Cohesion and behavioral synchrony among females in a wild group of Japanese macaques

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2015

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Acknowledgements

Firstly, I am grateful to my supervisor Dr. N. Nakagawa, for his support and encouragement throughout the study. I wish to express my deepest gratitude to Drs. J. Yamagiwa and E. Inoue for their helpful suggestions and comments on this study. I would like to thank Dr. M. Suzuki for her cooperation at the field site and helpful discussion on the study. I am extremely grateful for the valuable assistance and advice provided throughout this study by Dr. D. S. Sprague. I also thank Dr. S. Hayakawa for providing unpublished kinship data regarding the study group. I appreciate Drs. H. Sugiura and N. Agetsuma for their valuable productive comments. I am indebted to Dr. K. Mochida for his productive insights on the study and advice on statistical analyses. I would like to express deep gratitude toward the current and former members of the Laboratory of Human Evolution Studies, Kyoto University for their helpful advice and encouragement, particularly Drs. M. Nakamura, N. Itoh, H. Nishie, M. Kiyono-Fuse, and Mr. S. Hanamura.

The Yakushima Forest Environment Conservation Center and Kirishima-Yaku National Park gave me permission to study in the study area. The Sarugoya Committee and former Field Research Center of Primate Research Institute, Kyoto University (KUPRI) (presently, Wildlife Research Center) offered me excellent facilities. I am grateful to these organizations. I would like to express my respect toward researchers who conducted initial research on Yakushima Island, and individuals who have engaged in conservation movements on Yakushima. This study would not have been possible without their monumental efforts. During my research in Yakushima, Dr./Mr./Ms. S. Suzuki, T. Yumoto, N. Noma, Y. Yanagihara-Agetsuma, M. Matsubara, G. Hanya, R. Tsujino, H. Koda, M. Terakawa, H. Toju, M. Kajita, K. Tetsuka, M. Oka, T. Kawamura, and K. Iwakawa, as well as my colleagues and friends for their support and encouragement.

This study was partially financed by the Cooperative Research Fund of the Primate Research Institute, Kyoto University to M. Nishikawa., the Sasakawa Scientific Research Grant from The Japan Science Society to M. Nishikawa., Global COE Program A06 to Kyoto University, and a grant from the Japan Society for the Promotion of Science to N. Nakagawa.

Finally, I extend my gratitude to my parents, Tsugio and Rie, and my family, who for their moral support through my academic work and encouragement throughout the study.

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Chapter I

General introduction

1.1 Costs and benefits of group-living

Group-living is a widespread phenomenon in the animal kingdom [Krause & Ruxton, 2002]. By forming groups, animals may benefit from enhanced predator detection and avoidance through increased vigilance, predator confusion, and dilution of risk [Alexander, 1974; Bertram, 1978; van Schaik, 1983]. However, as group size increases, intra-group food competition may also increase, particularly when food resources are limited [Janson & Goldsmith, 1995; van Schaik, 1989]. Theoretical studies have reported that spatial cohesion of a group is maintained by the synchrony of activity of group members [Conradt & Roper, 2000; Engel & Lamprecht, 1997]. Indeed, animals that substantially benefit from spatial cohesiveness (i.e., decrease in predation) show higher behavioral synchrony (e.g., as fish shoals and bird flocks) [Aivaz & Ruckstuhl, 2011; Krause & Ruxton, 2002]. Contrastingly, animals that need to reduce costs (i.e., intra-group resource competition) exhibit lower behavioral synchrony [Conradt, 1998; King & Cowlishaw, 2009], which results in spatial dispersion of the group members. Individuals living in a group seem to adjust spatio-temporal cohesion and behavioral synchrony depending on the trade-offs between the risk of predation and/or intra-group food competition [Aureli et al., 2008; Kinzey & Cunningham, 1994].

1.2 Diversity of grouping dynamics in primates

The primate order is well-known for its diversity of social systems; inter- and intra-specific variation exists in social organization, social structure, and mating systems as groups adapt to ecological conditions [Chapman & Rothman, 2009; Kappeler & van Schaik, 2002]. Spatio-temporal cohesion among individual animals characterizes one aspect of the social organization of each primate society [Kappeler & van Schaik, 2002]. Because spatio-temporal cohesion relates to the frequency of communication with other group members and contributes to socio-spatial differentiation, it may affect the cognitive ability of individuals to store and process social information [Amici et al., 2008]. There is pronounced inter- and intra-species variation in spatio-temporal cohesion and grouping membership in primates. Social groups can range from being highly cohesive with stable group membership (lack of fission–fusion dynamics) to being highly fluid with relatively stable (low dynamics) or highly flexible subunit membership (high dynamics) [Aureli et al., 2008].

Individuals of a group are presumed to be competitive against conspecific neighboring groups to defend access to resources such as foods or mating partners [Cheney, 1987; Ghiglieri, 1984; Strier, 1994; Wrangham, 1980]. Most primates live in social groups with stable membership. A social group is composed of individuals of variable sex, age, size, or physiological state [Terborgh & Janson, 1986]. Individuals in a social group are familiar with each other and some species are characterized by a dominance hierarchy among group members [de Waal, 1986]. Therefore, each individual within a social group is obligated to regulate their own spatial position and behavior depending on both ecological situations and the social situation among group members. These individual regulations produce grouping dynamics (i.e., various aspects

of spatio-temporal cohesion, subunit membership, and behavioral synchrony/asynchrony among group members), and ultimately result in a social system within a group.

When we evaluate the spatio-temporal cohesion and behavioral synchrony among individuals, we must take into account an individual-based zone of interaction where individuals can interact directly with other individuals using their own sensory abilities (e.g., visual, auditory, and olfactory) [Zuberbühler, 2012]. Within the zone of individual spatial awareness of location and activities of others in a group, adjustment of spatial position and behavior over resources and/or direct social interaction can emerge. In an environment with poor visibility, such as in a forest, animals can interact with each other using auditory cues (e.g., contact call) when beyond visual range [Caine & Stevens, 1990], and an individual can confirm spatial location by responding to such calls [Ramos-Fernandez, 2005; Spehar & Di Fiore, 2013]. On the other hand, individuals located beyond the audible range of each other cannot interact directly.

1.3 Quantification of grouping dynamics

Previous studies have attempted to understand grouping dynamics in terms of grouping membership (i.e., subunit size and/or composition) [Asensio et al., 2009; Coles et al., 2012; Itoh & Nishida, 2007; Lehmann & Boesch, 2004] and the synchrony of activity among group members [Agetsuma, 1995; Fichtel et al., 2011; King & Cowlishaw, 2009]. However, quantitative studies of spatio-temporal cohesion are limited, and little attention has been paid to integrate spatial cohesion and behavioral synchrony. The scarcity of quantitative studies may be partly due to the difficulties in measurement of the distance between group members who may disperse over spatial ranges that are

wider than the visually observable limits. Similarly, studies of the synchrony of activity beyond the visual range of the observer are also limited. To understand holistic grouping dynamics, we have to consider the reactions of each individual to the dispersal of other group members into a wider spatial range where intra-group contact is not possible.

Traditionally, direct behavioral observation of animals used to be conducted by only one observer. Consequently, the examination of the range of grouping dynamics had previously been restricted to the visual range of one observer. This limitation has prevented clarification of the grouping dynamics of animals displaying dispersal beyond the visual range of the observer. However, in the last decade, technological advancements have facilitated the tracking of individuals with sufficiently high precision to enable understanding of intra-group spatial relations in animal groups spread over a wider range. Rapid progress in sensor technology using GPS has enabled accurate recording of the spatial position of an observed individual, leading to important advances in our understanding of animal spacing behavior. Applying these advanced technologies to simultaneous follows of multiple individuals ranging as a group provides a novel window into understanding the grouping dynamics of primates [Eckhardt et al., 2014; Hilgartner et al., 2012; Otani et al., 2014; Sugiura et al., 2011]. In this study, I applied this novel method (i.e., simultaneous focal animal sampling by two observers using GPS technology) to a group of wild Japanese macaques (*Macaca fusucata*).

1.4 Grouping dynamics of Japanese macaques

Japanese macaques live in multi-male and -female groups [Yamagiwa, 2010], feeding mainly on fruits, seeds, flowers, and leaves which are unevenly distributed [Maruhashi

et al., 1998]. The macaques have a linear dominance hierarchy based on kinship which is nepotistic among resident females [Hill & Okayasu, 1995]. Female Japanese macaques remain in the natal group throughout their lives [Yamagiwa & Hill, 1998], and associate most often with maternal kin [Takahashi & Furuichi, 1998].

Macaques use visual monitoring for vigilance in competitive situations [Yamamoto, 2005] and for locating group members to avoid separation from the group [Kazahari & Agetsuma, 2010; Suzuki & Sugiura, 2011]. Macaques uttered coo calls, which has been suggested as the vocalization used to maintain group cohesiveness [Green, 1975; Itani, 1963; Mitani, 1986; Sugiura, 2007], to avoid separation from the group [Sugiura et al., 2014, see also Koda & Sugiura, 2010 for review], and to ease tension or maintain appropriate distance in competitive situations, such as feeding and grooming in close proximity [Mori, 1975; Suzuki & Sugiura, 2011].

Recently, quantitative spatial cohesiveness (i.e., interindividual distance: IID) data of wild Japanese macaques collected during simultaneous observation of individuals by focal animal sampling using GPS in the Kinkazan [Sugiura et al., 2014; Sugiura et al., 2011] and Yakushima [Otani et al., 2014] Islands in Japan. Sugiura et al. [2011] revealed that female Japanese macaques show spatial cohesion that is adjusted depending on their activity. However, the effects of dominance rank and kinship on spatial cohesion and visual separation duration among group members are yet to be determined. Moreover, behavioral synchrony during periods when individuals disperse beyond the visual range remains to be identified.

1.5 Outline of the study

In this study, I investigated the dynamics of spatio-temporal cohesion and behavioral

synchrony among females in a group of wild Japanese macaques. In the following studies, simultaneous focal animal sampling by two observers was applied to provide a new insight into the grouping dynamics of this species.

In Chapter II, I examine the IIDs, the number and composition of group members within visual range (hereafter, termed visual unit size and visual unit composition), and the separation duration beyond visual range as the indicators of cohesion among individuals. I analyze whether individual activity, dominance rank, and/or kinship can explain these indicators. In Chapter III, I investigate the degree of behavioral synchrony (activity and travel direction) and the factors (IIDs, dominance rank, and/or kinship) that can affect the behavioral synchrony of female macaques including beyond visual and auditory ranges. Finally, in Chapter IV, I summarize the results and discuss the grouping dynamics of female Japanese macaques by integrating the results of Chapter II and Chapter III. I also discuss the grouping dynamics of wild Japanese macaques compared with other primate species, such as chimpanzees, spider monkeys, and southern muriquis, which have been presumed to display highly flexible spatial cohesion and subunit membership. I also mention the remaining challenges to reveal the whole picture of grouping dynamics of Japanese macaques.

Chapter II

Activity and social factors affect cohesion among individuals in female Japanese macaques: a simultaneous focal–follow study

2.1 Abstract

Understanding cohesion among individuals within a group is necessary to reveal the social system of group-living primates. Japanese macaques (*Macaca fuscata*) are female-philopatric primates that reside in social groups. I investigated whether individual activity and social factors can affect spatio-temporal cohesion in wild female Japanese macaques. I conducted behavioral observation on a group, which ranged over ca. 60 ha during the study period. The group was constructed by 38 individuals including 11 adult females and 13 non-natal males. Two observers carried out simultaneous focal animal sampling of adult female pairs during full-day follows using GPS which enabled us to quantify interindividual distances (IIDs), group members within visual range (i.e., visual unit), and separation duration beyond visual range as indicators of cohesion among individuals. I found considerable variation in spatio-temporal group cohesion. The overall mean IID was 99.9 m (range = 0–618.2 m, median = 47.4 m). The percentage of IIDs within visual range was 23.0%, within auditory range was 59.8%, and beyond auditory range was 17.1%. IIDs varied with activity; they were shorter during grooming and resting, and longer during foraging and traveling. Low-ranking females showed less cohesion than high-ranking ones. Kin

females stayed nearly always within audible range of coo calls, and they were rarely separated beyond audible range of loud vocalizations. The macaques were weakly cohesive with small mean visual unit size (3.15 counting only adults, 5.99 counting all individuals). The units composed of adults of both sex with juvenile(s) were the most frequently observed visual unit type when they were grooming or resting. Conversely, the units composed of adult female(s) were the most frequently observed visual unit type when they were foraging. The overall mean visual separation duration was 25.7 min (range = 3–513 min, median = 10 min). Separation duration was associated with dominance rank. These results suggest that Japanese macaques regulate cohesion among individuals depending on their activity and on social relationships; they were separated to adapt food distribution and aggregated to maintain social interactions.

