Title: Social relationships within and outside a troop in wild male Japanese macaques (Macaca fuscata) in Kinkazan Island, Japan

Author(s): Kawazoe, Tatsurou

Citation: Kyoto University (京都大学)

Issue Date: 2016-03-23

URL: https://doi.org/10.14989/doctor.k19528

Type: Thesis or Dissertation

Textversion: ETD

京都大学
Social relationships within and outside a troop in wild male Japanese macaques (*Macaca fuscata*) in Kinkazan Island, Japan

Tatsuro Kawazoe
TABLE OF CONTENTS

ACKNOWLEDGEMENTS ........................................................................................................... v

LIST OF TABLES ................................................................................................................... vii

LIST OF FIGURES ............................................................................................................... ix

ABSTRACT ................................................................................................................................. xi

CHAPTER 1: General introduction.................................................................................... 1

1-1. Male dispersal and benefits of all-male groups in non-human primates .......... 1

1.2. Social bonds and mechanism of altruistic behaviour ........................................... 2

1.3 Male–male social bonds and social style in genus Macaca ................................. 3

1-4. Life history and intra-specific variation of social organization in male
Japanese macaques ........................................................................................................... 5

1-5. Dominance hierarchy and effects of male–male social bonds in Japanese
macaques ....................................................................................................................... 6

1.6 Outline of the study ................................................................................................. 8

CHAPTER 2: Association patterns and affiliative relationships outside a troop in
wild male Japanese macaques (Macaca fuscata) during the non-mating season......... 11

2.1 Abstract.................................................................................................................... 11
3.3 Methods ................................................................................................................ 35

3.3.1 Study area, periods, and subjects................................................................. 35
3.3.2 Data sampling............................................................................................... 36
3.3.3 Data analysis................................................................................................. 38

3.4 Results ............................................................................................................. 40

3.4.1 Seasonal change and grooming reciprocity .............................................. 40
3.4.2 Seasonal change of aggression and linearity of dominance hierarchy ...... 40
3.4.3 Distribution, patterns, and reciprocity of coalition...................................... 41
3.4.4 Partial matrix correlation among grooming, aggression, and coalition...... 42

3.5 Discussion ....................................................................................................... 43

3.5.1 Reciprocal partner preference in affiliative interaction ......................... 43
3.5.2 Dominance hierarchy among males ......................................................... 44
3.5.3 Coalition and dominance hierarchy ......................................................... 45
3.5.4 Reciprocal partner preference in coalition and social tolerance .......... 47

3.6 Conclusion ....................................................................................................... 49

CHAPTER 4: General Discussion............................................................................. 51

4-1. Summary of male classification, male–male social bonds, and their influences on wild Japanese macaques ................................................................. 51

4-2. Methodological approach for reconsideration of intra-specific variation of social organization in male Japanese macaques ........................................ 54
4.3 Influence of between-group competition on formation of all-male groups and male–male social bonds................................................................. 55

4.4 Future perspectives .................................................................................. 56

REFERENCES ........................................................................................................ 59
ACKNOWLEDGEMENTS

I would like to express the deepest appreciation to Professor N. Nakagawa for his supports and encouragements through this study. I also would like to express my gratitude to referees of my doctoral thesis Drs. J. Yamagiwa, E. Inoue, S. Matsumura, Y. Muroyama for their helpful suggestions and comments on this study. Advices, comments, and encouragements given by members and alumni of the Laboratory of Human Evolution Studies, Graduate School of Science, Kyoto University have been a great help in conducting this study. I would like to thank Dr. C. K. Hemelrijk for the permission to use MatrixTester for analysis.

I would like to offer my special thanks to Dr. K. Izawa for the permission of field research, encouragements, and supports during the field study. I would like to thank all of my friends and colleagues in Kinkazan Island for their kind supports and discussions during my stay in the site.

Kinkazan Island which is the study site in the current study is the closest land from the epicentre of Great East Japan Earthquake occurred on March 11th, 2011. I would like to show my greatest appreciation to staffs of Koganeyama Shrine for their heart-warming supports during refuge life for the earthquake. Primate Society of Japan (PSJ), American Society of Primatologists (ASP), International Primatological Society (IPS), the members of PSJ, ASP, and IPS, and the Disney Wildlife Conservation Fund gave financial supports for reconstruction of the field
station in the island. Thanks to these supports, I am able to continue a study in this study site.

I would like to acknowledge the Cooperation Research Program of the Primate Research Institute, Kyoto University, the Global Centre of Excellence Program (A06 to Kyoto University) of the Ministry of Education, Culture, Sports, Science and Technology, Japan (MEXT), and a Grant-in-Aid for Scientific Research (B, No. 23370099 to Prof. N. Nakagawa) for providing funds and resources for this study.

I extend my gratitude to my parents, Yukihiro and Noriko, and my sister, Tomoko, who for their moral support through my academic work and encouragements throughout the study.

Finally, I would like to acknowledge macaques in Kinkazan Island for enduring my persistent observation. I am very glad if this study helps to understand their social life.
LIST OF TABLES

Table 2-1 Names, age classes, number of observation days (N), observation time, and mean observation time per day in each focal male ................................................................. 75

Table 2-2 Dataset of visual encounter ratio (VER), mean number of individuals within visual range, and proximity ratio entered into the principal component analysis ........................................................................................................................................ 76

Table 2-3 Components, factor loadings, eigenvalues, and cumulative contributions in principal component analysis run on six variables ................................................................................................................................. 77

Table 2-4 Mean ± SD of daily visual encounter ratio (VER), VER and mean number of males within visual range in the absence of females, proximity ratio, and grooming frequency at individual level .................................................................................................................. 78

Table 2-5 Matrix of dyadic proximity ratios among focal males and adult females in the subject troop ........................................................................................................................................ 79

Table 2-6 Matrix of dyadic grooming frequencies among focal males and adult females in the subject troop ................................................................................................................................. 80
Table 3-1 Dataset of visual encounter ratio (VER), mean number of individuals within visual range, and proximity ratio in the non-mating season 209 entered into the principal component analysis ................................................................. 81

Table 3-2 Names, age classes, number of observation days (N), and observation time in each focal male ........................................................................................................................................... 82

Table 3-3 Matrix of grooming indices in two seasons (non-mating season / mating season) among focal males.......................................................................................................................... 83

Table 3-4 Matrix of aggression indices in two seasons (non-mating season / mating season) among focal males and dominance rank in the mating season......................... 84

Table 3-5 Observed and expected frequencies of aggression in each activity .............. 85

Table 3-6 Matrix of coalition indices among focal males in the mating season ........... 86

Table 3-7 Distribution of coalitions according to patterns of coalition, initial aggression dyad, supporter, being supported male, common target, and the number of each instance.................................................................................................................. 87
LIST OF FIGURES

**Fig. 2-1** Principal component analysis (PCA) of focal males runs on six variables. See Table 2-3 for explanations of variables and loadings. ............................................. 89

**Fig. 2-2** Dyadic proximity ratios and results of multiple comparisons according to groups based on the combination of male attributes. P values were adjusted using the Holm’s method. *: P < 0.05 ................................................................. 90

**Fig. 2-3** Dyadic grooming frequencies per duration of proximity and results of multiple comparisons according to groups based on the combination of male attributes. P values were adjusted using the Holm’s method. *: P < 0.05 ................................................................. 91

**Fig. 2-4** Comparison of the direction in grooming frequencies between C1 males and C2 males. *: P < 0.05 ................................................................. 92

**Fig. 3-1** Principal component analysis of focal males for the classification of troop males and non-troop males run on six valuable in the non-mating season. See Table 2-1 for the data set of these six valuables ................................................................. 93
Fig. 3-2 Seasonal difference of dyadic interaction of (a) grooming rates and (b) aggression rates between non-mating season (NMS) and mating season (MS). ............ 94

Fig. 3-3 Number of coalitionary supports every three patterns according to dominance hierarchy. See methods for detail explanation of coalition patterns. .......... 95

Fig. 3-4 Results of partial tau $\tau_r$ test in grooming, aggression, and coalition in two seasons. (a) results of grooming given in the non-mating (NMS), grooming given in the mating season (MS), and aggression received in MS. (b) Results of grooming given in NMS, grooming given in MS, and coalition received in MS. Solid lines indicate significant correlation, and dotted lines indicate non-significant correlation. 96
ABSTRACT

Social bonds have been construed as differentiated enduring affiliative social relationships, which is a concept primarily derived from kin relations. In many primates, males disperse from their natal troop. Male–male social bonds have been supposed to be rare because their relatedness is expected to be low, and they compete over non-sharable fertile females. However, male–male social bonds are widespread phenomena even in male dispersal primate species. Male–male social bonds suggest formation of coalitionary support, social tolerance, and elevation of a dominance hierarchy in tolerant macaque species. Coalitions among males are hypothesized to depend on variation in the strength of contest competition over females.

Some males do not belong to bi-sexual troops, sometimes forming all-male groups. However, little is known about the association patterns and social relationships among these males and between troop and non-troop males. Studies on male–male social bonds and coalition formation have been conducted mainly in a tolerant social style. Knowledge about social relationships in despotic macaque species may contribute to elucidation of the evolutorial process of male–male social bonds.

Japanese macaques (*Macaca fuscata*) show male dispersal and the most despotic social style among macaque species, and non-troop males are observed in many populations. Male Japanese macaques have been classified qualitatively into troop/non-troop males. In the current study, I initially employed a novel method for quantitative classification of males based on their behaviour in the non-mating season through
principal component analysis (PCA) and revealed association patterns and affiliative
relationships in male Japanese macaques. I then analysed seasonal change and
correlation of affiliation, aggression, and coalition among males. I discussed
differentiation and its influence on affiliative relationships among males within and
outside a troop.

I conducted this study on Kinkazan Island, Japan. The island is about 10 km² in area
and is located 700 m from the main island of Japan. Six troops inhabit in the island, and
the socionomic sex ratio is skewed toward females. I conducted intensive field research
in 2007 and 2009. I chose Troop C₂ as the subject troop.

In 2007, I observed 12 wild male Japanese macaques for 809 h in non-mating season
with focal animal sampling. The number of other animals within visual range, the
amount of time males spent in the vicinity of other animals, and grooming interactions
were recorded. I examined male classification by PCA and analysed association pattern
and grooming frequencies.

In 2009, I observed 7 non-natal adult males including non-troop males for 350 h in
the non-mating and mating seasons with focal animal sampling. I recorded grooming,
aggression, and coalitions among males. The presence of other males was also recorded
to assess opportunities for social interaction. I analysed seasonal change and correlation
among these behaviours.

In the non-mating season of 2007, I was able to classify males into two distinctive
clusters (Clusters 1 and 2) according to their association and interaction patterns.
Cluster 1 males associated with females and participated in grooming with them.
Cluster 2 males had fewer visual encounters with females and did not groom them.
Although Cluster 2 males showed less proximity to one another than did Cluster 1
males, they frequently groomed one another according to proximity time. Cluster 2 males groomed Cluster 1 males more frequently than they were groomed.

