macaque live on Kinkazan (Izawa 2009). We studied Troop A, which lives in the north-western part of the island (Tsuji and Takatsuki 2009). Troop A have been habituated to observation at close proximity (< 10 m) since 1982. During the study period, the troop size varied from 29 to 39 individuals, including 2–5 adult males (> 5 y), 14–17 adult females (> 5 y), 8–9 juveniles (1–5 y) and 1–12 infants (< 1 y). Data on the maternal kinship and dominance ranks of 17 adult females was available prior to the study (Table I, see also Tsuji 2007). We confirmed the dominance hierarchy using a matrix based on submissive behaviours observed during *ad libitum* sampling (see Lehner 1979), giving 4 high-ranking (H), 6 middle-ranking (M), and 7 low-ranking (L) females (Table I). Landau's index of linearity (h) for the adult females was 0.926, reflecting an almost linear hierarchy (Lehner 1979). Japanese macaques are seasonal breeders, and females on Kinkazan mate mainly from October to November and give birth mainly between April and June (Fujita *et al.* 2004). From 1982 to 1995,

no female gave birth the year after a surviving infant was born (Izawa 2009). Thus, we assumed that all females without an infant during the mating season could potentially conceive (Fujita *et al.* 2004). Based on this, nine females had the potential to conceive in 2004 ($H = 2$, $M = 3$, and $L = 4$) and 13 in 2005 ($H = 3$, $M = 4$, and $L = 6$; Table I).

Data collection

We observed A-troop from late September to late November in both years (41 d in 2004 and 36 d in 2005). Total data collection time was 578 hrs (304 hrs in 2004 and 274 hrs in 2005). We followed the troop (17 females in 2004 and 14 females in 2005) from dawn to dusk, during which time we conducted focal animal observations as follows: in the morning we searched for females for whom we had less behavioural data than other females. Once we found an appropriate female we started a focal sample. When we lost the female during the sampling or we had obtained 6 hr of focal data, we terminated the given focal sample, and searched for the next candidate females and started a new focal sample after an interval of several minutes. We followed one to three adult females daily, conducting a total of 146 focal samples during the study (72 focal samples in 2004 and 74 focal samples in 2005) (Table I). Mean length of a focal sample was 257 ± 70 minutes ($N = 146$). We ensured that we sampled all females during both the morning (6:00–12:00) and afternoon (12:00–18:00) on different days (Table I). We did not follow

females in oestrus, who we identified by facial redness and/or consortship with adult males (Fujita *et al.* 2004), to eliminate the effect of this physiological status on foraging behaviour (Matsubara and Sprague 2004). Table I shows total sampling time for each female. Our methodology adhered to Japanese legal requirements.

Activity and food habits

We recorded the behavioural state of the focal animal every minute using instantaneous sampling. We classified activity into five categories: 1) feeding (including picking up, processing and chewing at one location), 2) moving (including quadrupedal walking, searching for food and running), 3) resting (including standing, sitting, lying without motion), 4) social grooming and 5) others (including drinking, fighting and alarm calling). If the animals were feeding at a given sampling point, we recorded the number of food items consumed (e.g., one leaf, one entire fruit and nut, or a single bite of bark). We categorised food items as 1) nuts (including *F. crenata*, *T. nucifera*, *Z. serrata*, *Carpinus* spp. and others), 2) fruits/seeds (except for nuts), 3) leaves, 4) other woody plant materials (including buds, bark, sap and gum), 5) herbaceous plants, 6) fungi, 7) animal materials and 8) others (including soil and unidentified materials). As the macaques fed on herbaceous plants with great rapidity, such plants were difficult to identify. The females rarely discarded any part of the feeding unit. When the focal

female fed on a given food item at locations where observation conditions were poor (e.g., within a tree crown or on a cliff), we recorded only the food item(s) and the number of instantaneous sampling points to determine the duration of the feeding episode. We defined the proportion of instantaneous sampling points for consuming food item i relative to all sampling points associated with feeding as the “feeding time percentage for food item i ”.

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

For each nut feeding bout on the ground, we recorded the onset (when the focal female ingested the first nut) and end of nut feeding (when the focal female left the feeding tree). We also visually estimated the crown diameters of feeding trees in 1-m intervals, from which we calculated the size of ground area (obtained by $\text{diameter}^2 \times \pi$) beneath the feeding tree (m^2). Finally, we recorded the number of adult females within 3 m of the focal animal every 5 min to provide an indication of inter-individual distances.

