OXFORD

Article

Low-ranking female Japanese macaques make efforts for social grooming

Yosuke KURIHARA*

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

*Address correspondence to Yosuke Kurihara. E-mail: kurihara.yosuke.35s@st.kyoto-u.ac.jp.

Abstract

Grooming is essential to build social relationships in primates. Its importance is universal among animals from different ranks; however, rank-related differences in feeding patterns can lead to conflicts between feeding and grooming in low-ranking animals. Unifying the effects of dominance rank on feeding and grooming behaviors contributes to revealing the importance of grooming. Here, I tested whether the grooming behavior of low-ranking females were similar to that of high-ranking females despite differences in their feeding patterns. I followed 9 Japanese macaques *Macaca fuscata fuscata* adult females from the Arashiyama group, and analyzed the feeding patterns and grooming behaviors of low- and high-ranking females. Low-ranking females fed on natural foods away from the provisioning site, whereas high-ranking females obtained more provisioned food at the site. Due to these differences in feeding patterns, low-ranking females spent less time grooming than high-ranking females. However, both low- and high-ranking females performed grooming around the provisioning site, which was linked to the number of neighboring individuals for low-ranking females and feeding on provisioned foods at the site for high-ranking females. The similarity in grooming area led to a range and diversity of grooming partners that did not differ with rank. Thus, low-ranking females can obtain small amounts of provisioned foods and perform grooming with as many partners around the provisioning site as high-ranking females. These results highlight the efforts made by low-ranking females to perform grooming and suggest the importance of grooming behavior in group-living primates.

Key words: dominance rank, *Macaca fuscata fuscata*, provisioning, space-use.

Grooming is an important activity for group-living primates. It has hygienic (Tanaka and Takefushi 1993; Zamma 2002, 2011) and physiological functions such as stress reduction (Schino et al. 1988; Keverne et al. 1989; Aureli et al. 1999). In addition, primates construct and maintain social relationships with group members through grooming exchanges (Silk et al. 2010a; Zhang et al. 2010). Such social bonds contribute to the fitness of an individual (e.g. offspring survival: Silk et al. 2009; survivorship: Silk et al. 2010b) and maintenance of the social cohesion of a group (preventing group fission) (Dunbar 1992; Henzi et al. 1997; Lehmann et al. 2007).

Despite the importance of grooming, conflicts could arise between feeding and grooming behaviors in group-living animals. To this end, trade-offs between feeding and grooming times have been previously reported (Majolo et al. 2008). Larger groups are known

to require longer feeding time than smaller groups, and consequently tend to find time for grooming at the expense of resting time (Iwamoto and Dunbar 1983); however, when resting time can no longer be decreased, grooming time is decreased to accommodate the feeding requirements (Dunbar et al. 2009). In addition, conflicts could arise between feeding and grooming areas. Spatial proximity among animals is essential for grooming behavior (Sugiura et al. 2011; Shaffer 2013); in fact, proximity networks or party-level associations within a fission–fusion society are known to be associated with grooming networks (Clark 2011; Crofoot et al. 2011). At the same time, animals must keep their distance from other individuals to avoid feeding competition (Sugiura et al. 2011; Shaffer 2013). In particular, when food resources are contestable, low-ranking animals tend to be located at the periphery of the group away from

high-ranking animals (Saito 1996; Hemelrijk 2000). Differences in the patterns of space-use could hamper the opportunities of low-ranking animals to aggregate with other group members for grooming, thereby limiting the diversity of grooming partners (Clark 2011). Nevertheless, maintaining grooming relationships with a range of individuals is also important for low-ranking animals.

Previous studies on provisioned groups of Japanese macaques have gathered data on grooming behavior, for example, influence of age, kinship, dominance rank, reproductive status, and group size on partner selection or reciprocity (Koyama 1991; Muroyama 1991; Nakamichi 2003; Nakamichi and Shizawa 2003; Katsu et al. 2013; Ueno et al. 2014, Zhang and Watanabe 2014, etc). At the same time, they have demonstrated that intragroup contest competition over food is more intense in provisioned groups than in wild groups (Hill 1999). Agonistic interactions are considerably more frequent in the presence of clumped, high-quality food than in wild groups (Hill 1999). Consequently, rank-related differences in feeding success at a provisioning site often develop within a group (Soumah and Yokota 1991; Kurita 2007). Thus, large variations in feeding patterns could cause variations in grooming behavior within a group. However, few studies have simultaneously examined the feeding patterns and grooming behavior of individuals of different ranks. Unifying the effects of dominance rank on feeding and grooming behaviors will contribute to understanding the importance of grooming behavior in group-living primates.

In this study, I tested whether the grooming behavior of low-ranking females were similar to that of high-ranking females in spite of differences in the feeding patterns. To this end, the effects of dominance rank on the feeding patterns and grooming behavior of adult females were investigated in a provisioned group of Japanese macaques. First, the feeding patterns of low- and high-ranking females were compared. Low-ranking females were predicted to access lower amounts of provisioned foods than high-ranking females; consequently, low-ranking females were expected to spend more time feeding and moving, consume more natural foods (other than provisioned foods), and make use of larger and more peripheral areas for feeding than high-ranking females (Soumah and Yokota 1991; Kurita 2007). At the same time, owing to the feeding advantages attained through successful competition, high-ranking females were expected to remain around the provisioning site (Soumah and Yokota 1991; Kurita 2007).

The grooming behavior of low- and high-ranking females was also compared. Overall, low-ranking females were predicted to spend less time grooming than high-ranking females due to the additional times used for feeding and moving (Agetsuma and Nakagawa 1998). Due to spatial differences during feeding, low-ranking females were predicted to make use of larger and more peripheral areas for resting than high-ranking females; however, low-ranking females would still be expected to perform grooming around the provisioning site similar to high-ranking females. This prediction was derived from previous studies that demonstrated that the spatial cohesiveness of a group during social interactions, including grooming, was less than that during other activities (Shaffer 2013).