Compared to the non-mating season in 2009, the subsequent mating season was characterized by a decreased rate of grooming and an increased rate of aggression. Coalition was observed only in the mating season, and most represented winner support. A linear dominance hierarchy was found in the mating season but not in the non-mating season. The higher-ranking male was involved in more frequent coalitions. Frequencies of grooming given in the non-mating season did not correlate with frequencies of coalition received in the subsequent mating season, but they were negatively correlated with frequencies of aggression received in the mating season.

The result of PCA suggested that Cluster 1 was made up of troop males, and Cluster 2 as made up of non-troop males. This means that males could be separated quantitatively by their behaviour. This method might contribute to clarifying the complexity of social structures. Non-troop males might have less opportunity to interact with females and form less cohesive all-male groups. Males in all-male groups engaged in more frequent grooming than did troop males, and they groomed troop males more frequently than they were groomed. Male–male affiliative relationships might be influenced by within-group potential competition.

The observed correlation among grooming, aggression, and coalitions between the two seasons suggested that social bonds construed as grooming relationships did not predict coalitions but, rather, social tolerance in despotic macaques. More grooming of troop males by non-troop males might derive social tolerance from troop males, which might enable non-troop males to approach fertile females in the mating season or immigrate into a troop in the near future.
Most coalitions were winner supports. Coalitions among subordinates against dominant males might be suppressed because of high risk of counter aggression and little benefit in terms of mating opportunities. The lack of coalitions among subordinates might contribute to a stable dominant hierarchy in despotic macaques.
CHAPTER 1

General introduction

1-1. Male dispersal and benefits of all-male groups in non-human primates

In many group-living species, members of one sex often remain in their natal group throughout their lives, whereas members of the other sex usually emigrate at sexual maturity (Greenwood 1980; Johnson & Gaines 1990). Dispersal of one sex is thought to avoid inbreeding, increase access to mates, or make available better habitats and dietary niches (Greenwood 1980; Pusey & Packer 1987). In many primates, females remain in their natal groups throughout their lives, and males disperse from their natal groups when they mature (Pusey & Packer 1987). Male dispersal is thought to be promoted as a result of eviction from females and sexual attraction to females in other groups (Pusey & Packer 1987). While some males transfer from one bisexual troop to another, others become solitary or join nonbreeding all-male groups for variable periods (Nishida 1966; Sugiyama 1976; Pusey & Packer 1987; Rajpurohit et al. 1995).

Dispersing males are likely to face the risk of mortality (Alberts & Altmann 1995) and the loss of opportunities for nepotistic and altruistic behaviour (Moore 1992). The risk of predation and aggression from other conspecifics may influence whether males form all-male groups or remain solitary (Pusey & Packer 1987). Individuals benefit from predation avoidance by forming groups (van Schaik 1983), and male
gregariousness may be an adaptation to predation (Pusey & Packer 1987). In several mammals, males obtain benefits of having social interaction partners and sharpening competitive skills (*Loxodonta africana*: Chiyo et al. 2011; *Giraffa camelopardalis*: Bercovitch & Berry 2015). However, benefits of acquiring interaction partners in all-male groups have rarely been examined in non-human primates.

1.2. Social bonds and mechanism of altruistic behaviour

The accumulation of the occurrence and outcome of social interaction construct social relationships within a group (Hinde 1976). When the affiliative relationships are differentiated across group mates and endure for a long period, they are regarded as social bonds (Silk 2002). Kin selection theory predicts that individuals perform altruistic behaviour and preferentially form affiliative relationships and social bonds with their relatives to maximize inclusive fitness (Hamilton 1964a, b; Trivers 1971; Clutton-Brock 2009). In many male dispersal and female philopatric primates, kinship has a strong effect on the establishment and maintenance of social bonds between females (Silk 2006).

In the fields of primatology, social grooming interaction has been widely adopted as a good indicator of affiliative relationships and social bonds (Silk 2002). Grooming is a widespread behaviour and has a function of hygiene (Tanaka & Takefushi 1993; Zamma 2002) and tension reduction between individuals (Schino et al. 1988). Moreover, several references show that grooming is exchanged with grooming (Muroyama 1991; Barrett et al. 1999) or interchanged with agonistic support (Seyfarth 1977; Schino 2007), social tolerance (Barrett et al. 2002; Tiddi et al. 2011), and allomothering behaviour
There are two general mechanisms explaining altruistic behaviour between non-kin primates (Schino & Aureli 2016). The first mechanism involves strong temporal relations within a dyad; in this mechanism, each dyad is conceptually independent from the other (Trivers 1971). The second mechanism involves comparative relations across dyads. In this mechanism, each dyad is not an independent but, rather, a comparative component. This mechanism is called ‘reciprocal partner choice’ (Schino & Aureli 2009). Although there is little evidence for temporal relations, reciprocal partner choices have been found in many primates (e.g. Schino 2007; Tiddi et al. 2011).

1.3 Male–male social bonds and social style in genus \textit{Macaca}

Male–male relatedness within a group is expected to be low because, in male dispersal primates, they disperse from their natal groups (Pusey & Packer 1987). In addition to this lower relatedness between males than between females, males struggle with one another over non-sharable fertile females (van Hooff & van Schaik 1994; Paul 2002). Therefore, male–male social relationships have been focused on competition (e.g. Mitani et al. 1996), and male–male social bonds are presumed to be rare. However, social bonds and altruistic behaviour among males are widespread phenomena especially in primate species and even in male dispersal species (van Hooff & van Schaik 1994; Ostner & Schülke 2014). Male–male social bonds have evolved as long-term alliances with adaptive functions of within-group potential contest competition (Ostner & Schülke 2014).

Aside from social bonds, male–male coalitions are widely observed in primates
(Bissonnette et al. 2014). The occurrence of male–male coalitions within a group is hypothesized to be influenced by the strength of contest competition (Pandit & van Schaik 2003; van Schaik et al. 2004). According to this theoretical model, male–male social bonds are likely to occur more frequently in low-contest competition and tolerant groups and less frequently in high-contest competition and despotic groups.

Macaque species are classified into four social style grades according to the tolerant–despotic continuum (Matsumura 1999; Thierry et al. 2000). The *Sinica–arctoides* lineage and most of the *silenus–sylvanus* lineage except for pig-tailed macaques (*M. nemestrina*) are classified as tolerant macaques (Matsumura 1999; Thierry et al. 2000). These macaques have a relaxed dominance hierarchy and display high rates of affiliative contacts and tension reduction behaviour. On the other hand, the *fascicularis* lineage and pig-tailed macaques showed a strict and steep dominance hierarchy and high nepotism as well as low rates of reconciliation (Matsumura 1999; Thierry et al. 2000).

Male social bonds and their influence have been examined recently in tolerant macaques in the aspect of reciprocal partner choice. Male social bonds predict the formation of coalitionary support (*M. sylvanus*: Berghänel et al. 2011), social tolerance (*M. thibetana*: Xia et al. 2013), cooperative defence of fertile females (*M. radiata*: Silk 1994), increase of access to mates (*M. sylvanus*: Bissonnette et al. 2011), and elevation of dominance rank and reproductive success (*M. assamensis*: Schülke et al. 2010), albeit low relatedness is expected among males. Compared to accumulation of references in tolerant macaques, there is little knowledge about the influences of social bonds on the above behaviour in despotic macaques, though the tolerant–despotic continuum may affect them.
1-4. Life history and intra-specific variation of social organization in male Japanese macaques

Japanese macaques (*M. fuscata*) live in multi-male and multi-female troops (Yamagiwa 2010) and show strict seasonal breeding (Fujita 2010). These macaques are classified into the most despotic social style according to their high nepotism and steep linear dominance hierarchy (Matsumura 1999; Thierry et al. 2000). Females remain with their natal troop throughout their lives (Yamagiwa & Hill 1998), whereas males disperse from their natal troop before reaching sexual maturity at about five years old (Nishida 1966; Sugiyama 1976; Sprague et al. 1998).

After dispersing, some males immigrate to other troops as troop males, and others form all-male non-breeding groups or range alone as non-troop males outside troops (Nishida 1966; Sugiyama 1976). Males repeat transfer between troops/groups even if they immigrate to a troop, becoming members of troops for approximately three years on average (Sugiyama 1976; Sprague et al. 1998). Male transfers are likely to occur during the mating season (Sprague 1992) as it is expected that sexual attraction is the main motivation for transfer (Pusey & Packer 1987). Non-troop males are observed in many populations, and living outside troops is typical in the life history of Japanese macaques even in the non-mating season (Nishida 1966; Sugiyama 1976; Sprague et al. 1998; Yamagiwa & Hill 1998; Muroyama et al. 2000; Otani et al. 2013; Kawazoe 2016).

There are intra-specific diversities in the socionomic sex ratio (SSR) in male Japanese macaques (Sprague et al. 1998; Yamagiwa & Hill 1998). The SSR is defined as the number of males vs. the number of adult females within a troop (Clutton-Brock et
al. 1977) and differs across Japanese macaque populations (Sprague et al. 1998; Yamagiwa & Hill 1998). In some populations, almost all males are members of troops (Yamagiwa & Hill 1998), in other populations, solitary males and all-male groups are found outside troops (Sprague et al. 1998). Although a considerable number of males live outside troops as members of all-male groups or solitary males, little is known about their social relationships.

We have little knowledge about the quantitative evaluation of the factors that explain the difference in social structure of male Japanese macaques across populations. Males are classified into troop males and non-troop males qualitatively rather than quantitatively (e.g. Sprague 1991; Horiuchi 2005). The classification is not able to cover the factor explaining the diversity of social organization in males between populations. Quantitative analysis on male classification and social relationships outside troops is required for full understanding of the diversity of intra-specific variation of social organization in Japanese macaques.

In the current study, I employ a novel approach to classify troop and non-troop males. Principal component analysis (PCA) is widely adopted to examine animal behaviour through a quantitative approach (Whitehead 2008). I apply this methodological approach to quantitatively classify males into troop and non-troop males based on their behavioural traits.

1-5. Dominance hierarchy and effects of male–male social bonds in Japanese macaques

Dominance hierarchy and affiliative interaction among males within troops have been
examined in wild Japanese macaques. Male macaques show a linear dominance hierarchy within troops (Sprague 1992). Age and dominance rank are often correlated in Japanese macaque troops (Sprague 1992). The dominance ranks of males correlate with age (Sprague 1992) and tenure (Sprague et al. 1998). The dominance hierarchy among males within troops is stable and rises with the death or departure of higher-ranking males (Sprague et al. 1998). Non-troop males are predicted to be subordinate to troop males because they are frequently attacked by troop males in the mating season (Horiuchi 2005). There are few data, however, on the dominance hierarchy between non-troop and troop males or among non-troop males. In the present study, I examine the dominance hierarchy among not only troop males but also non-troop males to clarify dominant–subordinate relationships among them as well as how a stable dominance hierarchy is achieved in Japanese macaques.