Three metres has been shown to be the minimum distance tolerated by Japanese macaques before agonistic interactions become more common while foraging (Saito 1996).

Nut availability

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

species in the feeding patches for 2004 and 2005, we positioned 0.5×0.5-m quadrats at ground level under randomly selected nut-producing trees ($N = 36$ for each species), and estimated the number of nuts ($\#/m^2$) from these quadrats. To calculate temporal changes, we repeated this procedure every 2 to 3 weeks (2004: five times, 2005: six times), using different trees each time. In 2004 only *T. nucifera* produced fruit so sampling was limited to this species, while in 2005 all four species fruited and were sampled.

Agonistic interactions

We recorded agonistic behaviour on a continuous basis. We recorded only agonistic interactions directed by the focal female toward other individuals, not those received by the focal female, to simplify the analyses. Following previous studies (Barton 1993; Saito 1996), we recorded both overt (e.g., attack) and subtle (e.g., displacement and threat) agonistic interactions.

Estimation of foraging success

a) Estimation of metabolizable energy intake (MEI)

During the study period, we collected almost all food items consumed by the study subjects (72 of 80 food items). Of these, we reported the nutritional characteristics of 37 items elsewhere (Tsuji *et al.* 2007; Tsuji and Takatsuki 2008). We report the nutritional characteristics of the remaining 35 food items here. We dried each food item and

weighed it according to its feeding unit (g) ($N = 5$). Then we milled and analysed the item for crude proteins (%CP, obtained by C.N. coder), neutral detergent fibre (%NDF, obtained from the remnants left after neutral detergent boiling), crude lipids (%CL, determined in a Soxhlet tube) and crude ash (%CA, obtained from the ignition loss) (Tsuji *et al.* 2008). We measured the nutritional contents in duplicate and took the mean of the results. We calculated the gross energy content of food item i (e_i , kcal/g) using the following formula (Maynard *et al.* 1979):

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

We calculated the rate of consumption of different food items as the dry weight consumed/min, and the rate of energy intake (EIS) by multiplying this number by the gross energy content/g of that food item.

We estimated the amount of energy intake (kcal) for a focal female during an focal sample, which provides a good indicator of foraging success, by combining behavioural data from the subjects and EIS for each food item, as employed by Iwamoto (1982), Nakagawa (1989) and Tsuji *et al.* (2008). First, we calculated the gross energy intake (GEI) for a focal female during a focal sample (kcal), using the following formula:

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

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

item i . To estimate the energy intake from food item i when observation conditions were poor, we used the average EIS for the given food item (Nakagawa 1989; Tsuji *et al.* 2008). Then we multiplied the apparent energy digestibility for a given wild food item (55%, Nakagawa 1989; Tsuji *et al.* 2008) by GEI to estimate the digestible energy intake. Finally, we calculated metabolizable energy intake (MEI, kcal) during the focal sample by subtracting the energy lost in urine (estimated as 4% of GEI, Nagy and Milton 1979) from the digestible energy intake.

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

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

We estimated daily energy requirements according to Nakagawa (1989): a non-nursing adult female (8 kg in body weight) requires 517.9 kcal during one whole day in autumn (600 min). This gave us the energy required per minute, and we calculated the energy requirement during the focal sample i (ER_i) (kcal) using the following formula:

$$ER_i = \left(517.9 / 600 \right) \times OT_i, \\ = 0.863 \times OT_i$$

where OT_i represents the duration of the focal sample i . When MEI_i was inferior to ER_i , we considered the focal female to be experiencing an energy shortage.

Population parameters

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

and the presence of each adult female. We assumed that females who had disappeared during our observations in the two seasons had died. For each dominance rank, we calculated a modified birth rate and adult mortality (Fujita *et al.* 2004):

$$\text{Modified birth rate} = \frac{[\# \text{ of females that delivered}]}{[\# \text{ of adult females with no infant} < 1 \text{ y}] \times 100}$$

$$\text{Adult mortality} = \frac{[\# \text{ of females disappeared}]}{[\# \text{ of adult females in last May}] \times 100}$$

Statistical analyses

We employed the Kruskal-Wallis tests and post hoc Steel-Dwass tests to test the temporal change in nut availability. We employed the Mann-Whitney U tests to test the difference in the average crown size of nut producing trees between 2004 and 2005. For these analyses we set significant levels at 5%.

