Feeding and reproductive strategies of ranging behavior in male Japanese macaques

Yosuke Otani

2013

Table of Contents

CHAPTER II: DENSITY OF JAPANESE MACAQUE (MACACA FUSCATA YAKUI) MALES RANGING ALONE: SEASONAL AND REGIONAL VARIATION IN MALE COHESIVENESS WITH THE GROUP

3 Methods

4 Results

5 Discussion

CHAPTER III: SHORT-TERM SEPARATION FROM GROUPS BY MALE JAPANESE MACAQUES: COSTS AND BENEFITS IN FEEDING BEHAVIOR AND SOCIAL INTERACTION

3 Methods

4 Results

5 Discussion

CHAPTER IV: REPRODUCTIVE STRATEGIES OF RANGING BEHAVIOR EMPLOYED BY MALE JAPANESE MACAQUES IN YAKUSHIMA

3 Methods

4 Results

5 Discussion

LIST OF FIGURES AND TABLES

FIGURES

TABLES

ACKNOWLEDGEMENTS

This work was conducted under the guidance of Dr. G. Hanya. I am very grateful for his constant encouragement and detailed advice during my six years of study, and companionship for almost a decade. I would like to thank Dr. A. Sawada for her cooperation at field site and our institute. I appreciate Drs. N. Nakagawa, T. Yumoto, T. Furuichi, and C Hashimoto for their valuable comments. Dr. A. MacIntosh provided me useful advice on this manuscript.

I would like to express deep gratitude toward current and past members of Primate Research Institute who offered helpful advice, especially Drs. Y. Sugiyama, A. Mori, K. Wada, K. Watanabe, Y. Kawamoto, T. Mouri, B. Fred, M. Huffman, Y. Tsuji, and I. Matsuda.

I feel deep gratitude toward over 800 participants of Yakuzaru-chosatai. The present work could not have been completed without their voluntary effort. Moreover, they constantly motivated me and shared their valuable academic experiences. In particular, Dr. S. Yoshihiro taught me the nature of field work. Drs. Y. Takahata, T. Oi, K. Zamma, and S. Hayaishi offered detailed advice and suggestions on my study. Similarly, Dr./Mr./Ms. M. Nagai, M. Kanie, M. Fujino, K. Sugaya, M. Sudo, S. Amanai, M. Kaneda, Y Tachikawa, Y Okahisa, and K. Higashi provided me ample support during publication.

I thank the Yakushima Forest Office and Kirishima-Yaku National Park for permitting the study, as well as The Sarugoya-Committee and the Wildlife Research Center, Kyoto University for offering excellent facilities. Furthermore, I would like to express my respect toward researchers who conducted initial research on Yakushima, and people who engaged in conservation movements in Yakushima. This study would not have been possible without their monumental efforts. During my research in Yakushima, Dr./Mr./Ms. H. Sugiura, N. Agetsuma, Y. Agetsuma, S. Fujita, M. Terakawa, M. Suzuki, M. Koda. R, M. Fujita, M. Nishikawa, K. Mochida, H. Taniguchi, H. Bouchet, K. Tetsuka, and T. Kawamura, as well as my colleagues and friends offered me tremendous support and encouragement. I also greatly appreciate my late friend Mr. K. Iwakawa.

This study was financed in part by a Teijin Scholarship Foundation grant to YO, a MEXT Grant-in-Aid for JSPS Fellows to YO, and JSPS-MEXT Grants-in-Aid for Challenging Exploratory Research and for Young Scientists to GH, as well as the 21st Century COE Program and the Global COE Program "Formation of a Strategic Base for Biodiversity and Evolutionary Research: from Genome to Ecosystem."

Finally, I am indebted to my friends and high-school teachers who encouraged me to choose a career as a scientist. Most of all, I extend my gratitude to my family, Takashi, Naoko, Hiroyuki, and Yuya, who always understood my academic work and supported me.

Chapter I

General Introduction

Most primate species form social groups as a unit for ranging, foraging, and mating [Terborgh and Janson, 1986]. Previous studies have shown that group formation provides benefits and costs. Group formation can help individuals reduce the costs associated with monitoring the surrounding environment for predators and increase the probability of detecting predators [Alexander, 1974]. Individuals in groups can increase foraging efficiency because they usually rapidly locate food patches [Eisenberg et al., 1972], or as a result of joint protection of food patches against other individuals [Wrangham, 1980]. In addition, group living helps maintaining social interactions, where individuals exchange various social services, such as removal of external parasites [Henazi and Barrett, 1999]. In contrast, group-living animals always suffer from intra-group contest (or direct) competition, which indicates a decline in foraging efficiency because of direct agonistic behavior among group members. Scramble (or indirect) competition indicates the collective depletion of limited resources, which results in a reduced foraging efficiency for all group members [Chapman et al., 1995; Snaith and Chapman, 2008]. In addition, to maintain group coherence, each individual is required to pay the cost associated with social monitoring in order to keep up with other group members, which reduces the time available for feeding [Kazahari and Agetsuma, 2008]. Moreover, individuals of different age-sex classes range together within the group representing an additional cost, as each class often presents a different feeding strategy because of variations in nutritional requirements and vulnerability to predation [van Schaik and van Noordwijk 1986], and also because males have greater velocity than females do [Wrangham, 2000].

Fission-fusion is a known strategy used by primates to manage costs and benefits [Chapman et al., 1995, van Schaik, 1999, Lehmann et al., 2007]. Van Schaik [1999] distinguished “individual-based fission-fusion” and “group-based fission-fusion”. The variations of costs and benefits related to the dynamics of group formation have been mainly studied on species presenting individual-based fission-fusion.

In species exhibiting individual-based fission-fusion behavior, the individuals usually form subgroups with changing membership, although each group does have a stable home range and membership. The size and composition of the subgroups are determined by the balance between the costs and benefits of group living. For example, individuals of chimpanzees (*Pan troglodytes*) in large subgroups have higher mating opportunities [Hashimoto et al., 2001] and a decreased predation risk [Goodall, 1986]. In addition, spider monkeys (*Ateles geoffroyi*) in larger subgroups have advantages related to the formation of coalitions between females [Chapman et al., 1995], and can minimize ranging cost by adjusting subgroup size depending on food availability [Asensio et al, 2009].

In the group-based fission-fusion societies, individuals live in permanent social groups that have stable memberships but occasionally form subgroups or range alone [van Schaik, 1999]. However, in such societies, functions of fission-fusion behavior associated with the costs and benefits of group formation have not been completely addressed. Unlike individual-based fission-fusion, group-based fission-fusion is observed in many species, including the mangabey (*Lophocebus albigena*) [Olupot and Waser 2005], the long-tailed macaque (*Macaca fascicularis*) [van Schaik and van Noordwijk 1998], the Tonkean macaque (*Macaca tonkeana)* [Sueur et al., 2010], and the snub-nosed monkey (*Rhinopithecus* spp.) [Kirkpatrick and Grueter, 2010]. To expand our understanding of fission-fusion behavior and the reasons for group formation, studies on both individual-based and group-based fission-fusion are necessary.

Japanese macaques (*Macaca fuscata*) belong to the genus *Macaca*, which comprises 19 species. This medium-sized species has been studied for over 60 years, and is one of the most studied non-human primate species in the world [Nakagawa et al., 2010]. They form female-bonded multi-male multi-female groups that are generally cohesive; therefore, they are classified as a group-based fission-fusion species [Aureli et al., 2008]. To maintain group coherence, group members conduct contact calls [Suzuki and Sugiura, 2011] and social monitoring [Kazahari and Agetsuma, 2008]. Females remain in their natal group throughout their life; therefore, they tend to develop and maintain closer relationships with each other [Nakamichi and Yamada, 2010] than males. Thus males and females possibly have different strategies associated with group participation.

Males emigrate from their natal groups when they approach sexual maturity at approximately 4 to 5 years of age. Although most males join other bisexual groups, some join all-male groups or become solitary males [Sugiyama 1976; Sprague et al. 1998]. Individuals in a group exhibit a stable and linear dominance hierarchy [Suzuki et al., 1998]. Although female rank is inherited from mothers to daughters, the rank of males is mainly determined by their tenure in the group. This is because most males join a group at the bottom of the rank order, and their rank rises because of the death or emigration of higher ranked males [Suzuki et al., 1998]. Even during the early stages of the study of Japanese macaques, it was pointed out that males present a double-layered (central and peripheral) spatial structure within a group [Kawai, 1964]. The spatial configuration of males is affected by social position [Yamada, 1966, Soltis, 1999], which may be a consequence of the distribution of food, because these studies focused on populations provisioned by human. There are no examples confirming a spatial pattern associated with the social position of males in a wild, non-provisioned group by quantitative data. In fact, it is known that lower ranked males tend to copulate in the periphery of the group by hiding from other individuals [Hayakawa, 2007]. However, not much is known about the behavior of males ranging outside the groups.

Even if males belong to groups, sometimes they tend to temporarily separate from their group [Fukuda 1989]. For example, during mating seasons, several males are seen visiting from outside the group and succeed in copulation [Yamagiwa, 1985, Okayasu 2001, Hayakawa, 2008]. However, there are no data on how many males range outside the groups and in which social and environmental circumstances they choose to join a group. The cost and benefits associated with group ranging and separate ranging could be better understood by assessing the factors that affect their decision to range separately or in groups.

The purpose of this study was to examine group association and the management of costs and benefits related to ranging with/without other group members in male Japanese macaques. This research is based on two separate surveys: a broad-scale census on males ranging outside a group, and an intensive observational survey on males affiliated to groups.

In Chapter II, I described and analyzed the data obtained by full-day point censuses. These data are used to estimate the density of males ranging alone and to examine the seasonal and regional variation on density of males ranging alone. A large number of observers covered an area, including the home range of several groups. “Male ranging alone” was defined as a male who was detected at the census points on its own and no group was detected for at least 1 h both before and after its detection. I compared the density of males ranging alone among different vegetation types in a region to reveal the influence of food availability on the density of males ranging alone. In addition, I compared the results between mating (autumn) and non-mating (summer) seasons to reveal the influence of estrous females. I also compared the results between two regions with differing intensity of inter-group competition in order to understand the influence of inter-group competition on the recorded density of males ranging alone. Through these comparisons, I examined whether or not males can modify their pattern of group-association with seasons and regions that differ in food condition, competition intensity, and reproduction. Males ranging alone would avoid within-group competition while losing opportunities for social interaction, though the degree of these costs and benefit would differ depending on the duration of the period spent ranging alone.

In Chapter III, the term “males ranging separately from group” is introduced to define those males who are affiliated to a group but are seen temporarily ranging without other group members. For quantitative evaluation of males’ spatial position, I tracked in parallel a male and a female. Assuming that females mostly stayed in the group, I defined a male as separated from the group when he maintained a distance of > 100 m from the focal female for over 10 minutes. By conducting intensive observation during non-mating season, I could evaluate the influence of feeding strategy avoiding any confounding effect of the reproductive strategies on the male behavior. I compared the feeding behavior, ranging behavior, and social interaction of males ranging separately with those of males moving with their group. I also compared the frequency and the duration of separate ranging shown by males of different ranks. In addition, I compared the incidence of separate ranging in relation to the distributions of major food items. Through these comparisons, I determined whether males modify their separate ranging behavior with environmental and social conditions. Group males are a valid subject for this purpose because each male would have both options to range with or without other animals for a short period of time.

In Chapter IV, I conducted parallel tracking both during mating and non-mating seasons to examine the costs and benefits of ranging without groups, particularly from the perspective of reproductive strategy. In addition, by recording individuals presented in the sight of focal animals (presence data), I was able to study the factors affecting the choice among three main spatial positions for males; staying in central part of the group, staying in the periphery of the group, and ranging outside the group (separate ranging). To clarify the effect of reproduction and social position on the positions of males, I determined the males' spatial position based on the male-female distance and presence data and compared them among seasons and differently ranked males. To examine the benefit of separate ranging on mating, I recorded mating behavior during separate ranging, particularly in relation to females of other group. In addition, I compared travel distances between males ranging separately and ranging with the group to examine the cost of ranging separately. Moreover, I compared the rate of separate ranging and presence among years and days, which showed different number of estrous females in order to determine the influence of reproductive potency on the spatial position of males. Through these comparisons, I aimed to understand how males choose the main three possible spatial options concerning the mating strategies.

The general discussion includes integrative interpretations on the costs and benefits related to separate ranging, particularly feeding and reproduction and decision making of the spatial position of males. I also discussed the necessity for further research on males to further understand how males associate with other individuals. I proposed possible additional methods to reveal how males decide their affiliation, and dispersal behavior. These combined approaches would provide novel information and significantly enhance our understanding of the life history of males.

Chapter II

Density of Japanese macaque (*Macaca fuscata yakui*) males ranging alone: seasonal and regional variation in male cohesiveness with the group

1 Abstract

We conducted point censuses in Yakushima island to estimate the density of Japanese macaque (*Macaca fuscata yakui*) males ranging alone, focusing on its vegetational, seasonal, and regional variation. In highland areas, the detection frequency of males ranging alone did not differ among different types of vegetation, despite the latter's effect on overall population density. The detection frequency of males ranging alone in the mating season was a third of that in the non-mating season. In the mating season, males exhibit strong cohesiveness with a group, probably in search of resident estrous females. Outside the mating season, we detected 25% fewer males ranging alone in lowland areas, which have high population densities and strong inter-group competition, than in highland areas. The absolute density of males ranging alone was estimated to be 1.2-5.7 individuals /km^2. Meanwhile, the group and population densities were 1.25/km^2 and 19.3/km^2, respectively. A considerable number of males therefore remained outside groups, and male cohesiveness with groups is flexible in relation to ecological and social circumstances.

2 Introduction

Group size is an important parameter for social mammals [Reiczigel et al. 2008]. The benefits of grouping increase with group size, but simultaneously so do the costs. Grouping enables individuals to obtain the benefits of defending resources and avoiding predators [Hamilton 1971; Isbell and Young 1993], but incurs costs such as within-group feeding competition [Clutton-Brock et al. 1999], reduced foraging efficiency and increased travel costs [Chapman et al. 1995]. Depending on the circumstances, the degree to which costs and benefits vary, and the resultant optimal group size, changes [Brown 1982].

Many primate species form groups [Terborgh and Janson, 1986], but these groups are neither fixed nor closed. For example, in the fission-fusion societies of chimpanzees [*Pan troglodytes*] and Geoffroy's spider monkeys (*Ateles geoffroyi*), individuals form subgroups of fluctuating size and composition. The number of adult males in a subgroup is a function of food density and travel costs [Chapman et al. 1995]. Also, in a female-bonded society, gray-cheeked mangabey (*Lophocebus albigena*) males were often found several hundred meters away from their own groups [Olupot and Waser 2005]. In other species, many extra-group males can achieve some mating success [*Macaca mulatta*, Lindburg 1969; *Erythrocebus patas*, Harding and Olson 1986; *Cercopithecus mitis albogularis*, Henzi and Lawes 1987; *Macaca Fascicularis*, van Schaik and van Noordwijk 1998; *Mandrillus sphinx*, Abernethy et al. 2002]. In addition, groups of *M. fascicularis* tend to fission when there are no large fruit trees [van Schaik and van Noordwijk 1988]. In the above studies, the duration of males occurring outside or within groups ranges from hours to months or even years

[*Macaca mulatta*, Lindburg 1969; *Erythrocebus patas*, Harding and Olson 1986; *Cercopithecus mitis albogularis*, Henzi and Lawes 1987; *Macaca fascicularis,* van Schaik 1988; *Mandrillus sphinx*, Abernethy et al. 2002]. Regardless of the duration, as long as they are separated from groups, they lose the benefits of group-living, but also avoid or decrease the associated costs. As the degree of cost and benefit changes depending on circumstance [Steenbeek and van Schaik 2001; Ramesh et al. 2012], the number of individuals ranging separately from groups should change accordingly.

Japanese macaques (*Macaca fuscata*), which form female-bonded multi-male, multi-female groups, are another species in which males exist outside of groups [Nishida, 1966]. Males emigrate from their natal groups when they approach sexual maturity at around 4 to 5 years old, and although most males join other groups, some join all-male groups or become solitary males [Sugiyama 1976; Sprague et al. 1998]. Even if males belong to groups, sometimes they are separated temporarily from them [Fukuda 1989]. Therefore, it is difficult to determine whether males who range alone are solitary or simply separated temporarily from their group.

In most previous studies, males were classified on the basis of sociological perspectives such as group attendance or social interactions. For example, males who remained in the subject group and socially interacted for at least a few months were classified as group males [Sprague 1992]. In the same way, males who visited a subject group only temporarily during the mating season and those who were not known to be resident in any group were classified as non-group males and solitary males, respectively [Nishida 1966;

Okayasu 2001]. On the other hand, such perspectives ignore variation in males' proximity to groups during daily ranging, which is also important. For example, even a few hours of isolation from a group can significantly affect food intake because it allows males to feed without competition [Chapman et al. 1995].

In addition, previous studies have defined the tenure status of males by continually observing bisexual groups [e.g. Yamagiwa and Hill 1998]. This method allows for collection of detailed information within groups, such as group composition and kin-relationships among males, both of which may influence male group- cohesiveness. However, it is then impossible to understand population-level dynamics, which is necessary to speculate about the functions of individual cohesiveness with groups. Alternatively, censusing large areas that cover multiple habitat types and include many groups may enable us to obtain new information that could not otherwise be obtained by continually observing groups.

In the present study, we conducted full-day point censuses using multiple observers to evaluate the density of male Japanese macaques ranging alone. Direct tracking and continuous observation is inadequate, because males ranging alone cover large areas and are almost impossible to detect as they rarely vocalize and have unstable ranging areas [Muroyama et al. 2000]. We hypothesize that the density of males ranging alone differs across vegetation types, seasons, and mean group densities, and we know that the vegetation types vary in terms of food availability [Hanya et al. 2005]. To elucidate the factors that affected male group-cohesiveness, we investigated the following three points:

(a) We compare among different vegetation types in a region, to reveal the influence of food availability: this comparison is conducted in one study site that includes about 10 groups. Males can move around vegetations in a short time. Males may change their ranging area flexibly in accordance with food availability.

(b) Comparisons between mating (autumn) and non-mating (summer) seasons, to reveal the influence of estrus females: In autumn, which corresponds to the mating season for Japanese macaques, males may change their ranging behavior because they have a demand for mating with females in groups that they do not have in the non-mating season.

(c) Comparison between two regions in which intensity of inter-group competition differs, to reveal the influence of inter-group competition: The two regions are separated from each other by about 7 km, which exceeds males' monthly ranging area [Muroyama et al. 2000]. Males cannot move between the two regions easily. The two regions have different intensities of inter-group competition because of the different vegetation and food availability. Males may converge on a high food availability place or apply a different ranging strategy because females allow more males to stay in their groups as inter-group competition becomes intense [Wrangham 1980].

In addition, we estimate the absolute density of males ranging alone and compared this with the group density to determine the regularity with which males do range alone. We thereby aimed to clarify variation in male group-cohesiveness, particularly whether males change their group-association patterns in accordance with environmental conditions. We discuss the significance of our results in relation to foraging and reproductive strategies. Revealing the factors that influence an individual’s group cohesiveness can contribute to a greater understanding of the factors determining group size and group formation among mammals.

3 Methods

3-1 *Study site*

Yakushima is a 503 km^2 island in southern Japan (30°N, 131°E). Japanese macaques (*M. f. yakui*) are distributed across the entire island. Yakushima exhibits clear altitudinal gradation in habitat types, which results in variation in macaque diet, population density, and strength of feeding competition [Yoshihiro et al. 1999; Hanya et al. 2004; Hanya et al. 2008], although genetic diversity of the macaques is low [Hayaishi and Kawamoto 2006]. Beginning in the mid-1970s, many studies have been conducted in coastal, subtropical, warm-temperate areas, but since the late 1990s, studies have also been conducted in highland, cool-temperate areas [e.g. Yamagiwa 2008]. Our census team has focused on the population dynamics of Japanese macaques using a point census method [Hanya et al. 2005; Hanya et al. 2008]. Thus in Yakushima, we can compare the behaviors of males with the same genetic background in different environments.

3-2 *Regions and Vegetation*

The census was conducted in highland (700 m-1300 m a.s.l.) and lowland regions (under 300 m a.s.l.)(Fig. II-1). The census area in the highlands and lowlands occupied 7.5 km^2 (30 points or specific locations) and 6.5 km^2 (14 points), respectively. The vegetation of the highlands is classified as either a warm-temperate/cool-temperate transitional forest zone or a cool temperate zone, and that of the lowlands is classified as subtropical-warm temperate transitional zone or warm-temperate evergreen broad-leaved forest zone [Kimura and Yoda 1984]. The highlands have lower food availability than the lowlands [Hanya et al. 2004], which translates into a lower population density in the highlands (13.8-27.1 individuals /km^2) than in the lowlands (62.4-99.8 individuals /km^2) [Yoshihiro et al. 1999; Hanya et al. 2005].

In accordance with the method described in Hanya et al. (2005), we classified the vegetation of the highland study site into the following categories: ‘primary’ forest is an undisturbed national park, ‘naturally regenerated’ forest was logged between 1985-1996 and subsequently managed with minimum human disturbance, and ‘plantation’ forest was logged between 1976-1984 and later planted with Japanese cedar (*Cryptomeria japonica*). These vegetation types have 12, 8, and 10 census points, respectively.

3-3 *Study period*

We conducted censuses during three periods listed below. The Japanese macaque is a strict seasonal breeder [Nozaki et al. 1992], with the mating season lasting from late September to early January in the lowlands [Sprague 1991] and from September to December in the highlands [Hanya unpublished data].

(a) During the non-mating season (summer), we conducted point censuses at the lowland site on 11 days from 23 July to 8 August 1993 using 35 observers, and on 14 days from 17 July to 5 August 1994 using 41 observers. Total observation time was 1,268 hours, including 144 points-day.

(b) During the non-mating season at the highland site, we conducted censuses on 77 days from August 8 to 31 between 2003 and 2008, using 41-54 observers/year. Total observation time was 10,061 hours, including 1,143 points-day.

(c) We conducted censuses during the mating season (autumn) only at the highland site, and at only 14 of the 30 points (3.5 km^2 of 7.5 km^2) consistently across years. Censuses were conducted on 17 days from 7 October to 8 November 2008, using eight observers. Total observation time was 331 hours, including 40 points-day.

3-4 *Operational definition for point census*

For the point census, we operationally defined a group and males ranging alone as follows:

Group: multiple individuals including females and/or juveniles detected visually or auditory.

Males ranging alone: the male was detected at census points on its own when no group was detected for at least one hour both before and after its detection (hereafter, the one-hour rule).

The one-hour rule is necessary because we must distinguish males ranging alone from males ranging with groups. To compare this index between vegetation types, seasons, or regions, the precondition that the detection frequencies of groups are similar must be met. If the detection frequencies of groups differ among categories of factors, we would need to confirm validity by simulation. Different methods should be applied in accordance with the type of error. When this index (detection frequency of males ranging alone by the one-hour rule) differs among categories of factors, there is a possibility of false-positives because of the difference in detection frequency of a group (type I error). In turn, even if this index does not differ between factors, there is a possibility that the difference in detection frequency of a group masks the difference in detection frequency of males ranging alone (type II error).

3-5 *Point census*

We used a point census approach for two reasons, first because the mountainous habitats of Japanese macaques on Yakushima preclude the use of line transects [Hanya et al. 2003] and second because of the necessity to census groups simultaneously with males ranging alone. The census area was divided into 500 × 500 m grid squares, and one observer was positioned in each grid square at a fixed point. If a grid square included a peak, the point was set there because it was easier to detect groups auditory. On the basis of auditory cues, groups can be detected from more than 200 m, so the locations of detected groups were not biased with topography [Hanya et al. 2003]. Home ranges of a single group included approximately six grid squares [Hanya et al. 200b]. The point census was conducted for 1-16 points simultaneously depending on the number of observers. Observers remained at each point from 0600-0800 to 1600, unless the weather was bad. Many of the observers were inexperienced, so they were trained for one day preceding the census. Moreover, to avoid bias, every observer was located at a different point every day. These observers could reliably estimate group density [Hanya et al. 2003]. When they detected one or more individuals, we judged whether it was a detection of a group or males ranging alone in accordance with the operational definition (see above). In addition, 1-3 researchers every 4-8 points followed groups that appeared in the census area to estimate detectability, except in the mating season.

3-6 *Detection frequency of males ranging alone*

We used detection frequency (detection events/observation time) as a relative index of density of males ranging alone. The numbers of males ranging alone detected each hour were averaged for each day and each point. We used this index to examine differences by vegetation type, season, and region.

Using this method, we could not classify males on the basis of a sociological perspective (for example, a solitary male or a male who separated from his group temporarily). However, the numbers of males ranging alone irrespective of affiliation needed to be compared to evaluate the factors that influence the decision of whether or not to range with groups.