2.2 Introduction

Spatio-temporal cohesion among individual animals characterizes one aspect of the social system of each primate society [Kappeler & van Schaik, 2002; Kummer, 1971]. The factors causing variation in cohesion among individuals have been mainly considered as responses to the costs (intra-group feeding competition) and benefits (reducing predation pressure) associated with living in groups [Krause & Ruxton, 2002; van Schaik, 1983]. The degree of spatio-temporal cohesion among individuals, which is determined by trade-offs between these costs and benefits, influences the mode and frequency of social interactions depending on communicative and cognitive abilities [Amici et al., 2008; Aureli et al., 2008; Barrett et al., 2003].

However, little research has been done to fully quantify the total extent of variation in spatio-temporal cohesion among individuals within a group [Hilgartner et

al., 2012; Sugiura et al., 2011], because highly dispersed group members are often beyond the visual range of one observer. One of the most effective methods for quantifying spatio-temporal cohesion is to measure the interindividual distances (IIDs) between group members. To capture patterns of spatio-temporal variation at larger spatial scales, it is necessary to carry out simultaneous follows of individuals in a group. Simultaneous follows permit the measurement of how far and how long an individual separates from another individual beyond the visual range.

When we evaluate the cohesion among individuals we must take into account not only IIDs but also an individual-based zone of interaction, where individuals can interact directly with other individuals by their own sensory abilities (e.g., visual, auditory, olfactory) [Zuberbühler, 2012]. Within the zone where an individual can see who is where and what they are doing with whom, coordination of spatial position over resources and/or direct social interaction can emerge. In a poor visibility environment, like in the forest, animals can interact with each other using auditory cues (e.g., contact call) beyond visual range [Caine & Stevens, 1990], and an individual can confirm spatial location by exchanging calls. Conversely, individuals located beyond audible range from each other cannot interact directly. Thus, I also considered the range of auditory communication to evaluate cohesion among individuals. Accumulating IID data with consideration for the visual and auditory ranges of animals enables us to increase our understanding of the contributions of spatio-temporal cohesion in primate social systems.

Under low predation pressure, individual activities mainly affect cohesion among individuals within a group. Foraging animals are likely to disperse in an attempt to reduce feeding competition [Altmann, 1974; van Schaik & van Noordwijk, 1988].

Traveling, which is considered to be a risky activity in terms of separation from group members, and affiliative social interactions (e.g., social grooming) might lead to group aggregation [Boinski, 1987; Cowlishaw, 1998]. As resting often occurs together with grooming, aggregation should also occur in resting. Besides individual activities, social relationships could influence patterns of cohesion among individuals. Dominance influences the spatial position of individuals within a group [Hemelrijk, 2000; Hirsch, 2007]. Dominant individuals may use their rank to gain access to preferred spatial positions [Barton, 1993; Saito, 1996]. Meanwhile, subordinates may avoid dominant animals as a strategy to reduce conflicts [Hall & Fedigan, 1997; Nakagawa, 1990]. In many primate societies, animals preferentially associate with kin, direct affiliative behaviors toward close relatives [Gouzoules & Gouzoules, 1987], and support close kin during agonistic interactions [Harcourt & de Waal, 1992; Silk, 2002]. As a result, individuals spend much of their time with their kin [de Waal, 1991; Furuichi, 1983].

In the current study, I quantified the cohesion among individual wild female Japanese macaques in Yakushima Island, Japan by making simultaneous focal follows of two individuals using global positioning system (GPS) devices to record location. I asked to what degree variability in IIDs, number and composition of individuals within sight (i.e., visual units size and composition), and separation duration beyond visual range can be explained by individual activity, dominance rank, and/or kinship. These determinants are not mutually exclusive, and I outline my predictions for each in turn.

Japanese macaques live in multi-male and -female groups [Yamagiwa, 2010], and they feed mainly on fruits, seeds, flowers, and leaves which are patchily distributed [Maruhashi et al., 1998]. Since macaques are likely to spread out over a wider area especially during foraging [Mori, 1977b; Sugiura et al., 2011], I predicted that IID will

increase (prediction 1.1) and visual unit size will decrease (prediction 1.2) when they engage in foraging. The macaques have a linear dominance hierarchy based on kinship which is nepotistic among resident females [Hill & Okayasu, 1995]. Macaques of the same rank class, including those of other kin lineages, should be found close to each other because of a commonality of needs and experience [de Waal & Luttrell, 1986; Matsumura & Okamoto, 1997]. I predicted that IIDs are expected to be shorter between same rank class females (prediction 2.1). Low-ranking animals tend to form small subunits away from the main group to avoid competition with other group members [Dittus, 1988; van Noordwijk & van Schaik, 1987]. I predicted that low-ranking females will also tend to spend time in smaller visual units than high-ranking ones (prediction 2.2), and separation duration of same rank class females are also expected to be shorter than that of different rank class (prediction 2.3). Female Japanese macaques remain in the natal group throughout their lives [Yamagiwa & Hill, 1998], and associate most often with maternal kin [Takahashi & Furuichi, 1998]. Maternal kin individuals are expected to spend more time at close distance because of their nepotism (prediction 3.1), and thus the more kin females, the larger the visual unit size (prediction 3.2) and separation duration is expected to be shorter between kin compared to non-kin females (prediction 3.3). Because the socionomic sex ratio (the number of non-natal males per adult females in a group) of the study group was 1.1, the visual unit composition of adult females might consist mostly of both-sex units (prediction 4).

2.3 Methods

2.3.1 Study site and subjects

The study was conducted on Yakushima Island (503 km^2), in southern Japan (30°N,

130°E). The study site lies within the western lowland (100–350 m a.s.l.) in Yakushima National Park. The study area is covered by primary and secondary warm temperate broad-leaved forest. Visibility in the study area is short with a median of about 20 m [Koda et al., 2008]. The island is inhabited by a large population of Japanese macaques [Yoshihiro et al., 1999]. Macaques have no natural predators, and it is likely that no predators have occurred on the island since the last glacial period [Environment Agency, 1985]. In addition, hunting has been forbidden by law since the 1970s.

I studied the E group, which contained 38 individuals, including 11 adult females (≥6-year-old), 13 non-natal males (≥5-year-old), 11 natal juveniles (1- to 5-year-old), and 3 infants. The members of E group have been individually identified since 2004 and were well habituated to human observers [Nishikawa & Mochida, 2010]. The maternal lineages for adult females of this group were known using non-invasive DNA analysis [S. Hayakawa unpub. data]. I defined kin dyads as those with maternal coefficient of relatedness ≥0.25 (i.e., mother–daughter and maternal sisters dyads in this study) based on the relatedness threshold for nepotistic aiding [Chapais et al., 1997]. I determined female dominance rank using agonistic interactions between two individuals, including both severe and mild aggression [Hill & Okayasu, 1995]. These interactions had been accumulated since 2004 on this group and I also recorded all agonistic interactions observed by *ad libitum* sampling during the study period. Dominance rank was stable throughout the study period.

Eleven adult females were classified into two rank classes, high-ranking and low-ranking. Six females, three from each rank class, were chosen as study subjects. In each rank class, two of the three females were kin related. The three high-ranking focal females had two, two, and one kin adult female(s), respectively, in the group. The three

low-ranking focal females had one, one, and one kin adult female, respectively, in the group. I excluded lactating females as study subjects because they might change their spacing behavior [Busse, 1984; Cowlishaw, 1999]. This study period (April–June 2008) was the non-mating season of the study species.

2.3.2 Data collection

Each of two observers (M. Suzuki and I), using coordinated watches and GPS, simultaneously followed an adult female for 34 days in April–June, 2008, using focal animal sampling from dawn to dusk. I observed all 15 possible pairs including two kin pairs. Each observation day was composed of more than 8 hr of simultaneous observation. The mean total observation time per individual was 130.8 hr (range: 125.9–142.7 hr). The mean observation time per pair per day was 11.0 hr (range: 8.4–13.6 hr).

The two observers recorded the activities (see below) of each focal individual every 1 min by instantaneous sampling. I classified activities into five categories: foraging, grooming, resting, traveling, and other. Foraging activities included searching, handling, and processing food. Grooming included grooming other individuals and being groomed. Resting included self-grooming and inactive states, mostly sitting without foraging, traveling, or grooming. Traveling referred to continuous movement without sitting. Other activities included agonistic interactions, playing, allo-mothering, and vomiting. The two observers recorded group members within sight (ca. ≤20 m) of each focal individual every 5 min by instantaneous sampling. I excluded infants because they were usually dependent on their mothers.

Both observers carried two light-weight GPS devices (i-Blue 821; TranSystem,

Taiwan) mounted on the shoulders or backpack. The GPS devices recorded a fix every second that included data on location (latitude, longitude), time, and positional dilution of precision (PDOP, an index of position accuracy). Mean dispersion of the GPS fixes during the study period was ±3.6 m for fixes matched to stationary locations. We usually remained within a horizontal distance of ≤5 m from the focal individual and considered the position of the observer to be that of the focal individual. The macaques ranged over ca. 60 ha during the study period.

2.3.3 Data analysis

Positional data

I converted location data to map coordinates in the Universal Traverse Mercator projection (Datum WGS84). To remove large location errors, I used only three-dimensional fixes with PDOP value ≤6 [D'Eon & Delparte, 2005], and did not use GPS location data recorded when either observer had lost the focal individual. To smooth positional data, a location point was calculated as an average of fixes within the 1 min duration (max. 60 fixes) centered on the minute corresponding to the moment the observers recorded behavioral data. Interindividual distances (IIDs) were calculated as the average of the planimetric distances from the two GPS devices carried by one observer to each of the two devices carried by the other observer (total four pairs). If a GPS device had failed to produce a data point, the IID was calculated from the remaining devices.

Typical activity

To represent relatively long and stable activity around the sampling time, I analyzed

activities observed during 5 min periods at 5 min intervals (i.e., five instantaneous sampling points of activity at –2, –1, 0 (the same time), +1, and +2 min from sampling time). I defined a typical activity as "foraging" and "resting" when a focal female exhibited these behaviors at four or five of five sampling points (≥80%). I defined a typical activity as "grooming" when a focal female exhibited this behavior at four or five sampling points (≥80%), or three grooming sampling points and two resting sampling points, or two grooming sampling points and three resting sampling points. I defined a typical activity as "traveling" when a focal female exhibited this behavior at ≥3 sampling points (≥60%). I relaxed the criterion for "traveling" because movement did not last as long as foraging, resting, or grooming. I defined any combination of activity other than these categories as "mixed".

Concurrent activity

To analyze the relationship between IIDs and activity, dominance rank, and kin (predictions 1.1, 2.1, and 3.1), I identified the concurrent activities using the 5 min typical activities of each focal individual. I defined concurrent activity types as "both foraging", "both grooming", "both resting", and "both traveling" when both focal females exhibited the same typical activity. I defined any combination of concurrent activity other than these four categories as "other combinations".

Visual unit size and composition

I defined a visual unit as all visible individuals within sight of each observer (ca. 20 m radius). The threshold was chosen from the observer's view [Koda et al., 2008], which was assumed to be similar to that of the focal animal. I defined adult visual unit size as

all visible adults (i.e., adult females and non-natal males) around the focal animal, and total visual unit size as all visible individuals around the focal animal, including juveniles. I classified visual units into seven types according to unit composition: 1) solitary (no other individual); 2) male (≥1 non-natal males); 3) female (≥1 adult females with/without juveniles); 4) juvenile (≥1 juvenile); 5) adult (≥1 non-natal males and ≥1 adult females without juveniles); 6) both-sex (≥1 non-natal males and ≥1 adult females with juveniles); and 7) other (≥1 non-natal males and juveniles). I examined the proportion of the unit type on each typical activity (prediction 4).