We constructed generalised linear mixed models (GLMMs) to examine the effects of year, dominance rank and their interaction on 1) the frequency of agonistic interactions, 2) the mean length of nut-feeding bouts in the focal sample, 3) time spent on a given activity (represented by the number of instantaneous scan samples), 4) number of neighbouring macaques and 5) MEI. We treated a single focal sample as a unit of data. We conducted the statistical tests using the glmmML, lme4, MASS and aod

packages in the statistical software package R.2.9.1 (R Development Core Team, Vienna, Austria). We included the identity of each individual as a random effect in our models (Bolker *et al.* 2008). We analysed the main effects of year and rank and their interaction on nut feeding and eating other food items separately. In order to eliminate the effect of difference in focal sample lengths on the given dependent variables, we added an offset term to the model for each analysis, except for the length of nut-feeding bouts, which are independent of focal sample length (Table II). We selected the best models using the “stepAIC” function in the MASS package in the statistical software package R.2.9.1 (R Development Core Team, Vienna, Austria). We omitted seven focal samples where we achieved less than 2 hrs of observation from the analyses.

Tables I and II should appear here

Results

Food habits in autumn

We obtained 19817 instantaneous scan samples (13859 in 2004 and 5958 in 2005) over 146 focal samples (Appendix 1). The females ate 60 different food items (excluding unidentified insects and soil) in 2004 and fed mainly on fruits and seeds other than nuts (5987 scans, 43.2% of all feeding time). Of the available nuts, the females spent more time feeding on *T. nucifera* than any other nut variety (1109 scans, 8.0% of all feeding

time and 64.1% of total feeding time for all nuts; Appendix 1). Herbaceous plants (4060 scans, 29.3%) were also important food items in 2004. Conversely, in 2005, focal females consumed 47 different food items, but fed mainly on nuts (3592 scans, 60.3% of all feeding time). Of the nuts, the percentage of *F. crenata* consumed was the largest (2872 scans, 48.2% of all feeding time and 79.9% of total feeding time for nuts) (Appendix 1). The contributions of fruits and seeds other than nuts (1144 scans, 19.2%) and herbaceous plants (560 scans, 9.4%) was lower in 2005.

Description of nut-producing trees

In 2004, 93 of the 128 nut-producing trees used by macaques were of the species *T. nucifera*. The next most commonly used species was *Quercus serrata* ($N = 31$). The mean $\pm$ SD nut tree size was $40 \pm 28 \text{ m}^2$ ($34 \pm 20 \text{ m}^2$ for *T. nucifera*). In contrast, 220 of the 294 nut-producing trees used by the macaques in 2005 were *F. crenata*. In addition, macaques fed on the nuts of *T. nucifera* ($N = 28$), *Q. serrata* ($N = 17$), *Carpinus* spp. ($N = 13$) and *Z. serrata* ($N = 9$). The average crown size of nut-producing trees was significantly smaller in 2004 than in 2005 (Mann-Whitney *U*-test: all trees: $U = 10895$, $N_1 = 128$, $N_2 = 294$, $p < 0.001$).

316 *Nut availability*

317 The density of *T. nucifera* nuts beneath the crowns of the trees examined peaked at
 318 $20/\text{m}^2$ in September 2004, and decreased dramatically to almost zero in early December.
 319 The temporal difference in nut availability was statistically significant (Kruskal-Wallis
 320 test: $H = 12.5$, $\text{df} = 4$, $p = 0.013$), though multiple comparisons did not show any
 321 significant differences among sampling times (Steel-Dwass tests, $p > 0.05$). In 2005, the
 322 nut density under the crowns of *F. crenata*, *Z. serrata* and *Carpinus* spp. increased until
 323 November, with densities maintained at over $50/\text{m}^2$ even in early December. All species
 324 exhibited statistically significant temporal changes in 2005 (Kruskal-Wallis tests: *F.*
 325 *crenata*: $H = 17.8$, $\text{df} = 5$, $p = 0.003$; *T. nucifera*: $H = 14.1$, $\text{df} = 5$, $p = 0.015$; *Z. serrata*:
 326 $H = 11.7$, $\text{df} = 5$, $p = 0.039$; *Carpinus* spp.: $H = 13.3$, $\text{df} = 5$, $p = 0.021$), although
 327 multiple comparisons did not show any significant differences among sampling times
 328 (Steel-Dwass tests, $p > 0.05$) except for *F. crenata*, in which number of nuts on the
 329 ground in early November was significantly greater than that in early December
 330 (Steel-Dwass test, $p < 0.05$).