3-7 *Absolute density of males ranging alone and group density*

We estimated density using distance sampling [Buckland et al. 2004]. If we can detect males ranging alone at probability (detectability) P_a, then we can estimate density (D) by dividing the number of detections by the total census area as follows

$D = \frac{n}{k\pi w^{2}\cdot P_a}$ *1

where *n*, *k*, and *w* indicate the number of detected individuals, the number of points, and the effective detection radius (range in which point observers can detect animals, calculated from the estimated detection function at zero-distance), respectively. Because P_a changes in accordance with the distance from points, we estimate P_a by modeling the detection function g(*r*)(0≦*r* ≦*w*). We assume that g(0)=1 because any animal at the point is certain to be detected. P_a can be expressed as [Buckland et al. 2004]

$P_a = \frac{2}{w^2}\int rg(r)dr$ *2.

From equations *1 and *2, we can obtain *D* using the values of *n*, *K*, and P_a as

$$D = \frac{n}{2\pi k \int_0^w rg(r)dr}$$

Using the software package “Distance 5.0” [Thomas et al. 2006], we adopted the best-fit model for P_a by maximum likelihood estimation.

The average duration of observation of males ranging alone was 4.19 minutes (*SD*= 5.71, N=132), and only 10.2% of all detection events lasted more than 10 minutes. We never detected multiple individuals in a single minute. If we applied a day as a unit, the density would be overestimated because animals would be regarded as remaining around the point all day, although they actually stayed for only a few minutes [Buckland et al. 2008]. To take the duration of observation into consideration, we should apply as short a unit as possible for estimation. To confirm that temporal auto-correlation does not significantly influence the results, multiple units should be examined. If the densities estimated by the multiple units do not differ substantially, the temporal auto-correlation is not serious. To maintain independence between units, only 1 of every 10 minutes (0610-0611, 0620-0621 etc.) or 15 minutes (0615-0616, 0630-0631 etc.) was used to estimate absolute density, and the remaining 9 and 14 minutes were discarded. When the male was observed for more than the unit time (10 or 15 minutes), the male was counted only once.

We calculated detection frequency in all three study periods but estimated group density only in (a) and (b) because estimation required a group follower. Since estimation of absolute density of males ranging alone requires a large sample size, we did so only in (b).

We estimated group density using the method described in Hanya et al. (2003). At each point, we counted the number of groups detected each hour (0600–0659, 0700–0759, etc.). When *y* and *g(y)* indicate the distance (m) from a point and the detectability that a group at distance *y* is detected, respectively, the number of groups detected (*n*) is given by the formula $n = 2D\pi\int_0^\infty yg(y)dy$. We calculated λ, which is the detectability constant of the half-normal model $g(y) = exp(-\lambda y^2)$ [Buckland et al. 2004]. Thus, we could calculate group density by the formula $D = \frac{\lambda n}{\pi}$ [Hanya et al. 2003b]. We applied different detectability constants in each vegetation type at the point.

3-8 *Statistical analysis*

We used a generalized linear mixed model (GLMM) to examine the association between vegetation type and detection frequency of males ranging alone and groups. We selected the best-fit model based on Akaike's Information Criterion

(AIC). In all models, we used the census point as a random effect. We used non-parametric statistical tests to examine associations among variables with alpha set at 0.05. All of the statistical analysis was conducted by freeware “R version 2.11” (R Development Core Team 2012).

4 Results

4-1 *Difference among vegetation types within a region (highlands, non-mating season)*

There was no difference in the detection frequency of males ranging alone among the three vegetation types in the highland study site, within which males can access all areas in just a few days (Table II-1). This indicates that males did not converge on high food availability areas. The average detection frequency in primary, naturally regenerated, and plantation forests were 0.0142, 0.0129, and 0.0107 individuals/hour, respectively. Vegetation did not influence the density of males ranging alone as the null model was found to be the best fit model (statistics not shown as no factors included). However, the best fit model for detection frequency of groups included vegetation types, which means the detection frequency varied among vegetation types; artificial forest was lower than the other two vegetation types (primary forest; estimate=0.246, SE=±0.0499, z=0.4919, naturally regenerated forest; estimate=0.609, SE=±0.0503, z=1.21). Therefore, the possibility of type II errors needs to be further investigated by simulation, as mentioned above. This is because the difference in the detection frequency of a group may mask differences in the detection frequency of males ranging alone.

We assumed that the detection frequency of a group was 1.90 times/day, which was the highest value in the three vegetation types. Under this assumption, during 452, 306, and 385 data points collected in primary, naturally regenerated, and plantation forests, respectively, and expected numbers of group detections in each vegetation type were 858, 581, and 731. These fictitious group detection events were randomly assigned to actual observation times (3869 h, 2696 h, and 3496 h in primary, naturally regenerated, and plantation forests, respectively). Then, we counted the number of detections of males ranging alone that were discarded/adopted under the one-hour rule. We repeated this trial 200 times. The simulated detection frequency of males ranging alone had significant vegetational variation at 0.015 (3/200). This means that even if the detection frequency of groups was the same among the three vegetation types, detection frequency of males ranging alone did not differ. Therefore, the possibility that the difference in detection frequency of groups masks the difference in detection frequency of males ranging alone can be judged as low.

There is a possibility that the difference in detectability among vegetation types masks the difference in density of males ranging alone. However, frequency distributions of detection of males ranging alone relative to the distance from the census point were similar among vegetation types (Fig. II-2). In addition, the values of effective detection radius (EDR; Buckland et al. 2004) did not differ greatly (EDR of primary, naturally regenerated, and plantation forests was 9.74, 9.96, and 10.22, respectively) and there was no significant difference in λ, which is the detectability constant of the half-normal model among vegetation types (λ of primary, naturally regenerated, and plantation forests was -0.163, -0.169, and -0.335, respectively; parallelism test, *P*=0.315). Therefore, the difference in detectability among vegetation types was negligible.

4-2 *Comparison between mating and non-mating season (highlands)*

In the highland, detection frequency in non-mating seasons (0.0126 individuals/hour, average from 2003 to 2008, 127 detection events for 1,143 data points collected) was three times as high as in the mating season (0.00402, average in 2008, one detection event for40 data points collected) (Mann-Whitney U test: *W* = 30543.5, *P*= 0.0448) (Table II-2). Detection frequency of group did not vary between the two seasons (Mann-Whitney U test: *W* = 24973.5, *P*= 0.162; 1.39 and 1.33 times/day; 1,143 and 40 data points collected in non-mating and mating season, respectively).

4-3 *Comparison between highland and lowland areas (non-mating season)*

The detection frequency of males ranging alone in the highlands (0.0126 individuals/hour) was four times as high as that in the lowlands (0.00363, average in 1993 and 1994, four detection events for 144 data points collected) (Mann-Whitney U test: *W* = 89154, *P*= 0.00184) (Table II-2). The detection frequency of groups varied between the two regions (Mann-Whitney U test: *W* =99327, *P*<0.001; 1.39 and 2.62 times/day: 1143 and 144 data points collected in the highlands and lowlands, respectively). Therefore, the possibility of type I errors also needs to be investigated by simulation.

We examined the null hypothesis that the density of males ranging alone did not differ between the highlands and lowlands. Under the null hypothesis, during the 1268-hour survey in the lowlands, the expected number of detections of males ranging alone was calculated as 1268 hours * 0.0126 times/hour (detection frequency in the highlands) =16 times. These 16 detection events were randomly assigned to actual data of the detection of groups in the lowlands. Then, we counted the number of male detections that were discarded/adopted under the one-hour rule. We repeated this trial 200 times and obtained the distribution of simulated detection frequency of males ranging alone (Fig. II-3). The simulated detection frequencies were never less than the actual detection frequency in the lowlands (0.00316 times /hour). Therefore, the null hypothesis was rejected at the alpha level of less than 0.005 (=1/200).

4-4 *Absolute density of males ranging alone and groups (highlands, non-mating season)*

The density of males ranging alone was calculated to be 2.6 individuals/km^2 (1.2-5.7; 95% confidence interval: 1 in every 10 minutes) and 2.3 individuals/km^2 (1.7-3.1; 95% confidence interval: 1 in every 15 minutes). Judging from their body size and secondary sexual traits, almost all individuals who appeared alone were mature males. No female was observed alone. The estimation may include error to some extent due to the topographically biased distribution of census points: 16 out of 30 points were at peaks. However, the detection frequency did not differ between the points at peaks versus other locations (Mann-Whitney U test: W = 161348, P= 0.899). Therefore, the potential error is not significant.

The average group density in the highlands between 2003 and 2008 was 1.25 groups /km^2. By multiplying the average group size of the five identified groups in the area (15.4), which was recorded by the group followers and the observed group density, we estimate the population density in the highlands to be 19.3 individuals /km^2.

5 Discussion

5-1 *Implications for foraging strategies: Vegetation and regional variation*

There was no significant difference in the detection frequency of males ranging alone among the different types of vegetation in highland areas, despite variable food availability. The detection frequency of males ranging alone in the highlands was higher than that in the lowlands, despite the lower food availability [Hanya et al. 2004]. This indicates that males did not converge on high food availability areas. On the other hand, group density was higher in the vegetation type that offered higher food availability than other types in our highland study site [Hanya et al. 2005]. These authors estimated the ground cover of herbs and the number of fleshy fruits eaten by macaques in 57 vegetation plots of 5 m^2 in the three vegetation types. Fruit production was higher in naturally regenerated forest than in primary forest and negligible in plantation forest. Herb availability was high in naturally regenerated forest but low in primary and plantation forests. The group density was high in the naturally regenerated forest, intermediate in the primary forest, and low in the plantation forest. Another study compared the total basal area of macaque food trees (m^2/ha) and the total annual fruit abundance among plots located in different altitudinal zones (0-400, 400–800, 800–1200 and 1200–1886 m) [Hanya et al. 2004]. Both variables indicated that fruits and seeds are most available in the coastal forest, which includes our lowland study site. The group density was higher also in coastal forest [Yoshihiro et al. 1999]. Therefore, food availability influenced groups but not males ranging alone.

Inter-group competition may be one factor underlying this difference (see van Hooff and van Schaik 1994). Inter-group competition was stronger in the lowlands because of a higher group density [Hanya et al. 2004; Hanya et al. 2008]. Under strong inter-group competition, females need many more males to defend resources, and thus allow a larger number of males to remain in the group [Wrangham 1980]. In the same way, males tolerate other males in the group, and form cooperative relationships [Takahashi and Furuichi 1998; see van Hooff and van Schaik 1994 for review]. In addition, males feeding alone must give up the feeding patch when encountering a group. At our lowland study site, males ranging alone that were observed to encounter a group left the area immediately in all three cases [Otani unpublished data]. For these reasons, it is likely profitable for males to feed with groups when inter-group encounter rates are high.

5-2 *Implication for reproductive strategies: Seasonal variation*

The detection frequency of males ranging alone in the mating season was lower than that in the non-mating season. There could be two explanations for this. One is that this indicates stronger cohesiveness with groups during mating seasons. This coincides with previous sociological studies reporting that non-group males approached groups during the mating season [Nishida 1966; Sprague 1992]. Additionally, we confirmed that males visit other group to copulate with females of other group [Chapter IV]. This explanation is supported by the fact that the attendance rate of group males in the mating season in an identified group in our highland study site was higher than that in the non-mating season [Hanya unpublished].

The other explanation is that the results indicate seasonal migration by males from highlands to lowlands. During mating season, males are attracted to groups by estrous females [Sprague 1992].The density of estrus females may be higher in the lowlands than in the highlands because of their higher population density [Yoshihiro et al. 1999]. Therefore, migration between these areas might be profitable for males. However, the two study sites are separated from each other by about 7 km, which exceeds the monthly ranging areas of males [Muroyama et al. 2000]. In addition, during the mating season in 2000 in the highlands, 12 non-group males appeared around the identified group which had six group males [Hanya unpublished]. This proportion of non-group males to group males (2.00) is comparable to the lowlands [3.00, Yamagiwa 1985; 3.05, Okayasu 2001, 0.20-2.17, Hayakawa 2007], suggesting that not all males ranging alone in the non-mating season migrated from highlands to lowlands in the mating season.

In either case, the benefits to males from being cohesive with groups must be related to the acquisition of estrous females as mating partners [Nishida 1966, Japanese macaques; Cords 1984, red-tailed monkey (*Cercopithecus ascanius*); Borries 2000, Hanuman langurs (*Semnopithecus entellus*). Males remaining in social units must therefore need to protect estrous females within their groups [Okayasu 2001]. To distinguish between these two possible explanations, point censuses in the lowlands during the mating season will need to be conducted in future studies.

5-3 *Absolute density of males ranging alone*

The absolute density of males ranging alone was estimated to be 2.6 and 2.3 individuals/km^2 in highland (1.2-5.7, 1.7-3.1; 95% confidence interval). Meanwhile, the group density was 1.25 groups/km^2 in the highlands. In comparison with group density, therefore, it appears that a considerable number of males remained outside of groups during the non-mating season in the highlands of Yakushima.

Why did so many males remain outside of groups? One advantage for males of moving alone is avoidance of within-group feeding competition [Steenbeek and van Schaik 2001; Isbell 1991]. In fact, according to studies of species that have fission-fusion societies, the number of males in subgroups is constrained by the density of feeding patches and travel costs [Chapman et al. 1995]. This is because an increase in group size will increase the area that must be traveled to find adequate food supplies to meet nutritional requirements [Terborgh and Janson 1986]. Moreover, individuals of different age-sex classes have different feeding strategies because of variation in nutritional requirements and the ability to overcome problems (e.g. predation) [van Schaik and van Noordwijk 1986], so they may benefit by separating from their group. In addition, the absence of predators on Yakushima [Fooden and Aimi 2005] may make it easier to range alone. The existence of a considerable number of males ranging alone shown in this study may indicate that the benefits of ranging alone is comparable with that of ranging with a group for male Japanese macaques.

5-4 *Possible limitations*

Although determining the distance between males and groups is an appropriate way to distinguish males ranging alone from groups, this was impossible using our point census method. Thus, in this study, we classified male cohesiveness using the time of detection (one-hour rule). However, in the point census, even if a detected male and other individuals were nearby, if the individuals remained quiet for one hour both before and after the detection, the male was recorded as a male ranging alone. This could lead to overestimation of the density of males ranging alone. However, the group density was low in the highlands (average detection frequency: 0.147 times/h), and males ranging alone were detected independently from groups along the time scale. Actually, detection events increased by only 17 cases (12.1% of all detection events) when we ignore the one-hour rule. Therefore, the degree of overestimation is not significant.

Furthermore, we repeated the census across time during the same day and at the same point, although this is not recommended [Buckland et al. 2008]. For this study, males ranging alone who are difficult to detect need to be sufficiently researched, and this must be done in parallel with group censuses. As a result of a tradeoff between validity of study design and the number of samples available, we applied this point census method. However, the eventual influence of this tradeoff was not significant. Although the biggest problem with repeating censuses is temporal auto-correlation, males ranging alone were detected only once in one point*day in most cases (88.6%). In addition, absolute densities estimated by two census units did not differ significantly (2.6 individuals/km^2: 1 every 10 minutes and 2.3 individuals/km^2: 1 every 15 minutes, see above), which confirms the minor influence of auto-correlation.

In conclusion, the present study showed that a considerable number of Japanese macaque males remained outside of groups, and that male group cohesiveness varied by region and by season. Possible underlying factors include inter- and within-group feeding competition, foraging strategies, and male reproductive strategies Although Hanya et al. (2008) suggested that the female social relationships of Japanese macaques are robust, male cohesiveness with groups can change flexibly in accordance with changes in environmental conditions. Social animals inevitably experience both costs and benefits by forming groups, and it is thought that optimal group size, which is determined by the balance of costs and benefits, changes with circumstance [Brown 1982]. However, how individuals react to variation in circumstance and change their patterns of cohesiveness has rarely been reported, especially in medium-sized mammals. This study investigated the actual reactions of animals to variable contexts, and showed that individuals can adapt quickly to changes in circumstance which influence the costs and benefits of group formation.

Chapter III

Short-term separation from groups by male Japanese macaques: costs and benefits in feeding behavior and social interaction

1 Abstract

To expand our understanding of fission-fusion behavior and determine its variability among primates, studies of both individual-based and group-based fission-fusion are necessary. We conducted a parallel tracking study of male and female Japanese macaques (*Macaca fuscata yakui*) during the non-mating season to clarify the general features of separate ranging by males of this species, an example of fission-fusion behavior, and to reveal its associated costs and benefits. Males frequently engaged in short-term separate ranging, leaving the company of females and ranging on their own for periods averaging 68 minutes in duration. However, the males did not venture outside the group's home range. When ranging separately from the group, males spent more time on feeding, stayed longer in each feeding tree, and fed at a lower rate than when ranging with the group. This would be because separated males had no necessity to catch up with other group members. Additionally, separated males received aggression at a lower frequency, had longer feeding time on fruits, and fed greater amount of food for one out of four main items. These behavioral changes suggest that males can avoid within-group contest feeding competition

by ranging alone. However, this behavior was also associated with higher traveling costs, and these separated males were more vulnerable to intergroup competition and had fewer opportunities for social interaction. The frequency of separate ranging was lower when highly clumped food plant species were the main food source. Lower ranked males, who received more aggression when ranging with the group, exhibited a higher frequency of separate ranging. This behavioral flexibility with respect to group cohesion may allow males to reduce the costs of group living without completely losing the benefits. Specifically, by ranging alone, males may acquire sufficient feeding time without being disturbed by other group members and without necessity of following up the group. Conversely, when ranging with the group, males can access grooming partners and advantages in intergroup competition.

2 Introduction

Most diurnal primates are gregarious, and group living provides ecological and sociological benefits for individuals in the group, such as avoidance of predation, better foraging efficiency, removal of external parasites, and social interactions [Alexander, 1974; Wrangham, 1980; van Schaik, 1983]. However, individuals also suffer costs associated with feeding competition, which may decrease foraging efficiency [Isbell, 1991; Chapman et al., 1995], and females and infants may suffer harassment by males [Smuts and Smuts, 1993; Clutton-Brock and Parker, 1995; van Schaik, 1996; van Noordwijk et al., 1999]. The balance of these costs and benefits varies according to the size and composition of the group. Some species of primates can facultatively change their group sizes and compositions through fission-fusion. The occurrence of fission-fusion behavior enables us to analyze the costs and benefits of group formation, as the formation, disbandment, and size of subgroups, as well as the overall group size, can be related to environmental or social factors.

Van Schaik [1999] distinguished “individual-based fission-fusion” and “group-based fission-fusion,” based on the degree of cohesion of group members. In species showing individual-based fission-fusion behavior, such as spider monkeys (*Ateles geoffroyi*) [Chapman et al., 1995], chimpanzees (*Pan troglodytes*) [Furuichi, 2009], and orangutans (*Pongo pygmaeus*) [van Schaik, 1999], it is rare that all members of a single group range together. Members habitually form subgroups with changing membership or even range alone, although each group does have a stable home range and membership. Observers can identify the members of the larger social unit only by accumulating data on the composition of subgroups [Chapman et al., 1994]. Orangutans exhibit an extreme form of such behavior, as they mostly range alone, except for females raising young offspring. This species sometimes forms small groups; however, these usually do not consist of more than 5 individuals [van Schaik, 1999]. The size and composition of subgroups in these fission-fusion systems seem to be determined by the balance between the costs and benefits of group living. The benefits of forming larger subgroups include the formation of coalitions of females [spider monkey, Chapman et al., 1995], increased mating opportunities [chimpanzee, Hashimoto et al., 2001; orangutan, van Schaik, 1999], avoidance of harassment by males, and experience of social interaction by adolescents [orangutan, van Schaik, 1999]. The costs include increased travel distance to find adequate food [spider monkey, Korstjens et al., 2006; chimpanzee, Terborgh, 1986, Chapman et al., 1995, Lehmann et al., 2007] and within-group feeding competition [chimpanzee, Chapman et al., 1994]. Subgroup size is known to change flexibly depending on food availability (density and distribution of food resources) [spider monkey, chimpanzee, Chapman et al., 1995; Asensio et al, 2009], the number of estrous females [chimpanzee, Hashimoto et al., 2001], and predation risk [chimpanzee, Goodall, 1986].

In group-based fission-fusion societies, by contrast, individuals live in permanent social groups that have stable memberships, and usually range with all group members [van Schaik, 1999]. Although these individuals may occasionally form subgroups or range alone, the degree of cohesion is stronger than that of individual-based fission-fusion species. Unlike individual-based fission-fusion, group-based fission-fusion is observed in many species [mangabey (*Lophocebus albigena*), Olupot and Waser, 2005; long-tailed macaque (*Macaca fascicularis*), van Schaik and van Noordwijk, 1988; Tonkean macaque (*Macaca tonkeana)*, rhesus macaque (*Macaca mulatta*), Sueur et al., 2010; snub-nosed monkey (*Rhinopithecus* spp.), Kirkpatrick and Grueter, 2010].

To identify the various forms of fission-fusion behavior among nonhuman primates, studies that compare group-based and individual-based fission-fusion are required. Studies of the behavior of individuals that range separately from the group are of particular interest, as this behavior reflects the single individual's evaluation of the costs and benefits of group living. Conversely, group splitting results from a mixture of decisions by multiple individuals, and the factors affecting this process might therefore be more difficult to elucidate. Studies of fission behavior by individuals in group-based fission-fusion societies are rare because observers typically focus on groups, and individuals that move off on their own are more difficult to detect and track; individuals are less conspicuous than groups and may vocalize only rarely [Muroyama et al., 2000].

Japanese macaques (*Macaca fuscata*) form female-bonded multi-male, multi-female groups. These groups are generally cohesive, and Japanese macaques are thus classified as a group-based fission-fusion species [Aureli et al., 2008], although temporary fission of their groups has been reported [Fukuda, 1989; Okayasu, 2001; Sugiura et al., 2011]. Both males and females sometimes separate from other group members and form subgroups [Fukuda, 1989]. In addition, males sometimes move away from other group members on their own. In Chapter II, we showed that the density of males ranging separately from groups fluctuated with season and the group density in the area that they occupied. Another study reported the ranging behavior of a solitary male using radio tracking [Muroyama et al., 2000]. However, no previous studies have reported detailed information regarding the conditions under which male Japanese macaques range separately from the group, which could provide insight into the costs and benefits of group living. At our study site, multiple neighboring groups are well habituated [Yamagiwa, 2008], and the home range of each group is known to be relatively small [Hanya et al., 2006]; this arrangement allowed us to track males ranging separately from their group relatively easily.

We aimed to clarify the general features of separate ranging performed by male Japanese macaques and thus to shed light on the costs and benefits of group living, especially for males, in this species. We distinguished the periods when males ranged with the group from those when they ranged separately through the parallel tracking of males and females. We then compared the feeding behavior (feeding time, intake rate, amount of food intake), ranging behavior (traveling time, travel distance, home range use), and social interaction (grooming and agonistic interactions) of males ranging on their own with those of males moving with their group. We also compared the frequency and the duration of separate ranging among males of different ranks. In addition, we compared the incidence of separate ranging in relation to the distributions of major food items. Through these comparisons, we determined whether males modify their separate ranging behavior in accordance with environmental and social conditions. We also compared these features with those of individual-based fission-fusion species. Because mature Japanese macaques have no predators [Takahata et al., 1998], we could eliminate the influence of anti-predation strategies. In addition, because Japanese macaques are strict seasonal breeders, we could exclude the influence of reproductive strategies by conducting the research during the non-mating season.

3 Methods

3-1 Study site, subjects, and term

Our study group (AT group) inhabited the western coastal area of Yakushima, which is covered by subtropical/warm-temperate forest. Because long-term studies of the macaques in this area have been conducted since the 1970s, the animals are well habituated without provisioning. The 29-member group included 7 mature males and 9 mature females, each of which was individually identifiable. We distinguished mature from immature individuals by their clear variation in physical size and secondary sexual characteristics [Sprague et al., 1998]. Our study subjects included 6 mature males and 9 mature females. We excluded the lowest-ranked male because he had joined the group only recently, during the previous mating season (approximately 5 months before the study), and was rarely observed at the start of this research. The ages of the males ranked 1st and 2nd, 3rd-5th, and 6th were ≥ 13 years, 10-13 years, and 7-9 years, respectively. We defined 'high-ranking' and 'low-ranking' males as males of 1st to 3rd ranked and 4th to 6th ranked males, respectively.

3-2 *Data collection*

We collected data over 40 days (19 March to 10 June, 2010) during the non-mating season. Two researchers (YO, AS) tracked either 1 male and 1 female (526 h total; 263 h for males, Mean ± SD = 43.8 ± 6.01 h/individual; 263 h for females; 29.2 ± 3.87 h/individual) or 2 females (80 h total, 8.89 ± 3.14 h/individual) in parallel. Each researcher recorded the focal animal's location with a GPS device (Garmin 60CSx) every 30 s, enabling the subsequent calculation of the distance between the two focal animals. We followed a single male for the entirety of each observation day but switched from one female to another every 3 hours. When 2 females were tracked in parallel, observers switched the focal subjects every 3 h. We chose the focal animals for each day in advance, taking care to equalize the sample size among individuals and to avoid disproportionate emphasis on specific male and female combinations.