In tolerant macaque species, male–male social bonds correlate with the formation of coalitions (Berghänel et al. 2011) or social tolerance (Xia et al. 2013) based on reciprocal partner preference. Male–male social bonds and their effects in despotic species have been examined in provisioned troops (Kutsukake & Hasegawa 2005; Higham & Maestripieri 2010) but not in wild non-provisioned troops. Kutsukake and Hasegawa (2005) and Higham and Maestripieri (2010) indicate that males form coalitionary supports with their relatives and achieve dominance turnover. The occurrence of male–male coalitions is expected to be influenced by the strength of contest competition among them (Pandit & van Schaik 2003; van Schaik et al. 2004). Hence, the frequency and patterns of coalitions are expected to differ between tolerant and despotic macaques. Few data exist, however, to show frequency and patterns of male–male coalitions and how social bonds influence coalition formation or social
tolerance among males in wild non-provisioned despotic macaques.

**1.6 Outline of the study**

In this study, I conducted quantitative evaluation of the classification of male attributes according to their behavioural traits in wild male despotic Japanese macaques. In addition, I investigated association patterns, affiliative relationships, and their influence on coalition formation and social tolerance among males in two seasons.

In CHAPTER 2, I employ a novel methodological approach to classify male attributes into troop and non-troop males based on their behaviour such as visual encounter ratio, the number of individuals within visual range. In addition, I examine the proximity ratio and grooming frequency among males to clarify the difference of association patterns and affiliative relationships between troop and non-troop males.

In CHAPTER 3, I present the data on frequency and patterns of coalition formation and investigate the reciprocity of partner preference in grooming, aggression, and coalitions in the two seasons. I also examine and discuss the influence of social bonds on coalition formation and social tolerance.

Finally, in CHAPTER 4, I summarize the results and discuss the perspective towards the understanding of intra-specific variation of social structure in Japanese macaques by integrating CHAPTER 2 and CHAPTER 3. I also discuss a methodological approach to understanding intra-specific diversity in social organization in male Japanese macaques and the influence of contest competition on the formation of all-male groups and male–male social bonds outside bi-sexual groups. I further mention the remaining viewpoints to understand the variability in social organization and male–male social bonds in male
dispersal species.
CHAPTER 2

Association patterns and affiliative relationships outside a troop in wild male Japanese macaques (Macaca fuscata) during the non-mating season

2.1 Abstract

In many mammals, males disperse more than females. Although males in some male-dispersing species form all-male groups, little is known about the association patterns or social relationships among them. Studies on male–male social relationships have primarily focused on competition over fertile females, but affiliative relationships among males have recently attracted much interest. I suggested a novel method for the classification of males based on their behaviour through PCA and investigated association patterns and affiliative relationships in male Japanese macaques (Macaca fuscata) during the non-mating season. I observed 12 wild male Japanese macaques during the non-mating season. The number of other animals within visual range, the amount of time that males spent in the vicinity of other animals, and the frequency of grooming interactions were examined. I classified males into two distinctive clusters (Cluster 1 and 2) according to their association and interaction patterns. Cluster 1 males associated with females and participated in grooming with them. Cluster 2 males had fewer visual encounters with females and did not groom them. Cluster 2 males showed proximity to other Cluster 2 males in all possible dyads. Although Cluster 2 males
showed less proximity to each other than did Cluster 1 males, they frequently groomed one another according to duration of proximity. Cluster 2 males groomed Cluster 1 males more frequently than they were groomed by them. These results suggested that Cluster 1 was made up of troop males, and Cluster 2 was made up of non-troop males. Cluster 2 males had less opportunity for social interaction than did Cluster 1 (troop) males, and they may form all-male groups. Males in all-male groups engaged in more frequent grooming than do troop males. In addition, they groomed troop males more frequently than they were groomed. These results suggest that males could be separated by their behaviour. Male–male affiliative relationships might be influenced by within-group potential competition, and imbalanced grooming appears to cause troop males to tolerate non-troop males that might be immigrated in the near future.

2.2 Introduction

In many group-living mammals, females show philopatry, and males disperse from their natal groups (Greenwood 1980). Some males do not belong to bi-sexual groups, and sometimes they form all-male groups as a result of male dispersal or sex segregation (e.g. Moss & Poole 1983; Pusey & Packer 1987; Rajpurohit et al. 1995; Funston et al. 1998; Lettevall et al. 2002; Fischhoff et al. 2009). Some studies also indicate that males may behave tolerantly within all-male groups (Pusey & Packer 1987; Rajpurohit et al. 1995; Robbins 1996) and obtain some benefits from one another such as reduction of predation risk (van Schaik et al. 1983; Hill & Dunbar 1998), sharing of spatial knowledge (Rajpurohit et al. 1995), or gaining interaction partners (Chiyo et al. 2011). Moreover, considerable inter- and intra-specific variations in the association pattern and
social relationships among non-troop males were reported (Pusey & Packer 1987).

However, it is difficult to evaluate the diversity among studies, because there are several definitions of a male attribute, and quantitative behavioural data based on the definition is still lacking. Further, group membership is an important factor to clarify the association pattern and social relationships among males. In species with dynamic social organization like fission–fusion, group compositions fluctuate in the short term (Connor & Whitehead 2005; Aureli et al. 2008). Seasonal male influxes may also affect membership and social relationships in a group (Cords 2000; Hirsch & Maldonado 2011). It is meaningful to quantitatively evaluate group composition within and outside of bi-sexual groups based on their behavioural data. PCA has been used to analyse and classify social relationship quality based on behavioural aspects (Fraser et al. 2008; Majolo et al. 2010). In the current study, I initially applied this method to provide a quantitative definition of troop/non-troop males and to clarify their attributes. This novel approach of applying PCA to classify males into troop and non-troop males using quantitative behavioural data may enable us to compare the association patterns among males between populations or species.

The ultimate cause of social structure has been explained by socioecological theory: In male dispersal species, male–male social relationships and their distribution are strongly influenced by female distribution (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). Studies on male–male social relationships have focused on their competitive relationships (e.g. Cox & Le Boeuf 1977; Dobson 1982; Mitani et al. 1996) because conceptions cannot be shared (van Hooff & van Schaik 1994; Paul 2002). However, male–male affiliative relationships have recently attracted much attention. Although strong social bonds and enduring social affiliative relationships have evolved
more often among females than among males, they have been found among males including male dispersal species (Packer & Pusey 1982; van Hooff & van Schaik 1994; Connor et al. 2001; Ostner & Schülke 2014). Male–male social bonds bring some benefits through aggressive coalitions (Berghänel et al. 2011), cooperative defence of oestrus females (Connor et al. 1992; Majolo et al. 2005), increased dominance rank and reproductive success (Schülke et al. 2010), and joint transfer (Schoof et al. 2009). Demography, female reproductive synchrony, and variation of within-group contest competition determine male co-residency, male–male social bonds, and formation of coalitionary support (Ostner & Kappeler 2004; Bissonnette et al. 2014; Ostner & Schülke 2014). A large number of males per group and female reproductive synchrony lead to low reproductive skew and low male–male contest competition. Low reproductive skew and male–male tolerance develop male–male social bonds (Ostner & Schülke 2014). Hence, males will be expected to affiliate more frequently with each other when the potential for direct male–male competition is weaker.

Japanese macaques (*M. fuscata*) have a male dispersal social structure, strict breeding season (Bercovitch & Harvey 2004; Fujita 2010), and despotic social style (Matsumura 1999; Thierry et al. 2000). Male Japanese macaques disperse from their natal troops before reaching sexual maturity (Sugiyama 1976). They live as solitary males or as members of all-male groups after dispersing and repeatedly transfer to other troops (Nishida 1966). Non-troop males have been observed in some populations (Nishida 1966; Sugiyama 1976; Sprague et al. 1998; Muroyama et al. 2000; Otani et al. 2013); however, behavioural data are not available for males living outside of bi-sexual groups.

The proportion of non-troop males differs across populations and is related to intra-
specific variations in the ratio of adult females to males within a troop, the SSR (Clutton-Brock et al. 1977; Yamagiwa & Hill 1998). Although a considerable number of males live outside of troops as non-troop males in high-SSR populations, little is known about their spatial structures and social relationships.

In addition, there are several definitions of males’ classification among Japanese macaques. Male macaques have been classified qualitatively rather than quantitatively into troop and non-troop males (e.g. Furuichi 1985; Sprague 1991; Takahashi 2001; Horiuchi 2005). The classification of males can be summarized as follows: troop males are associated with females in non-mating seasons and have stable memberships. In the mating season, some of them remain in the troop while others leave the troop to acquire mating opportunities. Even when following troop members in the non-mating season, non-troop males are not observed within and around a troop. They are observed only after the onset of the mating season. After the end of the mating season, some non-troop males remain in and around the troop and become troop males, and many others go elsewhere. Male Japanese macaques repeat troop transfer throughout their lives (Nishida 1966).

Kinkazan Island is one of the long-term study sites of wild and non-provisioned Japanese macaques (Nakagawa et al. 2010). All-male groups and solitary males are observed on the island, and observers routinely encounter these males at the periphery of troops even in non-mating seasons (Sprague et al. 1998). This suggests that the above male classification may not adequately reflect the spatial structure and social relationships of male macaques.

In the present study, I investigated the spatial structure and affiliative relationships among males on Kinkazan Island. First, I obtained behavioural data and classified troop
and non-troop males through PCA to suggest a novel approach to understanding the diversity of spatiotemporal structures among males. I then compared proximity ratios and affiliative interaction frequency among troop and non-troop males to determine the social interactions and differentiation of affiliative relationships among these groups. The aim of this study was to suggest a new approach to separating males by their behaviour. I also discuss the cause and benefit of the formation of all-male groups and the diversity of association patterns and affiliative relationships between males in a bisexual group and males in an all-male group.

2.3 Methods

2.3.1 Study area, period, and subjects

I conducted this study on Kinkazan Island (38°2’N, 141°4’E). This island is approximately 10 km² in area and located 700 m from the main island of northern Japan. There are no natural predators of macaques on the island (Takahata et al. 1998). The vegetation is dominated by deciduous broad-leaved forests at higher elevations and by coniferous forests in lowlands (Nakagawa 1997). Six troops of wild Japanese macaques inhabit the island with overlapping home ranges (Izawa 1999). The SSR is skewed towards females, and non-troop males can be observed during both non-mating and mating seasons (Sprague et al. 1998). Solitary males and all-male groups can easily be observed from long distances on the island, because heavy browsing by sika deer (Cervus nippon) suppresses forest regeneration and provides good visibility (Takatsuki & Gorai 1994). The visual range has been estimated at a radius of approximately 40 m
(Koda et al. 2008). The mating season on the island is between late September and December (Takahashi 2001; Fujita et al. 2004). Data were collected during the non-mating season, January–March, May–June, and August–September, 2007. The observation period was 126 days in total.