Despite similarities in grooming areas, different factors were predicted to determine the space-use during grooming by low- and high-ranking females. Specifically, I examined two predictions: 1) the number of neighboring individuals was predicted to constrain low-ranking females to perform grooming around the provisioning site, since spatial proximity among individuals is a prerequisite for grooming behavior (Clark 2011; Crofoot et al. 2011). Low-ranking females would experience difficulties in grooming in peripheral areas used for feeding and resting as the number of neighboring

individuals in such areas would be considerably lower than around the provisioning site. In contrast, the number of neighboring individuals would not constrain space-use during grooming by high-ranking females, because they would remain at the provisioning site, surrounded by many individuals, regardless of activity. 2) Feeding on provisioned food at the provisioning site was predicted to constrain high-ranking females to perform grooming around the site, given that the provisioning schedule could influence the activity rhythms of individuals in a provisioned group (Iwamoto 1982). High-ranking females would perform grooming around the provisioning site before or after feeding on provisioned foods at the site, owing to their higher dependence on such foods. In contrast, low-ranking females would not be constrained by the feeding at the provisioning site because they would be less dependent on provisioned foods. Due to similarities in the grooming area used, the range and diversity of grooming partners were not expected to differ between low- and high-ranking females, despite rank-related differences in grooming time (Clark 2011).

Methods

Ethics statement

All field data are based on observations and the author did not interact with the macaques at any time. Data collection was conducted with permissions from S. Asaba, the owner of the Arashiyama Monkey Park Iwatayama. This study was conducted with all necessary permissions, and complied with the ethical guidelines for field research on nonhuman primates of the Kyoto University Primate Research Institute and the legal requirements of Japan.

Study site, period, and subjects

This study was conducted between April 2011 and June 2012 (except during April 2012) in the Arashiyama Monkey Park Iwatayama, Kyoto, Japan (35°01′N, 135°67′E). This population has been provisioned since 1954 (Huffman 1991), and individual demographic data are available since the park opened. Detailed information on the study site is available elsewhere (Huffman 1991).

During the study period, the macaques received foods 3 times a day (10:30, 12:30, and 14:30; regular provisioning). They were mainly provisioned with wheat and soybeans, chestnuts, sweet potatoes, and apples. Some macaques received supplementary foods when they were unable to obtain food during the regular provisioning. In addition, visitors were allowed to feed the macaques at the regular provisioning site. Hereafter, "provisioning" refers only to regular provisioning, unless otherwise noted.

The subject group was the Arashiyama group. During the study period, this group comprised 130–136 individuals, including 8 adult males (>7 years old), 91–92 adult females (>7 years old), 7–16 sub-adults (4–6 years old), 9–13 juveniles (2–3 years old), and 8–15 infants (≤1 year old). All macaques were free to move away from the provisioning site, but many remained in the proximity of the provisioning site, whose center corresponded with the center of the group during daytime (Kurihara, unpublished data).

I chose 4 low-ranking females and 5 high-ranking females (8–15 years old) as study subjects for behavioral observations. All the individuals in the group were categorized as belonging to low- or high-ranking maternal lineages; thus, the 9 female subjects selected belonged to 3 different low-ranking maternal lineages (*Sy*, *Sh*, and *Ai*) and 3 high-ranking lineages (*Mi*, *Ko*, and *Co*). Dominance rank was determined based on the outcome of dyadic aggressive interaction (Asaba, unpublished

data). Total observation time was 216.7 h (mean ± *SD* = 24.1 ± 11.8 h/individual). Although low-ranking female subjects were related on average to 1.5 individuals (range: 1–3, defined as individuals with $r \geq 0.125$; Koyama 1991) in the group, high-ranking subjects were related to 5.2 individuals (range: 3–6).

Behavioral data collection

I followed the 4 low-ranking females from April 2011 to March 2012 and the 5 high-ranking females from May to July 2012 via 1-day focal animal sampling. When the focal animal disappeared from my visual range, I chose the one for which the accumulated observation time was the shortest at that point, and resumed observations. To increase sample size and minimize sampling bias toward a particular season, I included data of the 5 high-ranking females collected between September 2011 and March 2012 via 1-h focal animal sampling. During the data collection period, I changed the focal animal every hour, distributing the 1-h duration sampling evenly throughout the day. Specifically, I divided the time into 4 time periods: 9:00–11:00 (including the first provisioning event), 11:00–13:00 (including the second), 13:00–15:00 (including the third), and 15:00–17:00 (without the provisioning event), and minimized the sampling bias. This sampling method did not influence any of the feeding and grooming behavioral parameters examined herein.

I recorded activities (feeding, moving, resting, grooming, and other), feeding items consumed, and the identities of grooming partners of the focal animal via 1-min instantaneous recording. Feeding items were categorized into provisioned foods (wheat, soybeans, apples, peanuts, or sweet potatoes) and natural foods (other items not provisioned by park staff). Whenever the focal animal was observed feeding on provisioned foods, I recorded the number of food units ingested (defined per food item, e.g. one grain or one piece of fruit). The number of individuals within a 3-m radius of the focal animal (neighboring individuals, hereafter) was recorded via 5-min instantaneous recording. It took about 10 s for 1 scan. I recorded the locations of the focal animal every minute using a hand-held GPS device (GARMIN60CS and GARMIN60CSx, GARMIN).

Data analysis

Opportunistic provisioning by park staff and visitors and their effect on macaque behavior were not included in the analyses because 1) opportunistic provisioning was available to high-ranking subjects and it was difficult to distinguish the effects of opportunistic provisioning by visitors from those of dominance rank, and 2) low-ranking females did not alter their feeding patterns based on opportunistic provisioning events by park staff on a daily basis. In addition, although the study period included the mating season (October–March) (Takahata 1980), I discarded the data collected during days when sexual consortship (Takahata 1982) involving the focal animal was observed. Therefore, the possible effects of sexual activity on feeding or grooming behaviors were not included in the present study.

Energy intake from provisioned foods, activity budget, and dietary composition

Energy intake from provisioned food was estimated per provisioning event. For each provisioned item, I collected wet weight data per food unit and estimated its energy content based on the Standard Tables of Food Composition in Japan, Fifth Revised and Enlarged Edition (Ministry of Education Culture Sports, Science and Technology 2005) (Table 1). Total energy intake per provisioning

Table 1. Wet weight and energy of provisioned items

Provisioned item	Unit weight (g)	Energy (kcal/g)
Wheat	0.03	3.37
Soybean	0.39	4.17
Chestnut	6.28	1.64
Apple	7.36	0.54
Dried sweet potato	4.68	3.03

Means are shown. The value of unit weight was used for the estimation of energy intake. Energy was calculated based on Standard Tables of Food Composition in Japan Fifth Revised and Enlarged Edition (Resource Council, Council for Science and Technology, MEXT, 2005).

event was estimated as the sum of the product of the energy content (kcal) of a food unit and the number of food units ingested. Subsequently, I compared the total energy intake from provisioned foods between low- and high-ranking females ($n_{\text{low-ranking females}} = 4$, $n_{\text{high-ranking females}} = 5$) using a Wilcoxon rank sum test. Activity budget was calculated as the proportion of time spent for each activity in the observation time per day. Dietary composition was calculated as the proportion of time spent feeding on natural foods in the total feeding time per day. Activity budget and dietary composition for low- and high-ranking females were compared using a chi-square test. Standardized residuals analysis was conducted to estimate the valid *P* values for the chi-square test in activity budget (Haberman 1973).