The two researchers independently recorded other individuals that they detected visually throughout each hour of the day, which indicated spatial associates in the vicinities of focal animals. The visibility was generally restricted to within 30 m because of the dense forest and steep terrain. Additionally, individual identification was difficult when researchers were more than 30 m from the individual. We also recorded each location where members of the focal group exhibited some response to the presence of another group as the site of an intergroup encounter [Saito et al., 1998]. We recorded male activity with instantaneous sampling at one-minute intervals [Altmann, 1974]. Activity classes included agonistic behavior, feeding, grooming (including being groomed), terrestrial moving, arboreal moving, and resting (including self-grooming). We recorded the onset and offset of grooming and feeding to the nearest second. A feeding started when individuals placed food in their mouth. After the individual had stopped feeding for 20 s, the time of the last bite was recorded as the end of the bout. We recorded the location of feeding trees whose diameter at breast height (DBH) was > 5 cm. All aggressive interactions that involved a focal animal were also recorded continuously by the second. When interval of aggressive interactions was more than 10 minutes, we regarded them as different aggression bouts. During feeding, the following variables were recorded:

- Intake rate: expressed as time per mouthful, which we calculated by taking the average, over one feeding tree visit, of the inverse of the time taken for 20 hand movements to the mouth or 20 direct bites. We calculated this index only for arboreal leaves, flowers, and fruits, which constituted most of the total feeding time (see Results).

- Duration of feeding tree visit: time (seconds) spent in each tree in which the focal animal fed.
- Feeding tree size: diameter of the tree crown (m) was estimated visually as a relative index of feeding tree size. When the tree crown was not round, we chose a part of the crown with an intermediate diameter. We calibrated our visual estimation using a tape measure before research began and confirmed that we could visually measure the crowns with a precision of one meter.
- Feeding tree location: the locations of each tree in which the focal animals fed were recorded by GPS to evaluate the distribution of feeding trees (Morisita index, see Results).
- The number of co-feeders: we recorded all mature individuals who fed in the trees in which the focal animals fed and timed the duration of their stay in the tree.
- Food item: identified in terms of species and parts (e.g., fruit, leaf).

3-3 *Data Analysis*

We operationally defined a male as separated from the group when he maintained a distance of > 100 m from the focal female for more than 10 minutes. These criteria were based on observed male-female distances (see Results). This definition was designed such that when the male-female distance exceeded the criterion distance, the focal male was generally separated from most group members. The distance between the focal male and female occasionally fluctuated near 100 m over several minutes, e.g., when males and females were moving in the same direction but toward different locations. To avoid overestimating the occurrence of separate ranging, we excluded instances in which the males and females were separated for < 10 minutes. We calculated distance between the male and the female using GPS locations that were recorded every 30 s. When calculating the duration of separation bouts, we discarded those bouts in which the observers required > 20 minutes to change focal females. If changing focal females required < 20 minutes, and the distance between the focal male and female remained more than 100 m, we considered the male as ranging separately from the group throughout the period. We used this criterion distance to compare the behavioral parameters (e.g. intake rate, duration of feeding tree visit) between males ranging separately from the group and males ranging with the group. To estimate distributions of distance between the focal animals, we used inter-individual distances recorded at 10 minute intervals (Fig. III-1).

We calculated the proportion of adult males or females in the group that were visible to the observers. For example, if five out of the nine females in the group were observed in the vicinity of a focal male, the proportion of females around the focal male in that hour would be 56%. We averaged this value (/h) across all observation hours for both males and females. We discarded the data when we did not track the focal animal completely during the one hour period. We also calculated this proportion when the minimum distance between the focal males and females exceeded 100 m for 1 h to validate the definition of separate ranging.

Using the Kernel method [Worton, 1989], we estimated the home ranges (95%) and the core home ranges (50%) of the females and of the males that ranged separately from their group using ArcGIS 9.3 and 10 (ESRI, Inc.). We considered the location of the females as representative of the location of the group (see Results). We connected the locations of the focal animals at intervals of 10 minutes and calculated travel distance per 10 minutes.

Following Hanya [2009], we calculated the mean number of mature individuals co-feeding with the focal animal in each feeding tree visit. For example, if the number of co-feeders was 1 for the first minute and 2 for the next 3 minutes, the mean number of co-feeders during that feeding tree visit would have been 1.75. We calculated the density of co-feeders in each feeding tree. First, we calculated the crown area using the following formula: Crown area = π * (feeding tree size/2)^2. As we did not record DBH, based on the correlations in Hanya [2009] in the study site, we estimated basal area and crown height from the crown area as follows:

$$\text{Log(basal area)} = \log(\text{crown area}) / 0.505 + 0.064$$

$$\text{Log(crown height)} = \log(\text{basal area}) * 0.269 + 0.691$$

Second, we estimated the approximate crown height and calculate Crown volume as:

Crown volume = 1/3* crown area * crown height [Janson 1988]. Finally, we calculated the density of co-feeder in each feeding tree by dividing the number of co-feeder by crown volume. We calculated the feeding parameters (intake rate, duration of feeding tree visit, feeding tree size, amount of food intake per minute, and density of co-feeder) only for those food items eaten at least 30 times during observations. We estimated the amount of food intake of each male using the following formula: [(mean intake rate of the food item) × (feeding time when males range separately from/with the group)] / (observation time). If a single food item comprised more than 30% of the feeding time in a day, we defined it as the main food of the day. We also compared the proportion of fruit feeding time to the total feeding time for males ranging separately and with the group.

We evaluated the degree of patchiness of the feeding trees visited by focal animals using the Morisita index (I_δ) [Morisita, 1959]. This aggregation index represents spatial patterns of organisms, determined by counting the number of individuals in quadrats. We divided the home range of the group into quadrats and calculated I_δ using the following formula:

$$I_\delta = q \sum_{j=1}^{q} x_j(x_j - 1) \Big/ \sum_{j=1}^{q} x_j \left(\sum_{j=1}^{q} x_j - 1\right),$$

where q and x_j indicate the number of quadrats and the total number of feeding trees in the jth quadrat, respectively. I_δ = 1.0 when the trees are randomly distributed, I_δ > 1.0 when they are clumped, and I_δ < 1.0 when they are regularly distributed. We set the size of the quadrats as 100 m. We also calculated the density of the feeding trees visited by focal animals in the home range of the group.

We used a generalized linear mixed model (GLMM) with a Gaussian error structure to examine the influence of three predictor variables on feeding behavior (duration of feeding tree visit and intake rate). The predictor variables were (1) separation from the group (yes/no, based on male-female distances), (2) number of co-feeders, and (3) feeding tree size. The unit of analysis was one feeding tree visit. We regarded the male was separated from the group during the feeding tree visit when the male-female distance was more than 100 m throughout the visit. We log-transformed duration of feeding tree visit, the number of co-feeders, and feeding tree size to achieve an approximation of normality. We confirmed the approximation of normality in all three variables. In all models, we used the male individual as a random effect. Although we examined three factors, number of co-feeders and feeding tree size were included because they are already known to affect feeding behavior [Hanya, 2009, Kazahari et al., 2013] and we were interested only in whether or not the effect of separation from the group was significant. Therefore, we examined the effect of separation from the group on each independent variable by conducting a likelihood ratio test between the models with and without the separation from the group predictor variable. We conducted standardized residuals analysis [Haberman, 1973] to estimate the valid P values for the χ^2 tests in the proportion analyses, such as those of activity budget and dietary composition. For other analyses, we used nonparametric statistics (Spearman's rank correlation test, Mann-Whitney's U test and the Steel-Dwass test for multiple comparisons). The alpha level was set at 0.05 for all analyses. All of the models and tests were conducted using "R 2.13" (R Development Core Team 2012). We used the "lmer" function in the package lme4 to construct the GLMM.

4 Results

4-1 *Distance between individuals and definition of separate ranging*

The distance between males and females was greater than that between females (Fig. III-1; median = 47.8 and Interquartile Range (IQR) = 21.2-106 m for male-female dyads, median = 21.3 and IQR = 11.5-50.5 m for female-female dyads, U test , $P < 0.001$). The proportion of females around focal females (mean ± SE = 67% ± 27, N = 215, U test, $P < 0.001$) was greater than that of females around focal males (mean ± SE 46% ± 36, N = 215). According to the distance distribution (calculated every 10 minutes), female-female distances were less than 100 m for 91% of the cases (N= 235, 40 h) (Fig. III-1). Female-female distances exceeded 100 m for more than 10 minutes only in 2 instances. Moreover, when the minimum distance between a male and female exceeded 100 m for a period of 1 hour, the mean proportion of females around the focal male was 3% (N = 20), and that of males around the focal male was 5% (N = 20). This result indicates that when the male-female distance exceeded 100 m, the male was not in the vicinity of most of the group members and was often alone.

On average, males ranged separately from their group for 33% of the observation time (range: 7-53%, N = 6 males, each observed for 43.8 ± 4.8 hrs, for a total of 263 hours). The duration of each separation bout was 68 ± 77.5 SD min (N = 76 bouts). We never observed that males slept while ranging on their own. The males ranged separately from their group at least once on 90% of the observation days (36 of 40 days). Lower-ranked males showed higher frequencies of separate ranging and spent a greater proportion of their time away from the group (Spearman test, frequency: $r_s = 0.827$, $P = 0.0421$; proportion: $r_s = 0.815$, $P = 0.0481$, $N = 6$; Fig. III-2). We never observed a male involved in agonism before separating from the group.

4-2 *Ranging behavior of males when ranging separately vs. with their group*

The home range of the group (53.0 ha) included 98.0% of that of males ranging separately from their group (42.6 ha) (Fig. III-3). Males ranging separately also seemed to avoid areas in which inter-group encounters occurred: while the group's core home range included 6 of the 9 locations where inter-group encounters occurred, the home range of males ranging separately included only 1 of these 9 locations (Fig. III-3). Males ranging separately from the group encountered neighboring groups (E and Nina-A2) at the periphery of the group's home range three times. (The 2nd and 4th ranked males encountered other groups twice and once, respectively.) In all 3 cases, the males avoided neighboring groups without any display or aggression. In contrast, both males and females of AT group confronted neighboring groups (E, Nina-A2, Kw-Z) aggressively in 8 of the 9 instances in which they met, with the groups ignoring each other in the remaining encounter.

When males ranged separately from the group, travel distances per 10 minutes (mean ± SE = 36.2 ± 36.3 m/10 minutes) were greater than those of males ranging with the group (30.7 ± 30.7 m/10 minutes, Steel-Dwass test, $P < 0.01$) or than that of females (30.4 ± 30.2 m/10 minutes, Steel-Dwass test, $P < 0.01$). No significant differences were found between travel distances per 10 minutes of males ranging with the group and those of females ($P = 0.336$).

4-3 *Feeding behavior of males when ranging separately vs. with their*

group

Fruit feeding time when the males ranged separately was also longer (65.5% of total feeding time) than when they ranged with the group (53.5%, $P < 0.001$, $\chi^2 = 5556$, $df = 1$). Food items that were eaten at least 30 times included the leaves of *Rhus succedanea* and the fruits of *Ficus superba*, *F. erecta*, and *Myrica rubra*. All of the three predictor variables, separation from the group, feeding tree size, and number of co-feeders, to some degree had positive effects on the duration of feeding tree visits (Table III-1). Males that ranged separately from the group stayed in each feeding tree significantly longer (with group: mean ± SE 707 s ± 740; separate: 790 s ± 857, likelihood ratio test, $P < 0.05$).

In contrast, males ranging separately from the group had a significantly lower intake rate (with group: mean ± SE 0.285 /s ± 0.121; separate: 0.209 /s ± 0.113, likelihood ratio test, $P < 0.01$, Table III-2). The intake rate was calculated only for tree products. However, the results reflected the general tendency of the males' feeding behavior because the consumption of tree products constituted 91.8% of the males' feeding time for separate and group ranging combined.

The leaves of *R. succedanea* and the fruits of *F. superba* and *M. rubra* were the main food items on 5 days (April 4-28), 5 days (April 26-May 6), and 16 days (May 3-June 4), respectively. *Ficus erecta* was not a main food item on any of our observation days. When *M. rubra* fruit was the main food, the frequency of separate ranging tended to be lower (0.26 bouts/hour) than that observed on other days (0.32 bouts/hour) (U test, $P = 0.065$, $N = 40$). No such difference was observed when *R. succedanea* and *F. superba* were the main foods (U test, $P = 0.74$ and $P = 0.90$, respectively, $N = 40$). The density of *R. succedanea, F.*

superba, M. rubra and *F. erecta* that were visited by the focal animals in the home range of the group was 0.60, 0.30, 1.28, and 0.32 tree/ha. The density of co-feeders when males ranged with group was higher in *M. rubra* and *F. superba* (mean ± SE: 0.150 ± 0.333, 0.068 ± 0.177 /m^2), and lower in *R. succedanea and F. erecta* (mean ± SE 0.012 ± 0.030, 0.016 ± 0.046 /m^2, Steel-Dwass test, $P < 0.05$).

Although *R. succedanea*, *F. superba*, *M. rubra* and *F. erecta* had a clumped distribution, the degree of patchiness was stronger for *M. rubra* (mean ± SE I_δ: 6.61) than for the other species (*R. succedanea*: 3.35, *F. superba*: 3.66, *F. erecta*: 1.86). When we compared the amount of food intake per minute between males ranging separately from their group and males ranging with the group, a significant difference was found only for *F. superba* fruits (with group < separate, Steel-Dwass test, $P < 0.05$) (Fig. III-4).

4-4 *Activity budget and social interactions*

The proportion of time spent on feeding and terrestrial moving increased significantly, and that on grooming and resting decreased significantly, when males ranged separately from their group ($P < 0.01$, $\chi^2 = 904$, df = 5, standardized residuals = 20.0, 8.68, 16.5, 13.3, respectively, Fig. III-5). The time spent engaged in aggression and arboreal moving did not change (χ^2 test, standardized residual analysis, $P = 0.238$ and $P = 0.157$, respectively, $\chi^2 = 904$, df = 5, standardized residuals = 1.18, 1.32). Males received aggression more frequently when ranging with group (mean ± SE 0.00209 ± 0.00161 bouts/minute) than when ranging separately (0.00070 ± 0.00071 bouts/minute, U test, P < 0.05). The frequency of receiving aggression of low-ranking males (0.00234 bouts/minute) was higher than that of high-ranking males (0.00054 bouts/minute, U test, P < 0.01) (Fig. III-6). When males ranged with the group, the proportion of time spent grooming with females compared to the total observation time was lower among lower-ranked individuals (U test, P < 0.001) (Fig. III-7).

5 Discussion

We found that males separated temporarily from their group repeatedly; however, they did not move outside the group's home range. When males ranged separately from the group, their behavior was characterized by longer travel distances, larger proportions of time spent feeding, longer fruit-feeding times, longer durations of feeding tree visits, lower intake rates, and greater amount of food intake for one out of the four main items. When a highly clumped item was the main food on a given day, the frequency of separate ranging was low. Lower-ranking males showed higher frequencies of ranging separately.

5-1 *Benefits of separate ranging*

One of the benefits of separate ranging would be avoidance of within-group contest competition (interference or direct competition [Nicholson, 1954]). Individuals ranging with groups are subject to both contest and scramble competition for food resources [Snaith and Chapman, 2008]. Individuals can always be disturbed by others [Janson, 1988], which is a manifestation of contest competition. We found that visits in a feeding tree by separated males tended to last longer and separated males fed at lower intake rate. These would be partly because separated males rarely received aggression. Likewise, longer fruit-feeding time and greater amount of food intake of *F. superba* by separated males may be the result of avoiding within-group contest competition. As aggression among co-feeders increases when Japanese macaques eat fruits/seeds versus other foods [Hanya, 2009], the feeding duration or amount of intake for fruits may be constrained when males ranged with the group.

Separated males had greater amount of food intake of *F. superba* because contest competition would become intense when they fed the *F. superba* fruits in the group. Males may change the frequency of separate ranging in accordance with the density and the distribution of main food source which influence on the intensity of contest competition. *F. superba* showed a unique combination of characteristics: density of co-feeder was high, and the density of the tree was low. High density of co-feeder would indicate the greater influence of contest competition. In addition, because the density of *F. superba* tree was low, individual animals can hardly find alternative fruiting trees within the ordinary group spread when they are disturbed by other individuals. The density of co-feeder in *M. rubra* was also high, however, the density of the *M. rubra* tree was high. Additionally, *M. rubra* showed more clumped distribution than other species did. Therefore, even if the contest competition in a tree becomes intense, animals can find alternative *M. rubra* fruiting trees within the ordinary group spread. This would be a reason why males tended to remain in their group when *M. rubra* was main food item, and the amount of food intake of *M. rubra* did not differ when males ranged separately. The density of co-feeder in

F. erecta and *R. succedanea* was low, thus the effect of contest competition would be minor. Therefore, the amount of food intake for these two species would not increase when males ranged separately than when ranged with the group. Although we show the data that the density of *F. erecta* was low, the density would be underestimated as DBH of many of *F. erecta* tree was under 5 cm, which was not included in the density estimation.

One circumstantial evidence further supports the idea that separate ranging is a means of reducing contest competition. Higher-ranked males, which are less frequently disturbed by other group members, separated from their group less frequently.

An alternative interpretation could explain the results that feeding time increased and intake rate decreased when males ranged separately, although we consider it unlikely. Feeding time can increase as a result of intensive competition, when such competition forces individuals to feed on lower-quality food items [Saito, 1996]. There is a possibility that separated males had greater feeding time as they could get only low-quality food outside of group. However, this was not the case in the present study, as we found that feeding time for fruits increased when males ranged separately from group. Fruits are not low-quality foods for Japanese macaques, as they contain more readily available energy than other foods [Nakagawa, 1997], and Japanese macaques in Yakushima actually prefer fruits over other foods [Hanya, 2004].

Another benefit of separate ranging would be the lack of necessity to catch up with other group members. The comparatively longer duration of feeding tree visit during separate ranging could be explained not only by the absence of disturbance by group members but also by the lack of a necessity to catch up with group members. The decision as to when to leave a food patch is also determined by following of other group members [Nakagawa, 1990], and duration of feeding tree visit increases with the increasing number of co-feeders as they have less necessity to end up feeding to follow other members [Kazahari and Agetsuma, 2008]. Separated males would stay in one feeding tree longer as they have no necessity to catch up with others. Separated males did not need to increase their intake rate to ensure sufficient food intake over a limited time. Intake rate can also be constrained by the necessity of vigilance to mating competitors [Nakagawa, 2000] or increasing social monitoring cost to catch up with other group members [Kazahari and Agetsuma, 2008]. However, this was not the case of the present study because we studied during a non-mating season. As noted above, separated males would have no social monitoring cost. In fact, when males ranged separately from the group, we did not frequently observe vigilance behavior [Otani, pers. obs.].

5-2 *Costs of separate ranging*

Our findings suggest that there were three costs associated with separate ranging. First, males that ranged separately from the group suffered from increased traveling costs, as indicated by their longer travel distances and the greater proportions of time spent on terrestrial moving. One likely reason for this observation is that males must find the group when they wish to rejoin it. If males frequently conduct short-term separate ranging, this cost could be considerable. Travel distances have also been shown to increase as a result of within-group scramble competition [Snaith and Chapman, 2007], although this was not the case in the current study, as travel distances increased when males ranged separately from their group.

Second, males ranging on their own were more vulnerable to competition with other groups. Our study site has a high group density (4.8 groups/km^2) [Yoshihiro et al., 1999], and inter-group competition is intense [Takahata et al., 1994, Saito et al., 1998; Hanya et al., 2004]. When encountering other groups, males ranging on their own had no choice other than to retreat. Therefore, males that ranged separately from the group did not go outside the group's home range and tended to avoid areas where they were likely to encounter other groups. Vulnerability to competition with other groups could also be the reason why males separated from the group only for short periods. Another possible explanation for low frequency of separate ranging when *M. rubra* was the main food, other than the ease of access to alternative fruiting tree (see above), would be the effect of inter-group competition. The frequency of separate ranging may be low as the inter-group competition becomes intense when *M. rubra* is a main food [Hill and Agetsuma, 1995]

Third, males ranging separately from the group spent less time grooming than they did when in the group. When they ranged separately from their group, the grooming partners of these males were other males or juveniles who had separated from the group with them. Because lower-ranked males spent less time grooming than higher-ranked males even when ranging with the group, the loss of grooming opportunities due to separate ranging would be smaller for these individuals. This might explain the higher frequency of separate ranging by lower-ranked males. It is also logical to assume that lower-ranked males would try to maintain their few grooming opportunities in the group, but we found that this was not the case here. Such a scenario may arise only when males completely lose their grooming opportunities, which is unlikely to result from the short-term separate ranging exhibited by the current subjects.

5-3 *Comparison of group-based and individual-based fission-fusion societies*

One of the clear differences between separately ranging male Japanese macaques and individual-based fission-fusion primates is the duration and frequency of separation from the group. Male Japanese macaques left the group for short periods only and never slept alone, while in individual-based fission-fusion societies, there are no constraints to this behavior with respect to the duration of group formation or sleeping behaviors [Kappeler and van Schaik, 2002]. Thus, the size and composition of subgroups in individual-based fission-fusion societies may be adjusted in accordance with social and ecological conditions without any constraint in duration. By contrast, although male Japanese macaques had constraints in the duration of their separation, each individual could decide whether they ranged with other individuals or not when separated from their group.

In conclusion, the separate ranging of male Japanese macaques in the non-mating season had both costs and benefits associated with feeding and social behavior. Through short-term separate ranging behavior, males could avoid within-group contest competition; however, they lost grooming opportunities, became more vulnerable to inter-group competition, and suffered from higher travel costs.

Chapter IV

Reproductive strategies of ranging behavior employed by male Japanese macaques in Yakushima

1 Abstract

In bisexual groups, males obtain an opportunity to mate by defending females in their group. However, alternative strategies involving mating at the periphery of the group or mating with females belonging to other groups would be feasible. To clarify the effectiveness of the alternative mating strategies and factors that affect males' decision among these strategies, we analyzed male-female distance through a parallel tracking of male and female Japanese macaques (*Macaca fuscata yakui*), and the presence rate of males and females during mating and non-mating seasons. During the mating seasons, separated males ventured outside of the group's ranging area and succeeded in mating with females of other groups. During the non-mating season, they did not venture and avoided areas where they were likely to encounter other groups. Males had a greater travel cost when they ranged separately, particularly when they visited other groups. High-ranking males tended to range separately when the reproductive potency of their group was low, but low-ranking males ranged separately more often than did high-ranking males during any season. Low-ranking males tended to stay in the more peripheral part than high-ranking males during the non-mating season; however, they tended to stay in a similar

part of the group during mating seasons. Low-ranking males moved more to the periphery to copulate with their group females, while high-ranking males did not. Social position and the reproductive potency of their group would affect the males’ decision on the reproductive strategy.

2 Introduction

Reproductive benefit is one of the important factors of group-living [Terborgh and Janson, 1986]. The males’ reproductive strategy involves defending females and mating within their own group [Berenstain and Wade, 1983]. However, males being affiliated in groups cannot monopolize estrous females in their own group [Berenstain and Wade, 1983]. Unaffiliated males are also attracted from outside to estrous females in groups [Cords, 1984, Matsumoto et al., 1998] and can also mate with group females [Ohsawa et al., 1993, Zhao et al., 2005]. These males may come from other bisexual groups, all-male groups, or may be a solitary [Cords, 1986, Zhao et al., 2005]. It is evident that the purpose of visiting other groups is to obtain mating partners; however, the reasons for resident males leaving their group and visiting other groups remain unclear. Males leaving their own bisexual groups would pay an opportunity cost, as their original group also has females and the males would lose a chance to mate with them. They may also incur the cost of being attacked by the resident males in the group they visit [Boggess, 1980]. In addition, they would lose other benefits of group-living, such as avoidance of predation and better foraging efficiency [Wrangham, 1980; van Schaik, 1983]. To reveal the factors influencing the pivotal decision to leave their group, continuous tracking of males, not of the group, would be effective for clarifying the conditions when males move away from the group.

The basic reproductive strategy of males living in a bisexual group is to range with females and increase the chances of mating [Boyd et al., 2000]. Individuals compete for favorable spatial positions within their group [Janson, 1990a], with dominant members occupying the advantageous central part while subordinates range in the periphery [Janson, 1990b]. As not all the males can occupy a favorable space to gain exclusive access to females in the group, some males may adopt alternative strategies [Ellis, 1995]. One such strategy is sneak mating, whereby males hide from other individuals to mate with their group females [Soltis, 1999]. This strategy would be effective for lower-ranking males in preventing monopolization of estrous females by high-ranking males. Another alternative strategy would be for the males to leave their group temporarily and copulate with females of other group. This strategy would be particularly effective where the home ranges of multiple groups are contiguous. Males' rank and the number of estrous females in their group may determine whether they range with their group or not. This is because males have a better chance of mating when the number of estrous females is equal to or greater than the males' rank [Takahashi, 2004].

Some factors other than reproduction also influence males' decision to leave their group. Individuals ranging with groups are always subject to competition for food resources [Snaith and Chapman, 2008] and suffer from decreased foraging efficiency [Isbell, 1991; Chapman et al., 1995]. They also pay social monitoring cost to catch up with group members [Kazahari and Agetsuma, 2010]. In our own previous study, we confirmed that short-term separate ranging by male Japanese macaques mitigates within-group contest feeding competition. However, they lose grooming opportunities, become more vulnerable to intergroup competition, and suffer from higher travel costs [Chapter III]. Thus separate ranging has both costs and benefits associated with feeding and social behavior. However, mate search tactics employed by males and inter-male competition appears to influence male habitat use patterns more than the need to maximize foraging efficiency [Watts, 1994].