I studied Troop C2, one of the six troops that inhabit the northern part of the island. Not counting adult males, the troop included 7 adult females, 1 young female, and 11 juveniles during the study period. In the present study, I attempted to quantitatively classify males into troop or non-troop males using PCA based on their associations with both females and males during the non-mating season. I identified and observed all non-natal males found within a home range of the troop, regardless of whether they ranged with females (Table 2-1). I classified them into three age classes according to their body size and the size of their testes. Full adult (FA) males (10–13 kg) had large red testes, adult (A) males (7–10 kg) had medium-sized red testes, and young adult (YA) (5–7 kg) males had small, light red testes. Most of them were observed during all the study periods; however, two full adult males (Co and Tv) were observed only during one of three observation periods because they were never found within a home range of Troop C2 during the remaining two periods. There is no information on whether these two males moved into another troop during these study periods. I excluded these males from statistical analysis because of their insufficient observation time. The age–sex composition of the study troop has been confirmed since 2000 by individual identification. Among the subject males observed at the periphery or outside the troop, none had been natal or recognized as troop members before the onset of this study. Hence, these males were not considered to be in the process of emigrating from the troop. Members of the troop and subject males were well habituated to the presence of
humans, and I was able to follow them within a 10-m distance without any disturbance.

2.3.2 Data collection

The focal animal sampling method (Altmann 1974) was used for observation. It is difficult to observe male–male grooming in a short observation time because it appears to occur with low frequency (Sprague et al. 1998). Hence, I followed only one male each day as long as possible. Although I found subject males ranging alone or with a few other males in some cases, I usually chose focal animals within or around the troop after locating the troop, because the efficiency of finding each male differed depending on whether it ranged with females. The focal animal changed from the initially chosen male to another if the latter male had only been minimally observed up to that point to reduce variations in the observation time among focal males. I followed the 12 males for a total of 809.4 h. The mean ± SD observation time per day was 6.4 ± 1.3 h (Table 2-1, range: 5.0–10.6 h).

Horiuchi (2005) studied male–male affiliative relationships in wild Japanese macaques. He considered individuals who stayed within 5-m of the focal male as associates. Following his definition, I recorded the presence and the number of males and females within the observer’s visual range to assess their spatial traits using the instantaneous sampling method (Martin & Bateson 2007) with 5-minute intervals. I recorded the individuals located in close proximity (within 5 m) to the focal male as well as the start and end time of proximity using the continuous sampling method (Martin & Bateson 2007). Grooming partners, the number of grooming bouts, and the direction of grooming were also recorded using the continuous sampling method. A
grooming bout began when the hands of an animal touched the body of another to
groom and ended when the two animals broke contact.

2.3.3 Data analysis

All statistical analyses were performed in the R 3.0.0 software statistical environment
(R Core Team 2013).

The visual encounter ratio (VER) was calculated by dividing the number of sampling
points at which other adult individuals were present within the visual range by the
number of total sampling points. The visual range was a radius of approximately 40 m
(Koda et al. 2008). I also calculated the VER for each observation day to assess
fluctuations in the association across days. These values were defined as daily VER. I
calculated the mean number of individuals within the visual range over all sampling
points. I also divided the total duration of proximity with at least one individual by the
total observation time to calculate the proximity ratio. Each of these calculations was
performed separately for both sexes, and the resulting six variables were used for PCA
(Table 2-2). I extracted PCA components with eigenvalues > 1. For a given component,
high loadings were considered variables with absolute values > 0.5. After the PCA, I
conducted a cluster analysis using Ward’s method to generate clusters of males
according to the loading factors of PC1 and PC2.

I defined the dyadic proximity ratio and dyadic grooming frequency according to the
following equations:

\[
\text{Dyadic proximity ratio}_{AB} = \frac{P_A(B) + P_B(A)}{O_A + O_B}
\]
Dyadic grooming frequency $A \rightarrow B = \frac{G_{A \rightarrow B}}{P_A(B) + P_B(A)}$

where $O_A$ (or $O_B$) is the total observation time of individual $A$ (or $B$), $P_A(B)$ [or $P_B(A)$] is the duration of proximity between $A$ and $B$ when $A$ (or $B$) was followed, and $G_{A \rightarrow B}$ indicates the number of grooming bouts in which $A$ groomed $B$. I calculated the dyadic grooming frequency using duration of proximity rather than observation time as the denominator because individuals in some male–male dyads had few opportunities to groom each other as males exhibit less spatial cohesion than do females (Otani et al. 2014). For the calculation of dyadic proximity ratio and dyadic grooming frequency with females, I treated $O_B$ and $P_B(A)$ as 0.

I used a randomization test to compare the dyadic proximity ratio and dyadic grooming frequency among males because dyadic data cannot be regarded as independent. Each value of proximity ratios and grooming frequencies was maintained, and dyads of proximity and grooming interaction were randomized. I conducted randomization tests of the frequency and direction of grooming with 10,000 iterations. Using PCA, I classified subject males into two clusters (see Results). For the test statistics, I subtracted the mean dyadic proximity ratio (and dyadic grooming frequency) among Cluster 2 males (C2) from the mean dyadic proximity ratio (and dyadic grooming frequency) among Cluster 1 (C1) males. I also defined the test statistic for the analysis of the direction of grooming by subtracting mean dyadic grooming frequency with which C1 males groomed C2 males from the frequency with which C2 males groomed C1 males. For comparison of difference in grooming frequency between C1 males or C2 males, the test statistic was defined by subtracting the mean frequency of grooming from individual $A$ to individual $B$ from the mean frequency of the reverse. P-
values of all multiple comparisons in proximity ratio and grooming frequency were adjusted appropriately using Holm’s method.

2.4 Results

2.4.1 Classification of males by PCA

I obtained two components from the PCA conducted on the six variables at the individual level (Table 2-3). The first component explained 70% of the variance and was characterized by negative loadings for all variables except for the proximity ratio with males. I tentatively considered this component to indicate association with other individuals. The second component explained 19% of the variance and indicated high negative loadings for the proportion of time spent in close proximity to other males. The second component was considered as proximity with males.

The cluster analysis for the first and second component scores revealed two distinctive clusters (Fig. 2-1), C1 and C2, and males in each cluster were termed C1 males (i.e. Kl, Rc, Pp, Ha) and C2 males (i.e. Th, Ng, Bl, Mk, Rb, Mc). I performed the subsequent analyses according to these classifications.

2.4.2 Stability of visual encounter group

I analysed the fluctuations in daily VER to assess the stability of visual encounters with other individuals. Although daily VER with males showed low variation, C2 males showed low variation in daily VER with males and higher variation in daily VER with
females (Table 2-4). Out of 6 C2 males, 4 did not visually encounter females at all during some observation days. C1 males maintained high and stable VER with females throughout the observation days.

VER only with males in the absence of females was higher in C2 males than in C1 males (Table 2-4). In the absence of females, the mean number of males and SD within visual range was 1.1 ± 1.6 for C1 males (N = 457) and 2.1 ± 1.8 for C2 males (N = 3060) excluding the focal male. Significant negative correlation was found between VER with females and VER only with males (Spearman’s rank correlation test: S = 322, ρ = −0.95, P < 0.001); males who rarely visually encountered females tended to gather only with other males within visual range.

2.4.3 Proximity with other individuals

Table 2-5 shows the dyadic proximity ratio (see Table 2-4 for the proximity ratios at the individual level). Male–female proximity was observed in 100% (28/28) and 33% (14/42) of the possible male–female dyads in C1 and C2 males, respectively. The occurrence of male–female proximity differed significantly between C1 and C2 (Fisher’s exact test: P < 0.05). Among the males who showed proximity to females, the mean ± SD dyadic proximity ratios were 0.082 ± 0.0047 and 0.0047 ± 0.0038 for C1 male–female and C2 male–female proximity, respectively. C2 males were significantly less proximate to females than were C1 males (Mann-Whitney U test: N1 = 28, N2 = 14, U = 0.0, P < 0.001).

Male–male proximity was observed in 100% of the possible male–male dyads among both C1 males (6/6) and C2 males (15/15) and was observed in 92% (22/24) between
C1 and C2 males. There was no significant difference across dyads (Fisher’s exact test: \( P = 1.0 \)). Among the males who showed proximity to other males, the mean ± SD proximity ratios among C1 males, between C1 and C2 males, and among C2 males were 0.022 ± 0.014, 0.007 ± 0.005, and 0.011 ± 0.006, respectively. The randomization test and multiple comparisons revealed significant differences between all groups (Fig. 2-2, Randomization test: between C1–C1 and C1–C2, \( P < 0.05 \); between C1–C1 and C2–C2, \( P < 0.05 \); between C1–C2 and C2–C2, \( P < 0.05 \)).

### 2.4.4 Grooming frequency

Table 2-6 shows the dyadic grooming frequencies and their direction (see Table 2-4 for the grooming frequency at the individual level). I excluded from this analysis dyads in which dyadic proximity was 0 because I could not calculate their dyadic grooming frequency.

Male–female grooming was observed only in C1 males. Although some C2 males showed proximity to females, they did not groom females. The occurrence of male–female grooming differed significantly between C1 and C2 males (\( \chi^2 = 5.0 \), df = 2, \( P < 0.05 \)).

Male–male grooming was observed in 67% (4/6) of possible dyads among C1 males, 50% (11/22) between C1 and C2 males, and 93% (14/15) among C2 males. There was no significant difference in the occurrence of male–male grooming among dyads (\( \chi^2 = 1.43 \), df = 2, \( P = 0.49 \)). C2 males groomed one another more frequently than among C1 males and between C1 and C2 males (Fig. 2-3, Randomization test: between C1–C1 and C2–C2, \( P < 0.05 \); between C1–C2 and C2–C2, \( P < 0.05 \)). Grooming frequency among
C1 males showed no significant difference from that between C1 and C2 males (Fig. 2-3, Randomization test: P = 0.85).

Grooming direction comparison showed that C2 males groomed C1 males more frequently than they were groomed by C1 males (Fig. 2-4, Randomization test: P < 0.05). C2 males were groomed more frequently than C1 males groomed them in 72.7% (8/11) of dyads in which grooming was observed. On the other hand, there was no significant difference in the direction of grooming frequency among C1 males (Randomization test: P = 0.88) and C2 males (Randomization test: P = 0.63).

2.5 Discussion

2.5.1 Classification of troop and non-troop males

Males could be classified into at least two social categories based on behavioural data regarding their associations and interactions, even during non-mating seasons. C1 males showed high gregariousness with females, and C2 males were characterized by high proximity with other males.

C1 males not only maintained associations with females throughout observation periods but also had affiliative interactions with females (Table 2-4). These results suggest that C1 males have stable membership in the bi-sexual group and may be considered troop males. When I considered C1 males as troop males, the SSR of the subject troop, 1.75 (4 adult males and 7 adult females), was consistent with a previous report (Sprague et al. 1998). C2 males showed lower proximity to females than did C1 males despite the good visibility of the study site (Koda et al. 2008). In C1 males, daily
fluctuations of associations with females were small, whereas those in C2 males were relatively high. Moreover, C2 males did not groom females at all throughout the observation periods. These results suggest that they are not stable members of the subject troop; consequently, C2 males are considered non-troop males.

I excluded 2 full adult males from statistical analyses because of their short overall observation time. These males showed less visual encounter and did not have any affiliative interactions with others (see Table 2-2). Hence, they might be considered solitary males at least during the period in which they were observed. The current sampling method is likely to overestimate associations and affiliative interactions among individuals because I chose a focal animal near the subject troop in many cases. In other words, I collected the data in the situations in which interactions were likely to occur. However, these two focal males did not show any interaction with other individuals in these sampling conditions. These facts presume that these males did not interact with other macaques even when I did not observe them.