Space-use

A data point was defined as the location data collected in a minute. All of the data points were plotted on a 25×25 m grid map of the area (Figure 1). The cell and the provisioning site was the same in size, and the total grid area was designed to place the cell, G10, over the provisioning site. The center of the group is located at the provisioning site during daytime (see "Study site, period, and subjects" section), and consequently, the distance between each individual and the provisioning site can be regarded as the distance between each individual and the center of the group. I geometrically analyzed the areas used per individual using a dispersion index (DI) calculated as follows: First, I calculated the distance (d_i) between the G10 center (provisioning site) and the center of cell *i* used by the focal animal. Subsequently, d_i was multiplied by the number of minutes spent in cell *i* by the focal animal (m_i). Finally, the sum of $d_i \times m_i$ was divided by the sum of m_i.

$$\text{DI} = \frac{\sum_i (d_i \times m_i)}{\sum_i m_i}.$$

A Tukey–Kramer test was used to assess the effect of rank (low- and high-ranking) and activity (feeding, resting, and grooming) on DI. I confirmed that the data were normally distributed (Kolmogorov–Smirnov test: $D = 0.08$, $P = 0.10$).

Factors influencing space-use during grooming: effect of the number of neighboring individuals

To examine whether the number of neighboring individuals constrained macaques to perform grooming around the provisioning site, I used generalized least square regression (GLS) for each rank separately, using data per cell per focal animal as the analytical unit.
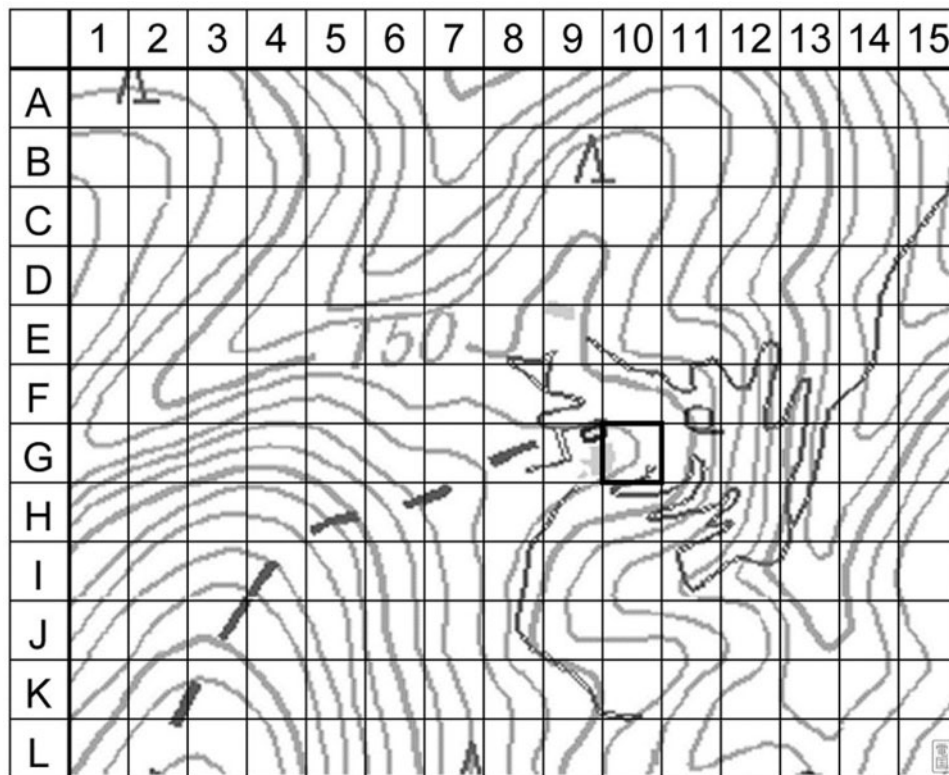
Figure 1. Map of areas around Arashiyama Monkey Park Iwatayama, Kyoto, Japan (GeoSpatial Information Authority of Japan). The size of each cell is 25×25 m and the contour line is every 10 m. Double lines indicate trails on which visitors can walk. Regular provisioning was conducted in G10 (bold lines).

For these models, percentage of grooming time in each cell among the total grooming time (Figure 2E and F) was set as the dependent variable, and mean number of neighboring individuals excluding the grooming partners (individuals/scan; number of scans per focal female: $n = 288.7 \pm 141.2$) in each cell was set as independent variable (Figure 4). I examined the significance of the independent variable in the full model. GLS enables to control for spatial autocorrelation among cells (Beale et al. 2010), but it does not allow including the identity of the focal animal as random effect in the model. However, the same results were obtained using generalized linear mixed models (GLMMs) including the identity of the focal animal as random effect. Therefore, only the results of GLS are shown here.

Factors influencing space-use during grooming: effects of feeding at the provisioning site

To examine whether feeding on provisioned foods at the provisioning site constrained macaques to perform grooming around the site, I investigated whether the timing of grooming around the site was dependent on the timing of feeding at the site. Grooming bout was defined as the time used by the focal animal for social grooming. Another bout was assumed to start when the focal animal exchanged roles or changed grooming partners (Fujimoto and Takeshita 2007). These data were used to calculate the time interval elapsed between the initiation of a grooming bout and the initiation of the closest feeding event on provisioned foods at the provisioning site. Bouts whose start or end time points were not observed were not included in the analyses. The distribution of grooming bouts was compared with the distribution of the observation time (defined as the expected distribution of grooming bouts) using a two-sample Kolmogorov–Smirnov test.

Grooming partners

To examine rank-related differences in the diversity of grooming partners, I calculated the grooming diversity ratio (GDR) for each individual (Di Bitetti 2000; Nakamichi and Shizawa 2003), as follows:

$$\text{GDR} = \frac{H}{H_{\max}} = -\frac{\sum_{i}^{n} p_i \log p_i}{\log (n-1)},$$

where p_i is the proportion of grooming time with individual i in the total grooming time, and $n - 1$ represents the number of potential grooming partners (n: group size). GDR reaches 1 when the grooming time for the focal animal is evenly distributed across all potential partners, and reaches 0 when it only engages in grooming with 1 potential partner. I compared GDR values for low- and high-ranking females using a t-test. I confirmed that the data were normally distributed (Kolmogorov–Smirnov test: $D = 0.18$, $P = 0.90$). All statistical analyses were performed using R 3.0.1 (The R Foundation for Statistical Computing). I used the *nlme* package for GLS and the *lme4* package for GLMMs. The level of significance was set at $P < 0.05$.