331

332 *Agonistic interactions (Prediction 1)*

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

SD) frequency of agonistic interactions initiated by the focal animals (times/sampling hour) was significantly greater in 2004 (0.68 ± 0.78 , $N = 17$) than in 2005 (0.22 ± 0.27 , $N = 14$; paired t -test, $t = 2.62$, $df = 13$, $p = 0.021$). Agonistic interactions occurred more frequently during feeding (both nut feeding and other feeding) in 2004, whereas they occurred more frequently during resting and grooming in 2005 (Table IIIa). Selected models showed that year affected the occurrence of agonistic interactions during all activities with the exception of resting (i.e., the frequencies of agonistic interactions were greater in 2004; Table IIIa). The frequency of agonistic interactions was greater during resting in 2005 than in 2004 (Table IIIa). Moreover, rank showed a negative association with the frequency of aggressive behaviour during feeding and moving (Table IIIa). Finally, we found an interaction between rank and year for feeding on other food items, showing that dominance status affected the frequency of agonistic interactions during feeding in 2004, but not in 2005 (Table IIIa).

Table III should appear here

Foraging-related behaviour (Prediction 2)

The frequencies of total feeding, feeding on other items and moving all decreased from 2004 to 2005, whereas resting and grooming both increased from 2004 to 2005 (Table IIIb). Furthermore, rank showed a negative association with total feeding ($H > M > L$).

Our models showed an interaction between rank and year for nut feeding, moving and resting such that rank was negatively correlated with nut feeding in 2004 ($H > M > L$), but this effect was not clear in 2005 ($H > M = L$; Table IIIb). Subordinates spent longer moving and resting than dominants ($H < M < L$) in 2004 during the nut shortage, whereas this relationship was not apparent in 2005 ($H = M = L$), when many nuts were available (Table IIIb).

Year had a positive effect on the number of neighbours within 3 m of a focal female during moving and resting (2005 > 2004; Table IIIc). Rank showed a negative association with the number of neighbours a focal female had while moving ($H > M > L$). Finally, an interaction between rank and year affected the number of neighbours a focal female had during feeding (on both nuts and other items) and grooming. During feeding, rank showed a negative association with the number of neighbours in 2004 ($H > M > L$); however, there was no clear relationship in 2005 ($H > M < L$; Table IIIc). Similarly, rank was negatively related to the number of neighbours while grooming in 2004 ($H > M > L$); however, this effect was not apparent in 2005 ($H = M < L$; Table IIIc).

Year, rank and their interaction in our models all affected the length of feeding bouts on nuts, on other food items and on all food items. Rank showed a negative

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

Foraging success (Prediction 3)

We found clear differences in the association between MEI and rank in 2004 (Fig. 2, Table IV). Most of the dominant individuals obtained enough energy from nuts to exceed their estimated ER (Fig. 2a); they generally obtained less energy from other food items than did subordinates (Fig. 2b). Furthermore, the MEI from all food items was greater for dominant than for subordinate individuals (Fig. 2c). These differences in MEI among females of different rank disappeared in 2005, when all females were able to satisfy most of their ER by consuming nuts. We found no difference in MEI between individuals of different rank in 2005 (Fig. 2, Table IV).

Table IV should appear here

Survival and reproduction (Prediction 4)

Three adult females (two middle-ranking and one low-ranking) died during the winter of 2004 (mortality: 0% [0/4] for H , 33% [2/6] for M and 14% [1/7] for L), whereas no adult females died during the winter of 2005 (Table I). However, the mortality of adult females, as a group, did not significantly vary between 2004 and 2005 ([3/17] vs [0/14];

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

Only one high-ranking female gave birth in the spring of 2005 (modified birth rate: 50% [1/2] for *H*, 0% [0/3] for *M* and 0% [0/4] for *L*). In contrast, 12 females gave birth in the spring of 2006 (modified birth rate: 100% [4/4] for *H*, 75% [3/4] for *M* and 83% [5/6] for *L*; Table I). One of the high-ranking females with a surviving infant born in 2005 (*Kr*) also gave birth in 2006. The difference in birth rate between 2004 and 2005 was close to significant ([1/9] vs [12/14]; Fisher's exact test, $p = 0.060$).

Figure 2 should appear here

Discussion

The frequency of agonistic interactions during each activity, with the exception of resting, was greater in 2004 than in 2005, and decreased with dominance during feeding (both on nuts and other food items) and moving in 2004 but not in 2005. Thus, our results support Prediction 1. We found an interaction between year and dominance rank during “other feeding” in 2004, when dominant females frequently initiated agonistic interactions, however we did not find this same interaction during 2005 season. This finding reflected differences in the main food items in the two years: food items other

than nuts consumed during the autumn of 2004 mainly consisted of fruits and seeds. In 2005, competition for such food items decreased because the macaques spent significantly more time feeding on nuts, the availability of which was markedly higher than in 2004, particularly those of *F. crenata*.