Separation duration

I defined separation duration as follows. I took 20 m, the general range of visibility in this study site, as the criterion of convergence and separation. I defined "converged" when the IID of two focal females was less than 20 m, and "separated" when the IID of two focal females were 20 m or further apart. I defined the last minute of "converged" leading to "separated" as "separation-start", and the first minute of "converged" following "separated" as "separation-end". A continuous separation bout between separation-start and separation-end was defined as "separation duration". I counted as separation in the analysis lasting more than 2 min to avoid small GPS fix variability around the borderline of visibility. That is why minimum separation duration was 3 min. I excluded separations for which I could not record either separation-start or separation-end from the analysis.

Statistical analyses

To quantify the factors affecting spatio-temporal cohesion among individuals, I used

generalized linear mixed models (GLMMs). All analyses were computed using R statistical software, version 2.15.2 [R Development Core Team, 2012]. I used the R package glmmADMB to construct GLMMs based on the maximum likelihood method, and this package estimates the maximum likelihood of parameters using Laplace approximation. I performed model selections on the basis of an information-theoretic approach [Burnham & Anderson, 2002]. I determined that GLMM having the smallest Akaike Information Criterion (AIC) value was the best model. Significance was tested using the Wald statistic, evaluated against the Chi-squared distribution. Before analysis, I calculated Cramer's coefficient (V) or Correlation ratio (η^2) among all explanatory variables to account for the possibility of correlations between them.

For the analysis of spatial cohesion among individuals, I set the IID as a response variable. Then I set concurrent activity (prediction 1.1), dominance rank pair (prediction 2.1), and kinship (prediction 3.1) as the explanatory variables. Cramer's coefficient between explanatory variables was small (All V <0.5), thus ruling out correlation [Dormann et al., 2013]. I used the Gamma distribution and a log-link function in the models. IID data were collected repeatedly within and across days, and so observation date and pair ID were fitted as random factors, to control for the non-independence of observations. I also set the adult visual unit size as a response variable. Then I set typical activity (prediction 1.2), dominance rank (prediction 2.2), and the number of maternal kin adult females (prediction 3.2) as the explanatory variables. Correlation between explanatory variables was ruled out (V <0.5, and all η^2 <0.5). I used the Poisson distribution and a log-link function. Observation date and macaque ID were fitted as random factors. For the analysis of temporal cohesion among individuals, I set the separation duration as a response variable. Then I set rank pair

(prediction 2.3) and kinship (prediction 3.3) as the explanatory variables. Correlation between explanatory variables was ruled out (All V <0.5). I used the Gamma distribution and a log-link function in the models. Observation date and pair ID were fitted as random factors. I concluded a χ^2 test of independence and residual analysis to determine if the composition of visual units were associated with typical activity (prediction 4).

2.4 Results

2.4.1 Interindividual distances (IIDs)

Variation in IIDs experienced by six focal adult female macaques is shown in Figure II–1A and Table II–1. The overall mean IID was 99.9 m (N = 4,368, range = 0–618.2 m, median = 47.4 m). The percentage of the macaques located within visual range (IID <20 m) was 23.1%, within auditory range (20 ≤ IID < 200 m) was 59.8%, and beyond auditory range (IID ≥200 m, [Oi et al., 2003]) was 17.1% of overall observation time. The two focal females never converged throughout the day in two of 34 observation days. One such pair was a non-kin and high–low-ranking pair and the other was a non-kin and low–low-ranking pair. However, these focal females converged within 2 days.

The AIC values for the full model and all possible sub models are shown in Table II–2. The best model (Model 1a, Table II–2) indicated that concurrent activity, dominance rank pair, and kinship influenced IID (AIC = 45,585.8). The coefficients and standard errors of the explanatory variables in the best model are shown in Table II–3. IID was longest when female-pairs engaged in foraging concurrently and the shortest when they engaged in grooming concurrently. High-ranking pairs decreased IID. In

contrast, low-ranking pairs increased IID. Kinship decreased IID. However, since the ΔAIC between Model la (best model) and Model 1b was <2 (Table II–2), they can be considered broadly equivalent [Burnham & Anderson, 2002], meaning that an independent effect of kinship on IID was caution.

IIDs between kin female pairs were within audible range of contact calls (i.e., <200 m) during 99.8% of the observation time. They were almost always within the audible range of coo calls emitted during calm situations (i.e., <100 m [Oi et al., 2003]) and rarely beyond the audible range of loud vocalizations (i.e., <200 m), whereas non-kin female pairs dispersed beyond the audible range (i.e., ≥200 m) during 19.9% of the observation time.

2.4.2 Visual unit size and composition

I observed 7,464 visual units. Mean visual unit size was 3.15 ± SD 3.20 (range = 1–17, potential max = 23) counting only adults and 5.99 ± SD 5.40 (range = 1–28, potential max = 34) counting all individuals, although the modal size was just one adult (Figure II–1B). I never observed the entire group together concurrently during a single 5 min sampling point.

The best model (Model 2a, Table II–2) indicated that typical activity and dominance rank influenced adult visual unit size (AIC = 1,5648.9). The number of kin adult females was not included in a best model. Females engaged in foraging and traveling showed smaller adult visual unit size compared with grooming and resting. Low-ranking females showed smaller adult visual unit size than high-ranking one's (Table II–3).

Female units as well as both-sex units constituted the frequent visual unit types.

I found that females spent similar time in both-sex (35.3%) and female (37.0%) visual units, and also spent time in juvenile (9.4%), solitary (8.9%), adult (2.7%), male (2.3%), and other (4.5%) units although the proportion was smaller than the two former ones. The types of visual unit composition differed significantly among the typical activities (χ^2 test for independence: χ^2 = 1,234.9, df = 16, P <0.001). Residual analysis revealed that both-sex visual units were observed significantly more frequently than expected during grooming (P <0.001) and resting (P <0.001). Conversely, female visual units were observed significantly more frequently than expected during foraging (P <0.001) and traveling (P = 0.032) (Figure II–2).

2.4.3 Separation duration

Variation in separation duration is shown in Figure II–1C and Table II–1. The overall mean separation duration was 25.7 ± SD 50.0 min (N = 431, range = 3–513 min, median = 10 min). However, potential separation duration may be longer, because I could not record long separation durations when the focal females never converged in the whole day (N = 2 days) or did not converge at nearby sleeping sites (N = 12 days).

The best model (Model 3a, Table II–2) indicated that dominance rank pair influenced separation duration (AIC = 3,604.6). Separation duration was the shortest between high-ranking females, intermediate between high and low-ranking females, and the longest between low-ranking females (Table II–3). Kinship was not included in a best model. However, since the ΔAIC between Model 3a (best model) and Model 3b was <2 (Table II–2), they can be considered broadly equivalent, meaning that the significance of kinship on separation duration should be treated with tenuous.

2.5 Discussion

2.5.1 Features of group cohesion of female Japanese macaques

It is known that Japanese macaques disperse when they forage and travel within a day [Furuichi, 1983; Mori, 1977a]. However, little had been known about the precise picture of cohesion among individuals beyond visual range [but see Sugiura et al., 2011; Otani et al., 2014]. In this study, I was able to quantify the IIDs between females with simultaneous focal follows. As a whole, female pairs were positioned beyond visual range but within auditory range (20–200 m) for more than half of observation time and occasionally beyond auditory range (≥200 m) (Figure II–1A). The overall median separation duration (10 min) could be explained by macaque feeding behavior. Female Japanese macaques that separated from other group members for foraging travel to catch up with other group members as soon as their foraging was finished at a certain food patch. Remarkably, females are found in a solitary unit in some instances. Although solitary females of Japanese macaques have been described as desertion of the group [Sugiyama & Ohsawa, 1982], my finding revealed that a solitary female is one expression of subunit composition during daily ranging and not an anomaly.

2.5.2 Effects of activity on cohesion among females

In the analysis of the variables that influence the IID and visual unit size, all models with the highest support included activity (Table II–2). I found that IIDs were larger and visual units were smaller during foraging (in support of predictions 1.1, 1.2, Table II–3). These results might be caused by their food distribution pattern characterized by small patches in this study site [Maruhashi et al., 1998]. The number of macaques which can co-feed within a certain food patch would be small, and the quality of a small food

patch may immediately decrease when a macaque uses it once. Therefore, macaques may have to make an effort not to overlap using food patches and they should use patches that have not been exploited by other macaques. Overall, mean IID during both focal females engaged in foraging (92.6 m) was larger than mean inter-food patch distance in this study site (70.1 m, [Maruhashi et al., 1998]). Patchy and limiting food sources lead to intra-group feeding competition [Koenig, 2002], and previous studies have shown that Japanese macaques exhibited agonistic interaction during feeding in this study site [Hanya et al., 2008; Hill & Okayasu, 1995]. With these points, macaques may have to maintain large distances from each other in order to not only adapt to food distribution but also reduce feeding competition. As a result, the number of individuals around focal animals might have been reduced and then visual unit size became small during foraging. Alternatively, individual preference for feeding sites could contribute to the exceptionally large IIDs, hence further analyses are needed. I found that females spent similar time in both-sex and female visual units (in failing to support prediction 4). Both-sex visual units decreased during foraging, suggesting that sexual segregation occurred more frequently during foraging compared to resting and grooming between adult Japanese macaques. Because body weights of adult males are much heavier than adult females in Japanese macaques [Hamada & Yamamoto, 2010], adult males may select lower quality but more abundant food items based on the Jarman–Bell principle [Agetsuma, 2001]. Such differences in dietary preference between males and females might lead to spatial sexual segregation.

Conversely, when the focal animals engaged in grooming and resting, IID was smaller and visual unit size was larger than in other activities (predictions 1.1, 1.2, Table II–3). This aggregation might be important for group members in this study area

where aggressive intergroup encounters often involve coalitions of group members [Saito et al., 1998], because grooming is important for strengthening social bonds between individuals [Schino, 2007; Spruijt et al., 1992]. Each group member might gain an advantage in forming coalitions for intergroup encounters from habitual aggregation during resting and grooming to maintain recognition as group members. The predominance of both-sex visual units during grooming and resting show that not only females but also males converged at one site during the day and females spent their time with males (Figure II–2), although this study period was during the non-mating season. Since females also show aggressive behavior during intergroup encounters in Yakushima [Saito et al., 1998], being together with females may also give males an advantage in home range defense including food resources.

When study animals engaged in traveling, IID increased and visual unit size decreased (predictions 1.1, 1.2, Table II–3), indicating that these Japanese macaques did not aggregate during traveling. Japanese macaques in the Kinkazan population also did not aggregate during traveling [Sugiura et al., 2011]. This traveling pattern differs from some primate species which are characterized as having high fission–fusion dynamics (e.g., chimpanzees (*Pan troglodytes*) and southern muriquis (*Brachyteles arachnoides*) which exhibit larger traveling subunits than both resting and feeding subunits [Coles et al., 2012; Reynolds, 2005]). One of the reasons might be the absence of predators in this study site. Predator free environments may allow spatial separation between individuals within a group. In addition, the home range size of the study animals (ca. 60 ha) is much smaller than these two other species (southern muriquis, >400 ha; chimpanzees, 700 ha) [Newton-Fisher, 2003; Talebi et al., 2009], and Japanese macaques often use specific grooming sites repeatedly [Iwamoto, 1989]. Considering these facts, macaques might

not need to converge when traveling to avoid losing group members.

2.5.3 Effects of dominance rank and kinship on cohesion among females

I also found that the dominance rank relationships of macaques have effects on IIDs, visual unit size, and separation duration. The IID and separation duration of high-ranking females were the smallest and they tended to stay in larger visual units, whereas, those of low-ranking females were the largest and they tended to stay in smaller visual units (not entirely consistent with predictions 2.1, 2.3, in support of prediction 2.2, Table II–3). Low-ranking females might avoid high-ranking females in order to reduce conflicts with not only high-ranking females but also low-ranking ones. In Kinkazan, low-ranking females were separated from high-ranking ones by using alternative low-quality food patches during foraging [Nakagawa, 1990; Saito, 1996]. As low-ranking individuals of some primate species should be more dispersed to avoid feeding competition and aggression from dominant animals [Janson, 1990; van Noordwijk & van Schaik, 1987], low-ranking females of Japanese macaques appear to spend much more time in small visual units or solitary units. High-ranking females aggregated relatively more often with each other, whereas non-kin low-ranking females were not only positioned separately from high-ranking individuals but also avoided each other (Table II–3). During this study, a certain low-ranking focal female sometimes showed persistent agonistic interactions toward the lowest ranking non-kin matriline [M. Nishikawa, unpub. data]. The lowest ranking matriline may have tried to keep their distance to avoid aggression from that certain female. This avoidance behavior may have contributed to the large IIDs between non-kin low-ranking females. We might need

to take into account not only dominance rank but also the social preference of the females in order to understand their spatial position within a social group.