In wild non-provisioned troops in Yakushima Island, adult males tend to acquire higher ranks than young males, and many males reach full adult body size without a solitary period (Sprague 1992). My observation may suggest that the older males tend to be solitary, and the younger males are likely to interact with other males even outside of bi-sexual groups. Association and interaction patterns of males might be influenced by age. Solitary males have been reported in several mammals (Greenwood 1980; Pusey & Packer 1987; Weigart & Whitehead 1997), but these reports have been anecdotal, and there is little or no quantitative data on the time these males spent alone (see, however, Yamagiwa 1986, 1987; Yamagiwa & Mwanza 1994 for eastern gorillas). My observations on two full adult males were surely short, but may suggest that some full
adult males live as solitary males outside of any social group.

Males have been classified into troop and non-troop males through qualitative definitions in previous studies of mammals, and these studies have not applied the same definition. Therefore, it can be difficult to compare the behaviour of males even between conspecific populations. The present study shows that troop and non-troop males can be defined quantitatively by their behaviour in the non-mating season. Quantitative definition of troop/non-troop males may enable comparison of spatial structures or social relationships of males between populations or species and contribute to a better understanding of male sociality.

In the current study, I classified the number of individuals in close proximity among male macaques using novel methods. In many group-living mammals, differences in sex, age, and dominance hierarchy lead to spatial dispersal, sex segregation, and substructure among group mates (van Schaik & van Noordwijk 1986; Lettevall et al. 2002; Hirsch 2007; Fischhoff et al. 2009). PCA based on individual behaviour has contributed to the determination of group boundaries, detection of substructures, and clarification of group membership fluctuation according to dynamic social organization (Connor & Whitehead 2005; Aureli et al. 2008) or male influx (Cords 2000; Hirsch & Maldonado 2011). Recently, social network analysis has been used to analyse complex social systems (Krause et al. 2007; Wey et al. 2008). Compared to social network analysis, the current method using PCA is able to simultaneously take multiple datasets into consideration. This PCA method could advantageous and contribute to clarifying the complexity of social structures.
2.5.2 Formation of all-male groups and affiliative relationships between non-troop males

I found that non-troop males spent time in close proximity to one another, although it was shorter than among troop males, and they frequently groomed one another. These results suggest that these males formed all-male groups with less cohesion. This all-male group was composed of one full adult male, three adult males, and two young adult males. One full adult male ($N_g$) has smaller body size than other full adult males (Kawazoe personal observation). Compared to other full adult males, he might have benefits to form all-male groups. Not only age (e.g. Rajpurohit et al. 1995) but also body size might be a factor influencing on the formation of all-male groups. In many cases, all young adult males were observed in the situation that there were other young adult males within visual range, and they were not be classified as solitary males. Hence, young adult males might tend to form all-male groups compared to full adult males.

In Japanese macaques, troop males repeatedly separate from their troops (Otani et al. 2014). When they range alone away from a troop, they are vulnerable to between-group competitions (Otani et al. 2014). Younger males are supposed to suffer more than older males from between-group competitions because of their smaller body size. It is effective for the detection of predators and competitors to increase group size (van Schaik et al. 1983). The formation of all-male groups will be beneficial for younger males than for older males. In hanuman langurs ($Presbytis entellus$), younger males form all-male bands with older males to avoid risk and to gain spatial knowledge of resources in an unfamiliar terrain (Rajpurohit et al. 1995). The difference of spatial knowledge between age classes might also be why younger males are likely to form all-
male groups. The difference in age class compositions between an all-male group and solitary males might be caused by the benefits for younger males in the formation of the all-male group.

Troop males who live in a low SSR troop (i.e. the number of adult females per adult male is small) have less opportunity to groom females; therefore, they might compensate for the scarcity of grooming partners by grooming other troop males (Hill 1994; Nakagawa 1998). Considering the intrinsic rate of natural lice increase, macaques need to be groomed almost every day (Zamma 2002). Non-troop males have no female affiliative partners, so they might compensate for the lack of alternative opportunities by gathering to gain grooming partners.

In the current study, though non-troop males form an all-male group, they spent shorter times in close proximity to other non-troop males than among troop males. The result might suggest that male–male competitions are less likely to occur in the all-male group than in the troop. Within-group potential contest competition influences male–male social bonds, and low contest competition promotes affiliative relationships (Ostner & Schülke 2014). These low male–male potential contest competitions in all-male groups will offer the foundation for male–male affiliative interaction, affiliative relationships. In such a situation, non-troop males might obtain social interaction partners and establish affiliative relationships.

In Japanese macaques, male–male coalition support is not customary but is observed repeatedly among adult males or under specific circumstances (Bissonnette et al. 2014), and subordinate males have attained a high dominance rank through coalitions (Kutsukake & Hasegawa 2005). Male–male affiliative relationships in the non-mating season enhanced the formation of coalition support in the following mating season in
another macaque species (Berghänel et al. 2011). In all-male groups, the necessity to obtain grooming partners and frequent grooming among them could establish affiliative relationships and social bonds that may provide coalition support (Berghänel et al. 2011) or social tolerance (Tiddi et al. 2011) in the future.

2.5.3 Affiliative relationships between troop and non-troop males

Imbalanced grooming interactions were observed between troop and non-troop males. Non-troop males groomed troop males more frequently than they were groomed. Males use either of the following strategies of immigration in male dispersal group-living primates: non-obtrusive transfer from the lowest dominance rank without agonistic interaction or bluff transfer from the top rank with agonistic interaction (van Noordwijk & van Schaik 1985). Non-obtrusive transfer is predominant in the Japanese macaques and constitutes most of the transfers in the present study site (Sprague et al. 1998). In Arashiyama, Kyoto, some young males in E troop groomed adult males in the adjacent F troop more frequently than they were groomed and soon immigrated to the F troop (Matsumura 1993). On Yakushima, non-troop males who visit a troop in mating season groom not females but troop males in the following non-mating season as the early stage of immigration (Furuichi 1985). Frequent grooming of troop males by non-troop males in the current study might promote social tolerance of troop males and immigration of non-troop males.

2.6 Conclusion
In the present study, I suggested a novel methodological approach to separating males according to their behavioural characteristics. PCA based on individual behaviour classified males without contradicting previous qualitative studies. This method will contribute to the reorganization of intra-specific diversity in attributes of males or to the elucidation of more complex social structures like fission–fusion dynamics or temporal male influxes. Non-troop males, especially young adult males, are likely to form all-male groups, most likely to avoid the risk of between-group competitions and to obtain grooming partners. Although males in all-male groups spent less time in close proximity to one another than males in troops, they showed stronger affiliative relationships (i.e. social bonds). The differences in male social bonds between inside and outside of troops may be determined by the variation in within-group male–male contest competition.
CHAPTER 3

Social bonds, coalitions, and social tolerance among males in despotic wild Japanese macaques (Macaca fuscata)

3.1 Abstract

Social bonds have been construed as differentiated enduring social relationships and are primarily derived from kin relations. Male–male social bonds, however, are widespread phenomena even in male dispersal species. Grooming is a good indicator to assess social bonds and interchange with coalitionary support or social tolerance. Coalitions among males are hypothesized to depend on the variation in strength of contest competition over fertile females. Although social bonds predict coalitionary support in many tolerant macaques, there is little related knowledge in despotic species. In the current study, I present data on frequency and patterns of male–male coalitions among troop and non-troop males in wild despotic Japanese macaques. I analysed seasonal change and correlation of grooming, aggression, and coalition among males and I examined whether social bonds predict coalitionary support and social tolerance. I observed 7 adult males including non-troop males in the non-mating and subsequent mating season on Kinkazan Island, Japan. Compared to the non-mating season, grooming was observed less frequently and aggression more frequently in the mating season. Coalition was observed only in the mating season, and most coalitions constituted winner support. Frequencies of grooming in the non-mating season were not
correlated with those of coalition in the subsequent mating season but were negatively correlated with those of aggression in the mating season. These results suggest that social bonds predicted not coalitions but social tolerance in despotic macaques. Coalitions against dominant males might be suppressed because of high risk of counter aggression and little benefit in terms of mating opportunities. The lack of coalitions among subordinates might contribute to a stable dominant hierarchy in despotic macaques.

3.2 Introduction

Social bonds have been construed as differentiated enduring affiliative social relationships and have been evaluated in non-human primates by proximity or grooming interaction among individuals within a social group (Silk 2002). Social bonds have been primarily derived from kin relations (Trivers 1971; Clutton-Brock 2009). Altruistic behaviours such as grooming among non-kin have been examined from the viewpoint of “reciprocal partner choice” (Schino & Aureli 2009). In this mechanism, each relation is not an independent but, rather, a comparative component across dyads (Schino & Aureli 2009). Studies on social bonds have revealed the positive relations between grooming and coalitionary supports (Schino 2007) and between grooming and social tolerance (Tiddi et al. 2011; Xia, 2013 #212).

Male–male relatedness within a group is expected to be low because males disperse from their natal troop in many primates (Pusey & Packer 1987). Moreover, males struggle with one another over non-sharable fertile females. Therefore, male–male social bonds have been thought to be rare (Clutton-Brock 2009). Social bonds are
observed, however, among males even in male dispersal species (van Hooff & van Schaik 1994; Ostner & Schülke 2014). Male–male social bonds have evolved as long-term alliances with an adaptive function in within-group contest (Ostner & Schülke 2014). Male–male coalitions are widespread phenomena in primates (Bissonnette et al. 2014) and are hypothesized to be influenced by the strength of contest competitions over fertile females (Pandit & van Schaik 2003; van Schaik et al. 2004; Bissonnette et al. 2014).

Macaque species are classified into four grades of social style according to the tolerant–despotic continuum (Matsumura 1999; Thierry et al. 2000). The hypothesis predicts that male–male coalitions are common in tolerant species and rare in despotic species (Pandit & van Schaik 2003; van Schaik et al. 2004). Male–male social bonds and their influences have been studied recently in tolerant macaque species. For example, social bonds predict formation of coalitionary supports (Berghänel et al. 2011), social tolerance (Xia et al. 2013), cooperative defence of fertile females (Silk 1994), increase of access to mates (Bissonnette et al. 2011), elevation of dominance rank, and reproductive success (Schülke et al. 2010). In provisioned despotic macaques, natal males form coalitions with their mothers or relatives to achieve turnover of the dominance hierarchy (Kutsukake & Hasegawa 2005; Higham & Maestripieri 2010). Few data exist, however, to show the frequency and patterns of male–male coalitions and how social bonds influence coalition formation or social tolerance among males in wild non-provisioned despotic macaques. Influence of social bonds in despotic species might differ from that in tolerant species because the difference in the strength of contest competitions might affect coalition formation (Pandit & van Schaik 2003; van Schaik et al. 2004). In despotic species, it is expected that social bonds are related not to
coalition but to other behaviour with little cost because steep a dominance gradient might suppress coalitions among subordinates against dominant males and cause counter aggression. Additionally, troop males are predicted to be involved in more coalitions in the mating season because they may have the lower risk and higher benefit involved in the elimination of extra males (Nunn 2000; Ostner & Schülke 2014).