Engaging in aggressive interactions is disadvantageous for subordinate individuals, because in addition to losing the opportunity to access quality food resources such as nuts, they run the risk of physical injury (Sutherland 1996). In the present study, low-ranking individuals were unable to remain at feeding trees for long periods in 2004, possibly because of the increased risk of agonistic interactions. Among long-tailed macaques (*Macaca fascicularis*) subordinate individuals tend to increase their foraging effort when faced with food restrictions, e.g., they prolong total feeding time (van Schaik and van Noordwijk 1985) and increase their inter-individual distances (van Noordwijk and van Schaik 1987). In the current study, subordinate individuals engaged in longer periods of moving (perhaps thereby increasing the amount of time available for searching for food on the ground) and appeared to avoid getting within close proximity to neighbouring macaques by increasing their inter-individual distances and often feeding alone. Therefore, it seems that low-ranking macaques in our study modified their foraging tactics in response to inter-annual variation in the food

environment. These findings support Prediction 2.

In 2004, the MEI from nuts available to subordinate individuals was much lower than that available to dominant females, due to differences in the length of nut-feeding bouts exhibited by the different dominance ranks. Previous studies have shown that the amount of time spent at feeding patches is important to an animal's foraging success (Janson 1985; van Noordwijk and van Schaik 1987), and our results support these findings. In the present study, subordinate individuals were able to increase their MEI by resorting to other food items and, in this way, some were able to obtain sufficient total energy. Such foraging tactics only occurred over the short term because *T. nucifera* nuts were not available in 2004 beyond late November, after which subordinate individuals fed on non-nut foods. As a consequence, the MEI after late November could not satisfy the ER of these individuals. From December to February, which corresponds to the food-scarce season, Japanese macaques expend body fat accumulated during the previous season (Muroyama *et al.* 2006), and it is possible that subordinate individuals were unable to deposit adequate amounts of body fat after late November, 2004. A food shortage at this time could thus cause more serious long-term consequences for lower-ranking individuals. The fact that two mid-ranking adults and one low-ranking adult died during the food-scarce season of 2004, and only one female gave birth the

next birth season, supports this hypothesis. However, nut production in 2005 was much greater (Tsuji 2010) and the macaques were able to feed on nuts until the following April (Tsuji personal observation). The MEI did not differ among females of different dominance rank in 2005. Nutritional conditions during the food-scarce season of 2005 were therefore the same regardless of the dominance rank of focal females. The fact that none of the females died during the food-scarce season of 2005, and 12 females gave birth in the spring of 2006 supports this notion.

The physical conditions of temperature and rainfall often affect population parameters (Pavelka *et al.* 2003); however, these conditions did not play a role in the results of the present study because both daily rainfall and temperature during the mating season (September to November) and following the food-scarce season (December to February of the next year) were similar in 2004 and 2005, with the exception of the temperature during the food-scarce season. The fact that no females died during the food-scarce season of 2005, when the temperature was lower (that is, more severe for the macaques) than that in 2004, further suggests that physical conditions were not a factor in the present study. Our results therefore support Predictions 3 and 4, although the findings for Prediction 4 are inconclusive owing to the small sample size. The large annual variation in birth rate and mortality on the island

reported by Izawa (2009) may be partially explained by the yearly variation in nut availability and consequent variation in feeding behaviour of animals in different dominance rank. However, a longer-term study of population parameters needs to be undertaken to confirm this hypothesis.

In conclusion, a great deal of evidence indicates that yearly changes in food availability can affect the physical condition of animals, in terms of energy intake (Knott 1998, Curran and Leighton 2000), body weight (Feldhamer *et al.* 1989), oestrus patterns (Takahashi 2002) and birth rate/infant mortality (Eiler *et al.* 1989). The present study tested the hypothesis that inter-annual variation in the food environment indirectly influences primate nutritional conditions through modification of their foraging behaviour. We also demonstrated that such variation in food supply differentially affected animals according to dominance rank; subordinate females faced serious food shortages during a year of low nut availability. In addition, the behavioural variation was reflected in survival and reproduction, although these results should be treated with caution due to small sample size and short-term measures of reproduction. Because yearly changes in food availability, especially nut fruiting, are common in temperate regions (Suzuki *et al.* 2005), yearly changes in staple food production may thereby ultimately affect the population dynamics of animals.