Results

Rank-related differences in feeding patterns

Low-ranking females were less dependent on provisioned foods than high-ranking females, and increased foraging effort to obtain natural foods. The amount of energy obtained from provisioned food was lower for low-ranking females than for high-ranking females (low-ranking females: 27.4 ± 29.6 kcal/provisioning; high-ranking females: 105.7 ± 22.5 kcal/provisioning; $n_{\text{low-ranking females}} = 4$, $n_{\text{high-ranking}}$
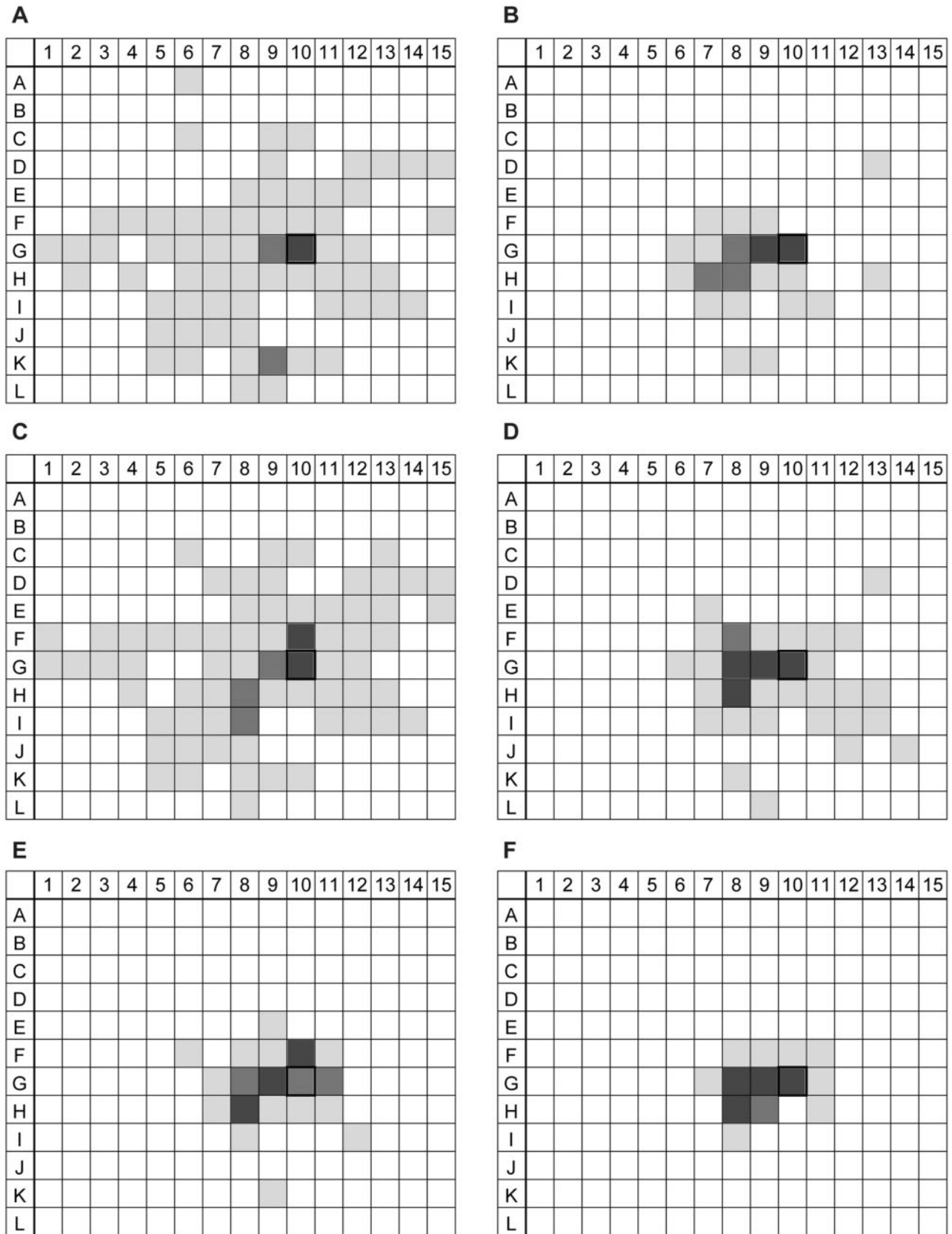
Figure 2. Space-use during each activity. (A) Feeding of low-ranking females. (B) Feeding of high-ranking females. (C) Resting of low-ranking females. (D) Resting of high-ranking females. (E) Grooming of low-ranking females. (F) Grooming of high-ranking females. Time spent for a given activity in each cell relative to the total time spent for the activity is shown as percentage. *Dark gray*: $\geq$10%; *Gray*: 5%–10%; *Light gray*: 0–5%; *White*: 0% (not used).

$_{\text{females}} = 5$, $W = 0$, $P < 0.05$). Consequently, they spent more time feeding, in particular, feeding on natural foods, and moving than high-ranking females (feeding time: low-ranking females: $21.2\% \pm 10.4\%$, high-ranking females: $18.7\% \pm 11.3\%$, $\chi^2 = 280.9$, $df = 4$, standardized residuals = 7.4, $P < 0.001$; moving time: low-ranking females:

$12.2\% \pm 3.5\%$, high-ranking females: $6.7\% \pm 2.6\%$, $\chi^2 = 280.9$, $df = 4$, standardized residuals = 9.9, $P < 0.001$; proportion of natural foods: low-ranking females: $73.4\% \pm 17.4\%$, high-ranking females: $26.6\% \pm 5.6\%$, $\chi^2 = 356.8$, $df = 1$, $P < 0.001$). In addition, low-ranking females used larger and more peripheral areas for feeding than they did for grooming and high-ranking females did for all activity types (Table 2, Figures 2 and 3; low-ranking females: feeding: $DI = 69.1 \pm 18.6$, number of cells = 65; grooming: $DI = 36.3 \pm 9.4$, number of cells = 19). They also used more peripheral areas for feeding than for resting, although the areas used for resting were slightly larger than those used for feeding (low-ranking females: resting: $DI = 43.1 \pm 16.1$, number of cells = 67). High-ranking performed all their activities within the same area (feeding: $DI = 26.7 \pm 8.6$, number of cells = 21; resting: $DI = 36.2 \pm 9.9$, number of cells = 31; grooming: $DI = 33.0 \pm 5.6$, number of cells = 13).
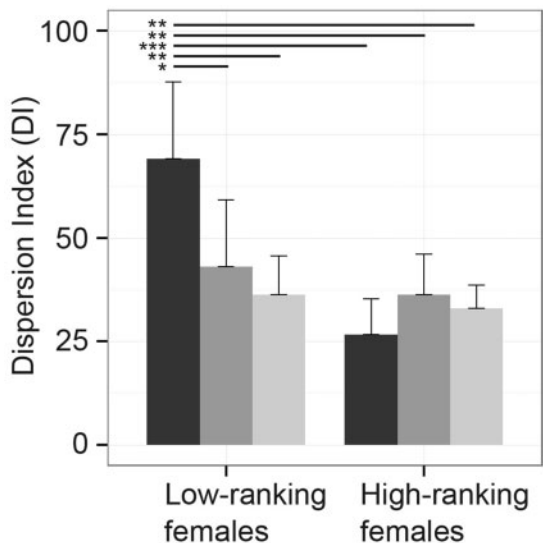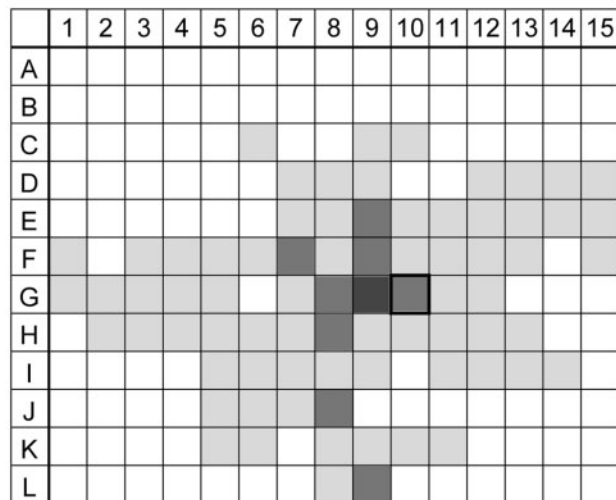
Rank-related differences in grooming behavior

Overall, low-ranking females spent less time grooming than high-ranking females (low-ranking females: $16.5\% \pm 9.9\%$, high-ranking females: $25.2\% \pm 15.1\%$, $\chi^2 = 280.9$, $df = 4$, standardized residuals = 5.5, $P < 0.001$); however, both low- and high-ranking females engaged in grooming around the provisioning site (G10), although low-ranking females tended to use larger and more peripheral areas for resting than they did for grooming (Table 2, Figures 2 and 3). Factors determining space-use during grooming differed with rank. For low-ranking females, space-use during grooming was influenced by the number of neighboring individuals, but not by the

Figure 3. DI of each activity. *Dark gray*: feeding; *Gray*: resting; *White*: grooming. Means ± SDs are shown. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
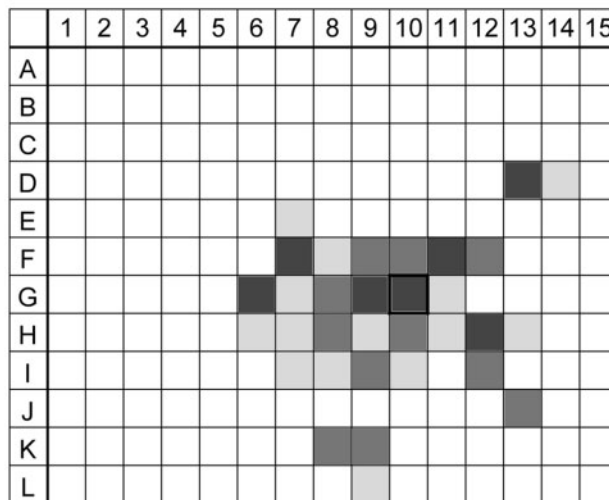
Figure 4. Grid map for the number of neighboring individuals. Mean number of neighboring individuals in each cell is shown. (A) Low-ranking females. (B) High-ranking females. *Dark gray*: ≥2 individuals; *Gray*: 1–2 individuals; *Light gray*: 0–1 individuals; *White*: 0 individuals.

Table 2. Summary of Tukey–Kramer test for the effects of rank and activity on DI

	Low-ranking × Resting	Low-ranking × Grooming	High-ranking × Feeding	High-ranking × Resting	High-ranking × Grooming
Low-ranking × Feeding	$t = 3.1$, $P < 0.05$	$t = 3.9$, $P < 0.01$	$t = 5.4$, $P < 0.001$	$t = 4.2$, $P < 0.01$	$t = 4.6$, $P < 0.01$
Low-ranking × Resting		$t = 0.8$, $P = 0.96$	$t = 2.7$, $P = 0.08$	$t = 2.1$, $P = 0.33$	$t = 1.3$, $P = 0.79$
Low-ranking × Grooming			$t = 1.2$, $P = 0.82$	$t = 0.1$, $P = 0.99$	$t = 0.4$, $P = 0.99$
High-ranking × Feeding				$t = 1.3$, $P = 0.79$	$t = 0.9$, $P = 0.95$
High-ranking × Resting					$t = 0.4$, $P = 0.99$

Table 3. Models for the effect of number of neighboring individuals on the space-use during grooming of (a) low-ranking females and (b) high-ranking females

A. Low-ranking females

	Coefficient	SE	t	P
(Intercept)	2.57	6.20	0.41	0.68
Number of neighboring individuals	9.56	2.50	3.82	<0.001

B. High-ranking females

	Coefficient	SE	t	P
(Intercept)	9.66	13.56	0.71	0.48
Number of neighboring individuals	1.38	2.66	0.52	0.61

feeding at the provisioning site (Table 3, Figures 4A and 5). They spent more time grooming in areas surrounded by a larger number of individuals (Table 3, Figure 4A), and they engaged in grooming randomly, independent of feeding at the provisioning site ($\chi^2 = 41.44$, $df = 2$, $P < 0.001$; Figure 5). In contrast, for high-ranking females, space-use during grooming was not influenced by the number of neighboring individuals but by the feeding at the provisioning site (Table 3, Figures 4B and 5). The timing of grooming by high-ranking females did depend on the timing of feeding at the provisioning site ($\chi^2 = 2.71$, $df = 2$, $P = 0.52$; Figure 5). They tended to perform grooming more frequently before feeding.