Japanese macaques (*Macaca fuscata*) form female-bonded multi-male/multi-female groups, in which males emigrate from their natal group when they approach sexual maturity. Although groups are generally cohesive [Sugiura et al., 2011], subgrouping is occasionally reported,; and a considerable number of males are observed to range alone [Chapter II]. During mating seasons, many males visit from outside of the group and succeed in copulation [Yamagiwa, 1985, Okayasu 2001, Hayakawa, 2008]. These males from outside the group are ascertained to include males who belong to other groups [Fukuda, 1989, Sprague, 1991]. Even within groups, Japanese macaque males had a double-layered spatial structure [Yamada, 1966]. In a previous study of a provisioned Japanese macaque group, it was reported that high-ranking males ranged in the central part, while low-ranking males ranged in the peripheral part [Yamada, 1966]. As provisioning influences demography and social behavior (e.g., group size, sex ratio, and affiliative and agonistic interaction) [Hill, 1999], we need to confirm the patterns of spatial positioning associated with males' social position in a wild, non-provisioned group as well. The spatial position of males would be related with their reproductive strategy. Low-ranking males tend to copulate in the periphery of the group by hiding from other individuals [Hayakawa, 2007]. The peripheral position would increase the chance of mating, particularly for low-ranking males. Therefore, to evaluate the effect of spatial position on reproductive strategy, we should clarify whether males copulate in the sight of other members or copulate in the periphery of the group, and also whether males range with the group.

To distinguish these spatial positions of males, we collected two types of data in this study: male-female distance and presence rate. We calculated male-female distance by parallel tracking of two individuals. We also recorded individuals detected in the vicinity of focal males or females. We regarded the focal female’s position as the central part of the group because cohesiveness among females was strong [Chapter III]. We used these data to distinguish whether males range with their group or separately from the group by setting an operational definition. We used these 2 types of data in a complementary manner because each has different features. By parallel tracking, we could record the male-female distance at a fine resolution (30 s), but as we needed to track two individuals simultaneously, there was a constraint on the amount of data we could collect. As presence rate could be recorded for all individuals at one time and we needed to track only one individual, much more amount of data could be collected. However, we recorded on an hourly basis; therefore, time resolution was low. In addition, the absence of particular individuals from the sight of the focal individual does not indicate how far they are separated.

In this study, we aimed to clarify spatial positioning of Japanese macaque males, which would be related with the reproductive strategy, particularly for the situations where males are likely to leave their group. Males would have the following 3 spatial options: stay in the central part of the group, stay in the periphery of the group, or range outside the group (separate ranging). First, in order to distinguish separate ranging from ranging within the group, we made an operational definition of separate ranging based on male-female distance and the presence rate of mature individuals in the vicinity of the focal male. Second, as background information affecting the spatial position of males, we compared reproductive potency between the 2 mating seasons and the number of births during the subsequent birth season. Third, we determined the spatial position of males and compared it among seasons and differently ranked males. We applied the following 4 variables as indices of the spatial position; the proportion of time spent ranging separately, male-female distance when males ranged with the group, presence rate of males in the vicinity of focal females, and presence rate of females in the vicinity of focal males. Fourth, to reveal the influence of reproductive potency on males' separate ranging also on the scale of day, we compared the proportion of time spent ranging separately among days with varying numbers of estrous females. We predict that the frequency of separation is higher when there are fewer estrous females in the group because the option to seek females of other groups would be more advantageous. We conducted the same analysis on high- and low-ranking males separately to detect different responses to the variance in reproductive potency. Fifth, we reported mating behaviors during separate ranging and ranging within the group. We confirmed that males moved away from their own group to mate with the females of other groups. To reveal the spatial position for mating behavior with their group females, we compared the presence rate of females in the vicinity of focal males and the male-female distance for each copulation event between high- and low-ranking males. Finally, we estimated the ranging areas of the group and separated males and compared these among seasons to identify the difference in land use during separate ranging among seasons. Moreover, we compared the travel distance per 10 min between males ranging separately from the group and within the group to evaluate the travel cost during ranging separately. Through these comparisons, we aimed to reveal how males choose from the 3 options of spatial positions with regard to mating strategies.

This study requires extracting the effect of mating on ranging behavior. As Japanese macaques are strict seasonal breeders, and mature individuals have no predators [Takahata et al., 1998], we can identify the influence of reproduction. Furthermore, direct tracking on individuals moving among multiple groups is feasible in our study site because multiple neighboring groups are well habituated [Yamagiwa, 2008] and the home range of each group is relatively small [Hanya et al., 2006]. Therefore, the subjects were ideal for the study of separate ranging.

3 Methods

3-1 *Study site, subjects, and term*

Our study subjects were from the AT group that inhabits the western coastal area of Yakushima, which was the same group as that in Chapter III. We directly tracked both males and females during 3 terms: from September 9 to November 23, 2009; from October 21 to November 10, 2010 (which corresponded to mating season–hereafter mating season I, mating season II, respectively); and from March 19 to June 10, 2010, which represented non-mating season. In addition, we tracked only females from November 24, 2009 to January 24, 2010. We also observed the group in May 2011 to confirm the birth of infants sired during mating season II.

The group included 8, 7, and 7 mature males in mating season I, mating season II, and non-mating season, respectively, and also included 9 mature females through the 3 terms. None out of the 9, and 7 out of the 9 females had infants in mating season I and mating season II, respectively. Our study subjects comprised 7, 5, and 6 mature males in mating season I, mating season II, and non-mating season, respectively, as well as 9 mature females throughout the 3 terms. One mature male immigrated to another group between mating season I (autumn in 2009) and non-mating season (spring in 2010). Throughout the 3 terms, we excluded 1 male (ranked 8th in mating season I) because he had only joined the group during mating season I. During mating season II, another male was excluded from the study because he was absent from the group most of the time. Based on agonistic interactions, the subject males were ranked from 1st to 7th, 1st to 2nd and 4th to 6th, and 1st to 6th in mating season I, mating season II, and non-mating season, respectively. All males had immigrated from other groups. The age of the males was estimated to be 7 - 14 years.

3-2 *Data collection*

We conducted parallel tracking in 3 terms: 16 days in mating season I, 12 days in mating season II, and 35 days in non-mating season. Two researchers tracked 1 male and 1 female, including estrous female (99 h in mating season I, 95 h in mating season II, 263 h in non-mating season) simultaneously using GPS devices (Garmin 60CSx) to record their locations every 30 s. In mating season I and non-mating season, we switched from 1 female to another every 3 h while tracking the same male throughout the day. In mating season II, each male and female was tracked all day. Each male was tracked for 2.4 days (± 0.49 SD), 2.4 days (± 0.48 SD), and 5.8 days (± 0.37 SD) in average during mating seasons I and II, and the non-mating season, respectively. Because the data amount of each male was not sufficient, males were divided into high-ranking and low-ranking males indicating males of 1st to 3rd ranked and 4th to 7th ranked males, respectively. We applied this category for the analysis of effect of males' rank on separate ranging, presence rate, and frequency of copulation. To calculate the duration of separation bouts, we made a rule when we switched our focal female (3-3 Analysis). To avoid the bias of focusing on a particular combination of males and females, we selected the focal animals in advance, taking care to equalize sample size among individuals. We also recorded each location where members of the focal group exhibited some response to the presence of another group as the site of an intergroup encounter [Saito et al., 1998]. We regarded the male visited another group when at least 1 individual from the other groups was observed and the distance from the focal female exceeded 100 m.

The 2 researchers independently recorded other mature individuals that they detected visually throughout each hour of the day (e.g., 6:00–6:59) in mating season I and the non-mating season. The male-following researcher recorded these data during parallel tracking, and the female-following researcher recorded during 42 days from September 9, 2009 to January 24, 2010; and 35 days from March 19 to June 10, 2010. The female-following researcher during mating season II did not record these data.

The number of estrous females in each day was recorded. We judged females’ estrous state from copulation and male sexual behaviors such as sexual attack, hindquarters display, and hand-on-back [Takahata, 1980]. Copulation bout was defined as a male/female mounting series accompanied by ejaculation: the number of copulation bout of focal males was recorded.

3-3 *Analysis*

Based on male-female distance, we standardized a definition to compare separate ranging throughout the multiple terms. Following Chapter III, we operationally defined separation from the group as a distance of >100 m between the focal male and female for more than 10 min. Otherwise, males were regarded as ranging with other group members. We calculated the distance between focal animals based on their locations recorded every 30 s. We validated this criterion in the Results. In calculating the duration of separation bouts, we discarded instances where the observers required >20 min to change focal females. If changing focal females required <20 min, and the distance between the focal male and female remained >100 m, we considered separate ranging as having continued throughout the period. As these determinations may have led to underestimation of separate ranging in mating season I and non-mating season, we address this possible aberration in Results.

To clarify the spatial position of males within their group, we divided male-female distance data into 5-m classes and calculated the percentages of each class in the number of data points <100 m. Because the visibility in this study site was restricted to approximately 20 m [Koda et al., 2008], and cohesiveness among the females of the group was strong [Chapter III], we considered that a male stayed in the central part of the group when the male-female distance was <20 m. In addition, we calculated the male-female distance at the onset of a copulation event by a focal male with a non-focal female of the group and compared it with other distance data.

We defined the presence rate as the proportion of individuals that were visible to the researcher following a focal animal for each 1-h period. For example, if 9 of 15 individuals in the group were observed in the vicinity of a focal male, the presence rate of mature individuals in the vicinity of the focal male in that hour would be 60%. We applied this value in each hour as the data unit for analysis. In this manner, we calculated the presence rate of mature individuals in the vicinity of focal male, that of females in the vicinity of the focal male, that of males in the vicinity of focal females, and that of females in the vicinity of focal females. These were applied for validating the definition of separate ranging, confirming aggregation among females and examining the variation with respect to seasons, males' rank, and the number of estrous females per day.

Using the Kernel method [Worton, 1989] with Hawth's tool in ArcGIS 9.3 (ESRI, Inc.), we estimated ranging area (95%) of the females and males who ranged separately from their group, respectively. We set 10 m as the raster size and 50 m as the smoothing factor. The size of the ranging area can be affected by the number of data points. To examine the effect, we flattened out the data amount to the minimum number (separated males during mating season I: 536 min) by discarding the location data randomly. We connected the locations of focal animals at intervals of 10 min and calculated the travel distance per 10 min.

We built a general linear model [Mundry and Nunn, 2009] that included study terms as a predictor variable and duration of separate ranging as a response variable. We also examined the influence of 2 predictor variables (the proportion of separate ranging and male rank) on the response variable (the number of estrous females in each day). We log-transformed duration of separate ranging to achieve an approximation of normality. We used non-parametric statistical tests to examine associations among variables with the alpha level set at 0.05. All models and tests were conducted using R 2.13 (R Development Core Team 2012).

4 Results

4-1 *Validation for the definition of separate ranging*

The distance between males and females sometimes exceeded several hundreds of meters in all the study terms (Fig. IV-1). Median and maximum distances between focal males and females during mating season I, mating season II, and non-mating season were 32.4 m, 42.9 m, and 48.0 m, and 365 m, 973 m, and 632 m, respectively.

When the minimum male-female distance for 1 h exceeded 100 m, the proportion of mature individuals around the focal male was not zero only in 4 cases (N = 23, Fig. IV-1). This indicates that when distance exceeded 100 m, the male separated from most of the group members (separate ranging) and mostly ranged alone. In the 4 cases, subgrouping or consorting for mating may have occurred.

4-2 *Difference of reproductive potency between mating seasons I and II*

The group's reproductive potency was higher in mating season I than that in mating season II. The groups' mean number of estrous females during the mating season I (3.14/day ±0.814 SD) was greater than that during the mating season II (2.08/day ±1.14 SD) (U test , $P < 0.001$, Table IV-3). During both terms, all females, except 1 old female, exhibited signs of estrous behavior. Although the mean frequency of copulation with females in their own group did not differ between two mating seasons (U test, $P = 0.309$), the number of births in the following birth seasons was higher for mating season I (7 infants) than for mating season II (1 infant).

4-3 *Seasonal variations in separate ranging and presence rate*

Males ranged separately from their group for a shorter time during mating season. Duration of separate ranging bout was longer during non-mating season but shorter during mating seasons I and II (GLM, $P < 0.05$, Tables IV-1, 2). The proportion of separate ranging time relative to observation time was highest during non-mating season, intermediate during the mating season II, and lowest during the mating season I (χ^2 test with Bonferroni correction, $P < 0.05/3$, Table IV-1). We discarded 6 (non-mating season) and 4 (mating season I) possible separation bouts as we switched focal females. However, even when we included the possible separation bouts, the tendencies of duration and proportion of time for separate ranging remained the same (GLM, $P < 0.05$, χ^2 test with Bonferroni correction, $P < 0.05/3$). The proportion of separate ranging relative to observation time in each day was greater for low-ranking than for high-ranking males in mating season I and non-mating season; but not mating season II (Steel-Dwass test, mating season I and non-mating season, $t = 2.12$, 2.33, $P < 0.05$; mating season II, $t = 1.02$, $P = 0.43$, Fig. IV-2). The proportion of separate ranging of low-ranking males was greater in the non-mating season than in the mating seasons (Steel-Dwass test, the non-mating season vs mating season I and II, $t = 2.38$, 2.37, $P < 0.05$). The proportion of separate ranging of high-ranking males was lower during mating season I than during mating season II and the non-mating season (Steel-Dwass test, mating season I vs the non-mating season and mating season II, $t = 2.17$, 2.19, $P < 0.05$, Fig. IV-2).

When the focal male ranged within the group, the male-female distance was shorter for high-ranking males than that for low-ranking males during the non-mating season but did not differ during the mating seasons. In addition, the presence rate of females in the vicinity of focal males ranging with the group was lower in low-ranking males than in high-ranking males only during the non-mating season. When the male-female distance was < 100 m, the proportion of the distance <20 m was higher in high-ranking males than in low-ranking males only during the non-mating season (χ^2 test, mating season I, $\chi^2 = 2.18$, $P = 0.139$; mating season II, $\chi^2 = 0.41$, $P = 0.521$; non-mating, $\chi^2 = 690.62$, $P < 0.0001$, Fig. IV-3). When males ranged with their group, the presence rate of females in the vicinity of the focal male was lower in low-ranking males than in high-ranking males during the non-mating season (Steel-Dwass, $P < 0.05$), whereas no difference was observed between high- and low-ranking males during mating seasons I and II (Steel-Dwass, $P > 0.1$, Fig. IV-4). The presence rate of males in the vicinity of focal female was greater in high-ranking males than in low-ranking males both during mating season I (χ^2 test, $P < 0.001$) and the non-mating season (χ^2 test, $P < 0.001$, Fig. IV-5); data were not available for mating season II. The presence rate of males in the vicinity of the focal female did not significantly differ between mating season I (0.29 males ±0.28 SD) and the non-mating season (0.35 males ±0.29 SD). We applied the hours when more than half of 8 other group females were in the vicinity of the focal female (the presence rate of females in the vicinity of the focal female >0.5) for the analysis to ensure that focal females, based on whose position we examined the position of males, were in the central part of the group. The hours that met the condition were 49.4% of all observation hours (283 h of 573 h).

4-4 *Influence of reproductive potency on separate ranging and presence rate*

A negative correlation was observed between the number of estrous females on each day and the proportion of separate ranging relative to observation time (Spearman test, $r = -0.629$, $P < 0.001$, Fig. IV-6). When data were divided by males' rank, a similar tendency was found only in high-ranking males, whereas this was not the case in low-ranking males (high-ranking, $r = -0.708$, $P < 0.01$; low-ranking, $r = -0.469$, $P = 0.106$, Fig. IV-7). However, there no correlation was observed between the number of estrous females and the presence rate of males in the vicinity of the focal female (r = 0.007, P = 0.977, Fig. IV-6). In addition, no correlation was observed when data were divided by males' rank (high-ranking, r = −0.247, P = 0.416: low-ranking, r = 0.019, P = 0.962). Even when we excluded the hours when the presence rate of females in the vicinity of the focal females was <0.5 from data of mating season I, the result did not change.

4-5 *Mating behavior*

The frequency of copulation with their group females did not differ between high- and low-ranking males both during mating seasons I and II (U test, mating season I, P = 0.7, N = 34; mating season II, P = 0.2, N = 29). When a focal male copulated with a non-focal female of the group, the distance between the focal male and the focal female was <100 m in all the 63 cases. For low-ranking males, the male-female distance was longer when the focal male copulated with a non-focal female of the group than the distance when they conducted anything except copulation (Wilcoxon signed-rank test with Bonferroni correction, P < 0.05/6, Fig. IV-8), whereas high-ranking males kept the same level of distance whether they copulated or did not copulate (Wilcoxon signed-rank test with Bonferroni correction, P = 0.020 > 0.05/6). Moreover, the presence rate of females in the vicinity of low-ranking males in the hours that included copulation events with group females was smaller than that in the vicinity of high-ranking males (U test, P < 0.001, Fig. IV-9). Even when we excluded the hours when the presence rate of females in the vicinity of focal females was <0.5 from data of mating season I, the difference was still significant (U test, $P < 0.05$).

Males visited other groups and copulated with the females of the other group during each mating season. During mating season I, each of the 5th and 6th males was observed to visit other groups (E, Nina-A2) once during 99 h of observation and copulated with the females of groups in both instances. During mating season II, each of 5 males was observed to visit other groups (E, Nina-A2, Kw-z) once each during 95 h of observation, and copulation with the females of these groups was observed twice (1st and 6th ranked males). In all the cases, the females of other groups approached them, and the males of other groups responded with aggression. The frequency of copulation with the females of other groups during separate ranging was 0.22 and 0.08 times/h during mating seasons I and II, respectively, while the frequency of copulation with the females of their group during ranging with their group was 0.38 and 0.40 times/h during mating seasons I and II, respectively.

4-6 *Ranging behavior*

Males ranging separately from their group ventured outside of groups' home range only in mating seasons. In mating season I and mating season II, the ranging area of the separated males (37.9, 51.1 ha, respectively) spread out the group's ranging area (48.1, 48.8 ha, respectively, 21.3% and 28.5%, respectively, of separated males' ranging area was outside of group's ranging area), whereas during non-mating season, the entire ranging area of the group (53.0 ha) included almost all the ranging area of the separated males (42.6 ha). This meant that males hardly ever range outside of the groups' ranging area (2.00%

of separated males' ranging area was outside of group's ranging area: Fig. IV-10). When we flattened out the data amount by discarding the location data randomly, separated males' ranging area still spread out the group's ranging area during each mating seasons, but not during non-mating season.

The core ranging area of separated males included a lower number of encounter points in non-mating season, in contrast to mating seasons I and II. The group's core ranging area (50% Kernel estimate) in mating seasons I, II, and non-mating season included 2 out of 4, 4 out of 7, and 6 out of 9 locations, respectively, where intergroup encounters occurred. The core ranging area of separated males in mating seasons I, II, and non-mating season included 2 out of 4, 4 out of 7, and 1 out of 9 locations of intergroup encounters (Fig. IV-10).

The travel distance per 10 min was greater for males ranging separately than that for males ranged with the group in all the 3 study terms (Steel-Dwass test, $P < 0,01$, Fig. IV-11). Moreover, the travel distance during 7 separate ranging bouts in which males visited other groups was greater than that during the other separate ranging bouts (χ^2 test, $P < 0.001$, Fig. IV-12).

5 Discussion

5-1 *Separate ranging as a reproductive strategy*

Males repeated short-term separate ranging in both mating and non-mating seasons. However, for both mating seasons, the duration of separate ranging bout was shorter than that in the non-mating season and the proportion of separate ranging was lower in the mating seasons than in the non-mating season. This would be because males are attracted to groups by estrous females. However, once they were separated, males moved outside of the group’s ranging area in mating seasons while they did not in the non-mating season. The core ranging area of the group and separated males included the same number of locations of inter-group encounters in the mating seasons. In non-mating season, the core ranging area of the separated males included a smaller number of encounter points. Separated males did not move outside the home range of their group in the non-mating season because they can avoid within-group contest competition, whereas vulnerability to inter-group competition is one of the costs of separate ranging [Chapter III]. During mating seasons, separated males appeared to actively search for other groups.

Copulation with the females of other groups by separate ranging can be one reproductive strategy option. In mating seasons, males visited other groups 7 times in total, and succeeded in copulating with females of other groups in 4 cases. The frequency of copulation with the females of their group during ranging with their group was greater than that with the females of other group during separate ranging. In this study, the small number of copulations observed outside the group was likely to be underestimated because aggressions by the males of other groups, which occurred every time the focal males visited, made continuous observation difficult. We sometimes temporarily lost sight of the focal males. Although we could not convincingly estimate its frequency, one of the benefits of moving outside of the groups’ ranging area during mating seasons would be the copulation with females of other group. By separate ranging, males could increase not only the number of copulations but also the number of potential mating partners. This strategy was feasible in the study site because group density is high [Yoshihiro et al. 1999]. This finding was in accordance with previous studies in this area. In Yakushima, males who appeared from outside the group are reported to account for 41% of copulations [Sprague, 1991] and sire 56% of offspring [Hayakawa, 2008].

The travel cost is one of the costs of separate ranging, and it is intensified as a reproductive strategy. The travel cost was greater when males ranged separately than when males ranged with the group both during mating and non-mating seasons. This would partly be because separated males need to identify their group to rejoin them [Chapter III]. In addition, the travel cost was greater when separated males visited other groups than when they were separated from the group but did not visit other groups. Males have to pay additional travel costs to identify another group or to escape from the aggression by the males of other groups.

Males chose to range separately when their group's reproductive potency was low, both on the scale of day and year. On the scale of year, proportion of time spent separate ranging in the mating season I, when the number of estrous females in the group was higher, was less than that in the mating season II. Because the interbirth interval is approximately 2 years at the study site [Takahata et al., 1998], reproductive potency varies by year, particularly when group females give birth in synchrony. Actually, in mating season II, because 7 out of 9 mature females had infants, the probability of giving birth next birth season was quite low. Actually, the number of birth in the following birth season was only 1. Differences in separate ranging were also found on the scale of day. For mating seasons, a negative correlation was found between the number of females in estrous per day and the proportion of separate ranging. Males decided to range separately on the basis of females' estrous state on that day. When the number of estrous females in their group was extremely low, males would take a chance of seeking the females of other group rather than losing an opportunity for mating by staying in the group.

5-2 *Rank and seasons as factors for spatial position of males in and out of group*

Males would have the following 3 spatial options: stay in the central part of the group, stay in the periphery, or range separately from the group. Males would apply different reproductive strategies with respect to their social position, which would affect their spatial position.

High-ranking males changed the proportion of time spent ranging separately in response to fluctuations in the reproductive potency of their group, but low-ranking males did not do so, and they ranged separately more often than did high-ranking males during any seasons. During mating season II, when the reproductive potency of the group was lower, even high-ranking males tended to separate from the group, whereas during mating season I, the proportion of time spent ranging separately by high-ranking males was extremely low. In contrast, low-ranking males tended to range separately even when reproductive potency was higher. Moreover, high-ranking males increased the proportion of separate ranging on days when the number of estrous females was low, while low-ranking males did not have such a tendency. Compared with low-ranking males, high-ranking males were less likely to range separately because they experienced greater benefits and fewer costs through group-living (receiving more grooming while receiving less influence of contest competition) [Chapter III], which holds true both during mating and non-mating seasons. As for reproduction, dominant males use the strategy of mate guarding within their group [Matsubara, 2003] and would therefore need to range with the estrous females for quite a while. However, both the high- and low-ranking males tended to range separately when they had difficulties in copulation with their group females because of the low reproductive potency of their group at that time.

Spatial variations with respect to seasons and social positions were also found when males ranged with the group. When focusing on males ranging with their group, low-ranking males tended to stay in more peripheral parts than high-ranking males during the non-mating season. However, during mating seasons, such a difference was not found, as low-ranking males increased the proportion of time they spent in the central part of the group. This is indicated by the finding that the male-female distance was <100 m, and the presence rate of females in the vicinity of focal males ranging with the group differed by rank during the non-mating season but not during the mating seasons. During mating seasons, low-ranking males would venture close to the central part of their group when they ranged with their group probably because they were attracted to estrous females. During the non-mating season, low-ranking males tended to stay more in the peripheral part than did high-ranking males when they ranged with the group. This would be because individuals compete for favorable spatial positions within their group [Janson, 1990a], with dominant members occupying the advantageous central part while subordinates range in the periphery [Janson, 1990b]. In fact, low-ranking males in the subject group have smaller benefits and greater costs through social interaction among group members [Chapter III].