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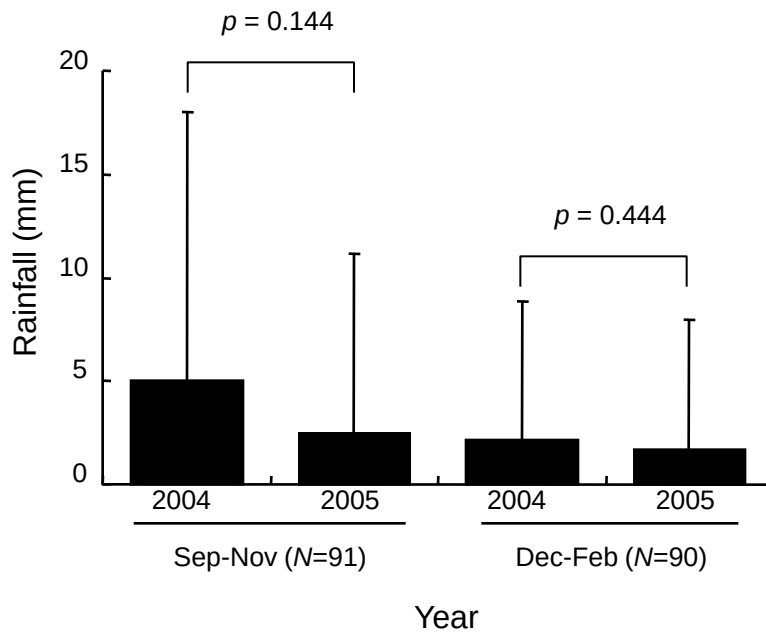
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610 Figure legends

611 Figure 1. Mean daily rainfall a) and temperature b) from September to November
 612 (mating season, left) and from December to February (food-scarce season, right) in
 613 2004 and 2005. Data source: Ishinomaki Weather Station.
 614 (<http://www.data.kishou.go.jp>). *p*-values were obtained from paired *t*-tests for
 615 yearly comparisons (see text).

616 Figure 2. Metabolizable energy intake (MEI, kcal) from a) nuts, b) other food items and
 617 c) all foods during the study periods, 2004 (left) and 2005 (right). ●: high-ranking
 618 (*H*); ●: middle-ranking (*M*); and ○: low-ranking (*L*). Energy shortage is
 619 highlighted in grey (for details, see Methods).