Previous studies found kinship to be one of the most influential factors structuring proximity including affiliative contact [de Waal, 1991; Furuichi, 1983]. However, surprisingly, the independent effect of kinship on IIDs and separation duration was tenuous in this study (predictions 3.1, 3.3). This discrepancy might suggest that the effect of kinship was weakened when the proximity was assessed over a wider range (e.g., beyond visual range). However, kin females largely remained within audible range of coo calls which emitted in calm situation (i.e., <100 m [Oi et al., 2003]) and rarely separated beyond audible range of loud vocalizations (i.e., <200 m [Oi et al., 2003]) when they separated from one another beyond visual range (Table II–1). Japanese macaques use vocal communication to maintain contact with group members [Itani, 1963], and can identify the contact calls of individuals [Ceugniet & Izumi, 2004; Mitani, 1986]. My results suggest that it must be important for kin females to remain within audible range to able to communicate using vocalizations. In Japanese macaques, animals who belonged to the same matrilineal group allied with one another [Watanabe, 1979]. Because other macaque species (e.g., rhesus macaques (*M. mulatta*) and pigtailed macaques (*M. nemestrina*)) can distinguish screams between kin and non-kin [Fugate et al., 2008; Gouzoules & Gouzoules, 1990], Japanese macaques also can be assumed to discriminate screams between kin and non-kin. Ranging within an audible zone, especially of coo calls, may be important among kin individuals to respond to the emergency situations and make alliances with each other. The number of adult kin females did not affect adult visual unit size (failing to support prediction 3.2, Table II–3). In this study, the variation in number of adult kin among focal females was small

(range; 1–2), therefore further research is required to explore potential kin individual effects.

2.5.4 Perspectives

In conclusion, my results demonstrate that the cohesion among individuals of female Japanese macaques in Yakushima showed considerable spatio-temporal variation (i.e., variation in IIDs and separation duration) within short time periods, and variously changing visual unit size and composition. This study is a first essential step in illustrating cohesion among individuals of wild Japanese macaques. In the future it is hoped that I will able to elucidate the links between such spatio-temporal variation in grouping dynamics with fine-scale data on the availability and distribution of food resources. Detailed primary data, especially on IIDs and separation duration, from other species are awaited in order to make more precise interspecific comparisons which can help in illustrating link between the spatio-temporal variation in grouping dynamics and communicative and cognitive abilities among primates.

Chapter III

Behavioral synchrony in female Japanese macaques

3.1 Abstract

Many different types of grouping dynamics exist among social animals. Behavioral synchrony (i.e., synchrony of activity and travel direction) within a group is one aspect of grouping dynamics, and elucidation of behavioral synchrony can lead to the understanding of how individuals manage their needs within a heterogeneous group. However, past studies on behavioral synchrony have been restricted to narrow spatial ranges, generally to that of the visual range of an observer. Therefore, there is an inadequate understanding of grouping dynamics when members are dispersed across a wider range in terms of behavioral synchrony. In the current study, I investigated the degree of behavioral synchrony and studied if IID, dominance rank, and kinship can affect behavioral synchrony in female Japanese macaques (*Macaca fuscata*). In the current study, two observers performed simultaneous focal animal sampling using global positioning system (GPS) devices to record locations, enabling the monitoring of the behavior of dispersion of focal females beyond the visual range. I found that the degree of overall synchrony of activity was positive (Cohen's $k = 0.13$) compared with the expected value. The factors which affected synchrony were dependent on behavioral categories. Spatial cohesion affected synchrony in grooming and resting, and the degree of synchrony was highest when paired macaques were located within visual range.

Synchrony during foraging and grooming also varied depending on dominance rank, with high-ranking female pairs displaying the highest synchrony. Kinship also affected traveling synchrony with kin females displaying a higher traveling synchrony. The frequency of synchronous travel direction was similar up to 100 m, beyond which it sharply declined. Current results suggest that low-ranking females generally adjust their behavioral timing to avoid intra-group feeding competition and/or conflicts with other females within a group. Female Japanese macaques use coo calls to synchronize their travel direction within ca. 100 m and probably belong to a same ranging-unit, even when visually separated as far as ca. 100 m.

3.2 Introduction

Group-living is a widespread phenomenon in the animal kingdom, and many social animal groups are constructed by individuals of variable sex, age, size, physiological, or social state [Krause & Ruxton, 2002]. Because of the heterogeneity among group members, individuals differ in their optimal timing of activities [Ruckstuhl, 1998] or where they prefer to travel [King et al., 2008]. These interindividual conflicts can yield asynchrony of activity and travel direction among group members, and lead to temporary spatial dispersion of group members without risking permanent group fission [Kerth et al., 2006; King et al., 2008]. Such fluctuations in spatial cohesion, synchrony of activity, and travel direction produce grouping dynamics, which vary across groups and species based on their socioecological, communicatory, and cognitive aspects [Amici et al., 2008; Aureli et al., 2008; Kinzey & Cunningham, 1994].

Group cohesion brings benefits to group-living animals because of shared vigilance or predator confusion [Alexander, 1974; Krause & Ruxton, 2002]. Theoretical

studies have shown that group cohesion is maintained by synchronous activity of group members [Conradt & Roper, 2000; Engel & Lamprecht, 1997]. However, synchronization of activity to maintain group cohesion is not beneficial on an individual level because group members compromise on the activities that would be of optimal benefit to themselves to match the behavior of their companions and may face increased competition over resources [Symington, 1988; Wittig & Boesch, 2003]. Therefore, animals that substantially benefit by spatial cohesiveness (i.e., decrease in predation) show higher behavioral synchrony (as fish shoals and bird flocks) [Aivaz & Ruckstuhl, 2011; Krause & Ruxton, 2002]. On the other hand, animals that obtain fewer benefits by spatial cohesiveness show lower behavioral synchrony [King & Cowlishaw, 2009], because group members exhibit different behavior to reduce costs (i.e., intra-group resource competition) resulting in spatial dispersion of group members.

The degree of spatial cohesion among individuals changes and is determined by trade-offs between costs and benefits associated with group-living [Eckhardt et al., 2014; Hilgartner et al., 2012; Otani et al., 2014; Sugiura et al., 2011]. Despite the knowledge of spatial cohesion within various animal groups, previous empirical studies considering synchrony of activity have been restricted to a narrow range (i.e., within the visual range of an observer) [Agetsuma, 1995; Harrison, 1985; King & Cowlishaw, 2009]. Therefore, synchrony of activity and travel direction (hereafter termed behavioral synchrony) has been unresolved in terms of various forms of changing spatial cohesion within animal groups relating to grouping dynamics.

Under low predation pressures, two major factors can be attributed to behavioral synchrony of social group-living animals which have similar nutritional demands, namely spatial cohesion and social relationships. Temporal spatial-related

processes such as visual or auditory isolation, as a consequence of interindividual distances (IIDs), may result in reduced synchrony due to a reduced opportunity for the use of socially transmitted information such as signals or cues [Fichtel et al., 2011; King & Cowlishaw, 2009]. A dominance hierarchy exists among individuals within groups of many social animals. Nevertheless, previous research on the synchrony of activity has mainly focused on the differences of nutritional demands among group members (e.g., sex, body size, or age classes) [Conradt & Roper, 2000]. However, little attention has been paid to the effect of social relationships among individuals on synchrony of behavior. Differentiation among individuals in dominance rank can skew access to resources and dominant individuals use their rank to gain access to preferred spatial positions [Barton, 1993; Hirsch, 2011; Saito, 1996]. Meanwhile, subordinates avoid dominant animals as a strategy to reduce conflicts [Hall & Fedigan, 1997; Nakagawa, 1990]. Therefore, low-ranking females are obligated to expend effort to adjust their behavior due to their subordination. In many animal societies, animals preferentially associate with kin individuals [Wiszniewski et al., 2010], direct affiliative behaviors, such as social grooming toward close kin [Takahashi & Furuichi, 1998], and support close kin during antagonistic interactions [Gompper et al., 1997; Harcourt & de Waal, 1992; Silk, 2002; Watanabe, 1979]. Therefore, there are less conflicts between kin-related individuals [Furuichi, 1983; Holekamp et al., 1997], which may considerably contribute to synchrony of behavior among kin individuals.

Japanese macaques (*Macaca fuscata*) form large matrilineal multi-male and -female groups with stable membership. These groups are characterized by ephemeral spatio-temporal cohesiveness changing within short time periods, e.g., 1 day (see Chapter II) [Otani et al., 2014; Sugiura et al., 2011]. The macaques display a linear

dominance hierarchy based on kinship among resident females and are nepotistic [Hill & Okayasu, 1995; Kawamura, 1965], and females remain in the natal group throughout their lives [Yamagiwa et al., 1998]. Kinship strongly constrains the associations among females during collective movements [Jacobs et al., 2011]. Japanese macaques use visual monitoring for vigilance in competitive situations [Yamamoto, 2005] and for locating group members to avoid separation from the group [Kazahari & Agetsuma, 2010; Suzuki & Sugiura, 2011]. Japanese macaques emit coo calls, which has been suggested as a vocalization to maintain group cohesiveness [Green, 1975; Itani, 1963; Mitani, 1986; Sugiura, 2007], to avoid separation from the group [Sugiura et al., 2014; see also Koda & Sugiura, 2010 for review], and to ease tension or maintain appropriate distance in competitive situations, such as feeding and grooming in close proximity [Mori, 1975; Suzuki & Sugiura, 2011].

In the current study, I aimed to clarify the general features of behavioral synchrony among female Japanese macaques over all spatial extents of a group. I examined effects of spatial cohesion (i.e., visual and auditory ranges) and social relationships (dominance rank and kinship) on their behavior. Because mature Japanese macaques at the study area had no natural predators [Environmental Agency, 1985], I could eliminate the influence of anti-predation strategies on behavioral synchrony to maintain group cohesion. To quantify the spatial cohesion between individuals, my collaborator and I conducted simultaneous focal animal sampling from dawn to dusk using GPS devices. First, I describe the general pattern of the degree of overall synchrony of activity and relation of synchrony of each activity to spatial cohesion. Next, I explore factors (spatial cohesion and social relationships) that may influence each behavioral synchrony. In addition, I discuss a ranging unit and sub-grouping in

terms of the relationship between spatial cohesion and synchrony of travel direction. My analyses provide a quantitative scale of the behavioral synchrony, facilitating the discussion regarding the mechanisms that drive grouping dynamics and by which individuals coordinate their behavior.

3.3 Methods

3.3.1 Study site and subjects

The study was conducted on Yakushima Island (ca. 500 km^2), in southern Japan (30°N, 130°E, 100–350 m a.s.l.). The study site lies within the western lowland in Yakushima National Park. The study area is covered by primary and secondary warm temperate broad-leaved forest. The island is inhabited by a large population of Japanese macaques [Yoshihiro et al., 1999]. Macaques have no natural predators, and it is likely that no predators have occurred on the island since the last glacial period [Environment Agency, 1985]. In addition, hunting has been forbidden by law since the 1970s.

I studied the E group, which contained 38 individuals, including 11 adult females (≥6-year-old), 13 non-natal males (≥5-year-old), 11 natal juveniles (1- to 5-year-old), and 3 infants during this study period (April–June 2008). The members of E group have been individually identified since 2004 and were well habituated to human observers [Nishikawa & Mochida, 2010]. The maternal lineages for adult females of this group were known using non-invasive DNA analysis [S. Hayakawa unpub. data]. I defined kin dyads as those with maternal coefficient of relatedness ≥0.25 (i.e., mother–daughter and maternal sisters dyads in this study) based on the relatedness threshold for nepotistic aiding [Chapais et al., 1997]. I determined female dominance rank using agonistic interactions between two individuals, including both severe and

mild aggression [Hill & Okayasu, 1995]. These interactions had been accumulated since 2004 on this group and I also recorded all agonistic interactions observed by *ad libitum* sampling during the study period. Dominance rank was stable throughout the study period.

Eleven adult females were classified into two rank classes, high-ranking and low-ranking. Six females, three from each rank class, were chosen as study subjects for this study. In each rank class, two of the three females were kin related. I excluded lactating females as study subjects because they might change their spacing behavior [Busse, 1984; Cowlishaw, 1999]. This study period was the non-mating season of the study species.