The proportion of time spent in the central part over the whole observation time was higher in high-ranking males than in low-ranking males. This is indicated by the fact that the presence rate of males in the vicinity of focal females was lower in low-ranking males than in higher-ranking males both during mating and non-mating seasons. This is seemingly contradictory to the fact that, when focusing on males ranging with the group, low-ranking males spent as much time in the central part as high-ranking males during the mating seasons (see above). However, the presence rate of males in the vicinity of the focal female indicates the males' position, not over the time only when ranging with the group, but over the whole observation time. Therefore, the males' absence from the sight of females implies 2 following possibilities: males may stay in the peripheral part of the group or they may range separately from the group. During the non-mating season, both frequent separate ranging and more time spent in the periphery of the group would explain the low proportion of time spent in the sight of group females by low-ranking males than high-ranking males. During mating season I, the difference would be due solely to much more frequent separate ranging by low-ranking than high-ranking males, although both stayed in a similar position when ranging with the group.

High-ranking males tended to mate with their group females in the central part of the group, while low-ranking males did so more often in the periphery. During the mating season, when males ranged with their group, both high- and low-ranking males stayed in a similar position within the group, but only low-ranking males moved more to the periphery to copulate with their group females. In contrast, high-ranking males stayed in the same position even when they copulated. Explanations for these scenarios may be as follows: (1) the spatial position within their group did not differ between high- and low-ranking males when they conducted anything except copulation (2) the male-female distance when the focal male copulated with a non-focal female of the group was longer in low-ranking males than in high-ranking males, and (3) the presence rate of females in the vicinity of low-ranking males when they copulated with group females was smaller than that in the vicinity of high-ranking males. Low-ranking males succeeded in copulation with their group females by hiding from other mature females, whereas high-ranking males would apply the tactic of mate guarding in the central part of the group.

A previous study [Hayakawa 2007] conducted in the present study site reported that low-ranking males did not copulate in the sight of other group members, but that study did not reveal the absolute position where these sneak-matings occurred. We reveal the entire process of sneak mating as follows: low-ranking males usually stay in a similar position within the group as high-ranking males, and they move more to the peripheral part only when they copulate but never separate from the group >100m. Low-ranking males stay in the central part of the group during the mating seasons probably to monitor estrous females and escape from other members to avoid disturbance when they copulate. Moreover, as the frequency of copulation did not differ between high- and low-ranking males, sneak mating would be as effective as the mate guarding strategy. In addition to copulation with group females, low-ranking males were more likely to range separately to copulate with the females of other groups. Therefore, their mating success would not necessarily be lower than high-ranking males. However, they would pay substantial costs of travel or aggression by the males of other groups. In contrast, high-ranking males succeed in copulation using the mate-guarding tactic without such costs. Due to the Westermark effects [Westermarck, 1921; Takahata, 1982] males with long tenure may become less acceptable as copulation partners, and it may become more difficult for them to succeed in copulation using by mate-guarding behavior. Males would be able to copulate with the females of other groups; however, this strategy of separate ranging involves larger costs. The delicate balance of cost and benefit of the strategies by high- and low-ranking males, which have been shown in this study, and such chronic changes in males' attractiveness seem to drive males to repeat intergroup transfer.

In conclusion, the three options for males' spatial positioning were affected by seasons, the males' social position, and reproductive potency of their group. Differently ranked males had different reproductive strategies associated with their spatial position.

Chapter V

General Discussion

1 Summary of the results

In the present study, we revealed that males decide to preferentially range with other animals depending on the intensity of inter- and within-group competition, their social position, and the reproductive potential of their group.

Data from point census described in Chapter II suggest that a considerable number of males remained outside groups, and the male cohesiveness with groups is flexible and varies with ecological and social circumstances. The density of males ranging alone did not differ among different types of vegetation despite population density was shown to be affected. During mating season, males showed strong cohesiveness with a group, probably in search of resident estrous females. Outside the mating season, males also showed strong cohesiveness with a group where inter-group competition was strong.

In Chapter III, parallel tracking was carried out during non-mating season revealing that group males frequently engaged in short-term separate ranging. Low-ranking males were able to avoid within-group contest competition for food by ranging alone. However, this behavior was associated with higher traveling costs and these separated males were more vulnerable to inter-group competition and had fewer opportunities for social interaction. Therefore, the duration of separate ranging was relatively short, and they hardly moved outside the home range of the group.

In Chapter IV, parallel tracking was carried out during mating seasons and the spatial position of males in relation to their group was recorded. Males separately ranged as a mating strategy, but the proportional time spent within the group increased compared with the non-mating season. Low-ranking males were more likely to stay in the central part of the group during the mating season than during the non-mating season. However, low-ranking males moved to a more peripheral part when copulating with their group females. High-ranking males mostly stayed in the central part of the group. However, both of high- and low-ranking males conducted separate ranging when the reproductive potential of their group was extremely low to seek females of other groups.

2 Double-layered spatial structure of males within a group

Wild Japanese macaque males had a double-layered spatial structure within their group: the central part of the group or the periphery. We showed that high-ranking males were likely to be observed in the central part than low-ranking males were. When focusing on males ranging with the group during the non-mating season, low-ranking males tended to stay in the more peripheral part than did high-ranking males. In contrast, during the mating season, high- and low-ranking males were observed in the central part of the group at the same rate. However, high-ranking males mated with their group females in the central part of the group, whereas low-ranking males did so in the periphery. Although previous studies on Japanese macaques reported that high-ranking males tend to copulate in the sight of other group members [Hayakawa, 2007], I determined the absolute position where sneak-mating occurred and where males stayed when not copulating. Studies on other primate species reported that individuals compete for favorable spatial positions within their group [Janson, 1990a]. Baboons (*Papio cynocephalus ursinus*) present different spacing patterns between sexes and vary if infants are present [Cowlishaw, 1999]. In capuchin monkeys (*Cebus apella*), dominant members range around those areas where foraging success is expected to be the greatest, juveniles choose to occupy those spaces with the lowest predation risk, and the positions adopted by subordinate adults neither maximized foraging success nor minimized predation risk [Janson, 1990b]. In the present paper, we revealed that the spatial positioning of Japanese macaque males varied with social position in a wild, non-provisioned group, which is an observation that has to date only been reported in provisioned groups [Yamada, 1966, Soltis, 1999]. Males also varied their spatial positioning with seasons and reproductive behavior.

3 Separate ranging as the third option of spatial position

To range outside the group is a third spatial positioning option for males. We gathered data covering the entire process of short-term separate ranging, from the time they left their group until they returned. In previous studies on Japanese macaques, it was reported that several males visit from outside the group and succeed in copulation [Yamagiwa, 1985, Okayasu 2001, Hayakawa, 2008]. However, the source of those males was not identified. This study showed that some of the males visiting from outside the groups during mating seasons are often group males. In addition, in previous studies, the absence of males from their group or visiting from outside has been considered to be related to reproduction [Yamagiwa, 1985, Sprague, 1991]. However, present study showed that males also chose to range outside their group as a feeding strategy. Males conducted separate ranging during non-mating season, and this behavior is related to the intensity of inter- and within-group competition. Males may compensate the costs of group living without losing benefits completely.

4 Difference of affiliations of “males ranging alone” and “separated males”

It is worth pointing out that “males ranging alone” (as defined in Chapter II) and “males ranging separately from the group” (Chapters III and IV) are different concepts. Japanese macaque males emigrate from their natal groups when they approach sexual maturity, and although most males will rapidly join another group, some join all-male groups or become solitary males [Sugiyama 1976; Sprague et al. 1998]. The males ranging separately from the group included only males who were affiliated to a group, whereas males ranging alone would include group males, solitary males, and males belonging to an all-male group. In previous studies, the affiliations of males have been defined as follows. Group males are usually defined as those ranging with a bisexual group both during the mating and non-mating seasons [Yamagiwa, 1985, Sprague, 1991, Takahashi, 2004]. In an all-male group, several males range together unaccompanied by females [Sprague, 1998]. Males are regarded as solitary when they range alone for at least several months [Muroyama, 2000]. In Chapter II, males ranging alone are defined as those that were detected at census points on their own and no group was detected for at least 1 h before and after the detection. Therefore, males ranging alone could include not only solitary males but also group males temporarily ranging separately, as well as males from an all-male group. In contrast, in Chapter II and IV, we operationally defined a male as separated from the group when he maintained a distance of > 100 m from the focal female for over 10 minutes. The separated males included only group males, because the focal males were observed with the group both in the mating and non-mating season.

Despite the difference in definition between males ranging alone and separated males, some common points can be readily identified in the results. Repeated observation of short-term separate ranging allowed analysis of the factors likely determining the decision of ranging separately or to stick with a group (Chapters III and IV). During the non-mating season, separated males obtained benefits associated with feeding, but paid costs in social interaction and because of inter-group competition. The vulnerability of separated males to inter-group competition also follows the results presented in Chapter II because the density of males ranging alone decreased where inter-group competition intensified. During the mating season, group males were more likely to remain with their group in order to mate with females of their group. However, when the males ranged separately from their group, they sometimes visited other groups and successfully mated there. This also coincides with the low density of males observed ranging alone during the mating seasons described in Chapter II. Therefore, regardless of their affiliation and the length of separation from the group, the costs and benefits arising from ranging without group would be common and are likely to include the necessity of social interaction, finding a mating partner, or escaping from competition. However, further data on males from all-male groups and solitary males would be necessary to test this hypothesis.

5 Separate ranging and immigration as mating strategy

In this study, it is confirmed that males could access multiple females from their own group or different groups by separate ranging. In contrast, when males immigrate to another group, males would obtain new mate partners but will lose the females of the previous group. This suggests that short-term separate ranging has an advantage over migrating to another group in terms of the number of mating partners. However, Japanese macaque males are known to migrate to other groups every few years [Sprague et al., 1998]. This would be because dominant males who attain their social position by long tenure cannot necessarily achieve higher mating success than low-ranking males. Most males join a group at the bottom of the rank order, and their rank rises with their tenure [Suzuki et al., 1998]. However, male and female Japanese macaques with intimate relationships do not tend to copulate [Takahata, 1982], and males with long tenure are rejected or hardly chosen by periovulatory females from their group [Inoue and Takenaka, 2008]. In fact, the frequency of copulation with their group females did not differ between high- and low-ranking males [Chapter IV]. Even if males are rejected by the females of their group, they may be able to aim to mate with the females of other groups by separate ranging; however, males can easily monitor the estrous state of females of their own group, whereas it is more difficult to monitor females of other groups. Therefore, immigration to other groups would be advantageous for males with long tenure.

6 Future research: strategies of males in all-male groups and solitary males

Chapters III and IV deal with group males and their ranging behavior. However, continuous observations on males of all-male groups and solitary males would be necessary to understand how males choose to associate with conspecifics throughout their life. Males of all-male groups and solitary males may have no interaction with females or other individuals for extended periods of time. If this situation is maintained throughout the mating season, they would have no opportunity to mate; however it remains unclear how males manage the cost of losing opportunities for mating and social interaction. These males may intermittently interact with females regardless of their affiliations, but continuous observation of males of all-male groups and solitary males would be necessary to examine this possibility. All-male groups may be the transient residence for males who cannot be affiliated to bisexual groups. Another possibility is that males of all-male groups may avoid daily ranging with females but they approach them during mating season. Males in all-male groups may also need to spend less effort in defending females, than their counterparts in bisexual groups. As individuals from different age-sex classes have different nutritional requirements and ranging ability, traveling with other age-sex classes may also incur additional costs [van Schaik and van Noordwijk, 1986]. As a result, travelling would be less costly for males of all-male groups. Alliances among males are important in reproductive competition [Chapais, 1995]; therefore, associating with other males may be advantageous in obtaining mating partners. Although group males ranging separately from the group were vulnerable to inter-group competition, males in all-male groups may not be vulnerable. At the same time, although group males had frequent opportunities to socially interact with females of their group, males in male-only groups are not presented with such opportunities. By forming all-male groups, males may reduce the costs associated with group living but at the same time may obtain fewer benefits from the group. Continuously tracking all-male groups would help in understanding other aspects of this strategy.

In addition, solitary life may be a transient state for males who cannot be affiliated to groups or are seeking a group to emigrate. Solitary males do not incur the cost associated with group living, but eventually need to visit groups to obtain mating partners. Observation of solitary males would also provide further data on this specific male strategy and their dispersal behavior. In Japanese macaques, males emigrate from their natal groups when they approach sexual maturity [Sprague et al., 1998; Sugiyama, 1976] and during emigration to another group, males would range on their own. The observation of this process would shed light on how they locate and choose a group to emigrate to and how far do males disperse. However, observing solitary males continuously is seeded with difficulties as their ranging area is not stable and they hardly vocalize [Muroyama, 2000].

Combining traditional observational methods with new technologies may facilitate the continuous observation of solitary males. Radio and GPS tracking systems would be a suitable option. Radio tracking may facilitate locating specific animals by receiving signals from a radio-transmitter attached to the individual. GPS telemetry collars can automatically record locations of animals and store them. Some models even allow fro remotely retrieving this data through the GSM cell phone network. GPS tracking allows for continuously tracing the migration pathway of males as long as their ranging area is covered by the network. GPS telemetry would also be suitable to follow their long-distance movements. The radio telemetry tags are cheaper and have a longer battery life than GPS telemetry collars; however, we cannot follow long-distance movements by radio tracking because its maximum detectable range is restricted to few kilometers, whereas males have been known to travel for several hundreds of kilometers [Yoshimi and Takasaki, 2003]. The main problem of GPS collars is the short battery life. For collars small enough to be attached to a Japanese macaque without altering their behavior, the battery would last for approximately 2 or 3 months if programed to record 24 locations per day.

One significant shortcoming of these methods is the technical limitation to collect enough data from a large number of animals. To clarify the factors determining the decision of males to affiliate to a group and in order to understand the costs and benefits associated with group behavior, it would be necessary to trace different individuals for a long period of time. Facial recognition systems could be useful for collecting data on migration and affiliation transition for a large number of males. Face recognition system are able to identify animals from photographs and register this identity into a database, allowing the identification of the same animal again. Thus far, individual identification depends on the skills and recollection abilities of each individual researcher. In addition, identification databases of each researcher are difficult to share among researchers. Furthermore, to ensure accurate identification, the same individual must be frequently observed. The area that can be covered by an individual researcher is very limited and can rarely cover the entire range of a solitary male. This makes it unfeasible to monitor solitary males by individual identification. This limitation is not observed with the use of the face recognition software. In addition, the face recognition software allows us to use past photographs for identification; therefore, it makes it possible to trace past movements. Face recognition systems for humans have already achieved high accuracy and have been applied [Li and Jain, 2011]. However, the programs and applications should be remodeled for Japanese macaques and expert cooperation would be required.

Another option to examine the dispersal distances of males is to analyze patterns of gene flow at the population level from mtDNA data. mtDNA is matrilineally inherited [Giles et al. 1980] and females remain in their natal groups; specific mtDNA haplotypes in females are observed for each region or group. Six different haplotypes have been described from individual macaques from Yakushima, with some being observed only in the lowlands [Hayaishi and Kawamoto, 2006]. Males inherit mtDNA from their natal group and may immigrate to other groups, which are commonly characterized by a different set of haplotypes. Therefore, by identifying the main female haplotypes in each region and comparing them with male haplotypes, we can reveal the group of origin for each male and identify patterns of gene flow among populations. In addition, we can clarify the range of hereditary interchange and gene flow in the population. This would be essential information to understand the role of males in gene dispersal and the life history of males.

References

Abernethy, K. A., White, L. J. T., & Wickings, E. J. (2002). Hordes of mandrills (*Mandrillus sphinx*): extreme group size and seasonal male presence. Journal of Zoology, 258(01), 131-137.

Agetsuma, N., & Noma, N. (1995). Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) in response to heavy fruiting of *Myrica rubra*. International Journal of Primatology, 16(3), 247-260.

Alexander, R. D. (1974). The evolution of social behavior. Annual review of ecology and systematics, 5, 325-383.

Altmann, J. (1974). Observational study of behavior: sampling methods. Behaviour, 49, 227-267.

Asensio, N., Korstjens, A. H., & Aureli, F. (2009). Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. Behavioral Ecology and Sociobiology, 63(5), 649-659.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Fiore, A. D., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson J. H., Ramos-Fernandez, G., Strier, K. B., & van Schaik, C. P. (2008). Fission-Fusion Dynamics. Current Anthropology, 49(4), 627-654.

Berenstain, L., & Wade, T. D. (1983). Intrasexual selection and male mating strategies in baboons and macaques. International Journal of Primatology, 4(2), 201-235.

Boggess, J. (1980). Intermale relations and troop male membership changes in langurs (*Presbytis entellus*) in Nepal. International Journal of Primatology, 1(3), 233-274.

Borries, C. (2000). Male dispersal and mating season influxes in Hanuman langurs living in multi-male groups. In Kappeler, P. M., editors. Primate Males. Cambridge University Press. p 146-158.

Boyd, R., Silk, J. B., Walker, P. L., & Hagen, E. H. (2000). How humans evolved (Vol. 8). New York: WW Norton.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. I., Borchers, D. L., & Thomas, L. (2004). Advanced Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press.

Buckland, S. T., Marsden, S. J., & Green, R. E. (2008). Estimating bird abundance: making methods work. Bird Conservation International, 18(S1), S91-S108.

Brown, J. L. (1982). Optimal group size in territorial animals. Journal of Theoretical Biology, 95(4), 793-810.

Chapais, B. (1995). Alliances as a means of competition in primates: evolutionary, developmental, and cognitive aspects. American Journal of Physical Anthropology, 38(S21), 115-136.

Chapman, C. A., White, F. J. & Wrangham, R. W. (1994). Party size in chimpanzees and bonobos. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors. Chimpanzee cultures. Cambridge: Harvard University Press. p 41-58.

Chapman, C. A., Chapman, L. J., & Wrangham, R. W. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behavioral Ecology and Sociobiology, 36(1), 59-70.

Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in primates: the importance of travel costs. On the move: how and why animals travel in groups. University of Chicago Press, Chicago. p24-41.

Clutton-Brock, T. H., & Parker, G. A. (1995). Punishment in animal societies. Nature, 373(6511), 209-216.

Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P., Manser, M., Skinner, J. D., & Brotherton, P. N. M. (1999). Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. Journal of Animal Ecology, 68(4), 672-683.

Cords, M. (1984). Mating patterns and social structure in redtail monkeys (*Cercopithecus ascanius*). Zeitschrift für Tierpsychologie, 64(3-4), 313-329.

Cowlishaw, G. (1999). Ecological and social determinants of spacing behaviour in desert baboon groups. Behavioral Ecology and Sociobiology, 45(1), 67-77.

Crook, J. H. (1970). The socio-ecology of primates. Social behaviour in birds and mammals, 103-166.

De Waal, F. (2007). Chimpanzee politics: Power and sex among apes. JHU Press.

Eisenberg, J. F., Muckenhirn, N. A., & Rundran, R. (1972). The relation between ecology a social structure in primates. Science, 176(4037), 863-874.

Ellis, L. (1995). Dominance and reproductive success among nonhuman animals: a cross-species comparison. Ethology and Sociobiology, 16(4), 257-333.

Fooden, J., & Aimi, M. (2005). Systematic review of Japanese macaques, *Macaca fuscata* (Gray, 1870). Fieldiana Zoology, 1-198.

Fukuda, F. (1989). Habitual fission-fusion and social organization of the Hakone troop T of Japanese macaques in Kanagawa Prefecture, Japan. International Journal of Primatology, 10(5), 419-439.

Furuichi, T. (2009). Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study. Primates, 50(3), 197-209.

Giles, R. E., Blanc, H., Cann, H. M., & Wallace, D. C. (1980). Maternal inheritance of human mitochondrial DNA. Proceedings of the National academy of Sciences, 77(11), 6715-6719.

Goodall, J. (1986). The chimpanzees of Gombe: patterns of behavior. Cambridge: Harvard University Press.

Haberman, S. J. (1973). The analysis of residuals in cross-classified tables. Biometrics, 205-220.

Hall, C. L., & Fedigan, L. M. (1997). Spatial benefits afforded by high rank in white-faced capuchins. Animal Behaviour, 53(5), 1069-1082.

Hamilton, W. D. (1971). Geometry for the selfish herd. Journal of theoretical Biology, 31(2), 295-311.

Hanya, G., Yoshihiro, S., Zamma, K., Kubo, R., & Takahata, Y. (2003). New method to census primate groups: estimating group density of Japanese macaques by point census. American Journal of Primatology, 60(2), 43-56.

Hanya, G. (2004). Diet of a Japanese macaque troop in the coniferous forest of Yakushima. International Journal of Primatology, 25(1), 55-71.

Hanya, G., Yoshihiro, S., Zamma, K., Matsubara, H., Ohtake, M., Kubo, R., Noma, N., Agetsuma, N., & Takahata, Y. (2004). Environmental determinants of the altitudinal variations in relative group densities of Japanese macaques on Yakushima. Ecological Research, 19(5), 485-493.

Hanya, G., Zamma, K., Hayaishi, S., Yoshihiro, S., Tsuriya, Y., Sugaya, S., Kanaoka, M. M., Hayakawa, S., & Takahata, Y. (2005). Comparisons of food availability and group density of Japanese macaques in primary, naturally regenerated, and plantation forests. American Journal of Primatology, 66(3), 245-262.

Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y., & Chijiiwa, A. (2006). Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. Primates, 47(3), 275-278.

Hanya, G., Matsubara, M., Hayaishi, S., Zamma, K., Yoshihiro, S., Kanaoka, M. M., Sugaya, S., Kiyono, M., Nagai, M., Tsuriya, Y., Hayakawa, S., Suzuki, M., Yokota, T., Kondo, D., & Takahata, Y. (2008). Food conditions, competitive regime, and female social relationships in Japanese macaques: within-population variation on Yakushima. Primates, 49(2), 116-125.

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

Harding, R. S., & Olson, D. K. (1986). Patterns of mating among male patas monkeys (*Erythrocebus patas*) in Kenya. American Journal of Primatology, 11(4), 343-358.

Hashimoto, C., Furuichi, T., & Tashiro, Y. (2001). What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. International Journal of Primatology, 22(6), 947-959.

Hayaishi, S., & Kawamoto, Y. (2006). Low genetic diversity and biased distribution of mitochondrial DNA haplotypes in the Japanese macaque (*Macaca fuscata yakui*) on Yakushima Island. Primates, 47(2), 158-164.

Hayakawa, S. (2007). Female Defensibility in a Small Troops of Japanese Macaques vis-à-vis Nontroop Males and Copulation on the Periphery of the Troop. International Journal of Primatology, 28(1), 73-96.

Hayakawa, S. (2008). Male-female mating tactics and paternity of wild Japanese macaques (*Macaca fuscata yakui*). American Journal of Primatology, 70(10), 986-989.

Henzi, S. P., & Lawes, M. (1987). Breeding season influxes and the behaviour of adult male samango monkeys (*Cercopithecus mitis albogularis*). Folia primatologica, 48(3-4), 125-136.

Henazi, S. P., & Barrett, L. (1999). The value of grooming to female primates. Primates, 40(1), 47-59.

Hill, D. A., & Agetsuma, N. (1995). Supra-annual variation in the influence of Myrica rubra fruit on the behavior of a troop of Japanese macaques in Yakushima. American Journal of Primatology, 35(3), 241-250.

Hill, D. A. (1999). Effects of provisioning on the social behaviour of Japanese and rhesus macaques: implications for socioecology. Primates, 40(1), 187-198.

Inoue, E., & Takenaka, O. (2008). The effect of male tenure and female mate choice on paternity in free-ranging Japanese macaques. American Journal of Primatology, 70(1), 62-68.

Isabirye-Basuta, G. (1988). Food competition among individuals in a free-ranging chimpanzee community in Kibale Forest, Uganda. Behaviour, 135-147.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. Behavioral Ecology, 2(2), 143-155.

Isbell, L. A., & Young, T. P. (1993). Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. Behavioral Ecology and Sociobiology, 32(6), 377-385.

Itoh, N., & Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. Primates, 48(2), 87-96.

Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. Behaviour, 1-17.

Janson, C. H. (1990a). Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour, 40(5), 910-921.

Janson, C. H. (1990b). Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. Animal Behaviour, 40(5), 922-934.

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. International Journal of Primatology, 23(4), 707-740.

Kawai (1964) Ecology of Japanese macaques [Nihonzaru no seitai]. Kawadeshobo, Tokyo (in Japanese).

Kazahari, N., & Agetsuma, N. (2010). Mechanisms determining relationships between feeding group size and foraging success in food patch use by Japanese macaques (*Macaca fuscata*). Behaviour, 147(11), 1481-1500.

Kazahari, N., Tsuji, Y., & Agetsuma, N. (2013). The relationships between feeding-group size and feeding rate vary from positive to negative with characteristics of food items in wild Japanese macaques (*Macaca fuscata*). Behaviour, 150(2), 175-197.

Kimura, K. (1984). Structure and regeneration process of evergreen conifers and broad-leaved trees in the Yaku-shima Wilderness Area, Yaku-shima. Conservation Reports of the Yaku-Shima Wilderness Area, Kyushu, Japan.

Kirkpatrick, R. C., & Grueter, C. C. (2010). Snub-nosed monkeys: Multilevel societies across varied environments. Evolutionary Anthropology, 19(3), 98-113.

Koda, H., Shimooka, Y., & Sugiura, H. (2008). Effects of caller activity and habitat visibility on contact call rate of wild Japanese macaques (*Macaca fuscata*). American journal of primatology, 70(11), 1055-1063.