a) Rainfall



b) Temperature

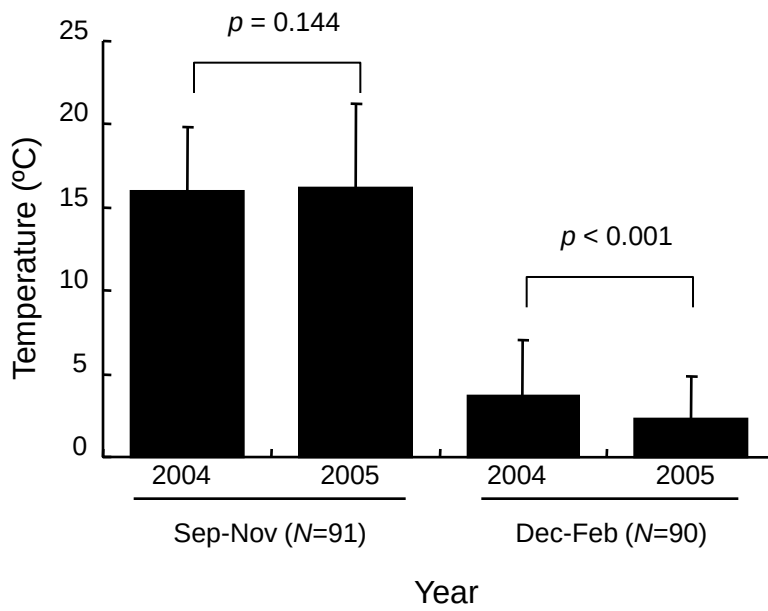


Fig. 2

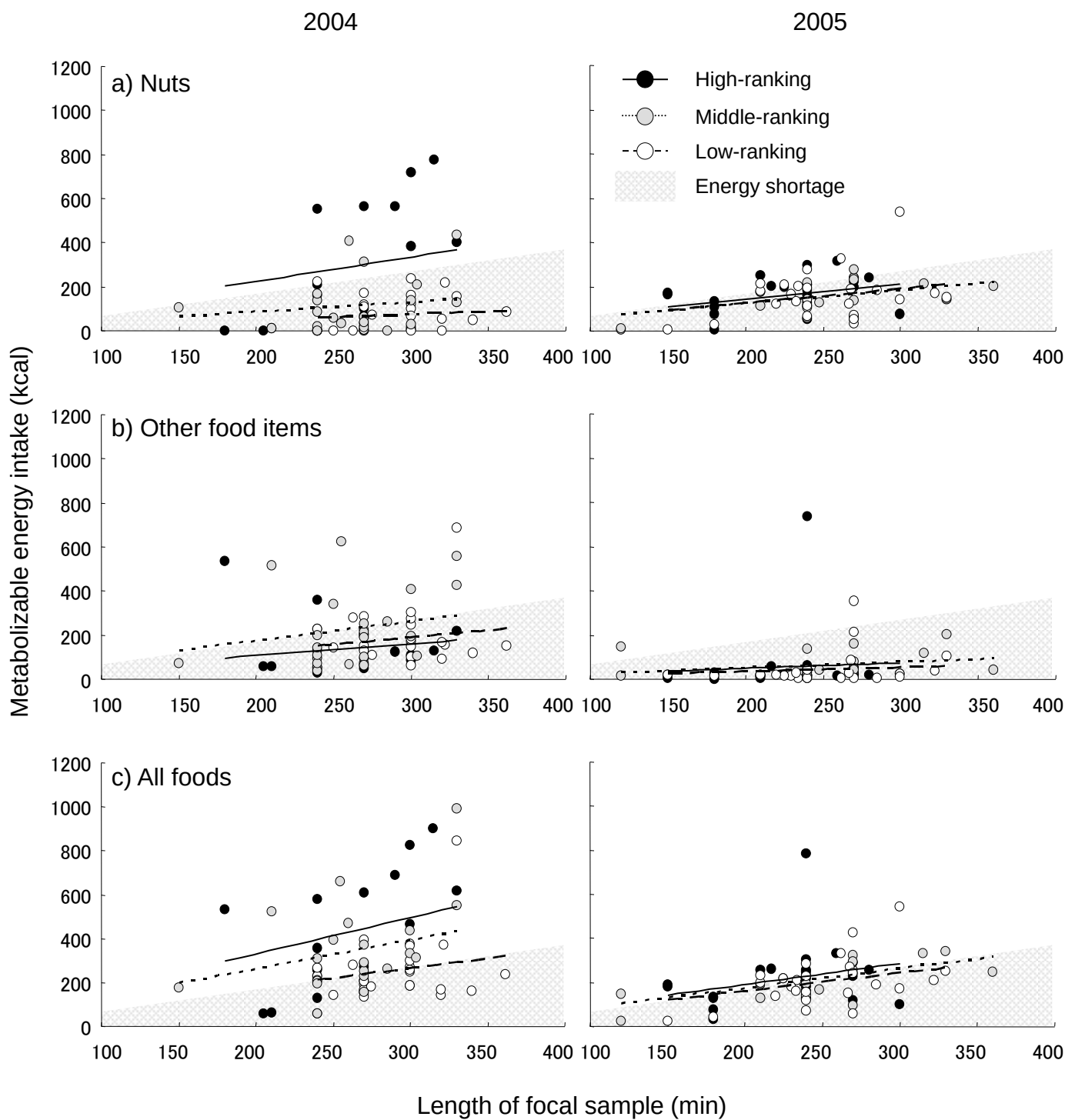


Table I. Details of the study subjects

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

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

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

^{a)} from Tsuji (2007), ^{b)} Age at April in 2004.