The range and diversity of grooming partners did not differ between low- and high-ranking females. The mean number of grooming partners and the mean number of unrelated grooming partners did not differ either (for all partners: low-ranking females: 18.3 ± 7.7, high-ranking females: 13.2 ± 8.1, $n_{low-ranking\ females} = 4$, $n_{high-ranking\ females} = 5$, $W = 15$, $P = 0.29$; for unrelated partners: low-ranking females: 17.3 ± 7.7, high-ranking females: 11.4 ± 8.0, $n_{low-ranking\ females} = 4$, $n_{high-ranking\ females} = 5$, $W = 15$, $P = 0.29$). GDR values did not differ significantly between low- and high-ranking females (low-ranking females: 0.44 ± 0.12; high-ranking females: 0.34 ± 0.18; $df = 7$, $t = 1.0$, $P = 0.35$).

Discussion

Feeding patterns
Low-ranking females increased foraging effort, due to the disadvantage in feeding competition at the provisioning site. In fact, low-ranking females obtained less energy from provisioned foods than high-ranking females. They also were observed to compensate this for energy deficit by spending more time feeding and moving, consuming more natural foods, and using larger and more peripheral areas for feeding than high-ranking females. At the same time, high-ranking females had access to larger amounts of provisioned foods, and therefore did not need to forage outside the provisioning site. These feeding patterns are similar to those previously described from other provisioned populations (Iwamoto 1988; Soumah and Yokota 1991; Mori 1995; Kurita 2007).

Grooming behavior: grooming time
Low-ranking females spent less time grooming than high-ranking females, possibly due to differences in their feeding patterns. According to Agetsuma and Nakagawa (1998), there might be a trade-off among feeding, moving, and grooming time. However, even low-ranking females in the present study spent more time resting than did macaques in the wild (Table 4). Consequently, it is likely that additional factors caused the difference in grooming time between low- and high-ranking females. One possible factor is that

rank-related differences in the number of unrelated grooming partners might be associated with differences in grooming time. Adult females in the Arashiyama group exchanged roles less frequently and performed shorter sequences of grooming bouts with unrelated females than they did with related females (Fujimoto and Takeshita 2007). This was also in the case of low-ranking females in the present study: they were related to a smaller number of individuals (see "Methods" section) and tended to have more unrelated grooming partners than high-ranking females. Consequently, low-ranking females might have found it more difficult to engage in grooming for a longer duration, possibly leading to shorter grooming time.

Grooming behavior: space-use during grooming
Despite differences in feeding patterns, including differences in space-use during feeding, both low- and high-ranking females performed grooming around the provisioning site. The factors determining space-use during grooming differed with rank; low-ranking females spent more time grooming around the provisioning site surrounded by a larger number of individuals, whereas high-ranking females performed grooming around the provisioning site along with feeding at the provisioning site.

Low-ranking females frequently moved away from the provisioning site for feeding; however, grooming in those peripheral areas would be inefficient or even impossible due to the small number of neighboring individuals. In fact, they were only in the proximity with <1 individual per cell in the periphery (Figure 4A). In addition, they used larger areas for resting than for grooming (Figure 2), which suggested that grooming did not necessarily occur in resting areas and supported that the number of neighboring individuals could be the factor limiting grooming areas. In contrast, high-ranking females were not constrained in performing grooming by the number of neighboring individuals, because they performed all activities around the provisioning site, surrounded by many individuals. Thus, the concentration of the group members around the provisioning site also constrained the grooming areas for low-ranking females to the site.

High-ranking females tended to engage in grooming around the provisioning site before feeding at the site. To this end, Iwamoto (1982) suggested that provisioning schedule could influence individual behavior in provisioned groups. This is supported by my results, which provide quantitative evidence of the effect of food provisioning on the timing of grooming. The concentration of grooming bouts of high-ranking females before feeding could reflect a need to cope with social stress or anticipated anxiety. Similarly, captive capuchin monkeys and chimpanzees are known to perform grooming more frequently before provisioning times, reducing the stress caused by anticipated aggression before provisioning times and the frequency of aggressive interactions during them (Koyama and Dunbar 1996; Di Sorrentino et al. 2010). On the other hand, the timing of grooming was not influenced by that of feeding at the provisioning site for low-ranking females. This refuted the hypothesis linking grooming around the provisioning site to the mere attraction to the food available at the site. Thus, even though both low- and high-ranking females performed grooming around the provisioning site, space-use during grooming was determined by different factors associated with rank-related differences observed in feeding patterns.