3.3.2 Data collection

Each of two observers (M. Suzuki and I), using coordinated watches and GPS devices, simultaneously followed an adult female for 34 days in April–June, 2008, using focal animal sampling from dawn to dusk. I observed all 15 possible pairs including two kin pairs. Each observation day was composed of more than 8 hr of simultaneous observation. The mean total observation time per individual was 130.8 hr (range: 125.9–142.7 hr). The mean observation time per pair per day was 11.0 hr (range: 8.4–13.6 hr).

The two observers recorded the activities (see below) of each focal individual with instantaneous sampling at 5 min intervals. I classified activities into five categories: foraging, grooming, resting, traveling, and other. Foraging activities included searching, handling, and processing food. Grooming included grooming other individuals and being groomed. Resting included self-grooming and inactive states,

mostly sitting without foraging, traveling, or allo-grooming. Traveling referred to continuous movement without sitting. Other activities included agonistic interaction, playing, allo-mothering, and vomiting.

Both observers carried two light-weight GPS devices (i-Blue 821; TranSystem, Taiwan) mounted on the shoulders or backpack. The GPS devices recorded a fix every second that included data on location (latitude, longitude), time, and positional dilution of precision (PDOP, an index of position accuracy). Mean dispersion of the GPS fixes during the study period was ±3.6 m for fixes matched to stationary locations. I usually remained within a horizontal distance of ≤5 m from the focal individual and considered the position of the observer to be that of the focal individual. The macaques ranged over ca. 60 ha during the study period.

3.3.3 Data analysis

Positional data

I converted location data to map coordinates in the Universal Traverse Mercator (UTM) projection (Datum WGS84). To remove large location errors, I used only three-dimensional fixes with PDOP ≤6 [D'Eon & Delparte, 2005], and did not use GPS location data recorded when either observer had lost the focal individual. To smooth positional data, a location point was calculated as an average of fixes within the 1 min duration (max. 60 fixes) centered on the minute corresponding to the moment the observers recorded behavioral data. Interindividual distances (IIDs) was calculated as the average of the planimetric distances from the two GPS devices carried by one observer to each of the two devices carried by the other observer (total four pairs). If a GPS device had failed to produce a data point, the IID was calculated from the

remaining devices.

Categorization of IIDs

Visibility in the study area is short with a median of about 20 m [Koda et al., 2008]. The coo call, which is the most frequently used vocalization within the vocal repertoire of this species, is often exchanged among group members [Koda, 2004; Koda et al., 2008; Sugiura, 1993, 1998]. The coo call can be heard from a distance of ca. 100 m [Oi et al., 2003]. The effective detection distance of other loud vocalizations (e.g., loud calls, loud screams, loud aggressive vocalization, and loud alarm calls) is ca. 200 m [Oi et al., 2003]. To estimate the effect of spatial cohesion on the synchrony of activity between paired macaques, I categorized IID into six types based the visual and auditory senses of macaques as follows: 0–20 m, 20–50 m, 50–100 m, 100–150 m, 150–200 m, and ≥200 m for the overall synchrony of activity and GLMM statistical analysis on each synchrony of activity. Because sample sizes were small in the ranges 100–150 m and 150–200 m, I combined these to form a 100–200 m range, resulting in five types of IID: 0–20 m, 20–50 m, 50–100 m, 100–200 m, and ≥200 m, for GLMM statistical analysis of synchrony in travel direction.

Synchrony of activity

For the analysis of synchrony of activity, I included only the sampling points in which both partners of a pair could be observed, resulting in a total of 4,425 sampling points. In modeling, in which factors do affect the synchrony of each activity, I considered four activity states, namely foraging, traveling, resting, and grooming. The “other” was not considered because I had very few records of this category (1% of all records).

Although I used “typical activity” (i.e., relatively long and stable activity) for analysis in Chapter II, in this chapter, I used 5 minute interval sampling points for each activity datum.

For evaluating the degree of synchrony of activity, I used Cohen’s *k*, which provides a measure of the extent of synchrony in the behavior of two focal animals [Asher & Collins, 2012; Cohen, 1960]. The Cohen’s *k* ranges from −1 to 1; $k = 1$ indicates that complete synchrony is observed, whereas $k = 0$ indicates that the level of observed synchrony is exactly equal to the expected proportion. Thus, $k > 0$ indicates more synchrony than is expected purely by chance. Landis and Koch [1977] defined the following arbitrary divisions for qualitatively evaluating Cohen’s *k*: ≤0.00 indicates poor agreement, 0.00–0.20 indicates slight agreement, 0.21–0.40 indicates fair agreement, 0.41–0.60 indicates moderate agreement, 0.61–0.80 indicates substantial agreement, and 0.81–1.00 indicates almost perfect agreement. I calculated Cohen’s *k* for the aforementioned six IID types for overall activity as a whole and individually for each activity.

For statistical analysis using GLMM, each synchrony of activity was assessed by one-zero assessment of whether activity of one focal animal agreed with the activity of another focal animal at every sampling point. I defined activities of two focal animals as synchronized when the activity of each focal animal were same on the sampling point.

Synchrony of travel direction

For the analysis of synchrony of travel direction, I used positional data at 15 min intervals in which both focal animals could be observed and traveled more than 30 m

during 15 min, resulting in a total of 483 sampling points. The 30 m cutoff was chosen to discount small positional movement, and the overall median travel distance during 15 min was 31.6 m during the study period. Travel of each focal animal during 15 min was represented as a vector. I defined travel of one focal animal as vector A and that of another as vector B. Next, I calculated the angle between vector A and vector B, which defined angle θ, ranging between 0° and 180°. I defined travel direction of two focal animals as synchronized when $0° \leq \theta < 45°$.

Statistical analyses

I used generalized linear mixed models (GLMMs) to estimate the factors affecting the synchrony of activity and travel direction among individuals. All analyses were computed using the "glmmADMB" function in the glmmADMB package of the R statistical software package, version 3.0.3 [R Development Core Team, 2014]. I performed model selections on the basis of an information-theoretic approach [Burnham & Anderson, 2002]. Determination of the best GLMM model to use was done on the basis of the smallest Akaike Information Criterion (AIC) value obtained. For the analysis of synchrony of each activity, I set 1 (synchronized) or 0 (asynchronized) as a response variable based on gathered data. For the analysis of synchrony in travel direction, I set 1 (synchronized) when $0° \leq \theta < 45°$, and set 0 (asynchronized) when the θ was $\geq 45°$. Then I set IID type (six and five types for each activity and travel direction synchrony, respectively), dominance rank pair, and kinship as the explanatory variables on each GLMM. I used the binomial distribution and a logit-link function in the models. Behavioral data were repeatedly recorded across days and pair, and so "observation day" and "pair ID" were fitted as random factors, to control for the non-independence of

observations. To remove the effect of the hour of the day on behavioral synchrony between pair partners, “hour” was also fitted as one of the random factors.

3.4 Results

3.4.1 Synchrony of overall activity

The value of Cohen’s *k* for overall activity was positive ($k = 0.13$, indicating slight agreement, $N = 4{,}425$) compared with the expected value ($k = 0$, means that individuals behave independently of one another).

The values of Cohen’s *k* were different in each interindividual distance (IID) (Figure III–1). The degree of synchrony of activity was the highest when paired macaques were located within visual range ($k = 0.31$, indicating fair agreement), whereas the degree was similar to the expected value when IID was above the range 50–100 m.

3.4.2 Synchrony of each activity

The values of Cohen’s *k* of each activity were also different in each IID (Figure III–2). Foraging and traveling synchrony decreased moderately with increasing IID. Grooming and resting synchrony showed a sharp decline when the IID changed from the range 0–20 m (visual range) to range 20–50 m (beyond visual range). The values of Cohen’s *k* for grooming became nearly constant above the range 50–100 m. The values of Cohen’s *k* for resting decreased to the same value as expected above the range 20–50 m to range 100–150 m.

The factors which affected synchrony were different among activities. The AIC values for the top five GLMMs of each activity are shown in Table III–1. The

coefficient and standard errors of the explanatory variables in the best model of each activity are shown in Table III–2.

In the case of foraging activity, dominance rank pair was selected in the best model (Model f1, N = 1,530, AIC = 2,114.94, Table III–1). The best model indicated that high-ranking pairs had the highest foraging synchrony. In contrast, low-ranking pairs had the lowest foraging synchrony (Table III–2).

In the case of traveling activity, kinship was selected in the best model (Model t1, N = 779, AIC = 743.20, Table III–1). The best model indicated that kin pairs had higher traveling synchrony than non-kin pairs (Table III–2). However, since the ΔAIC between Model t1 (best model) and Model t2 (null model) was <2.0 (Table III–1), they can be considered broadly equivalent [Burnham & Anderson, 2002], meaning that the independent effect of kinship on traveling synchrony should be treated with caution.

In the case of grooming activity, IID and dominance rank pair were selected in the best model (Model g1, N = 894, AIC = 1,071.70, Table III–1). The best model indicated that grooming synchrony was the highest when paired macaques were located within the range 0–20 m,(i.e., within visual range). High-ranking pairs had the highest grooming synchrony, whereas low-ranking pairs had the lowest grooming synchrony (Table III–2). However, since the ΔAIC between Model g1 (best model) and Model g2 was <2.0 (Table III–1), they can be considered broadly equivalent [Burnham & Anderson, 2002], meaning that the independent effect of dominance rank on grooming synchrony should be treated with caution.

In the case of resting activity, IID was selected in the best model (Model r1, N = 1,226, AIC = 1,454.81, Table III–1). The best model indicated that the resting synchrony was the highest when the paired macaques were located within the range

0–20 m (i.e., within visual range) (Table III–2).

3.4.3 Synchrony of travel direction

IID and dominance rank pair were selected in the best model (Model d1, N = 1,460, AIC = 1,834.60, Table III–1). The best model indicated that the synchrony of travel direction was higher when the paired macaques were located <100 m. High- and low-ranking pairs had the lowest synchrony in travel direction. However, since the ΔAIC between Model d1 (best model) and Model d2 was <2.0 (Table III–1), they can be considered broadly equivalent [Burnham & Anderson, 2002], meaning that the independent effects of dominance rank on synchrony of travel direction should be treated with caution.

Figure III–3 shows the declining pattern of frequency in synchronized travel direction on six IID types. The frequency of synchronized travel direction was similar as far as the range 50–100 m. The frequency decreased sharply in the range 100–150 m, and became nearly constant above this range.

3.5 Discussion

3.5.1 Effect of spatial cohesion on synchrony of activity

The value of Cohen's *k* for overall activity was 0.13, which indicates slight agreement [Landis & Koch, 1977]. This index value is similar to that obtained for red-tailed sportive lemurs (*Lepilemur ruficaudatus*), a nocturnal dispersed pair-living primate species [Fichtel et al., 2011]. Because Japanese macaques have no natural predators at this study site [Environment Agency, 1985], they may feel relatively less pressure to remain in a cohesive group. Therefore, they may have less need to synchronize their

activity to maintain group cohesion than they would in an environment inhabited by predators. The predator-free environmental condition occupied by the group of Japanese macaques observed in the current study seems to have resulted in the same degree of the synchrony of activity as nocturnal dispersed pair-living primates.

Theoretical studies have proposed models indicating that a social group can only be spatially coherent if its members synchronize activities [Conradt & Roper, 2000; Engel & Lamprecht, 1997]. Nevertheless, the current analysis using Cohen's *k* revealed that the degree of the overall synchrony of activity of Japanese macaques within visual range was in fair agreement ($k = 0.309$) [Landis & Koch, 1977]. This result also indicates that Japanese macaques do not necessarily synchronize their activities, even when they are spatially cohesive within a visual range (<20 m). One possible reason is their slow travel speed, with an average daily travel speed of 2.19 m/min at this study site [Maruhashi et al., 1998]. Therefore, even if individual macaques engaged in different activities with other group members, and as a result, got separated from other group members, they could easily catch up with the group. Another possible cause may be characteristic of their grooming sites, being spatially near to or the same as the feeding sites [M. Nishikawa, unpub. data]. In addition to predator-free environment and travel speed, this habitat characteristic enables macaques not to impose on same activity within visual range. Beyond the visual range, the degrees of the overall synchrony of activity were much lower than that within the visual range. In particular, the degree of overall synchrony of activity was close to the expected value above the range 50–100 m. These results raise the possibility that visual signals are needed for macaques to synchronize their activity, whereas auditory signals, such as the coo calls which are uttered during calm situations, are less influential in synchronizing

activity.