Korstjens, A. H., Verhoeckx, I. L., & Dunbar, R. I. (2006). Time as a constraint on group size in spider monkeys. Behavioral Ecology and Sociobiology, 60(5), 683-694.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. Evolutionary Ecology, 21(5), 613-634.

Li, S. Z., & Jain, A. K. (Eds.). (2011). Handbook of face recognition. Springer.

Lindburg, D. G. (1969). Rhesus monkeys: mating season mobility of adult males. Science, 166(3909), 1176-1178.

Matsubara, M. (2003). Costs of mate guarding and opportunistic mating among wild male Japanese macaques. International Journal of Primatology, 24(5), 1057-1075.

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A., & Kawanaka, K. (1998). Factors affecting party size in chimpanzees of the Mahale Mountains. International Journal of Primatology, 19(6), 999-1011.

Morisita, M. (1959). Measuring of the dispersion of individuals and analysis of the distributional patterns. Memoirs of the Faculty of Science, Kyusyu University. Series E Biology (2), 215-235.

Mundry, R., & Nunn, C. L. (2009). Stepwise model fitting and statistical inference: turning noise into signal pollution. The American Naturalist, 173(1), 119-123.

Muroyama, Y., Imae, H., & Okuda, K. (2000). Radio tracking of a male Japanese macaque emigrated from its group. Primates, 41(3), 351-356.

Nakagawa, N. (1990). Decisions on time allocation to different food patches by Japanese monkeys (*Macaca fuscata*). Primates, 31:459-468.

Nakagawa, N. (1997). Determinants of the dramatic seasonal changes in the intake of energy and protein by Japanese monkeys in a cool temperate forest. American Journal of Primatology, 41(4), 267-288.

Nakagawa, N. (2000). Foraging energetics in patas monkeys (*Erythrocebus patas*) and tantalus monkeys (*Cercopithecus aethiops tantalus*): implications for reproductive seasonality. American Journal of Primatology, 52(4), 169-185.

Nakamichi, M., & Yamada, K. (2010). Lifetime social development in female Japanese macaques. In Nakagawa, N., Nakamichi, M., and Sugiura, H., editors. The Japanese Macaques. Springer Japan. p241-270.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. Australian Journal of Zoology, 2(1), 9-65.

Nishida, T., Hiraiwa‐Hasegawa, M., Hasegawa, T., & Takahata, Y. (1985). Group extinction and female transfer in wild chimpanzees in the Mahale National Park, Tanzania. Zeitschrift für Tierpsychologie, 67, 284-301.

Nishida, T. (1966). A sociological study of solitary male monkeys. Primates, 7(2), 141-204.

Nozaki, M., Mori, Y., & Oshima, K. (1992). Environmental and internal factors affecting seasonal breeding of Japanese monkeys (*Macaca fuscata*). Topics in Primatology, 3, 301-316.

Ohsawa, H., Inoue, M., & Takenaka, O. (1993). Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). Primates, 34(4), 533-544.

Okayasu, N. (2001). Contrast of estrus in accordance with social contexts between two troops of wild Japanese macaques on Yakushima. Anthropological Science, 109(2), 121-140.

Olupot, W., & Waser, P. M. (2005). Patterns of male residency and intergroup transfer in gray-cheeked mangabeys (*Lophocebus albigena*). American Journal of Primatology, 66(4), 331-349.

Reiczigel, J., Lang, Z., Rózsa, L., & Tóthmérész, B. (2008). Measures of sociality: two different views of group size. Animal Behaviour, 75(2), 715-721.

Ramesh, T., Sankar, K., Qureshi, Q., & Kalle, R. (2012). Group size and population structure of megaherbivores (Gaur *Bos gaurus* and Asian elephant *Elephas maximus*) in a deciduous habitat of Western Ghats, India. Mammal study, 37(1), 47-54.

Saito, C. (1996). Dominance and feeding success in female Japanese macaques, (*Macaca fuscata*): effects of food patch size and inter-patch distance. Animal Behaviour, 51(5), 967-980.

Saito, C., Sato, S., Suzuki, S., Sugiura, H., Agetsuma, N., Takahata, Y., Sasaki, C., Takahashi, H., Tanaka, T., & Yamagiwa, J. (1998). Aggressive intergroup encounters in two populations of Japanese macaques (*Macaca fuscata*). Primates, 39(3), 303-312.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. Advances in the Study of Behavior, 22, 1-63.

Snaith, T. V., & Chapman, C. A. (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules?. Evolutionary Anthropology, 16(3), 94-106.

Snaith, T. V., & Chapman, C. A. (2008). Red colobus monkeys display alternative behavioral responses to the costs of scramble competition. Behavioral Ecology, 19(6), 1289-1296.

Soltis, J. (1999). Measuring male-female relationships during the mating season in wild Japanese macaques (*Macaca fuscata yakui*). Primates, 40(3), 453-467.

Sprague, D. S. (1991). Mating by nontroop males among the Japanese macaques of Yakushima Island. Folia Primatologica, 57(3), 156-158.

Sprague, D. S. (1992). Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). International Journal of Primatology, 13(4), 437-454.

Sprague, D. S. (1998). Age, dominance rank, natal status, and tenure among male macaques. American Journal of Physical Anthropology, 105(4), 511-521.

Sprague, D. S., Suzuki, S., Takahashi, H., & Sato, S. (1998). Male life history in natural populations of Japanese macaques: migration, dominance rank, and troop participation of males in two habitats. Primates, 39(3), 351-363.

Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. Behavioral Ecology and Sociobiology, 49(2-3), 100-110.

Stumpf, R. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2009). The context of female dispersal in Kanyawara chimpanzees. Behaviour, 146(4-5), 4-5.

Sueur, C., Petit, O., & Deneubourg, J. L. (2010). Short-term group fission processes in macaques: a social networking approach. The Journal of Experimental Biology, 213(8), 1338-1346.

Sugiura, H., Shimooka, Y., & Tsuji, Y. (2011). Variation in spatial cohesiveness in a group of Japanese macaques (*Macaca fuscata*). International Journal of Primatology, 32(6), 1348-1366.

Sugiyama, Y. (1976). Life history of male Japanese monkeys. In Rosenblatt, J.S., editors. Advances in the study of behavior, Academic Press. p255-284.

Suzuki, M., & Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. American Journal of Primatology, 73(7), 623-631.

Suzuki, S., Hill, D. A., & Sprague, D. S. (1998). Intertroop transfer and dominance rank structure of nonnatal male Japanese macaques in Yakushima, Japan. International Journal of Primatology, 19(4), 703-722.

Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). Behaviour, 117-134.

Takahashi, H., & Furuichi, T. (1998). Comparative study of grooming relationships among wild Japanese macaques in Kinkazan A troop and Yakushima M troop. Primates, 39(3), 365-374.

Takahashi, H. (2001). Influence of fluctuation in the operational sex ratio to mating of troop and non-troop male Japanese macaques for four years on Kinkazan Island, Japan. Primates, 42(3), 183-191.

Takahashi, H. (2004). Do males have a better chance of mating when the number of estrous females is equal to or greater than the males' ordinal rank? Testing the hypothesis in Japanese macaques. American Journal of Primatology, 63(2), 95-102.

Takahata, Y. (1980). The reproductive biology of a free-ranging troop of Japanese monkeys. Primates, 21(3), 303-329.

Takahata, Y. (1982). The Socio-Sexual Behavior of Japanese Monkeys. Zeitschrift für Tierpsychologie, 59(2), 89-108.

Takahata, Y., Suzuki, S., Okayasu, N., & Hill, D. (1994). Troop extinction and fusion in wild Japanese macaques of Yakushima Island, Japan. American Journal of Primatology, 33(4), 317-322.

Takahata, Y., Suzuki, S., Okayasu, N., Sugiura, H., Takahashi, H., Yamagiwa, J., Izawa, K., Agetuma, N., Hill, D., Saito, C., Sato, S., Tanaka, T., & Sprague, D. (1998). Does troop size of wild Japanese macaques influence birth rate and infant mortality in the absence of predators?. Primates, 39(2), 245-251.

Terborgh, J., & Janson, C. H. (1986). The socioecology of primate groups. Annual Review of Ecology and Systematics, 17, 111-136.

Thomas, L., Laake, J. L., Strindberg, S., Marques, F. F. C., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Hedley, S. L., Pollard, J. H., Bishop, J. R. B., & Marques, T. A. (2006). Distance 5.0. Version 5 0. UK: University of St. Andrews.

van Hooff, J. A., & Van Schaik, C. P. (1994). Male bonds: afilliative relationships among nonhuman primate males. Behaviour, 309-337.

van Noordwijk, M. A., & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. Primates, 40(1), 105-130.

van Schaik, C. P. (1983). Why are diurnal primates living in groups?. Behaviour, 120-144.

van Schaik, C. P., & van Noordwijk, M. A. (1986). The hidden costs of sociality: intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). Behaviour, 296-315.

van Schaik, C. P., & van Noordwijk, M. A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). Behaviour, 77-98.

van Schaik, C. P. (1996). Social evolution in primates: the role of ecological factors and male behaviour. Proceedings of the British Academy 88(1), 9-31.

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. Primates, 40(1), 69-86.

Watts, D. P. (1994). The influence of male mating tactics on habitat use in mountain gorillas (*Gorilla gorilla beringei*). Primates, 35(1), 35-47.

Westermarck, E. (1921). The history of human marriage (Vol. 2). Macmillan.

Williams, J. M., Liu, H. Y., & Pusey, A. E. (2002). Costs and benefits of grouping for female chimpanzees at Gombe. In: Boesch C, Hohmann G, Marchant LF, editors. Behavioural diversity in chimpanzees and bonobos. New York: Cambridge University Press. p192-203.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. Ecology, 70(1), 164-168.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe national park, Tanzania. In Clutton-Brock, T. H., editors. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Brighton: Academic Press. p 503-538.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. Behaviour, 262-300.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In Kappeler, P. M., Editor. Primate males: Causes and consequences of variation in group composition. Cambridge University Press. p248-258.

Yamada, M. (1966). Five natural troops of Japanese monkeys in Shodoshima Island (I). Primates, 7(3), 315-362.

Yamagiwa, J. (1985). Socio-sexual factors of troop fission in wild Japanese monkeys (*Macaca fuscata yakui*) on Yakushima Island, Japan. Primates, 26(2), 105-120.

Yamagiwa, J., & Hill, D. A. (1998). Intraspecific variation in the social organization of Japanese macaques: past and present scope of field studies in natural habitats. Primates, 39(3), 257-273.

Yamagiwa, J. (2008). History and present scope of field studies on *Macaca fuscata yakui* at Yakushima Island, Japan. International Journal of Primatology, 29(1), 49-64.

Yoshihiro, S., Ohtake, M., Matsubara, H., Zamma, K., Han'ya, G., Tanimura, Y., Kubota, H., Kubo, R., Arakane, T., Hirata, T., Furukawa, M., Sato, A., & Takahata, Y. (1999). Vertical distribution of wild Yakushima macaques (*Macaca fuscata yakui*) in the western area of Yakushima Island, Japan: preliminary report. Primates, 40(2), 409-415.

Yoshimi, I., & Takasaki, H. (2003). Long distance mobility of male Japanese macaques evidenced by mitochondrial DNA. Primates, 44(1), 71-74.

Zhao, D. A. P. E. N. G., Li, B., Li, Y., & Wada, K. (2005). Extra-unit sexual behaviour among wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains of China. Folia Primatologica, 76(3), 172-176.

Figures

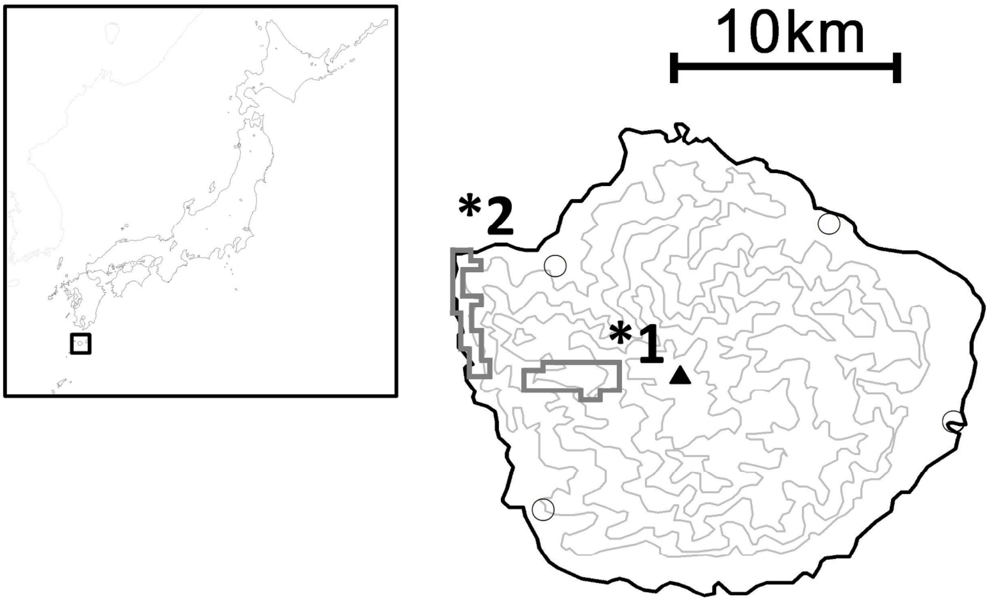


Figure II-1: Map of study site: *1 and *2 indicate study sites in highland and lowland areas, respectively.

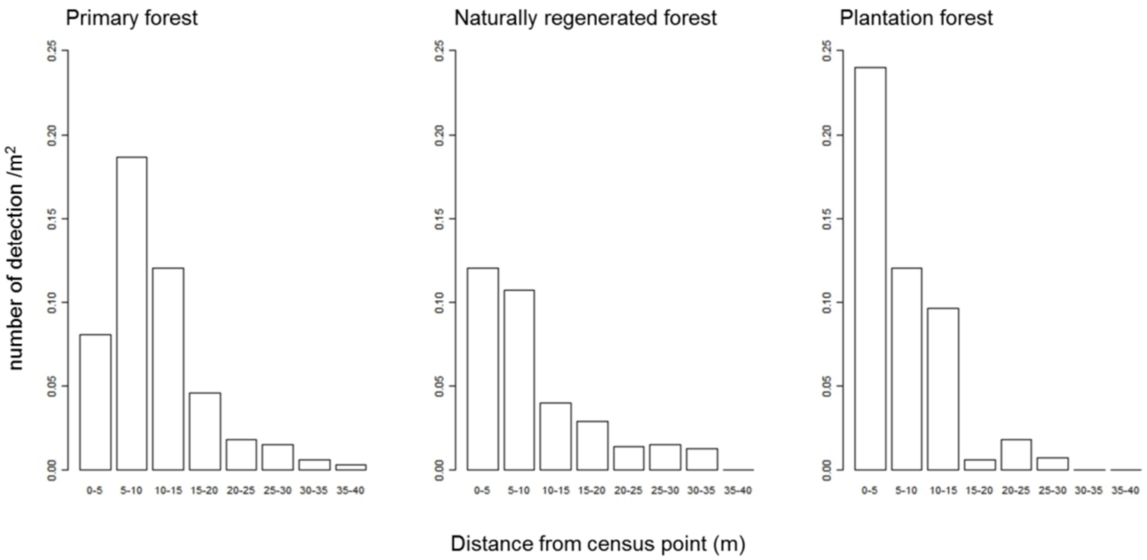


Figure II-2: Histogram of detection of males ranging alone in each vegetation type: the vertical axis indicates the number of detections per unit area (m2). The horizontal axis indicates the distance of detected males from census points (m). In each vegetation type, the number of detections decreases in accordance with distance from the census point.

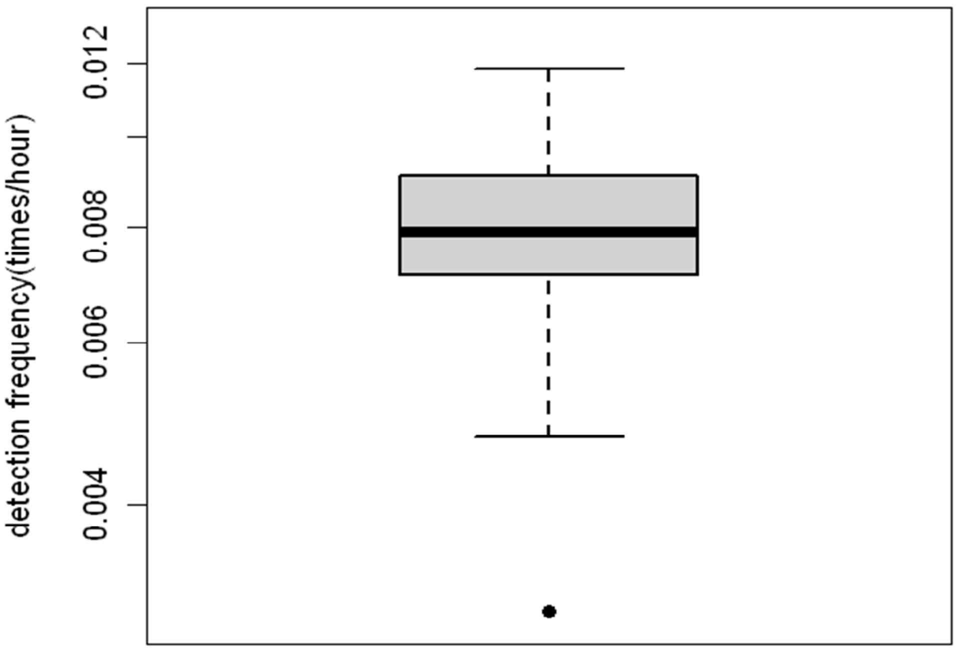


Figure II-3: Distribution of simulated detection frequency: the black dot indicates the value of the actual detection frequency in the lowlands. The boxplot indicates the distribution of the simulated detection frequency of males ranging alone across 200 trials. The top and bottom of the bar indicate the largest observation (sample maximum) and smallest observation (sample minimum), and the top and bottom of the grey box indicate the upper quartile (Q3) and lower quartile (Q1). The bold line in the grey box indicates the median (Q2).

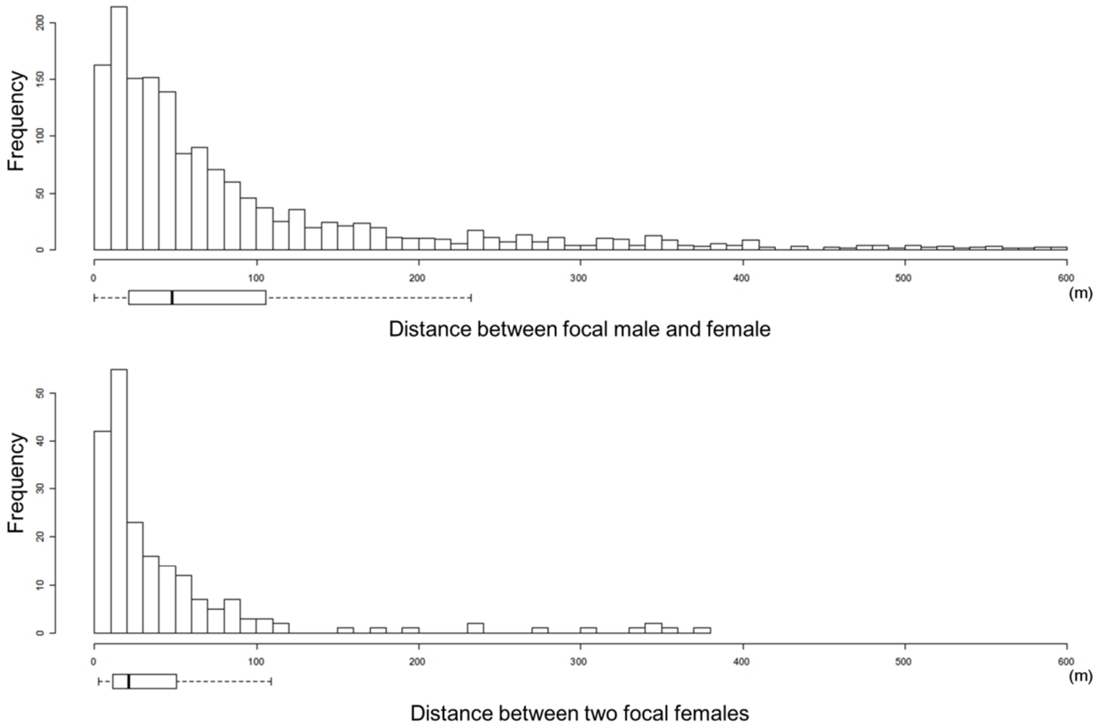


Figure III-1: Histograms of distance between focal animals; the upper and lower histograms show distances between focal male and female and two focal females, respectively. Distances were calculated every 10 minutes. The boxplots under the histograms indicate the degree of dispersion of distance samples. The left side, band, and right side of the box indicate the lower quartile (Q1), the median (Q2), and the upper quartile (Q3) of the distances, respectively. The left end and right end of the whiskers indicate the lowest distance within 1.5 times of range of the lower quartile, and the highest distance within 1.5 times of range of the upper quartile, respectively.

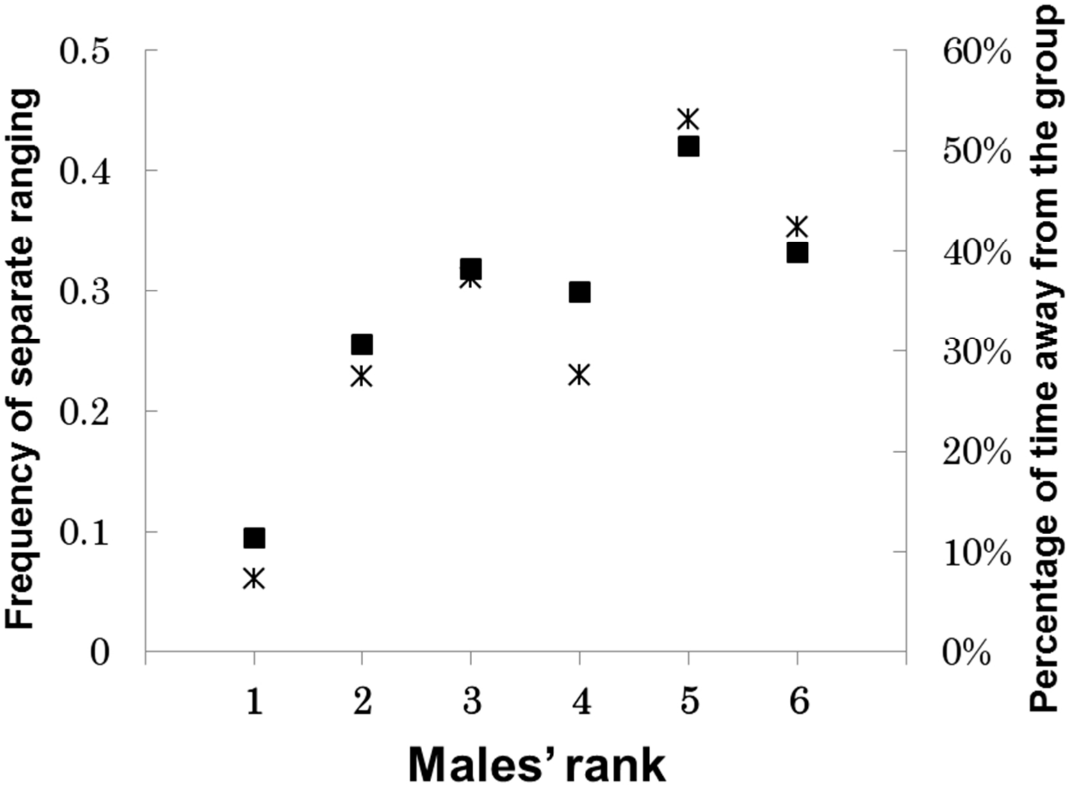


Figure III-2: Frequency of separate ranging (bouts per hour, solid square) and proportion of time away from the group (stars) as a function of male rank.