Grooming behavior: grooming partners
The range and diversity of grooming partners did not differ significantly between low- and high-ranking females, showing that both of
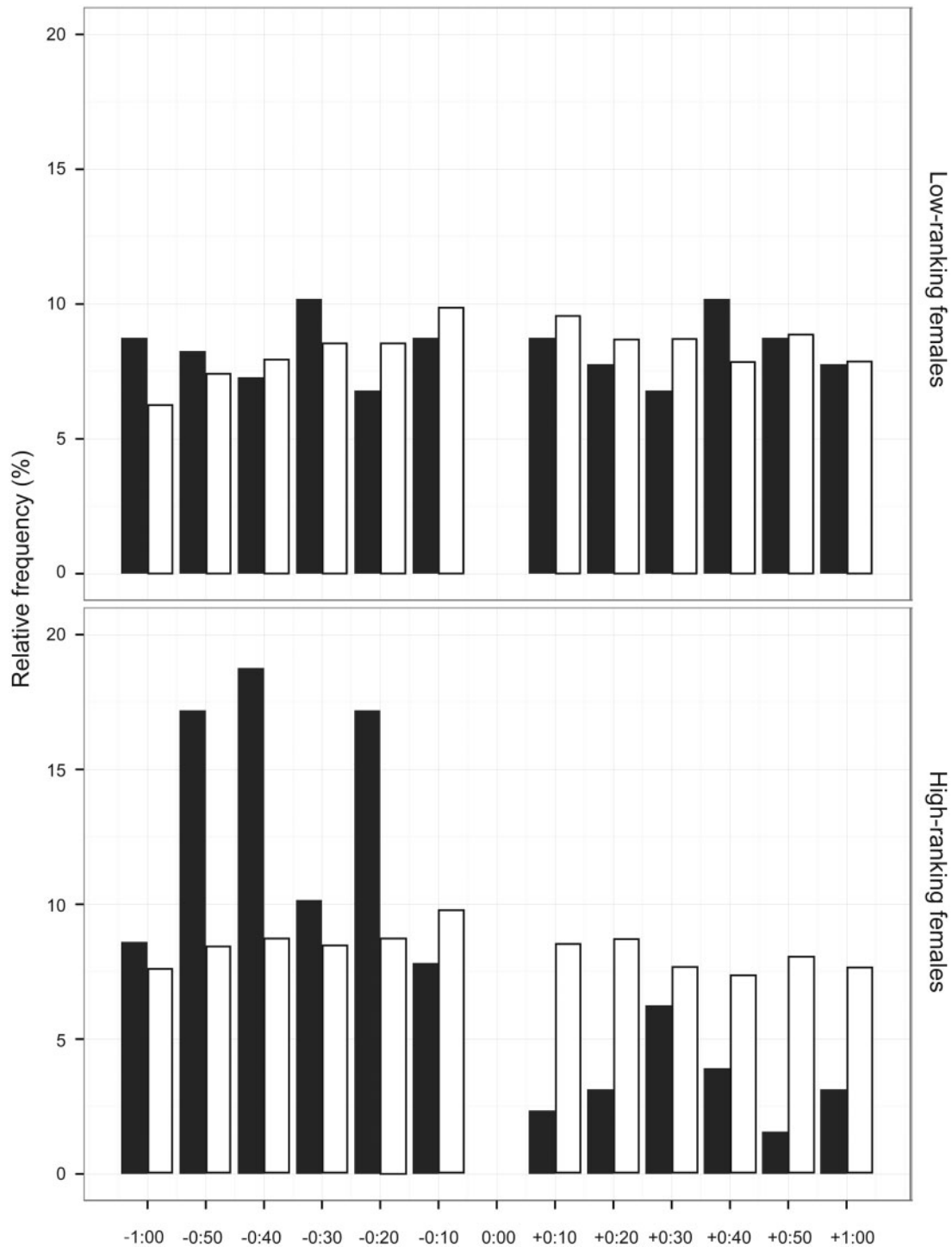
Figure 5. Histogram of observed and expected distributions of grooming bouts. *Black (Filled)*: observed distribution; *Gray (Open)*: expected distribution. The relative frequency of grooming bouts of low-ranking females (top) and high-ranking females (bottom) occurred during each time zone is shown. 0:00 is the onset time of feeding at the provisioning site, + means "after the onset time of feeding", and – means "before the onset time of feeding" on the *x*-axis. Only grooming bouts observed 1 h before and after the onset time of feeding are shown (low-ranking females: 206 of 274 bouts; high-ranking females: 128 of 162 bouts).

them were able to establish grooming relationships with as large range of partners. Attempting grooming with a large number of partners around the provisioning site might be effective for both low- and high-ranking females. Sueur et al. (2011) demonstrated using a computational model that limiting grooming partners to specific individuals, rather than reducing grooming time, can influence the social structure of

the group, potentially leading to its fission. Alternatively, demographic factors could outweigh the influence of rank on GDRs. GDR decreases as group size increases: even if group size (or the number of potential grooming partners, representing the denominator in GDR calculations) increases, animals can still have access only to a limited number of grooming partners, decreasing GDR (Nakamichi and Shizawa 2003;

Table 4. Comparison of activity budget among the Arashiyama group and wild groups of Japanese macaques

Study site	Group size	Feeding (%)	Grooming (%)	Resting (%)	Moving (%)	Reference
Arashiyama (Low-ranking females)	130–136	21.2	16.5	40.1	12.2	This study
Arashiyama (High-ranking females)	130–136	18.7	25.2	41.8	6.7	This study
Yakushima (coastal forest)	[a]	30.8	20.7	22.1	22.6	Agetsuma and Nakagawa (1998)
Yakushima (coniferous forest)	24	38	14	32	16	Hanya (2004)
Kinkazan	20–51	53.9	11.5	17.6	16.8	Agetsuma and Nakagawa (1998)
Shimokita[b]	51–79	35.6	19.8	19.8	24.7	Nakayama et al. (1999)

Means are shown. [a]Data on three groups (KO group: 48 individuals, P group: 5–19 individuals, T group: 7–10 individuals) were summarized. [b]Data on autumn and winter were averaged.

Lehmann et al. 2007). In the present study, GDRs (number of adult females: 91–92) were comparable to those calculated for a provisioned group in Katsuyama (number of adult females: 85) (Nakamichi and Shizawa 2003), suggesting that both low- and high-ranking females might have just formed a small clique of grooming partners in the Arashiyama group.

In conclusion, this study simultaneously investigated the feeding and grooming behaviors of individuals of different ranks and demonstrated how grooming behavior could change within a group according to rank-related feeding patterns. Low-ranking females performed grooming with as many partners around the provisioning site as did high-ranking females, despite rank-related differences in feeding patterns. This suggests that the areas around the provisioning site are not only important for low-ranking females to obtain small amounts of provisioned foods but also to construct and maintain grooming relationships with group members. Consequently, low-ranking females also made efforts to perform grooming there, and these efforts could contribute to maintaining the social cohesion of the group.

Acknowledgements

References

Agetsuma N, Nakagawa N, 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* **39**:275–289.

Aureli F, Preston SD, De Waal FB, 1999. Heart rate responses to social interactions in free-moving rhesus macaques *Macaca mulatta*: a pilot study. *J Comp Psychol* **113**:59–64.

Beale CM, Lennon JJ, Yearsley JM, Brewer MJ, Elston DA, 2010. Regression analysis of spatial data. *Ecol Lett* **13**:246–264.

Clark FE, 2011. Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. *Am J Primatol* **73**:748–757.

Crofoot MC, Rubenstein DI, Maiya AS, Berger-Wolf TY, 2011. Aggression, grooming and group-level cooperation in white-faced capuchins *Cebus capucinus*: insights from social networks. *Am J Primatol* **73**:821–833.

Di Bitetti MS, 2000. The distribution of grooming among female primates: testing hypotheses with the Shannon-Wiener diversity index. *Behaviour* **137**:1517–1540.

Di Sorrentino EP, Schino G, Visalberghi E, Aureli F, 2010. What time is it? Coping with expected feeding time in capuchin monkeys. *Anim Behav* **80**:117–123.

Dunbar RI, 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behav Ecol Sociobiol* **31**:35–49.

Dunbar RI, Korstjens AH, Lehmann J, 2009. Time as an ecological constraint. *Biol Rev Camb Philos Soc* **84**:413–429.