Japanese macaques have the most despotic social style among macaque species (Matsumura 1999; Thierry et al. 2000; see Nakagawa 2010 for exceptional populations) and a strict breeding seasonality (Fujita 2010). Male Japanese macaques show a linear dominance hierarchy within a troop (Sprague 1992). Non-troop males have been observed in several populations of wild Japanese macaques (Nishida 1966; Sugiyama 1976; Sprague et al. 1998; Kawazoe 2016). Though non-troop males are frequently attacked by troop males in the mating season (Horiuchi 2005), there are few data on dominance hierarchy between non-troop and troop males or among non-troop males. Further, there are no data to demonstrate how social bonds in non-troop males predict their social relationships in the following mating season, though non-troop males often groom one another and groom troop males more frequently than they are groomed (Kawazoe 2016).

In tolerant macaques, several references suggest that social bonds predict coalition among males (Berghänel et al. 2010; Schülke et al. 2010). In despotic macaques, however, male–male coalitions are supposed to be rare (Pandit & van Schaik 2003; van Schaik et al. 2004), and social bonds might not show significant correlation with coalition formation because of their despotic social style (Thierry 2013). In the current study, I aimed to present data on frequency and patterns of male–male coalitions in wild despotic Japanese macaques. I also examined whether male–male social bonds predict
coalition formation or social tolerance in despotic macaques. First, I analysed the dominance hierarchy among males including not only troop males but also non-troop males in the non-mating and subsequent mating seasons. Frequency and distribution of grooming, aggression, and coalition among males was also analysed. I then analysed the correlation between grooming in the non-mating season and coalition/aggression in the following mating season using a row-wise matrix correlation test. I discussed patterns of coalitions and relations among social bonds, dominance, coalition, and tolerance in male despotic Japanese macaques.

3.3 Methods

3.3.1 Study area, periods, and subjects

I conducted this study on Kinkazan Island (38°2′N, 141°4′E), Japan. The island is about 10 km² in area and located 700 m from the main island of Japan. A deciduous broad-leaved forest dominates the higher area and a coniferous forest the lower area (Nakagawa 1997). The composition of vegetation and the heavy browsing by sika deer, which suppresses the forest regeneration, allow for good visibility (Takatsuki & Gorai 1994) and favourable conditions for observation. Six troops of Japanese macaques inhabit the island with overlapping home ranges without any provisioning (Izawa 1999). Japanese macaques are strict seasonal breeders (Fred. B. Bercovitch & Harvey 2004; Fujita 2010), and mating season on the island usually lasts from late September to December (Takahashi 2001; Fujita et al. 2004). I conducted behavioural observation in May–June for the non-mating season and in October–December for the mating season.
in 2009. The observation periods included a total of 54 days in the non-mating season and 64 days in the mating season.

Among the six troops, I observed Troop C2, which sets up their home range in the northern part of the island. All the members of this troop have been identified since 2000. In the non-mating season, some non-troop males are observed occasionally around this particular troop, and they have affiliative interaction with troop males (Kawazoe 2016). Following CHAPTER 2 (Kawazoe 2016), I defined troop and non-troop males by conducting PCA on their behavioural traits (visual encounter ratio, the number of individuals within visual range, and proximity ratio) in the non-mating season (Table 3-1; Fig. 3-1). The troop included 3 adult males, 6 adult females, 1 adolescent female, 7 juveniles, and 1 infant through study periods. I observed the 3 troop males and the 4 non-troop males (estimated more than 7 years old) found around the troop in both study periods (Table 3-2). All subject males were regarded as non-natal to the troop from the long-term identification data.

3.3.2 Data sampling

I used focal animal sampling (Altmann 1974) for the observation. After locating the troop, I chose an adult male as a focal animal for the observation within or around the troop. I followed only one male as long as possible in each day. However, observation was changed from the focal male to another male if the second male had been minimally observed up to that point to reduce the deflection of observation time across subject males. I observed a focal male for more than 5 h in a day. Total observation time was 353 h 15 m in the non-mating season and 356 h 25 m in the mating season (Table
The mean observation time per male was 50.5 ± SD 10.2 h (range: 37.3–57.3) in the non-mating season and 50.9 ± SD 15.6 h (range: 23.8–68.2) in the mating season.

I recorded the participants and direction of grooming, aggression, and coalitionary support among males with continuous sampling (Martin & Bateson 2007). A grooming bout began when the hands of an animal touched the body of another to groom and ended when the two animals broke contact. Aggression was defined as chasing, grabbing, or biting. An aggressive interaction that occurred within 10 sec of a former aggression with the same direction was defined as the same bout as the former. However, when the direction of aggression was reversed without coalitions, it was defined as another bout even though it happened within 10 sec of the previous bout. I defined coalition formations as joint aggression of two males against a common target (de Waal & Harcourt 1992). When coalitionary support was observed, I recorded the individual supporting and being supported and the target of the coalition. At times, more than three males participated in aggressive interactions simultaneously in the mating season (N = 5). In such cases, the direction of attack or the presence of coalitions was unclear. Hence, I excluded such cases and analysed only the cases in which three males were involved in the coalition (i.e. two males against a common target).

I also recorded the activity of the focal male and males located within 5 m of the focal male as associates through instantaneous sampling with 5-min intervals (Martin & Bateson 2007). Activity was recorded with the following categories: feeding, moving, resting (including grooming), and mating (only in the mating season). Male Japanese macaques require multiple mounts before ejaculation (Enomoto 1974; Thierry et al. 2000). I recorded all the activities of the focal animals during mounting series as mating. It was possible to record mounting series from the beginning to the end by adopting
focal animal sampling methods.

### 3.3.3 Data analysis

I defined grooming, aggression, and coalition index with the following calculations. I drew out three sociometric matrices for grooming, aggression, and coalition among 7 focal males. Each index was calculated in the following formulae, controlling for their opportunities for interaction using the data from instantaneous sampling.

\[
Grooming\ index\ (GI)_{i\rightarrow j} = \frac{G_{i\rightarrow j}}{N_i(j) + N_j(i)}
\]

\[
Aggression\ index\ (AI)_{i\rightarrow j} = \frac{A_{i\rightarrow j}}{N_i(j) + N_j(i)}
\]

where \(G_{i\rightarrow j}\) and \(A_{i\rightarrow j}\) indicate the number of grooming and aggression bouts that individual \(i\) performed toward individual \(j\). \(N_i(j) [or N_j(i)]\) indicates the number of sampling points at which \(j\) (or \(i\)) was located within 5 m of individual \(i\) (or \(j\)) as associates. Coalition index \((CI)_{i\rightarrow j}\) was defined as the rate of the number of coalition formations in which individual \(i\) supported individual \(j\) to the number of aggressions in which individual \(i\) or individual \(j\) was involved.

I also calculated two indices at the dyadic level in the following formulae.

\[
GI_{i,j} = (GI_{i\rightarrow j} + GI_{j\rightarrow i})
\]

\[
AI_{i,j} = (AI_{i\rightarrow j} + AI_{j\rightarrow i})
\]

I tested seasonal change of grooming and aggression index at the dyadic level using the Wilcoxon signed rank test. I also analysed the linearity of the dominance hierarchy (de Vries 1995) in both seasons.
There are three patterns of coalitions according to those in the dominance hierarchy who formed coalitions (Chapais 1995; van Schaik et al. 2004). An all-down coalition (or conservative alliance in Chapais 1995) is the coalition in which the highest and the intermediate-ranking male jointly attack the lowest male; three males participate in the coalition. The highest and the lowest male attack the intermediate-ranking male in a bridging coalition, and the intermediate- and the lowest-ranking male form a coalition in the all-up pattern (revolutionary in Chapais 1995). I classified observed coalitions into these three patterns and compared them with the expected value of occurrence frequency.

In sociometric matrices, data are not independent since observations concerning the same individual recur; therefore, correlation analysis between two matrices requires special techniques (Hemelrijk 1990a; de Vries 1993). Data were analysed by means of the tau Kr and partial tau Kr test for matrix correlation tests (Hemelrijk 1990a, b). This row-wise matrix correlation test allows the researcher to avoid the problem of data dependence in different dyads and, at the same time, take into consideration inter-individual differences in the absolute rates of behaviour (Hemelrijk 1990a, b; de Vries 1993). When a Kr test or partial Kr test was performed, the significance P-value was calculated based on 10 000 permutations. Statistical tests were carried out using R 3.2.0 (R Core Team 2013) and MatrixTester 2.2.4 provided by Dr Charlotte Hemelrijk.

This study complied with research guidelines for the study of wild non-human primates of the Primate Research Institute, Kyoto University, Japan, and adhered to the Japanese legal requirements.
3.4 Results

3.4.1 Seasonal change and grooming reciprocity

Male–male grooming was observed in 71.4% (15/21) and 52.4% (11/21) of all possible dyads in the non-mating and mating season, respectively (Table 3-3). Grooming was performed much less in the mating season than in the non-mating season (Fig. 3-2a, Wilcoxon signed rank test: N = 21, Z = 120, P < 0.001). A Tau Kr test revealed a significant positive correlation between matrices in grooming given and received in both seasons (tau Kr test: non-mating season: tau Kr = 0.77, P < 0.001; mating season: tau Kr = 0.77, P < 0.001). These results indicate that males frequently groomed the males who often groomed them in both seasons.

3.4.2 Seasonal change of aggression and linearity of dominance hierarchy

Male–male aggression was observed in 19.0% (4/21) and 85.7% (18/21) of possible dyads in the non-mating and mating season, respectively (Table 3-4). Aggression was observed much more in the mating season than in the non-mating season (Fig. 3-2b, Wilcoxon signed rank test: N = 21, Z = 0, P < 0.001). Although linearity of the dominance hierarchy was not found in the non-mating season (h’ = 0.37, P = 0.56), it was found in the mating season, including non-troop males (h’ = 0.80, P < 0.05). Most of the non-troop males were subordinate to troop males, but dominant–subordinate relations between Ha (troop male) and Ga (non-troop male) were inconsistent with the tendency (Table 3-4).
There was no significant difference in activity phase when aggression occurred from the expected values in the non-mating season (Table 3-5, \( \chi^2 = 3.0, \text{df} = 2, P = 0.22 \)). However, in the mating season, aggression was observed more frequently in the resting and mating phase and less frequently in feeding and moving than expected (Table 3-5, \( \chi^2 = 131.2, \text{df} = 3, P < 0.001 \); Residual analysis: resting: \( P < 0.001 \); mating: \( P < 0.001 \); feeding: \( P < 0.001 \); moving: \( P < 0.001 \)).