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

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

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

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

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

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

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

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

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

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

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

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

56	<i>Miscanthus sinensis</i>	Gramineae	seed	0.01	—	0.014 ± 0.006	73.71 ± 0.50	8.12 ± 1.63	2.45 ± 0.06	1.73 ± 0.16	4.33	A
57	<i>Paederia scandens</i>	Rubiaceae	leaf	—	0.03							
58	<i>Perilla frutescens</i>	Labiatae	seed	30.67	1.56	0.004 ± 0.003	74.60 ± 1.31	17.18 ± 1.63	13.75 ± 0.06	1.66 ± 0.06	5.36	C
59	<i>Smilax china</i>	Liliaceae	fruit	0.38	0.15	0.060 ± 0.048	66.94 ± 0.87	10.59 ± 4.51	3.45 ± 0.26	0.29 ± 0.41	4.47	A
60	<i>Trifolium reoens</i>	Leguminosae	leaf	0.10	—	0.016 ± 0.017	59.84 ± 0.52	28.59 ± 0.30	0.12 ± 0.17	2.18 ± 0.03	4.50	A
61	<i>Tubocapsicum anomalum</i>	Solanaceae	fruit	0.02	0.02	0.056 ± 0.028	39.84 ± 2.51	13.40 ± 0.35	10.15 ± 0.90	0.16 ± 0.10	4.88	C
62	unidentified herbs		leaf	25.80	9.32	0.019 ± 0.022	41.23 ± 4.84	9.50 ± 1.06	0.07 ± 0.33	37.47 ± 3.70	2.74	C
Fungi												
63	Agaricales		-	0.69	1.54	1.318 ± 1.619	65.46 ± 3.56	7.82 ± 0.30	1.31 ± 0.19	1.24 ± 0.18	4.45	C
64	Polyporales		-	3.20	0.50	0.359 ± 0.143	47.78 ± 0.14	19.30 ± 0.02	5.60 ± 0.33	6.80 ± 0.10	4.28	C
Animal materials												
65	Acrididae spp.		adult	1.09	1.64	0.138 ± 0.116	76.74 ± 0.86	65.19 ± 0.82	1.81 ± 0.23	1.43 ± 0.34	5.16	C
66	Araneae		-	0.06	—	0.062 ± 0.028	40.50 ± 3.23	71.25 ± 0.09	7.81 ± 0.50	1.83 ± 1.94	5.55	C
67	<i>Dorcus rubrofemoratus</i>		adult	0.01	—	0.062 ± 0.028	40.50 ± 3.23	71.25 ± 0.09	7.81 ± 0.50	1.83 ± 1.94	5.55	C
68	gall on <i>Fagus crenata</i> leaves			2.69	—	0.012 ± 0.005	85.96 ± 0.03	3.08 ± 0.15	2.04 ± 0.09	2.69 ± 0.01	4.19	A
69	Gastropoda (periwinkle)			0.06	—	0.459 ± 0.592	32.00 ± 0.85	53.12 ± 3.98	7.15 ± 0.13	8.29 ± 0.20	6.31	A
70	Gastropoda (slug)		-	0.03	—	0.742 ± 0.812	27.93 ± 0.74	37.14 ± 5.70	6.31 ± 0.07	4.57 ± 0.00	4.85	C
71	Gastropoda (snail)		-	0.01	—	0.742 ± 0.812	27.93 ± 0.74	37.14 ± 5.70	6.31 ± 0.07	4.57 ± 0.00	4.85	C
72	Gryllidae spp.		adult	0.37	0.36	0.068 ± 0.055	74.22 ± 0.15	69.45 ± 1.92	2.07 ± 0.04	2.19 ± 0.17	5.21	C
73	Lepidoptera sp.		adult	0.01	—	0.062 ± 0.028	40.50 ± 3.23	71.25 ± 0.09	7.81 ± 0.50	1.83 ± 1.94	5.55	C
74	Mantodea spp.		egg	0.08	0.12	0.309 ± 0.114	80.84 ± 1.11	85.08 ± 0.87	6.29 ± 0.63	1.89 ± 1.13	5.68	C
75	Pyrilidae spp. in <i>Cirsium amplexifolium</i> stem		larva	0.53	0.40	0.034 ± 0.010	19.43 ± 0.27	24.01 ± 1.75	50.66 ± 0.00	0.43 ± 0.29	7.15	C
76	Pyrilidae spp. in <i>Senecio cannabifolius</i> stem		larva	0.07	0.08	0.034 ± 0.010	19.43 ± 0.27	24.01 ± 1.75	50.66 ± 0.00	0.43 ± 0.29	7.15	C
77	<i>Rana tagoi</i>		adult	0.00	—	1.900 ± 0.969	32.78 ± 0.98	58.47 ± 0.76	7.34 ± 5.45	9.87 ± 0.16	5.00	C
78	Tettigoniidae spp.		adult	0.06	0.15	0.138 ± 0.116	76.74 ± 0.86	65.19 ± 0.82	1.81 ± 0.23	1.43 ± 0.34	5.16	C
79	unidentified insects		-	0.40	0.40	0.062 ± 0.028	40.50 ± 3.23	71.25 ± 0.09	7.81 ± 0.50	1.83 ± 1.94	5.55	C
80	Soil			0.37	1.51							

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

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

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