Among the four activity types, synchrony of grooming and resting were explained by spatial cohesion (i.e., IID). Synchrony was the highest when paired macaques were located within the range 0–20 m (visual range) for both activities, with the synchrony declining sharply when IID increased to the range 20–50 m (Figure III–2). These results suggest that visual contact is especially fundamental for synchronizing grooming and resting activities.

3.5.2 Effects of social relationships on synchrony of activity

Synchrony of activity has been considered to be best maintained by individuals that are similar in size and reproductive state because they have similar activity budgets [Altmann, 1980; Muruthi et al., 1991; Rosetta et al., 2011], and thus, are more likely to synchronize their activities [Aivaz & Ruckstuhl, 2011; King & Cowlishaw, 2009]. Our focal females were all non-lactating and non-pregnant adult females. Nonetheless, why did female Japanese macaques show a low degree of the synchrony of activity? Dominance hierarchy seems to be one of the reasons. Japanese macaques are characterized by a very steep dominance gradient and a social system governed by strict rules [Thierry, 2007]. Among the four activity types, synchrony in foraging and grooming were explained by dominance rank. In the case of foraging, low-ranking females showed apparently lower synchrony as compared to high-ranking females. Because their food resources are unevenly distributed [Maruhashi et al., 1998], and the patches of available food resources are generally too small to satisfy the simultaneous foraging of all group members without competition [Hanya, 2009], subordinate females may delay foraging, giving way to dominant females. The characteristics of these foods

environment may impose adjustment behavior (such as traveling to an alternative feeding patch and/or delaying the timing of foraging) on low-ranking females to avoid aggressive interactions from other females. These adjustment processes mainly by low-ranking females may result in lower foraging synchrony between high- and low-ranking females. Because of the predator-free environment, subordinate individuals can adjust their activity fairly flexibly depending on their own needs and interests. This adjustment behavior would lead to no correlation between the dominance rank and reproductive success of females in this study population [Takahata et al., 1998]. In the case of grooming, as for foraging, low-ranking females showed lower synchrony as opposed to high-ranking females. As mentioned above, low-ranking females appear to be obligated to adjust feeding behavior to avoid competition. This would cause lower feeding efficiency for low-ranking females [Saito, 1996], and they need longer time for feeding and traveling than high-ranking females. As a result, the timing of grooming for low-ranking females is asynchronous with that of other females.

Kinship was the only influence on traveling synchrony. Kin females displayed higher synchrony of traveling than that of non-kin females. However, the significance of kinship on traveling synchrony should be treated with caution according to the result of the model selection (the ΔAIC between the best model and the null model were <2.0). Although kinship strongly constrained the associations in females during collective movements in Japanese macaques [Jacobs et al., 2011], the current result indicates that kinship is not necessarily an important determinant for synchrony during traveling. Because I recorded activity of macaques by instantaneous sampling using 5 min intervals, it is likely that instantaneous sampling was not adequate to detect traveling synchrony; temporally longer sampling durations may be more appropriate for assessing

traveling synchrony.

3.5.3 Effects of spatial cohesion and social relationships on synchrony of travel direction

The degree of synchrony in travel direction was the same for the range 0–20 m as for the range 50–100 m. However, the synchrony of travel direction declined sharply for the range 100–150 m (Figure III–3). Because coo calls can travel as far as ca. 100 m [Oi et al. 2003] and increase in frequency during resting and traveling when the group members are likely to be spread over a larger area [Suzuki & Sugiura, 2011], macaques can coordinate travel direction using coo calls within ca. 100 m without visual cues, suggesting that female macaques at Yakushima belong to the same ranging-unit, even when visually separated within ca. 100 m. A previous study conducted on Kinkazan showed the criteria as being 114 m at which sub-grouping occurred by analyzing the distribution of IIDs [Sugiura et al., 2011]. According to my result of frequency of synchronized travel direction (Figure III–3), individuals located beyond 100 m may be ranging independently to other ranging units, as supported by the same degree as the expected value of the overall synchrony of activity (Figure III–1) and the spatial distribution of macaques [Sugiura et al., 2011].

The lowest synchrony of travel direction was displayed between high- and low-ranking females. This result may be caused by difference in regard to spatial position (e.g., feeding patches) frequented by high- and low-ranking females, because low-ranking females position themselves at longer distances from other females to reduce intra-group competition and/or conflicts (see Chapter II).

Asynchrony of travel direction involves both the spatial separation and

convergence between two macaques. Although I did not discriminate between these two opposite movements in the current analysis, the lower synchrony in travel direction beyond the range 100–150 m would also include converging because macaques tend to move closer after 10 min when the distance to the other focal animals is larger [Sugiura et al., 2014]. The low synchrony in travel direction when IIDs are longer may be interpreted as a sign that either one or both the macaque(s) travel to converge with another macaque. In addition, low synchrony in travel direction could indicate a propensity for independently ranging, i.e., sub-grouping.

Chapter IV

General discussion

In this thesis, I revealed that female Japanese macaques show considerable variation in spatio-temporal cohesion among individuals and in visual unit size and composition within a group (see Chapter II). Also demonstrated was high variation in behavioral (activity and travel direction) synchrony including beyond the visual range (see Chapter III). These results were obtained using simultaneous focal animal sampling by two observers, which introduce a novel method of testing the relative contributions of activity and social factors on the adjustment of macaque individuals to achieve spatio-temporal cohesion and behavioral synchrony over a wider range than the visual range.

In this chapter, I present a summary of grouping dynamics of female Japanese macaques in relation to the content of Chapter II and Chapter III, and describe their grouping dynamics by integrating spatial variation and behavioral synchrony. In addition, I discuss the differences of grouping dynamics to other primate species and provide future perspectives on grouping dynamics of Japanese macaques.

4.1 Summary of grouping dynamics in female Japanese macaques

In Chapter II, simultaneous focal animal sampling by two observers revealed that female Japanese macaques are spatially distributed within the range of 0–618 m (median IID: 47.4 m). The female pairs were located beyond visual range but within

auditory range (20–200 m) for more than half of the observation time and occasionally ventured beyond the auditory range (≥200 m). The macaques spatially distributed themselves in different ways depending on their concurrent activity; IIDs were longer during foraging and traveling than during grooming and resting. They also adjusted their spatial position depending on their social relationships, with low-ranking females showing less cohesion than high-ranking females. Kin females almost always remained within audible range of coo calls (>100 m), and rarely ventured beyond the audible range of loud vocalizations (≥200 m). In addition, visual unit size and composition displayed considerable variation. The mean visual unit size was small (3.37 for adults and 6.33 for all individuals). Females engaging in foraging and traveling displayed smaller adult visual unit size compared with those engaging in grooming and resting. Low-ranking females displayed smaller adult visual unit size than high-ranking females. Both-sex units were the most frequently observed visual unit type when engaging in grooming or resting. Conversely, female units were the most frequently observed visual unit type when engaging in foraging. The overall median visual separation duration was 10 min (range: 3–513 min). Separation duration was associated with dominance rank, with the shortest duration between high-ranking females, and the longest between low-ranking females. These results suggest that Japanese macaques regulate cohesion among individuals depending on their activity and social relationships; they were separated to adapt to food distribution and aggregated to maintain social interactions.

In Chapter II, I mainly analyzed variation in spatial cohesion related to concurrent activity (i.e., both focal macaques engaged in the same activity, which means their activity was in synchrony). However, situations where each focal macaque engaged in a different activity remained unresolved. Therefore, I considered both

situations when focal macaques engaged in the same activity (synchrony) and different activities (asynchrony) in Chapter III. This data set allowed for the quantification of the degree of synchrony of activity and revealed factors causing synchrony of activity between female Japanese macaques. In addition to the synchrony of activity, I added analysis of synchrony in travel direction to clarify grouping dynamics.

In Chapter III, I revealed that the degree of the overall synchrony of activity was larger than the expected value (Cohen's $k = 0.13$). The degree of the synchrony of activity was the highest when paired macaques were located within visual range. The factors which affected synchrony were different across behavioral categories. Spatial cohesion affected synchrony during grooming and resting; the degree of synchrony was the highest when paired macaques were located within visual range. Synchrony also varied depending on the dominance rank during foraging and grooming; high-ranking pairs showed the highest synchrony. Kinship affected traveling synchrony with kin females showing higher traveling synchrony. The frequency of synchronous travel direction was similar up to 100 m and sharply decreased beyond that. These results suggest that visual information is important for allowing Japanese macaques to synchronize their grooming and resting activities. Auditory information of coo calls contributed to synchronizing their travel direction. This finding suggests that female macaques belong to a same ranging-unit even when visually separated within ca. 100 m.

Considering wider dispersion and smaller visual unit size during foraging (in Chapter II), and lower foraging synchrony in low-ranking female pairs than in high-ranking pairs (in Chapter III), macaques, particularly the low-ranking females, can adjust their spatial position and behavioral timing to avoid intra-group feeding competition among group members. Individuals ranging separately from the group are

vulnerable to encountering neighboring groups at this study site [Otani et al., 2014]. Relatively higher spatio-temporal cohesion and synchrony in travel direction among high-ranking females may indicate that females attempted to maintain aggregation within group members, resulting in higher foraging and grooming synchrony as a countermeasure against encountering neighboring groups. However, low-ranking females may be forced into asynchrony to a certain degree so as to avoid intra-group competition and/or conflicts with other females in the group.

4.2 Reconsideration of the effects of activity and social relationships on cohesion in the same ranging unit

According to the result of synchrony in travel direction presented in Chapter III, spatial criteria for belonging to the same ranging unit seemed to be ca. 100 m. In response to this result, I analyzed the effects of activity and social relationships on IID with limited data in which IID <100 m to remove the influence of sub-grouping using same statistical analysis as in Chapter II. In the analysis using GLMMs, activity and dominance rank pair were included as explanation variables in the best model (M. Nishikawa unpub. data). IIDs were shorter during grooming and resting and longer during foraging and traveling. Low-ranking females showed less cohesion than high-ranking females. Therefore, the effects of activity and dominance rank on IID showed the same tendency as the result of Chapter II which included IIDs ≥100 m. The second best AIC model included activity, dominance rank pair, and kinship as explanation variables, and the difference in ΔAIC between the best model and this model was 2.0, indicating that kinship has little effect on IID within 100 m.

4.3 Comparison with other primates

According to the conceptual framework proposed by Aureli et al. [2008], the relative degree of fission–fusion dynamics may be determined using three dimensions: subunit size, subunit composition, and spatial cohesion. In the current study, visual unit size and composition of Japanese macaques showed considerable variation and compositions were not stable. Females were also found in a solitary unit at some instances. It is known that females of chimpanzees, spider monkeys [Chapman et al., 1995], and southern muriquis [Coles et al., 2012] also spend time as a solitary unit within a group. In terms of visual unit size and composition, female Japanese macaques exhibit similar variation to chimpanzees, spider monkeys [Chapman et al., 1995], and southern muriquis [Coles et al., 2012] which are known as fission–fusion societies.

However, there is potentially a different aspect affecting the degree of spatio-temporal cohesion within Japanese macaques as compared with chimpanzees, which are renowned for having a fission–fusion society. Recently, Eckhardt et al. [2014] presented quantitative data on spatial cohesion collected by simultaneous focal animal sampling among individuals in male Chimpanzees at Taï National Park, Côte D'Ivoire. Their home range size was ca. 2,700 ha. Study of the IIDs revealed the maximum, median, and mean to be 7.2 km, 73 m, and 483 m, respectively. Although the quantitative data of separation duration has not been reported for chimpanzees, female chimpanzees visually observe one another only a few times during an entire year for some females [Goodall, 1986]. In the current study, IIDs of female Japanese macaques indicated that the maximum, median, and mean IIDs were 618 m, 47.4 m, and 99.9 m, respectively (Chapter II). Their home range size was ca. 60 ha. Given the IIDs and separation duration, Japanese macaques appear to demonstrate higher spatial

cohesiveness and converge relatively more often compared to chimpanzees.