Fujimoto M, Takeshita H, 2007. Analysis of behavioral sequences in grooming interactions between adult females in the Arashiyama-E group of Japanese monkeys *Macaca fuscata*. *Jpn J Anim Psychol* **57**:61–71. Japanese with English abstract.

Haberman SJ, 1973. The analysis of residuals in cross-classified tables. *Biometrics* **25**:205–220.

Hanya G, 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. *Am J Primatol* **63**:165–177.

Hemelrijk CK, 2000. Towards the integration of social dominance and spatial structure. *Anim Behav* **59**:1035–1048.

Henzi S, Lycett J, Piper S, 1997. Fission and troop size in a mountain baboon population. *Anim Behav* **53**:525–535.

Hill DA, 1999. Effects of provisioning on the social behaviour of Japanese and rhesus macaques: implications for socioecology. *Primates* **40**:187–198.

Huffman MA, 1991. History of the Arashiyama Japanese macaques in Kyoto, Japan. In: Fedigan LM, Asquith PJ editors. *The Monkeys of Arashiyama: Thirty-Five Years of Research in Japan and the West*. Albany (NY): State University of New York Press, 21–53.

Iwamoto T, 1982. Food and nutritional condition of free ranging Japanese monkeys on Koshima Islet during winter. *Primates* **23**:153–170.

Iwamoto T, 1988. Food and energetics of provisioned wild Japanese macaques *Macaca fuscata*. In: Fa JE, Southwick CH editors. *Ecology and Behavior of Food-Enhanced Primate Groups*. New York: Liss, 79–94.

Iwamoto T, Dunbar R, 1983. Thermoregulation, habitat quality and the behavioural ecology of gelada baboons. *J Anim Ecol* **52**:357–366.

Katsu N, Yamada K, Nakamichi M, 2013. Social relationships of nulliparous young adult females beyond the ordinary age of the first birth in a free-ranging troop of Japanese macaques *Macaca fuscata*. *Primates* **54**:7–11.

Keverne EB, Martensz ND, Tuite B, 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* **14**:155–161.

Koyama N, 1991. Grooming relationships in the Arashiyama group of Japanese monkeys. In: Fedigan LM, Asquith PJ editors. *The Monkeys of Arashiyama: Thirty-Five Years of Research in Japan and the West*. Albany (NY): State University of New York Press, 211–226.

Koyama NF, Dunbar RIM, 1996. Anticipation of conflict by chimpanzees. *Primates* **37**:79–86.

Kurita H, 2007. Comparison of artificial food intake between high- and low-ranking females among provisioned, free-ranging Japanese macaques *Macaca fuscata* at Takasakiyama: preliminary report. *Primate Res* **23**:25–32. Japanese with English abstract.

Lehmann J, Korstjens AH, Dunbar RIM, 2007. Group size, grooming and social cohesion in primates. *Anim Behav* **74**:1617–1629.

Majolo B, de Bortoli Vizioli A, Schino G, 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. *Anim Behav* **76**:1235–1247.

Ministry of Education Culture Sports, Science and Technology, 2005. *Standard Tables of Food Composition in Japan Fifth Revised and Enlarged Edition*. edition. Tokyo: National Printing Bureau. Japanese.

Mori A, 1995. Rank and age related feeding strategy observed through field experiments in the Koshima group of Japanese macaques. *Primates* **36**:11–26.

Muroyama Y, 1991. Mutual reciprocity of grooming in female Japanese macaques *Macaca fuscata*. *Behaviour* **119**:161–170.

Nakamichi M, 2003. Age-related differences in social grooming among adult female Japanese monkeys *Macaca fuscata*. *Primates* **44**:239–246.

Nakamichi M, Shizawa Y, 2003. Distribution of grooming among adult females in a large, free-ranging group of Japanese macaques. *Int J Primatol* **24**:607–625.

Nakayama Y, Matsuoka S, Watanuki Y, 1999. Feeding rates and energy deficits of juvenile and adult Japanese monkeys in a cool temperate area with snow coverage. *Ecol Res* **14**:291–301.

Saito C, 1996. Dominance and feeding success in female Japanese macaques *Macaca fuscata*: effects of food patch size and inter-patch distance. *Anim Behav* **51**:967–980.

Schino G, Scucchi S, Maestripieri D, Turillazzi PG, 1988. Allogrooming as a tension-reduction mechanism: a behavioral approach. *Am J Primatol* **16**:43–50.

Shaffer CA, 2013. GIS analysis of patch use and group cohesiveness of bearded sakis *Chiropotes sagulatus* in the upper essequibo conservation concession, Guyana. *Am J Phys Anthropol* **150**:235–246.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL et al., 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc Biol Sci* **276**:3099–3104.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL et al., 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. *Behav Ecol Sociobiol* **64**:1733–1747.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL et al., 2010b. Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* **20**:1359–1361.

Soumah AG, Yokota N, 1991. Female rank and feeding strategies in a free-ranging provisioned troop of Japanese macaques. *Folia Primatol* **57**:191–200.

Sueur C, Deneubourg JL, Petit O, Couzin ID, 2011. Group size, grooming and fission in primates: a modeling approach based on group structure. *J Theor Biol* **273**:156–166.

Sugiura H, Shimooka Y, Tsuji Y, 2011. Variation in spatial cohesiveness in a group of Japanese macaques *Macaca fuscata*. *Int J Primatol* **32**:1348–1366.

Takahata Y, 1980. The reproductive biology of a free-ranging troop of Japanese monkeys. *Primates* **21**:303–329.

Takahata Y, 1982. The socio-sexual behavior of Japanese monkeys. *Z Tierpsychol* **59**:89–108.

Tanaka I, Takefushi H, 1993. Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropol Sci* **101**:187–193. Japanese with English abstract.

Ueno M, Yamada K, Nakamichi M, 2014. The effect of solicitations on grooming exchanges among female Japanese macaques at Katsuyama. *Primates* **55**:81–87.

Zamma K, 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. *Primates* **43**:41–49.

Zamma K, 2011. Frequency of removal movements during social versus self–grooming among wild chimpanzees. *Primates* **52**:323–328.

Zhang J, Zhao DP, Li BG, 2010. Postconflict behavior among female Sichuan snub-nosed monkeys *Rhinopithecus roxellana* within one-male units in the Qinling Mountains, China. *Curr Zool* **56**:222–226.

Zhang P, Watanabe K, 2014. Intraspecies variation in dominance style of *Macaca fuscata*. *Primates* **55**:69–79.