### 3.4.3 Distribution, patterns, and reciprocity of coalition

Coalitionary support among males was never observed in the non-mating season and was observed in 28.6\% (6/21) of possible dyads in the mating season (Table 3-6), and 9.1\% (18/197) of all aggressions in the mating season. There was no significant correlation between the coalition given and received (Tau Kr test: \( \tau = 0.18, P = 0.23 \)). The third party formed coalitions more frequently with the aggressor than with the aggressee (Binominal test: \( N_1 = 16, N_2 = 2, P < 0.01 \)). The occurrence of coalition differed across the three patterns (Fig. 3-3, \( \chi^2 = 8.0, \text{df} = 2, P < 0.05 \)). All-down coalitions were observed much often than expected (Residual analysis: \( P < 0.05 \)), and all-up coalitions were never observed in the study periods (Residual analysis: \( P < 0.01 \)). Bridging coalition occurrence did not show significant difference from expectation (Residual analysis: \( P = 1.0 \)).

Most of the coalitions were formed between troop males against non-troop males (Table 3-7). Non-troop males were the main target of coalitions (\( N = 17 \)), and troop males were rarely targeted (\( N = 1 \)). Troop males did not form coalitions between troop males against other troop males. In the bridging coalitions, troop males (\( Kl \)) supported
non-troop males (*Rb*) against a troop male (*Ha*) in one case. Loser support was observed only between troop males against another non-troop male. Coalition formations between non-troop males were observed 4 times against non-troop males in a bridging pattern but not observed against troop males (Table 3-7). These 4 cases occurred when the target was resting.

3.4.4 Partial matrix correlation among grooming, aggression, and coalition

A partial tau Kr test was conducted among the matrices of grooming given in the two seasons and aggression received in the mating season (Fig. 3-4a). Significant positive correlation was found between the matrix of grooming given in the non-mating season and in the mating season when the effect of the aggression matrix in the mating season was partialled out (Partial tau Kr test: $\tau_{Kx,z} = 0.35$, $P < 0.05$). This result indicates that, in the mating season, males frequently groomed the males they often groomed in the previous non-mating season. Partial tau Kr test also showed a significant negative correlation between the matrix of grooming given in both seasons and the matrix of aggression received in the mating season (Partial tau Kr test: $\tau_{Kx,z} = -0.30$, $P < 0.05$, controlling for the matrix of grooming indices in the mating season; $\tau_{Kx,z} = -0.30$, $P < 0.05$, controlling for the matrix of grooming indices in the non-mating season). These results indicate that males less frequently received aggression from the males they often groomed in the non-mating and mating seasons.

The matrix of grooming given in the non-mating and mating seasons also showed significant correlation when the effect of the matrix of coalition received was partialled out (Fig. 3-4b, Partial tau Kr test: $\tau_{Kx,z} = 0.47$, $P < 0.01$, controlling for the
coalition matrix). On the other hand, the matrix of grooming given in both seasons showed no significant correlation with the matrix of coalition received (Fig. 3-4b, Partial tau Kr test: tau Kr_{xy,z} = 0.17, P = 0.18, controlling for the grooming matrix in the mating season; Partial tau Kr test: tau Kr_{xy,z} = -0.010, P = 0.54, controlling for the grooming matrix in the non-mating season).

3.5 Discussion

3.5.1 Reciprocal partner preference in affiliative interaction

In both the non-mating and mating seasons, grooming given and received showed significant positive correlation. This result means that male Japanese macaques more frequently groomed the same males that groomed them more frequently. Reciprocal partner preference in grooming has been reported in male tolerant macaque species (Silk 1992; Berghänel et al. 2011; Xia et al. 2013). Reciprocal partner preference in grooming is likely to be established relatively easily, because, unlike aggression, the interaction is accompanied with fewer costs and disadvantages for both groomer and groomee (Dunbar & Sharman 1984). Although the current study showed a steep dominance gradient in the mating season, reciprocal partner preference in grooming was found not only in the non-mating season but also in the mating season. These results suggest that partner preference in male–male grooming was performed reciprocally despite the steep dominance gradient among males found in the mating season.

The current study showed positive correlation not only between the matrices of grooming given and received within the seasons but also between the matrices of...
grooming given in the non-mating season and in the subsequent mating season. This result means that grooming partner preference was consistent in both seasons even though there was at least a 2-month time lag. Although social bonds are assumed to be formed between kin, they are widespread phenomena even between non-kin (Clutton-Brock 2009). Males need to take measures to maintain their bonds because temporal delays in returning benefits may provide cheating options to the receiver of the cooperative act between non-kin (Trivers 1971; Clutton-Brock 2009). Males might need to groom each other repeatedly in a short time span to ensure their affiliative relationships and avoid the disadvantage of free ride. Consequently, they might repeatedly groom the same partner in the mating season as in the preceding non-mating season.

3.5.2 Dominance hierarchy among males

Compared to the non-mating season, rates of aggression increased, and a linear dominance hierarchy including non-troop males was found in the mating season. Most of the non-troop males were subordinate to troop males.

Grooming with other males might provide opportunities to establish affiliative and dominance relationships. Non-troop males show less gregariousness than troop males in the non-mating season (Kawazoe 2016). Such a low cohesiveness might enable them to keep a distance from other males in case of a competitive situation like a feeding phase and to avoid contest competition among males. Hence, a dominance hierarchy including non-troop males might not likely become apparent in the non-mating season even if it exists. Males compete with each other over fertile females because fertilizations are
non-sharable resources (van Hooff & van Schaik 1994; van Schaik 1996). Male gregariousness may increase in the mating season because of females’ sexual attraction, and a dominance hierarchy might actualize in the mating season.

I observed not only troop males but also non-troop males in the current study. Non-troop males are likely to be classified into two categories according to their behavioural patterns. Some non-troop males, especially younger males, groom other non-troop and troop males, and the others, especially full adult males, have no affiliative social interaction in the non-mating season (Kawazoe 2016).

A full adult non-troop male (Ga) did not groom troop males at all in the non-mating season, and he dominated a troop male (Ha) in the mating season. The takeover of an alpha male can occur in Japanese macaques, though it is rare in the current population (Sprague et al. 1998).

Age is correlated with dominance ranking within a troop (Sprague 1992). The relation between age and dominance hierarchy might be applicable not only within but also outside of a troop, and non-troop males might adopt a different strategy of interaction with troop males according to their age class. Namely, younger non-troop males might establish affiliative relationships and a dominance hierarchy with troop males and immigrate to the troop at the bottom rank without antagonistic interaction. On the other hand, older males might not establish affiliative relationships and a dominance hierarchy with troop males and might try to take over from an alpha male through antagonistic interaction.

3.5.3 Coalition and dominance hierarchy
No third-party supported winner rather than loser or all-up coalition was observed in the current study periods. Most of the coalitions were formed between troop males against non-troop males. These results suggest that dominance hierarchy and male attribute are the important factors for the formation of coalitions, and they seem to predict patterns of coalitions.

In some primates, the number of males within a group in mating season fluctuates because of male influxes (Cords 2000; Ohsawa 2003). Reproductive competition caused by male influx brings disadvantages disproportionately for all males, and more dominant males suffer from the contest competition over fertile females (Cowlishaw & Dunbar 1991; Nunn 2000). The dominant male is predicted to prevent influx of extra males (Nunn 2000). The SSR in the current study site was skewed toward females (i.e. the number of adult males in a group was smaller than that of adult females), and many non-troop males inhabit in the area. Troop males might form coalitions to preclude influxes of these non-troop males and/or to ensure their dominance hierarchy in the mating season. Male Japanese macaques often groom one another and form social bonds against neighbouring troops in populations with high between-group contest competitions (Saito et al. 1998). Between-group contest competition might promote formation of male–male social bonds and coalitions within a troop even though it has smaller influence than within-group contest competition (Ostner & Schülke 2014).

I also showed a low rate of looser support and a lack of all-up coalitions in male Japanese macaques. Males showed significant linear dominance hierarchies in the mating season. These results suggest that subordinate males have the risk of counter aggression by dominant males. Alternatively, there may be another reason. All the cases of coalitions between non-troop males were observed when the target was not mating
but, rather, resting. This result might suggest that non-troop males do not form coalitions to gain mating opportunities. Male Japanese macaques need to guard oestrus females from other males for a long time because they require multiple mounts to ejaculate (Enomoto 1974), and dominant males sometimes aggressively disrupt the mating of subordinate males (Huffman 1987). Hence, even if non-troop males form coalitions with other non-troop males for access to the fertile females, they are less likely to gain mating opportunities for both non-troop males who form the coalition. Compared to troop males, non-troop males might have few benefits from forming coalitions against troop males, and there is the risk of counter aggression.

In contrast to the present results, all-up coalitions occurred in tolerant macaques (Ostner et al. 2008; Young et al. 2013). The lack of coalitions among subordinates might contribute to maintaining the steep and stable dominance hierarchy in despotic species. The evolutionary process of male coalitions has been discussed in terms of its frequency (e.g. Bissonnette et al. 2014). The current study suggests that not only frequency but also patterns of coalition need to be taken into consideration to clarify the evolutionary process of male–male social bonds.

3.5.4 Reciprocal partner preference in coalition and social tolerance

The present study showed no significant correlation between grooming given and coalition received among males. This is the first report to analyse the influence of affiliative relationships on coalition formation in male Japanese macaques. Most of the non-troop males are subordinate to troop males, and there is a linear dominance hierarchy among males. Non-troop males groomed one another more
frequently than did troop males (Kawazoe 2016). Although, in provisioned despotic macaques, natal males form coalitions with their mothers or relatives to achieve turnover of dominance hierarchy (Kutsukake & Hasegawa 2005; Higham & Maestripieri 2010), all-up coalition between non-kin males was not observed (Kutsukake & Hasegawa 2005). Subordinate males may not form all-up coalitions against a dominant male to avoid the risk of counter aggression for which they would gain few benefits because there is low probability to share the mating opportunities with all the participants. The lack of coalitions among subordinate males might be the reason why affiliative relationships did not predict coalitions in this study.

I found affiliation in the non-mating season to predict affiliation and tolerance in the following mating season. Grooming sometimes correlates with social tolerance in competitive situations other than coalition formation. For example, in Tibetan macaques (M. thibetana), dominant males tolerate their male grooming partners in the mating season, although not in competitive situations (Xia et al. 2013). Although Tibetan macaques are classified into the tolerant social style (Thierry et al. 2000), male Tibetan macaques have despotic characteristics in the aspect of reconciliation (Berman et al. 2006). Male despotic social style might predict that male–male social bonds affect not coalition formations but social tolerance.

In Japanese macaques, although dominant males can monopolize most copulations when a few females show oestrus, subordinates also have opportunities for copulation when many females show oestrus (Soltis et al. 2001; Takahashi 2001). Dominant males guard mating partners and aggressively disrupt the mating of subordinate males (Huffman 1987). Social tolerance among males in the mating season might enable subordinates to access and maintain close proximity to oestrus females. Consequently,
subordinates might acquire mating opportunities in the case of a high operational sex ratio without coalitions. Female macaques selected males with a shorter tenure as mating partners during the ovulation period (Inoue & Takenaka 2008). Hence, it might be a kind of strategy for subordinate non-troop males to stay near oestrus females to attract female attentions. Enhancement of tolerance in the mating season through social bonds might contribute to mating strategy in subordinate males (Xia et al. 2013). Although grooming does not show a positive correlation with coalition formation, subordinates might receive reproductive advantages by bringing out other males’ tolerance in the mating season.