Japanese macaques have previously been reported to show relatively low fission–fusion dynamics with stable group membership without data on spatio-temporal cohesion [Aureli et al., 2008]. However, given the results of the current study, we may have to redefine our recognition of the grouping dynamics of Japanese macaques with the results indicating less cohesion in terms of subunit size and composition than gelada baboons (*Theropithecus gelada*) [Altmann, 1974] and hamadryas baboons (*Papio hamadryas*) [Kummer, 1968], in which unit composition (one-male unit in gelada baboons and clans in hamadryas baboons) is predictable and temporally constant, with a similar cohesion in terms of subunit composition to that of tufted capuchins (*Cebus apella*) [Alfaro, 2007], and more cohesion than that of chimpanzees [Eckhardt et al., 2014]. Spider monkeys and southern muriquis have also been considered as fission–fusion societies [Aureli et al., 2008; Chapman et al., 1995; Coles et al., 2012; Ramos-Fernandez et al., 2011; Symington, 1990]. However, up to date, quantitative data of IIDs and separation duration are insufficient. Detailed primary data on IIDs, separation duration, and degree of behavioral synchrony from other species are awaited to allow more precise comparisons which can help in illustrating differences of the grouping dynamics among primates.

4.4 Remaining challenges

I point to several new areas for future research. First, the spatial and temporal patchiness in food dispersion and abundance has been an important ecological selection pressure leading to the evolution of grouping dynamics, namely fission–fusion social organization in chimpanzees and spider monkeys [Symington, 1990]. Female Japanese

macaques also show considerable variation in spatio-temporal cohesion (Chapter II). In addition, future studies of Japanese macaques involving ecological determinants and fine-scale data on the spatial and temporal distribution of food resources and comparative behavior are needed.

Second, the selection of foods and activity patterns by animals is related to body weight, age, and sex [Gautier-Hion, 1980; Hanya, 2003; Nakagawa, 2000; Watanuki & Nakayama, 1993]. These factors influence the nutritional requirements of the individual animals. Since I focused on the grouping dynamics of only adult females in the current study, the data on males and juveniles are needed to achieve a comprehensive understanding of grouping dynamics of Japanese macaques [but see Otani et al., 2014].

Third, the degree of spatial cohesion or temporal overlap in female receptive periods affects monopolization by males. Estrus females drive grouping membership in chimpanzees [Anderson et al., 2002; Matsumoto-Oda et al., 1998]. The studies conducted during mating seasons including following estrus females are also needed for Japanese macaques.

Fourth, the group size appears to affect group cohesiveness and behavioral synchrony. A decrease in group size led to an increase of group cohesion in chimpanzees [Lehmann & Boesch, 2004] and pig-tailed macaques [Oi, 1990]. The decrease in group size led to an increase in the synchrony of activity in Japanese macaques within visual range [Agetsuma, 1995]. We need to further investigate the influence of group size on grouping dynamics of Japanese macaques in multiple populations.

Finally, dominance style might cause differences of grouping dynamics. The

genus *Macaca* contains 20 species [Brandon-Jones et al., 2004]. They form multi-male and -female groups, however, different dominance styles occur in each species. Thierry [2000] classified the 20 species in the macaque genus into grades along the despotic–egalitarian continuum, and the Japanese macaque was graded as a despotic species. Dominance style may influence spacing behavior. Furthermore, some macaque species share habitat with predators. Therefore, they might show higher behavioral synchrony to maintain group cohesion to avoid predators.

Further investigation concerning these additional factors will help elucidate the suite of interacting social and ecological factors shaping the social system of Japanese macaques. Future studies with additional Japanese macaque groups of different habitats and a wider range of animal species groups are necessary to understand how individual animals and groups as a whole differ in their grouping dynamics.

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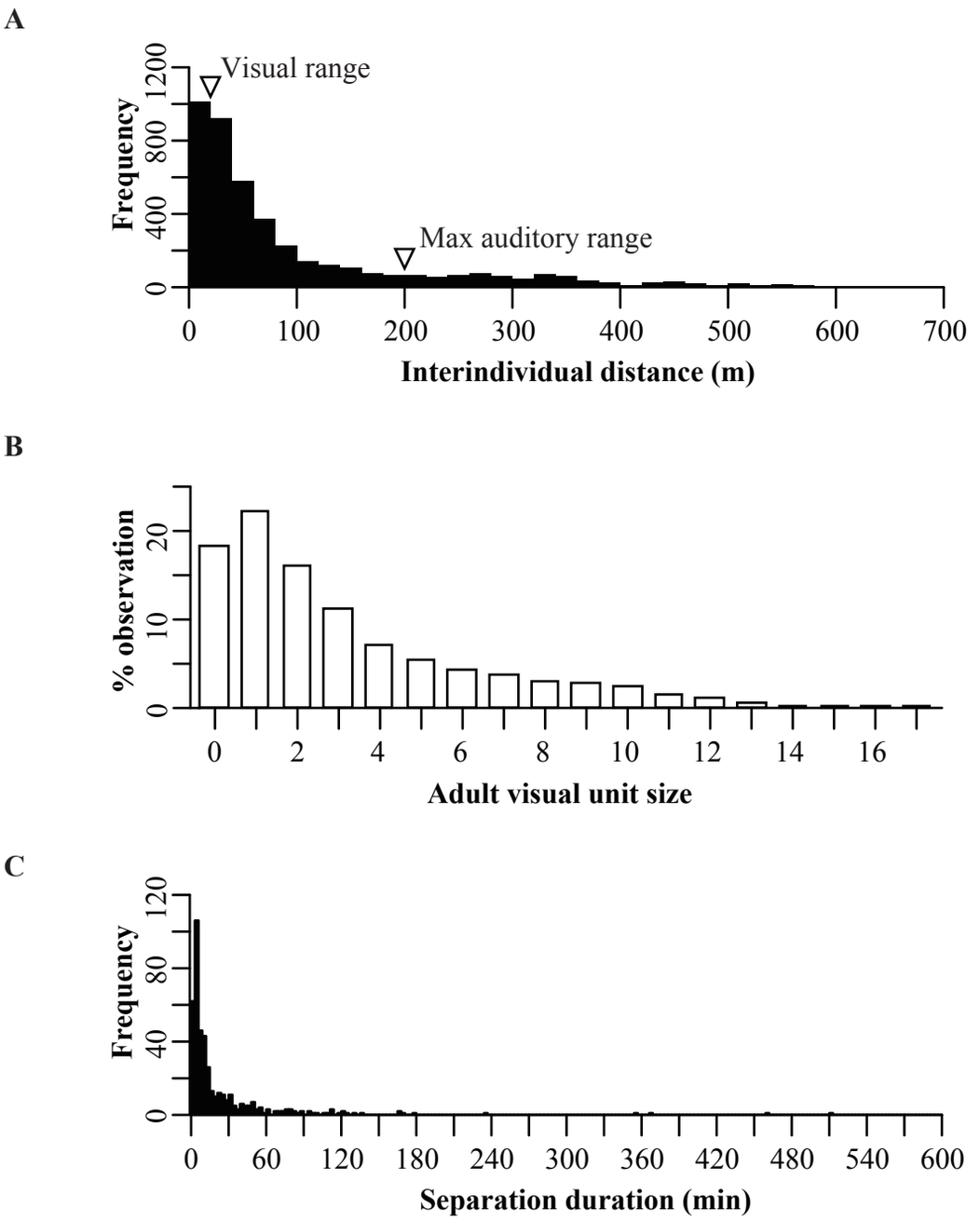

Figure II–1: **A**: Distribution of interindividual distances (IIDs) (N = 4,368 typical activity sampling points). **B**: Frequency distribution of adult visual unit sizes around focal female (N = 7,464 sampling points). Zero unit size means that there was no adult female/non-natal male within sight of the focal female. **C**: Frequency distribution of separation durations (N = 431 bouts). Class interval is 3 min.

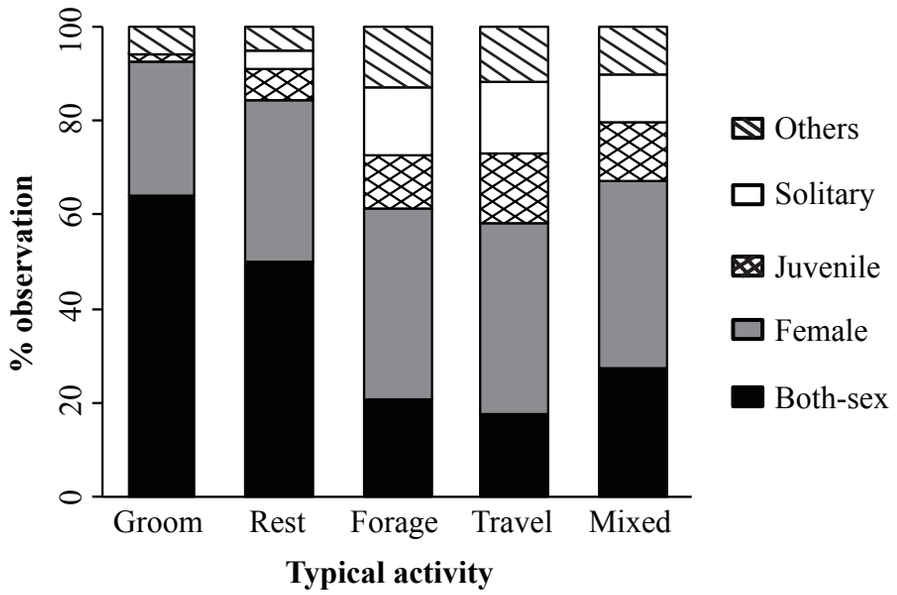

Figure II–2: Visual unit types for each typical activity of the focal female (*N* = 7,464 sampling points).

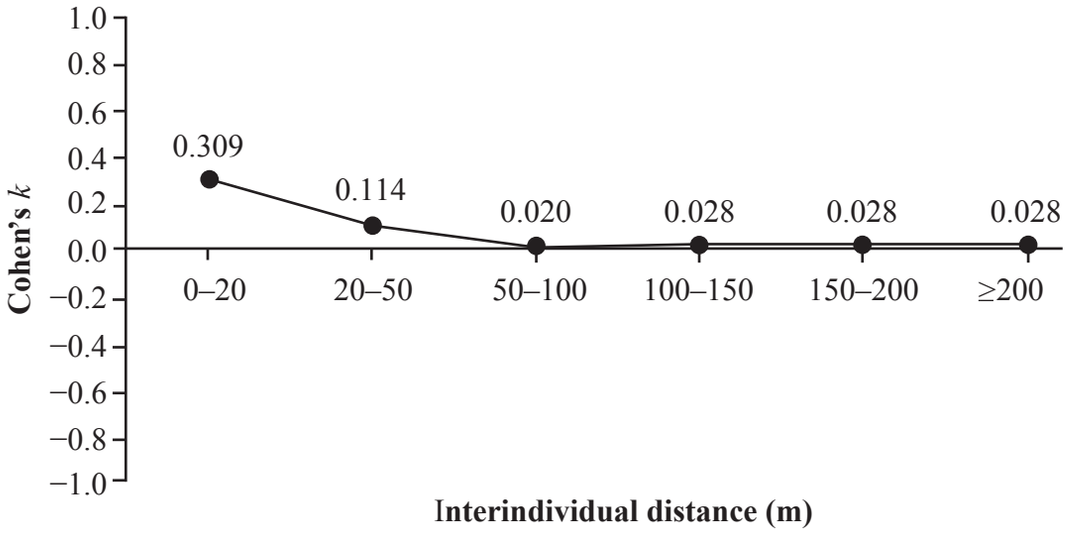

Figure III–1: Cohen's *k* of activity for six categorized IID ranges. The zero of Y-axis corresponds to the independent behavior.

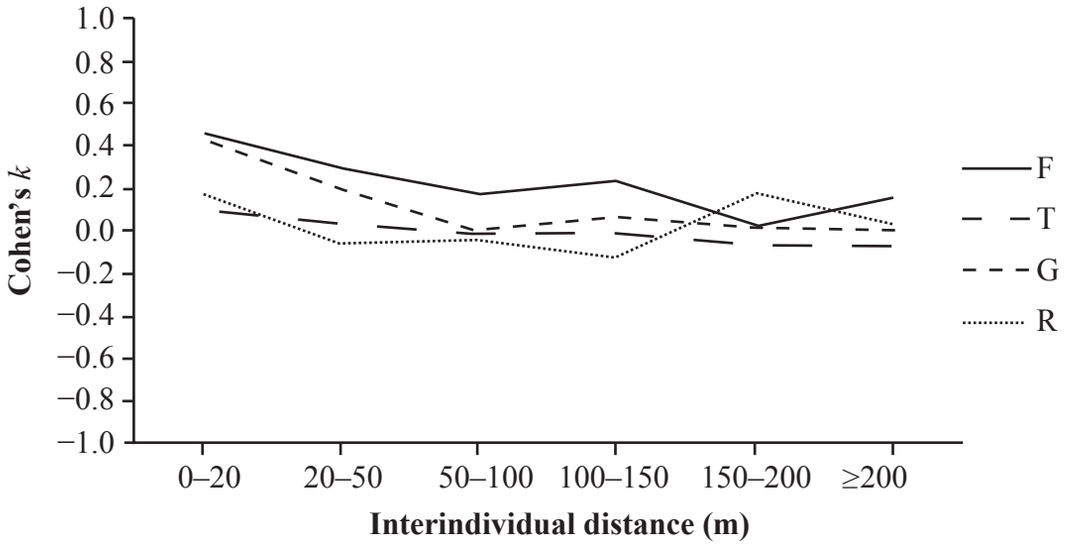

Figure III–2: Cohen's *k* of each activity for six categorized IID ranges. The zero of Y-axis corresponds to the expected value. F: foraging, T: traveling, G: grooming. R: resting.