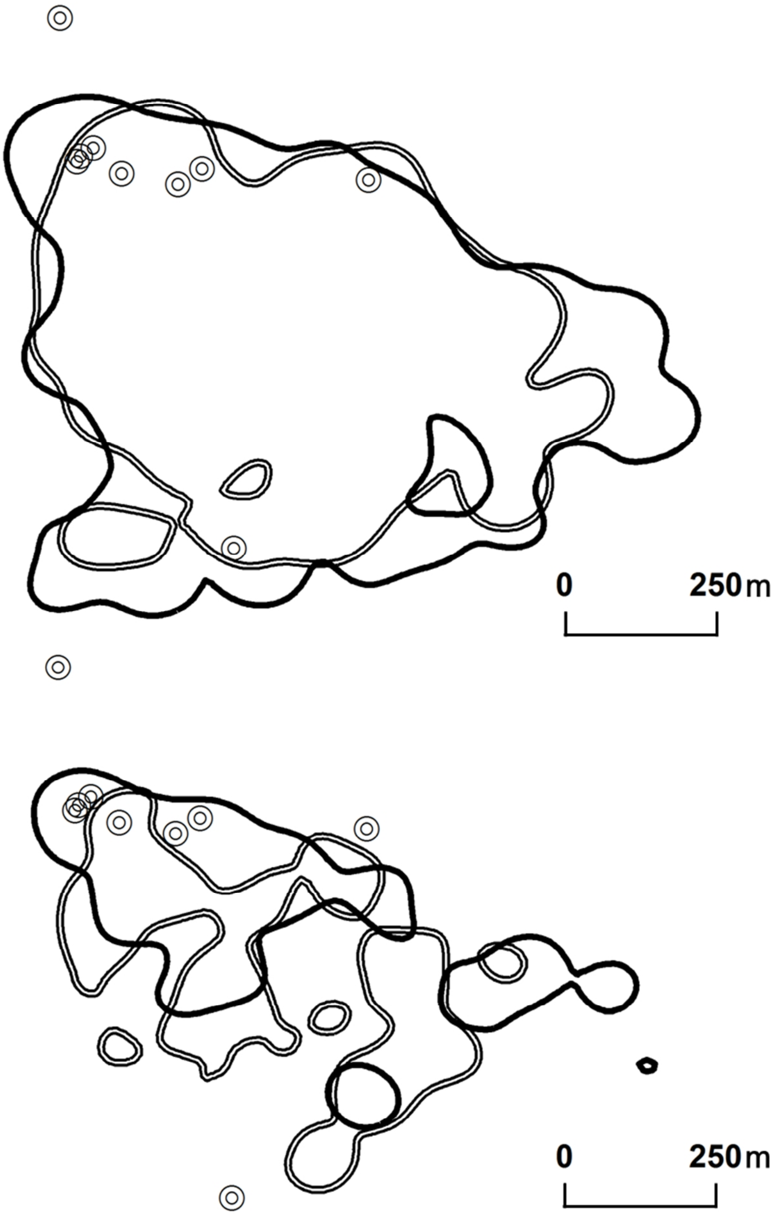


Figure III-3: Home ranges of group and males ranging separate from the group; the single line on upper and lower map indicates the group home range (53.0 ha) and core home range, respectively. The double line on upper and lower map indicates the home range of males ranged separate from the group (42.6 ha) and core home range, respectively. Double circles indicate locations of inter-group encounters.

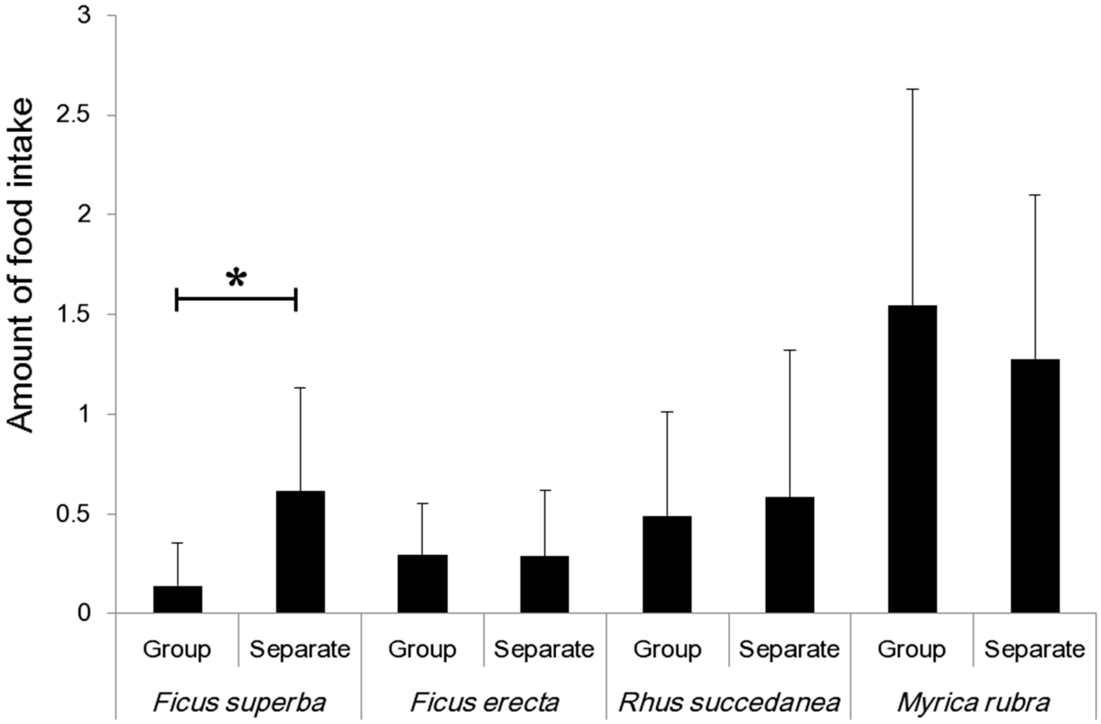


Figure III-4: Food intake per minute (mean ± SEM) when males ranged with (Group) or separately (Separate). Each of the four foods was eaten at least 30 times. * indicates P<0.05 (Steel-Dwass test). The bar shows SEM.

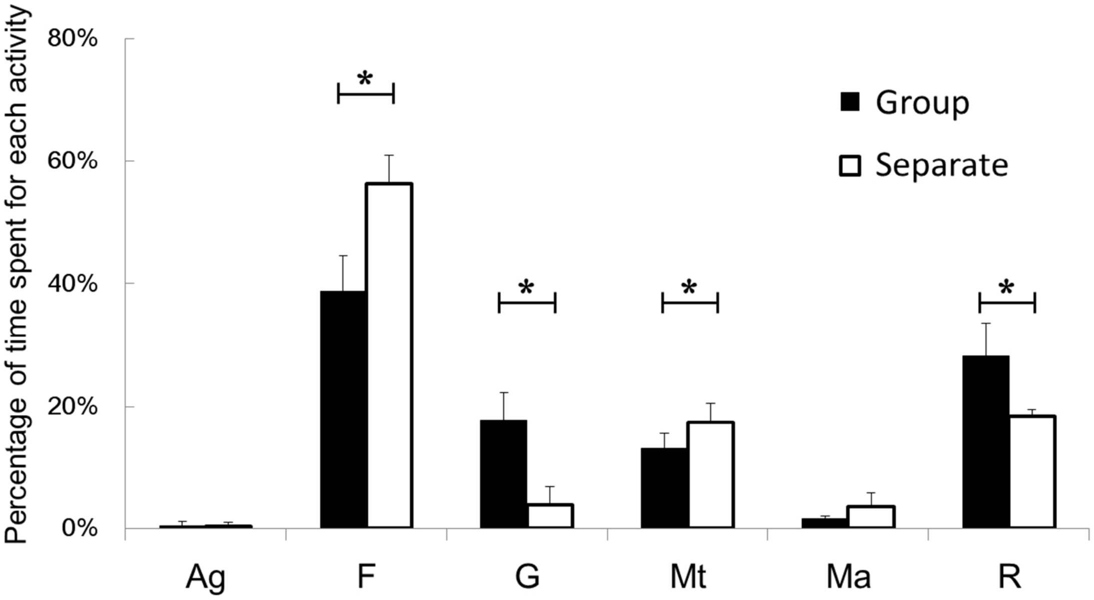


Figure III-5: Percentage of time spent in each activity when males ranged with the group (Group) and separate from the group (Separate); Ag, F, G, Mt, Ma, and R indicate agonistic behavior, feeding, groom/groomed, terrestrial moving, arboreal moving, and resting, respectively. The bar shows the standard deviation among males (N=6). * indicates $P<0.05$ (χ^2 test, standardized residual analysis).

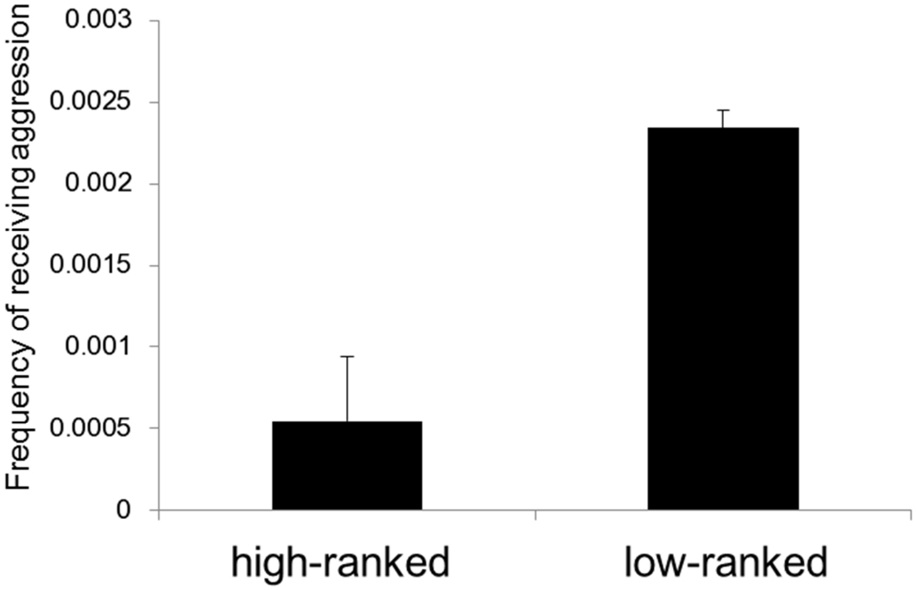


Figure III-6: Association between male rank and the frequency of receiving aggression. The high-ranking and low-ranking indicate 1st to 3rd ranked males and 4th to 6th ranked males, respectively. The bar shows SD.

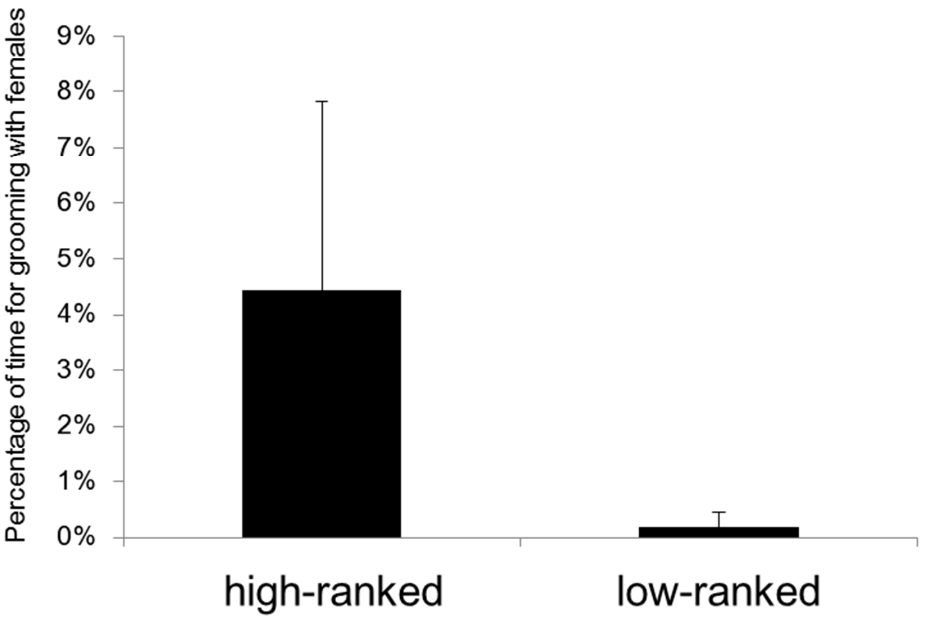


Figure III-7: Association between male rank and the percentage of observation time that each male groomed with females when he ranged with the group. The high-ranking and low-ranking indicate 1st to 3rd ranked males and 4th to 6th ranked males, respectively. The bar shows SD.

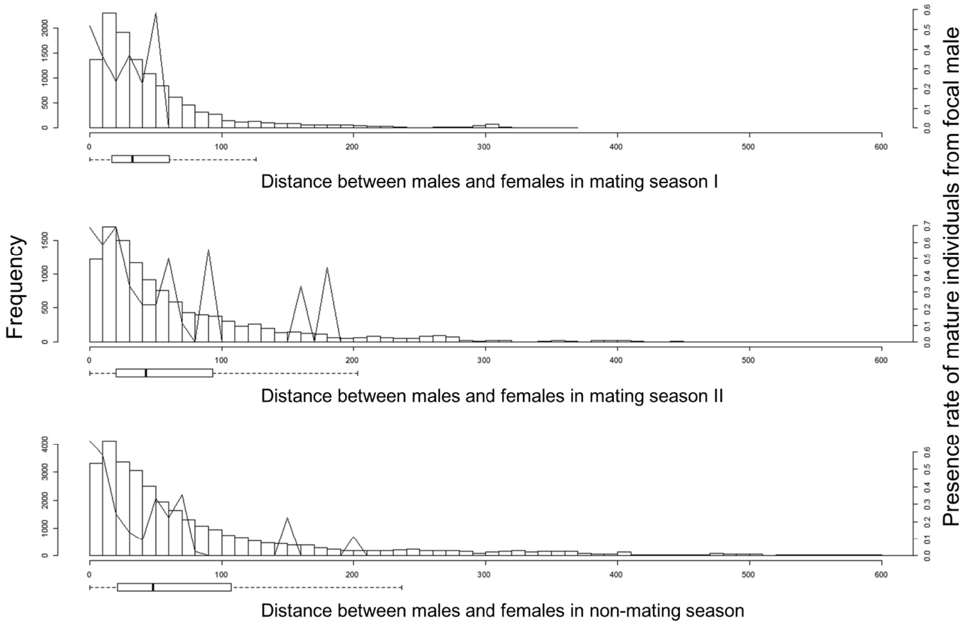


Figure IV-1: Histograms of distance between focal animals; the upper, middle, and lower histograms indicate distance between focal males and females during mating season I, mating season II, and the non-mating season, respectively. Distances were calculated every 30 s. Samples that exceed 600 m are omitted from the graphs as these were few. The boxplots under the histograms indicate the degree of dispersion of the distance samples. The left side, band, and right side of the box indicate the lower quartile (Q1), the median (Q2), and the upper quartile (Q3) of the distances, respectively. The left end and right end of the whiskers indicate the lowest distance within 1.5 times of the range of the lower quartile, and the highest distance within 1.5 times of the range of the upper quartile, respectively. The line plot indicates variations in the mean proportion of mature individuals that were visible to the male-following researcher.

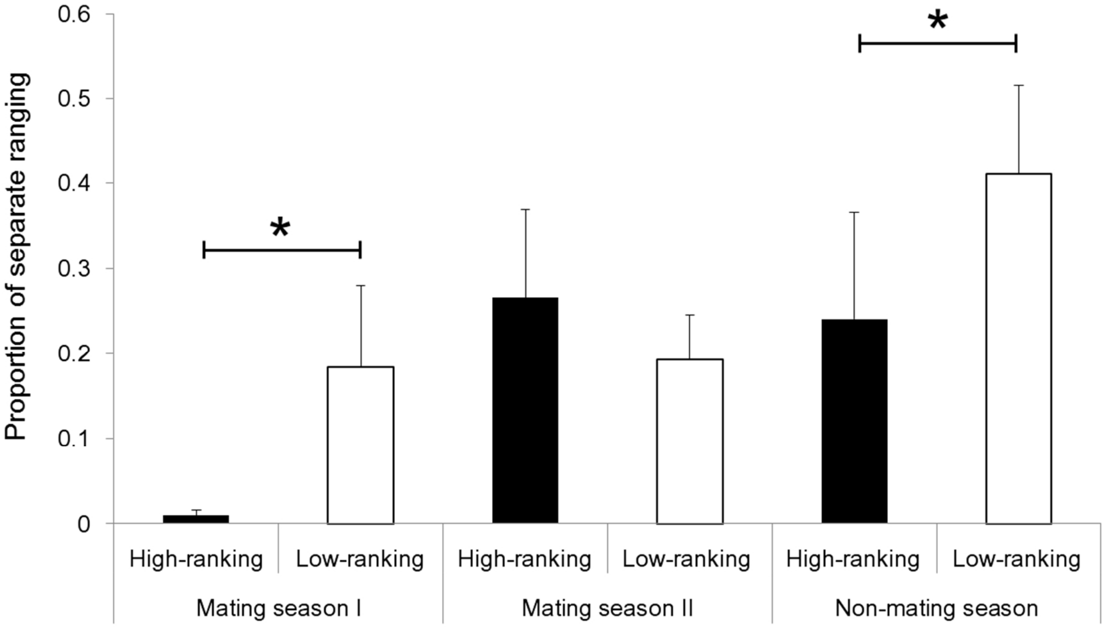


Figure IV-2: Proportion of separate ranging and males' rank; high-ranking and low-ranking indicate high-ranking males and low-ranking males, respectively. * indicates P<0.05 (Steel-Dwass test). The bar shows SEM.

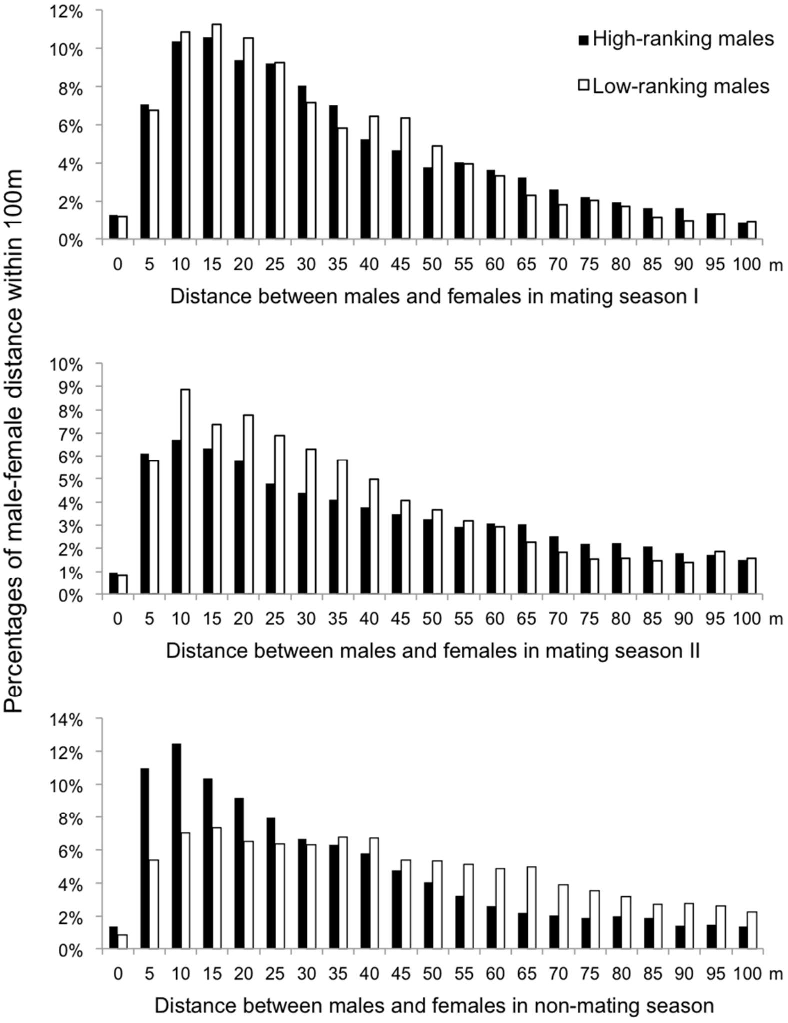


Figure IV-3: Percentages of male-female distance within 100 m: black and white bars indicate the proportion of the number of male-female distance in each class over the whole number within 100 m.

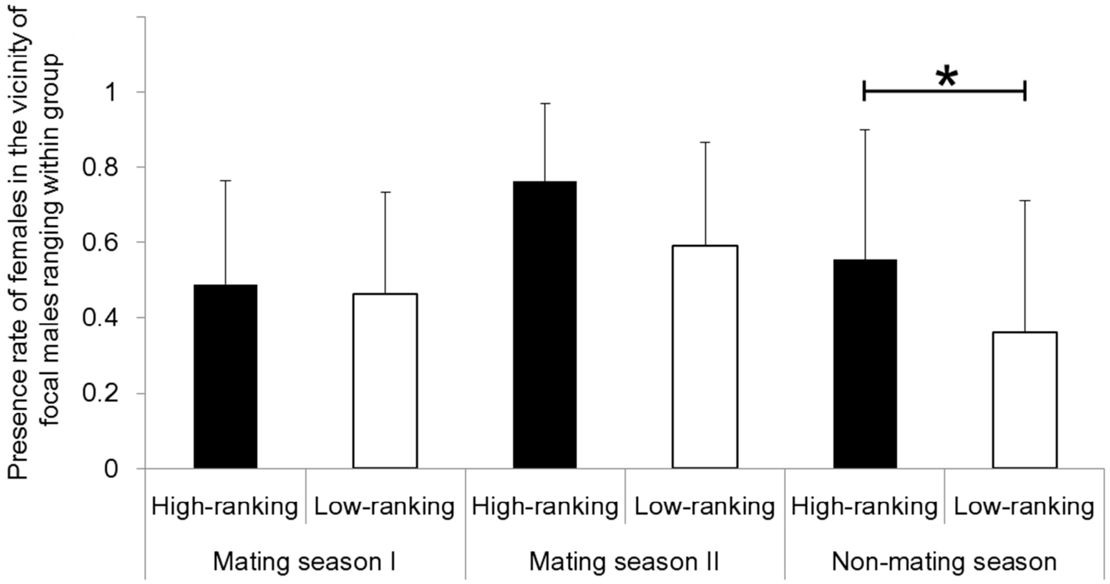


Figure IV-4: Presence rate of females in the vicinity of focal males when the focal males ranged with the group in the mating and non-mating season: high-ranking and low-ranking indicate high-ranking males and low-ranking males, respectively. We discarded the data when the male-female distance > 100 m. *indicates P<0.01 (Steel-Dwass test).

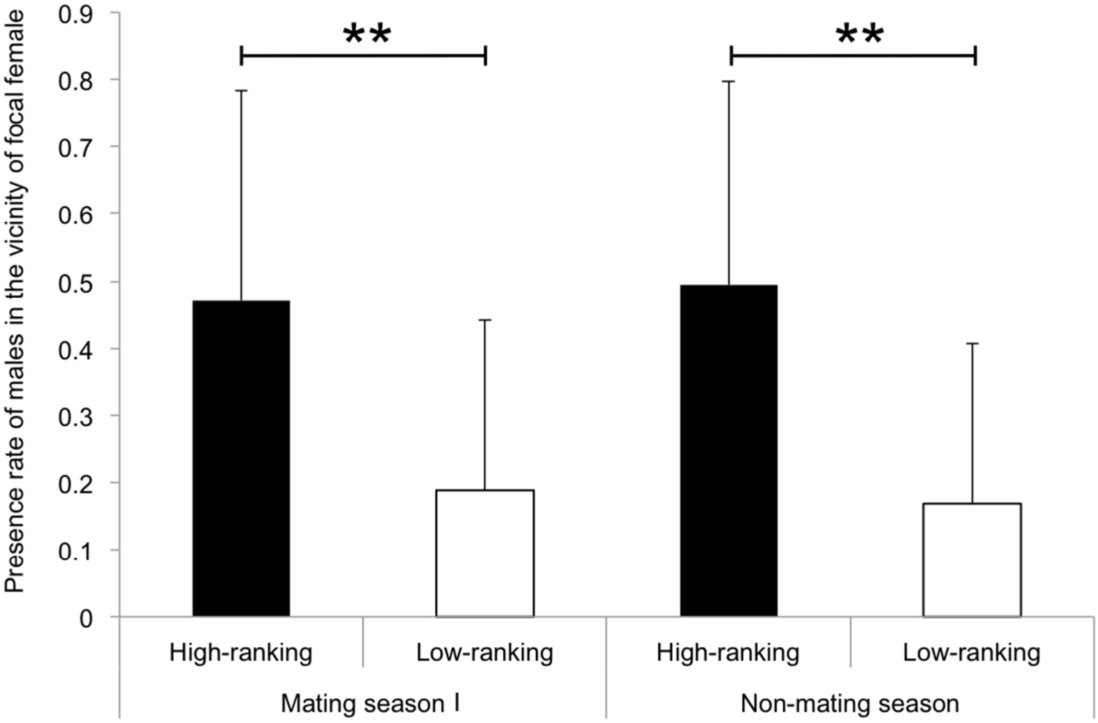


Figure IV-5: Presence rate of males in the mating and non-mating season: high-ranking and low-ranking indicate high-ranking males and low-ranking males, respectively. We discarded the hours when presence rate of females in the vicinity of focal female <0.5. **indicates P<0.001 (Steel-Dwass test). The bar shows SEM.