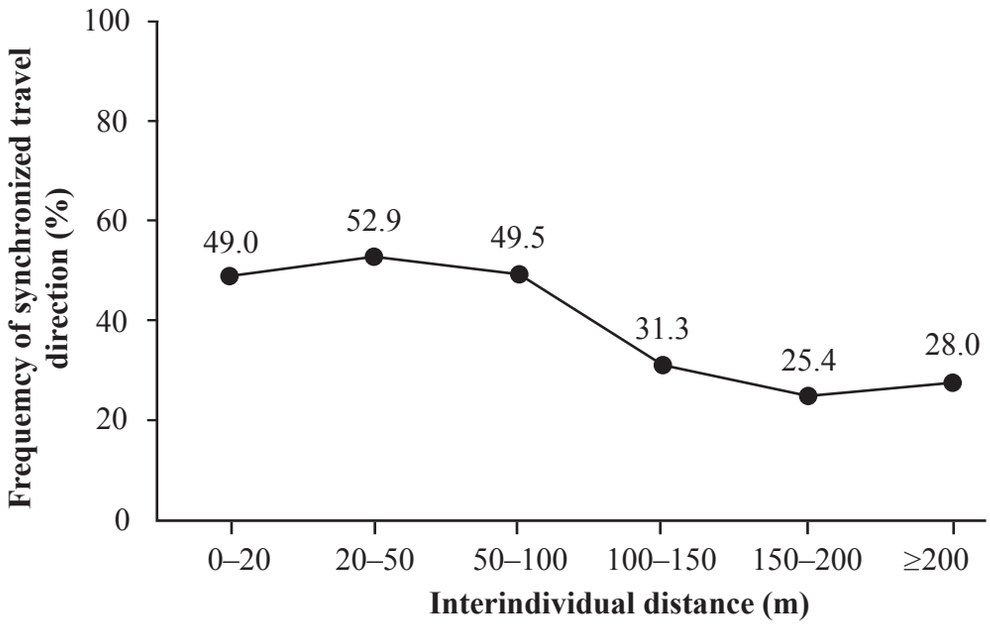

Figure III–3: Frequency of synchronized travel direction (%) for six categorized IID ranges.

Table II–1: Summary of interindividual distance (IID) (m), adult visual unit size, and separation duration (min) for each explanatory variable

Explanatory variables			*N*	Min.	Median	Mean ± SD	Max.
IID	Concurrent activity	Both foraging	483	2.5	48.9	92.6 ± 109.0	579.4
		Both grooming	367	2.4	16.6	63.4 ± 112.0	566.9
		Both resting	161	3.2	18.8	63.9 ± 110.7	516.9
		Both traveling	53	5.4	45.8	105.1 ± 132.2	562.1
		Other combinations	3,304	1.6	53.7	106.7 ± 123.2	618.2
	Dominance rank pair	High–High	808	2.9	24.6	38.6 ± 45.8	349.9
		High–Low	2,626	1.6	54.0	108.4 ± 126.1	615.0
		Low–Low	934	2.1	68.1	129.0 ± 134.0	618.2
	Kinship	No	3,758	1.6	52.7	110.0 ± 127.3	618.2
		Yes	610	2.1	29.6	38.0 ± 30.4	209.4
Adult visual unit size	Typical activity	Foraging	2,056	0	1	1.8 ± 1.9	13
		Grooming	1,591	0	5	5.8 ± 3.6	17
		Resting	989	0	4	4.7 ± 3.8	17
		Traveling	788	0	1	1.6 ± 1.6	8
		Mixed	2,040	0	2	2.3 ± 2.4	17
	Dominance rank	High	3,591	0	2	3.5 ± 3.2	17
		Low	3,873	0	2	2.8 ± 3.1	17
Separation duration	Dominance rank pair	High–High	132	3	8	16.3 ± 21.9	171
		High–Low	227	3	11	28.6 ± 52.6	462
		Low–Low	72	3	7	33.7 ± 72.1	513
	Kinship	No	354	3	10	26.6 ± 52.7	235
		Yes	77	3	9	21.8 ± 35.4	513

Table II–2: The best model and all sub-models that explain interindividual distance (IID), adult visual unit size, and separation duration

Response variable	Model	Model name	AIC	ΔAIC
IID	Concurrent activity + Dominance rank pair + Kinship	Model 1a (full model)	45,585.8	—
	Concurrent activity + Dominance rank pair	Model 1b	45,586.8	1.0
	Concurrent activity + Kinship	Model 1c	45,588.0	2.2
	Concurrent activity	Model 1d	45,590.6	4.8
	Dominance rank pair + Kinship	Model 1e	45,880.2	294.4
	Dominance rank pair	Model 1f	45,881.2	295.4
	Kinship	Model 1g	45,882.0	296.2
	Null	Model 1h	45,884.8	299.0
Adult visual unit size	Typical activity + Dominance rank	Model 2a	15,648.9	—
	Typical activity + Dominance rank + No. of kin adult females	Model 2b (full model)	15,650.9	2.0
	Typical activity + No. of kin adult females	Model 2c	15,651.7	2.8
	Typical activity	Model 2d	15,652.1	3.2
	Dominance rank	Model 2e	21,349.6	5700.7
	No. of kin adult females	Model 2f	21,351.2	5702.3
	Dominance rank + No. of kin adult females	Model 2g	21,351.5	5702.6
	Null	Model 2h	21,351.5	5702.6
Separation duration	Dominance rank pair	Model 3a	3,604.6	—
	Dominance rank pair + Kinship	Model 3b (full model)	3,606.5	1.9
	Null	Model 3c	3,607.1	2.5
	Kinship	Model 3d	3,608.6	4.0

AIC is Akaike information criteria, and ΔAIC is the difference between the AIC value for that model and the AIC value of the best model.

Table II–3: Summary of best models describing interindividual distance (IID), adult visual unit size, and separation duration

Response variable	Explanatory variables (no. of prediction)			Estimate	SE	*z* or *t*	*P*
IID	Intercept			3.998	0.295	13.55	<0.001
	Concurrent activity	(1.1)	Both foraging	0	0	—	—
			Both grooming	–0.799	0.055	–14.53	<0.001
			Both resting	–0.697	0.072	–9.69	<0.001
			Both traveling	–0.135	0.113	–1.19	0.233
			Other combinations	–0.081	0.039	–2.09	<0.05
	Dominance rank pair	(2.1)	High–High	0	0	—	—
			High–Low	0.510	0.328	1.56	0.119
			Low–Low	0.922	0.353	2.61	0.009
	Kinship	(3.1)	No	0	0	—	—
			Yes	–0.642	0.368	–1.74	0.081
Adult visual unit size	Intercept			0.716	0.086	8.34	<0.001
	Typical activity	(1.2)	Foraging	0	0	—	—
			Grooming	1.135	0.02	57.59	<0.001
			Resting	0.956	0.023	42.46	<0.001
			Traveling	–0.128	0.033	–3.87	<0.001
			Mixed	0.242	0.022	10.93	<0.001
	Dominance rank	(2.2)	High	0	0	—	—
			Low	–0.303	0.106	–2.85	<0.01
	No. of kin adult females	(3.2)		—	—	—	—
Separation duration	Intercept			2.783	0.179	15.52	<0.001
	Dominance rank pair	(2.3)	High–High	0	0	—	—
			High–Low	0.608	0.216	2.82	<0.01
			Low–Low	0.750	0.276	2.72	<0.01
	Kinship	(3.3)		—	—	—	—

Explanatory variables that were included in the best model are highlighted in bold-type face.

Table III–1: The top five models that explain synchronous activity in each activity type and travel direction

Response variable	Model	Model name	AIC	ΔAIC
Synchrony of activity				
Foraging	Rank	Model f1	2,114.94	0.0
	Rank + Kin	Model f2	2,115.92	1.0
	Rank + IID	Model f3	2,117.38	2.4
	Rank + Kin + IID	Model f4	2,118.94	4.0
	IID	Model f5	2,123.56	8.6
Traveling	Kin	Model t1	743.20	0.0
	Null	Model t2	744.79	1.6
	Kin + Rank	Model t3	745.88	2.7
	Rank	Model t4	746.86	3.7
	IID + Kin	Model t5	748.17	5.0
Grooming	IID + Rank	Model g1	1,071.70	0.0
	IID	Model g2	1,072.72	1.0
	IID + Rank + Kin	Model g3	1,073.53	1.8
	IID + Kin	Model g4	1,074.23	2.5
	Rank	Model g5	1,162.07	90.4
Resting	IID	Model r1	1,454.81	0.0
	IID + Kin	Model r2	1,455.24	0.4
	IID + Kin + Rank	Model r3	1,457.17	2.4
	IID + Rank	Model r4	1,457.64	2.8
	Null	Model r5	1,495.88	41.4
Synchrony of Travel direction	IID + Rank	Model d1	1,834.60	0.0
	IID	Model d2	1,835.46	0.9
	IID + Kin	Model d3	1,836.16	1.6
	IID + Rank + Kin	Model d4	1,836.58	2.0
	Kin	Model d5	1,868.98	34.4

“synchronous” = 1, “asynchronous” = 0, AIC represents Akaike information criteria, and ΔAIC is the difference between the AIC value for that model and the AIC value of the best model. “Rank” indicates dominance rank pair.

Table III–2: Summary of best models describing synchrony of each activity type and travel direction

Response variable	Explanatory variable		Estimate	SE	*z*	*P*
Synchrony of activity						
Foraging	Intercept		0.458	0.121	3.79	<0.001
	Rank	High–High	0	0	—	—
		High–Low	–0.411	0.137	–3.00	0.003
		Low–Low	–0.654	0.168	–3.89	<0.001
Traveling	Intercept		–1.583	0.102	–15.46	<0.001
	Kin	No	0	0	—	—
		Yes	0.484	0.249	1.95	0.051
Grooming	Intercept		0.780	0.187	4.17	<0.001
	IID	0–20	0	0	—	—
		20–50	–1.087	0.188	–5.79	<0.001
		50–100	–1.898	0.263	–7.21	<0.001
		100–150	–1.592	0.342	–4.66	<0.001
		150–200	–1.786	0.441	–4.05	<0.001
		≥200	–1.648	0.235	–7.01	<0.001
	Rank	High–High	0	0	—	—
		High–Low	–0.423	0.205	–2.07	0.039
		Low–Low	–0.499	0.249	–2.00	0.045
Resting	Intercept		–0.234	0.110	–2.13	0.034
	IID	0–20	0	0	—	—
		20–50	–0.857	0.163	–5.25	<0.001
		50–100	–1.065	0.197	–5.42	<0.001
		100–150	–1.376	0.313	–4.40	<0.001
		150–200	–1.0	0.394	–1.52	0.129
		≥200	–1.0	0.199	–3.78	<0.001

Table III–2: (continued)

Response variable	Explanatory variable		Estimate	SE	*z*	*P*
Synchrony of travel direction	Intercept		–0.082	0.154	–0.53	0.594
	IID	0–20	0	0	—	—
		20–50	0.199	0.154	1.29	0.196
		50–100	0.108	0.169	0.64	0.524
		100–200	–0.720	0.213	–3.39	<0.001
		≥200	–0.725	0.189	–3.83	<0.001
	Rank	High–High	0	0	—	—
		High–Low	–0.182	0.152	–1.20	0.231
		Low–Low	0.110	0.183	0.60	0.550

"Rank" indicates dominance rank pair.