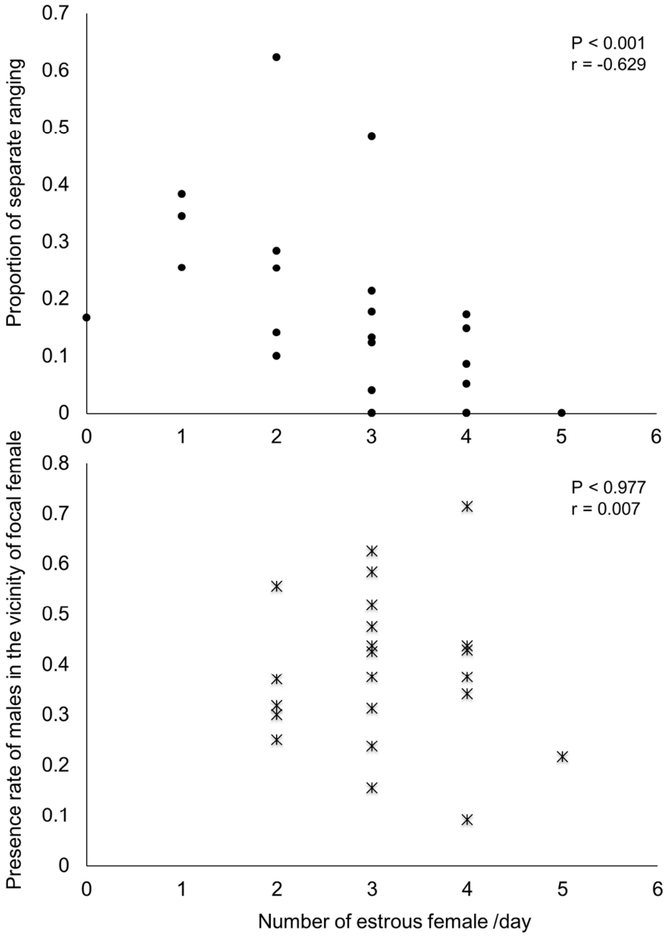


Figure IV-6: Proportion of separate ranging and presence rate of males as a function of number of estrous females; circles and stars indicate proportion of separate ranging relative to the total observation time and the average presence rate of males in the vicinity of focal female on each day. Correlation was found between the proportion of separate ranging and the number of estrous females, whereas correlation was not found between presence rate and the number of estrous females (Spearman test).

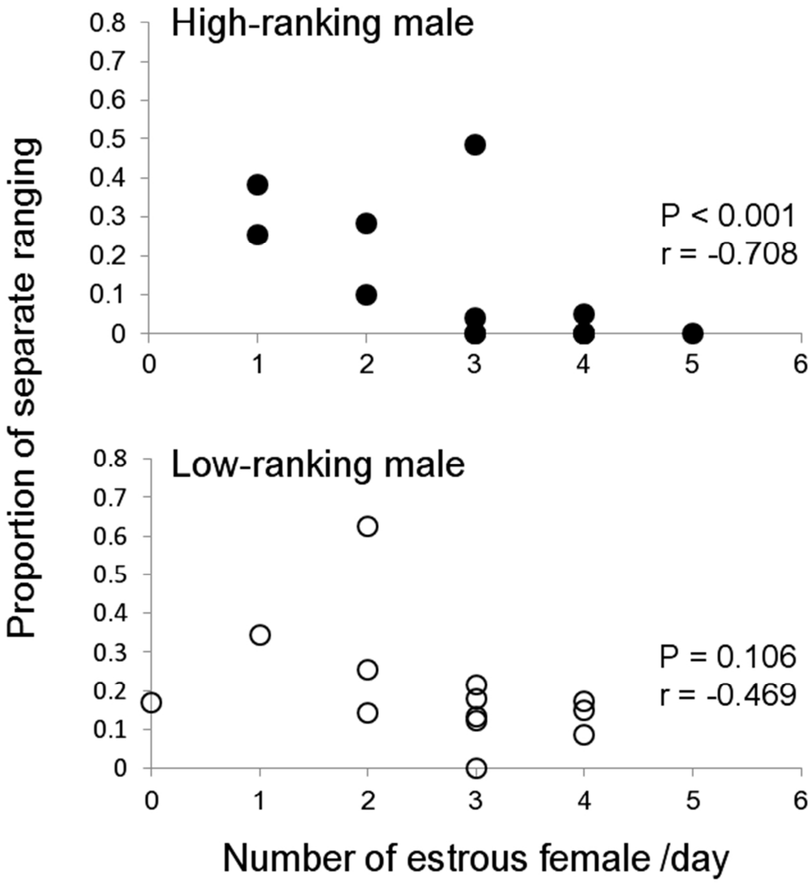


Figure IV-7: Proportion of separate ranging and the number of estrous females of high- and low-ranking males; circles indicate proportion of separate ranging relative to the total observation time on each day (Spearman test).

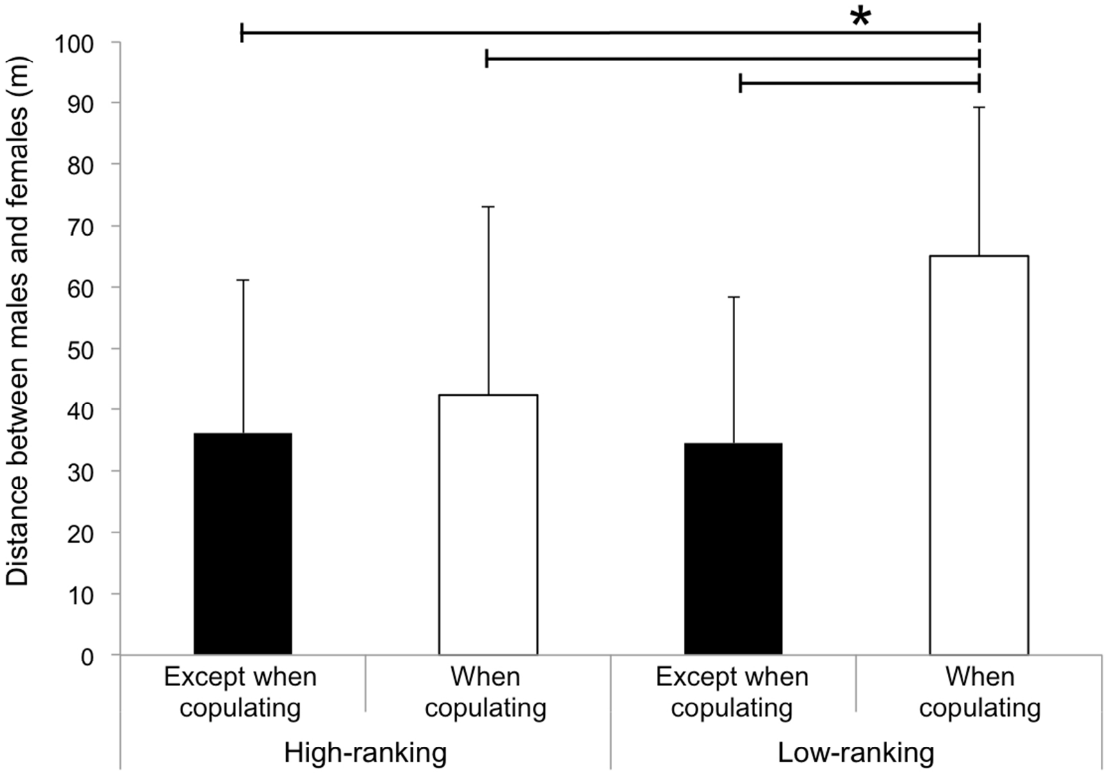


Figure IV-8: Distances between the focal male and the focal female when a focal male copulated with a non-focal female of the group (When copulating), and that when males ranged with the group and conducted anything except copulation during mating seasons I and II (Except when copulating). * indicates $P<0.01$ (Wilcoxon signed-rank test with a Bonferroni correction, significance level = 0.05/6). The bar shows SEM.

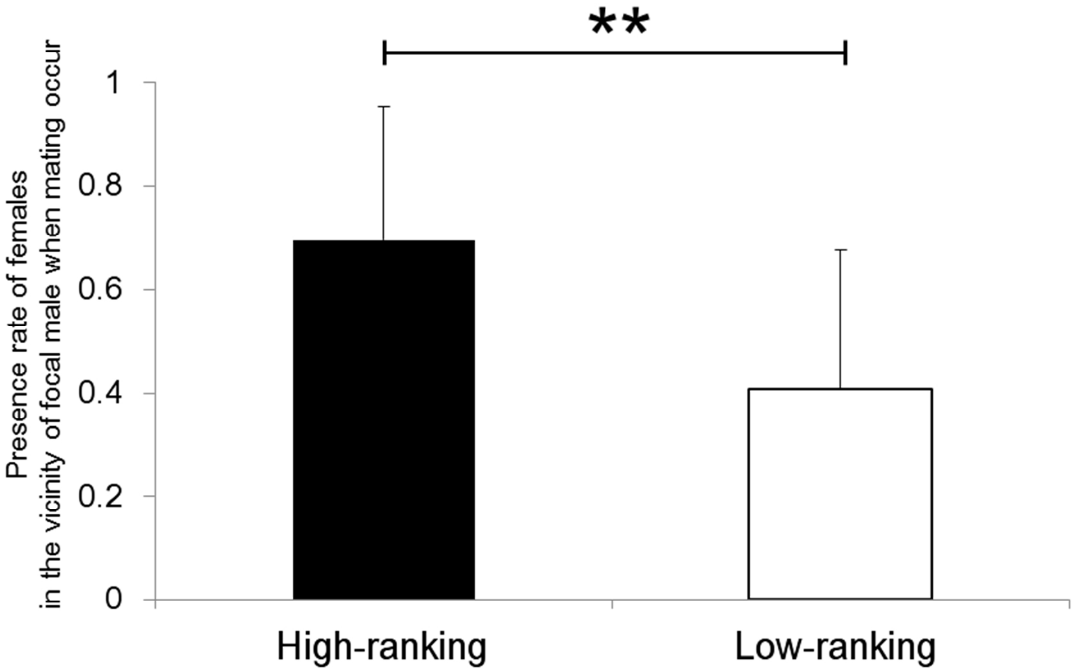
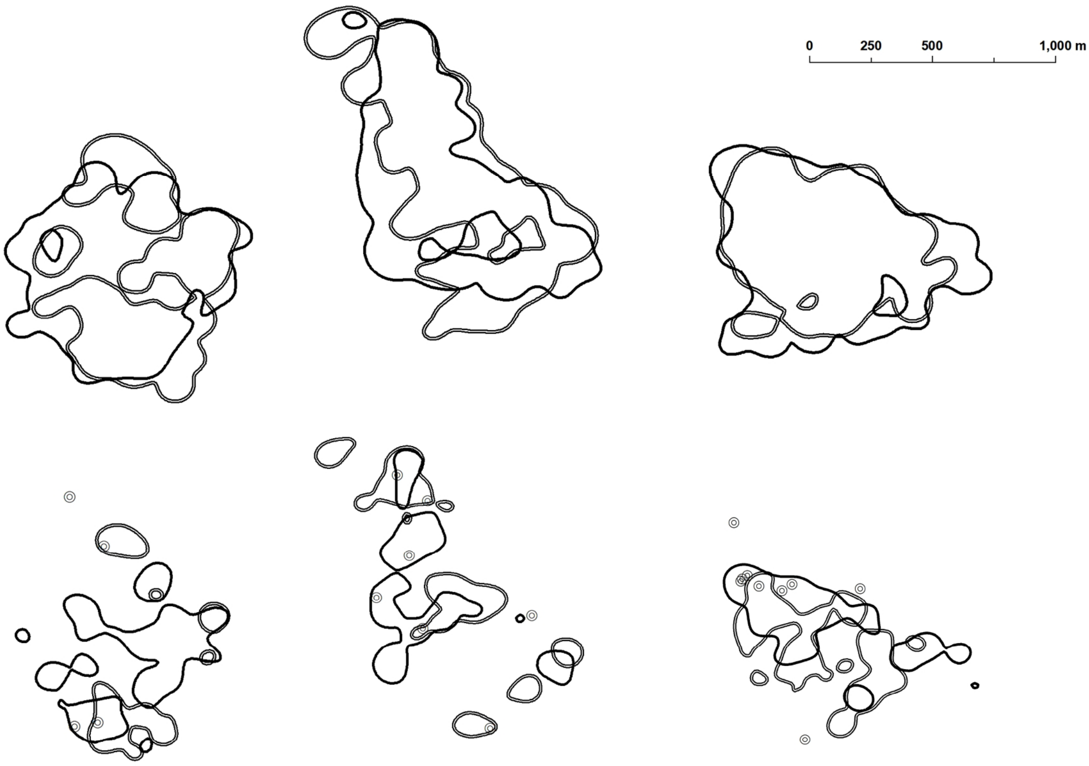


Figure IV-9: presence rate of females in the vicinity of male of hours that included the copulation event with their group females. ** indicates P<0.001 (U test). The bar shows SEM.



mating season I   mating season II   non-mating season

Figure IV-10: Ranging area of the group and separated males; the upper and lower maps show ranging areas (95% Kernel estimate) and core ranging areas (50% Kernel estimate), respectively. The single line and double line on each map indicate the group's ranging area and separated males' ranging area, respectively. The double circles indicate locations of inter-group encounters.

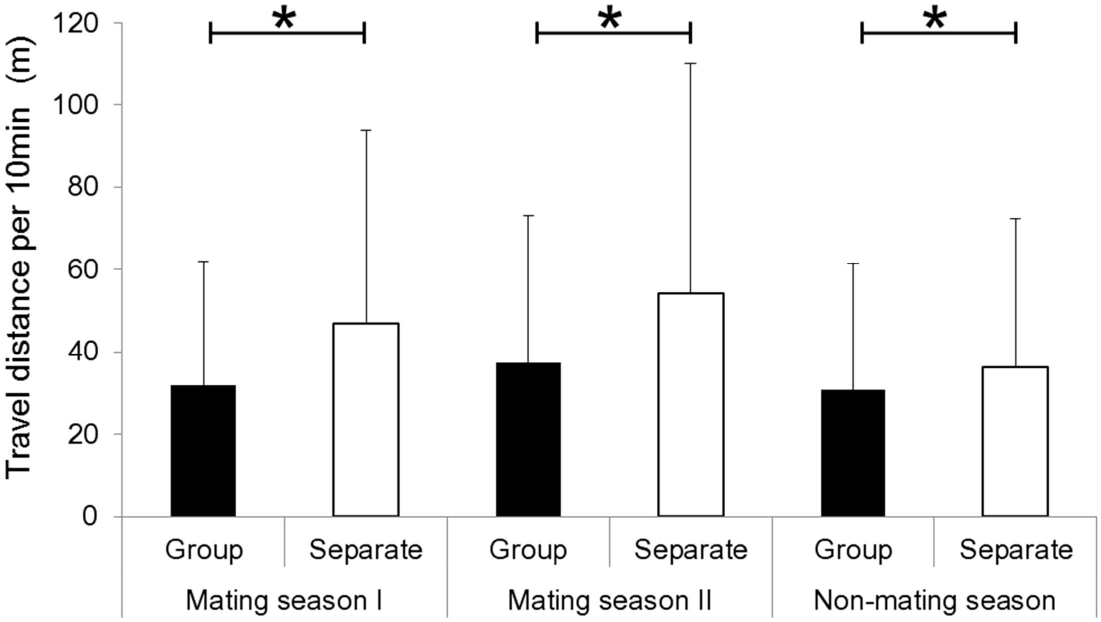


Figure IV-11: Travel distance of males ranging separately and with group in each study term. * indicates P<0.01 (Steel-Dwass test). The bar shows SEM.

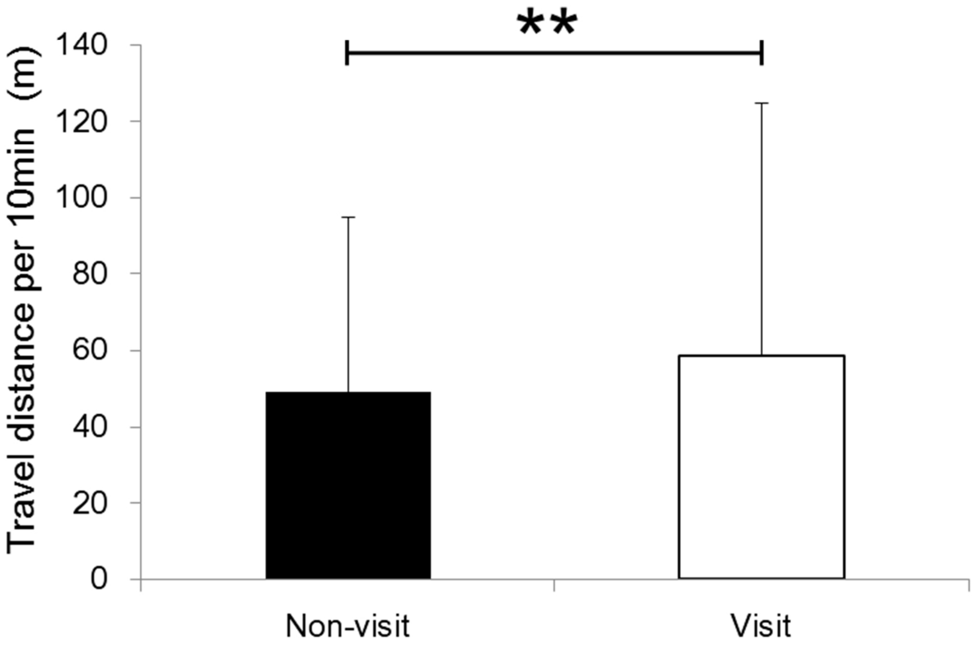


Figure IV-12: Travel distance when males visit other groups: each box indicate the travel distance during 7 separate ranging bouts (Visit), and that during the other separate ranging bouts (Non-visit). * *indicates P<0.001 (χ^2 test). The bar shows SEM.

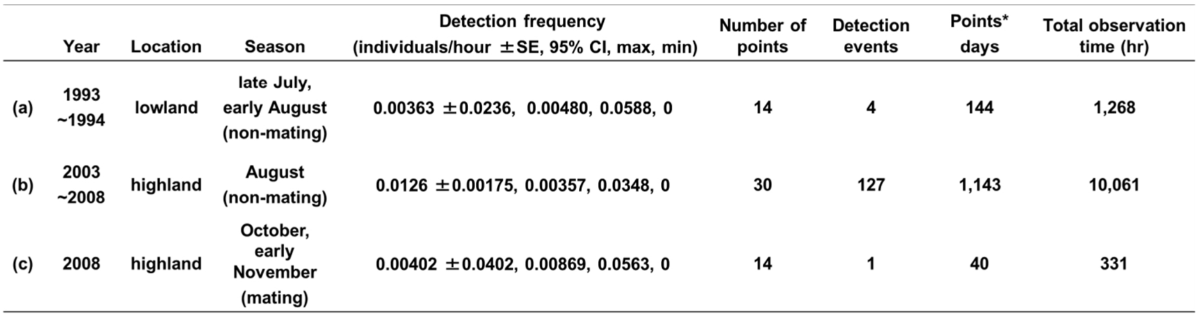
Tables

Table II-1: Detection frequencies of males ranging alone among three vegetation types

Vegetation	Detection frequency (individuals/hour ±SE, 95% CI, max, min)	Number of points	Detection events	Points* days	Total observation time (hr)
Primary	0.0142 ±0.00318, 0.00700, 0.0326, 0	12	54	442	3,857
Naturally regenerated	0.0129 ±0.00368, 0.00871, 0.0299, 0.003	8	33	311	2,738
Plantation	0.0107 ±0.00277, 0.00628, 0.0309, 0	10	40	390	3,466

Each census was conducted in highland in August (non-mating season) from 2003 to 2008. The numbers of detected males ranging alone were averaged for each day and each point (Points*days).

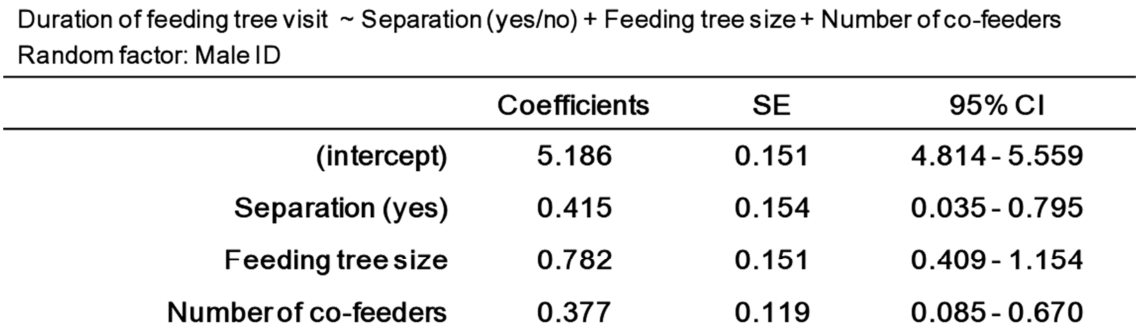
Table II-2: Summary of detection frequency of males ranging alone among three study terms



	Year	Location	Season	Detection frequency (individuals/hour ±SE, 95% CI, max, min)	Number of points	Detection events	Points* days	Total observation time (hr)
(a)	**1993 ~1994**	**lowland**	**late July, early August (non-mating)**	**0.00363 ±0.0236, 0.00480, 0.0588, 0**	**14**	**4**	**144**	**1,268**
(b)	**2003 ~2008**	**highland**	**August (non-mating)**	**0.0126 ±0.00175, 0.00357, 0.0348, 0**	**30**	**127**	**1,143**	**10,061**
(c)	**2008**	**highland**	**October, early November (mating)**	**0.00402 ±0.0402, 0.00869, 0.0563, 0**	**14**	**1**	**40**	**331**

The numbers of detected males ranging alone were averaged for each day and each point (Points*days).

Table III-1: Result of generalized linear mixed model (GLMM) for duration of feeding tree visit.



Duration of feeding tree visit ~ Separation (yes/no) + Feeding tree size + Number of co-feeders
Random factor: Male ID

	Coefficients	SE	95% CI
(intercept)	5.186	0.151	4.814 - 5.559
Separation (yes)	0.415	0.154	0.035 - 0.795
Feeding tree size	0.782	0.151	0.409 - 1.154
Number of co-feeders	0.377	0.119	0.085 - 0.670

Table III-2. Result of generalized linear mixed model (GLMM) for intake rate.

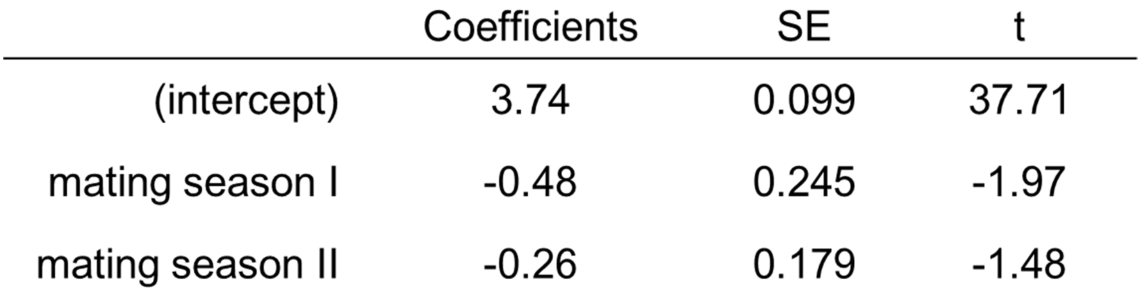
Intake rate ~ Separation (yes/no) + Feeding tree size + Number of co-feeders
Random factor: Male ID

	Coefficients	SE	95% CI
(intercept)	0.2879	0.0272	0.2208 - 0.3549
Separation (yes)	-0.0670	0.0213	-0.1195 - -0.0145
Feeding tree size	-0.0213	0.0159	-0.0605 - 0.0180
Number of co-feeders	-0.0004	0.0181	-0.0450 - 0.0442

Table IV-1: Number, duration, and proportion of separate ranging in each season

	Number of separate ranging	Mean duration (min)	Proportion of separate ranging (%)	Total observation time (hour)
mating season I	15	35.7	9.01	99
mating season II	34	41.6	24.8	95
non-mating season	76	68.0	32.7	263

Table IV-2: Result of general linear model for duration of separate ranging



	Coefficients	SE	t
(intercept)	3.74	0.099	37.71
mating season I	-0.48	0.245	-1.97
mating season II	-0.26	0.179	-1.48

Table IV-3: Reproductive potency of the group in the two mating seasons

	Mean estrous female (individual / day, SD)	Females with infant (individual)	Actual birth in the next birth season	Copulation with females of own group (times)	Copulation with females of other groups (times)	Visit to other groups (times)
mating season I	3.14 ±0.81	0	7	34	2	2
mating season II	2.08 ±1.14	7	1	29	2	5

ここに掲載した著作物の利用に関する注意

第 2 章:Otani Y, Yoshihiro S, Takahata Y, Zamma K, Nagai M. Kanie M, Hayaishi S, Fujino M, Sugaya K, Sudo M, Amanai S, Kaneda M, Tachikawa Y, Fukunaga Y, Okahisa Y, Higashi K & Hanya G (2013) Density of Japanese macaque (Macaca fuscata yakui) males ranging alone: seasonal and regional variation in male cohesiveness with the group. Mammal Study 38: 105-115. doi: 10.3106/041.038.0206.

第 3 章:Otani Y, Sawada A & Hanya G (in press) Short-term separation from groups by male Japanese macaques: costs and benefits in feeding behavior and social interaction. American Journal of Primatology. DOI: 10.1002/ajp.22241.