3.6 Conclusion

In the current study, I presented the frequency and patterns of coalitions in male despotic Japanese macaques. I also analysed seasonal change and correlation of grooming, aggression, and coalition among troop and non-troop males in Japanese macaques. A linear dominance hierarchy was found in the mating season. I found that reciprocal partner preferences in grooming were consistent throughout the study period. Social bonds predicted not coalitions but social tolerance in the mating season. The majority of coalitions were winner supports. All-down coalitions occurred most frequently, and no all-up coalition was ever observed. These results suggest that coalitions between non-troop males against dominant males might be suppressed because of high risk of counter aggression and few benefits in terms of mating opportunities. These patterns of coalitions might contribute to a stable dominance hierarchy in despotic species. Positive correlation between social bonds and social
tolerance might be the feature in despotic species and might contribute to a mating strategy for subordinate non-troop males.
CHAPTER 4

General Discussion

In this thesis, I examined quantitative classification of male attributes into troop and non-troop males based on their behavioural traits and revealed the difference of male–male affiliative relationships between those within and those outside of troops (see CHAPTER 2). In addition, male–male affiliative relationships were maintained between the non-mating and mating seasons, and such bonds might bring about not coalition formation but social tolerance among males (see CHAPTER 3).

In this chapter, I present a summary of a methodological approach to classify attributes and social relationships among not only troop males but also non-troop males among wild Japanese macaques in relation to the contents of CHAPTERS 2 and 3. I also discuss the methodological approach to understanding intra-specific variation in male social organization and the difference of social relationships from other primates. Finally, I provide future perspectives on social relationships and the life history of male Japanese macaques.

4-1. **Summary of male classification, male–male social bonds, and their influences on wild Japanese macaques**

In CHAPTER 2, I employed quantitative classification of male attributes in troop and
based on their behaviour. PCA of a VER dataset, the number of individuals within visual range, and the proximity ratio in the non-mating season revealed that males could be distinguished by association with other individuals and proximity with males. I also examined the stability of male memberships and concluded that some non-troop males formed less cohesive all-male groups, and the others were solitary. The number of troop males and the SSR led by this quantitative approach did not contradict previous report (Sprague et al. 1998). The result suggests that we are able to classify males not only qualitatively but also quantitatively regardless of study period.

In addition, following the above classification, I compared proximity ratio and grooming frequencies among males. Compared to troop males, non-troop males who formed all-male groups spent less time in proximity to other males and groomed other non-troop males more frequently. Some non-troop males groomed not only non-troop males but also troop males more frequently than they were groomed by troop males.

Dispersing males are likely to face the loss of opportunities for altruistic behaviour such as grooming (Moore 1992). Low proximity ratio between non-troop males suggests that non-troop males have less opportunity for social interaction than do troop males. Males compensate for the scarcity of female grooming partners by grooming other males (Hill 1994; Nakagawa 1998). Non-troop males might compensate for the lack of opportunities and female grooming partners by forming all-male groups and frequently grooming one another. Less opportunity for interaction may also suggest that contest competition among non-troop males is rare. Low potential contest competition might contribute to frequent grooming and establishment of social bonds among non-troop males (Ostner & Schülke 2014). The more frequent grooming by non-troop males toward troop males might promote tolerance in the troop males and resultant
immigration (Furuichi 1985; Matsumura 1993).

In CHAPTER 3, I examined the dominance hierarchy among males including non-troop males and showed a steep linear dominance hierarchy in the mating season. Almost all non-troop males were subordinate to troop males, but one non-troop male dominated one troop male. I revealed male–male social bonds as long-lasting affiliative relationships in the non-mating and mating seasons. Males showed reciprocal partner preference in grooming interaction between the 2 seasons. Such social bonds correlated with social tolerance in the mating season but did not correlate with coalition formations. I also presented the frequency and patterns of coalitions in Japanese macaques where coalition formations are thought to be rare (Pandit & van Schaik 2003; van Schaik et al. 2004). Coalitions frequently occurred with all-down patterns, and troop males formed coalitions against non-troop males.

Reciprocal partner preference in grooming was observed in many tolerant macaques (Silk 1992; Berghänel et al. 2011; Xia et al. 2013). These results suggest partner preference in male–male grooming performed reciprocally, although a steep dominance gradient among males was found in the mating season. Troop males are predicted to prevent influx of extra males (Nunn 2000) because they will suffer from the contest competition over fertile females (Cowlishaw & Dunbar 1991; Nunn 2000). Troop males might form all-down coalitions against non-troop males to prevent unfamiliar non-troop males from approaching fertile females. On the other hand, non-troop males might not form coalitions because of the risk of counter aggression by dominant males and because of low probability of sharing the mating opportunities with all the participants.

Although positive correlations are found between social bonds and coalition formations in tolerant macaques (Silk 1994; Berghänel et al. 2011), the current study
did not show such positive relations between social bonds and coalitions but, rather, between social bonds and social tolerance. Social style might influence the effect of male–male social bonds, and male despotic social style might predict social tolerance.

4-2. Methodological approach for reconsideration of intra-specific variation of social organization in male Japanese macaques

In CHAPTER 2, I introduced a new methodological approach for the classification of male attributes. According to the method, I confirmed that males could be classified quantitatively by their behavioural traits without contracting qualitative classification (e.g. Sprague 1998). Although the methodological approach I adopted brings the same results as a previous method, I believe that a quantitative approach is important to clarify and reconsider the intra-specific diversity of social organization in Japanese macaques.

The current thesis showed at least 3 categories of males based on their behaviour: troop males, non-troop males in all-male groups, and non-troop solitary males. In addition, non-troop males in all-male groups sometimes approach and travel around a troop and have affiliative interactions with troop males. On the other hand, in other Japanese macaque populations, different categories of males attributes are described in both non-provisioned and provisioned populations: central troop males, peripheral troop males, and non-troop males (e.g. Itani 1959; Yamada 1963; Nishida 1966; Koyama 1967; Kawai et al. 1968; Sugiyama 1976; Huffman 1992; Suzuki et al. 1998). The results in this thesis and these references seem to show both the common and different viewpoints in intra-specific social organization in Japanese macaques. In any
populations, males are classified into at least three categories. However, males at the periphery or outskirts of troops have been considered troop males in some populations and as non-troop males in others. On Kinkazan Island, where the current study was conducted, some males occasionally travel around the troops, although they are not regarded as troop members (Sprague et al. 1998), and I also conclude that they are non-troop males rather than peripheral troop males (CHAPTER 2).

The intra-specific variation in SSR among Japanese macaques has been mentioned (Sprague et al. 1998; Yamagiwa & Hill 1998). However, the confusion about the classification of males at the periphery of troops should be clarified for the full understanding of the variation of social organization. It seems that conventional qualitative aspects in male classification are not suitable for readjustment of such confusion, because it is not possible to compare the difference in male attributes across populations. The methodological approach I introduce in this thesis enables us to compare male attributes quantitatively and to discuss what factors influence the differences across populations. It might contribute to reconsideration of the social organization in Japanese macaques.

4.3 Influence of between-group competition on formation of all-male groups and male–male social bonds

Male–male social bonds have been examined within troops, and between-group contest has relatively low influence on social bonds (Ostner & Schülke 2014). Within-group contest competition is the main factor facilitating male–male social bonds, and males are likely to develop male–male bonds when within-group contest is low (Ostner &
Schülke 2014). However, between-group contest also promotes male–male bonds within troops (Saito et al. 1998). Males form bonds with one another to defend resources against other troops when high between-group contest exists (Saito et al. 1998).

Kinkazan Island, which is the current study site, is covered with deciduous forests (Nakagawa 1997), and the between-group contest is estimated to be low (Saito et al. 1998). In addition, no predators exist on the island (Takahata et al. 1998). Such low between-group contest and the absence of predation risk might enable males to range and feed away from troops to avoid within-group scramble competition (van Schaik 1989). In addition, dispersing males face the loss of opportunities for social interaction (Moore 1992). Non-troop males might form all-male groups to gain interaction opportunities and to develop male–male bonds, which relate with strategies of immigration and copulation. Not only within-group contest competition (Ostner & Schülke 2014) but also between-group contest competition is the important factor to facilitate formation of all-male groups and to develop male–male bonds outside of bisexual troops.

4.4 Future perspectives

In this thesis, I introduced a methodological approach for reconsideration and understanding of intra-specific diversity in social organization in Japanese macaques. Although I could show the validity of this approach within the population, it is necessary to confirm in other populations. Variability in SSR within and among species has been reported (Kappeler 2000). However, the causes and consequences of variation
are far more completely understood (Kappeler 2000). The approach I presented in this thesis has a strong possibility of contributing to the further understanding of variability in social organization.

In many primates, males disperse from their natal troops (Pusey & Packer 1987). Several references have mentioned that male dispersal is not random but influenced by kinship (Cheney & Seyfarth 1983; Jack & Fedigan 2004a, b; Albers & Widdig 2013). In addition, in long-tailed macaques (*M. fascicularis*), regarded as a despotic species, co-residence with related males in the same troop extended their tenure even after natal dispersal (Gerber et al. 2016). These references suggest that kinships or social bonds might influence dispersal patterns or post-dispersal life history in male dispersal species. Parallel dispersal occurs when individuals emigrate together with peers or close kin or immigrate to groups containing familiar or closely related individuals (Schoof et al. 2009).

In Japanese macaques, emigration and immigration with a cohort are also observed (Sugiyama 1976). Despotic social style is characterized by high nepotism (Matsumura 1999; Thierry et al. 2000). Hence, there is the possibility that kinships underlie dispersal patterns and social bonds in male Japanese macaques. In this thesis, I could not mention the influence of kinships among them because of insufficient data. Long-lasting observation and analytical methods adopting DNA analysis are required for further understanding of male–male social bonds and their function.
REFERENCES


unknown or tied relationships. *Animal Behaviour, 50*(5), 1375–1389


Schino, G., & Aureli, F. (2016). Reciprocity in group-living animals: partner control versus partner choice. *Biological Reviews*


Thierry, B. (2013). Identifying constraints in the evolution of primate societies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618)

*Ethology, 106*(8), 713–728


*Behavioral Ecology, 22*(3), 663–669


mountain gorillas (*Gorilla gorilla beringei*). *Primates, 28*(1), 1–30


Table 2-1 Names, age classes, number of observation days (N), observation time, and mean observation time per day in each focal male

<table>
<thead>
<tr>
<th>Name</th>
<th>Age class**</th>
<th>January–March</th>
<th>May–June</th>
<th>August–September</th>
<th>Mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N Observation time</td>
<td>N Observation time</td>
<td>N Observation time</td>
<td>Mean ± SD</td>
<td></td>
</tr>
<tr>
<td>Kl</td>
<td>FA</td>
<td>6 32.8</td>
<td>6 46.3</td>
<td>6 34.6</td>
<td>6.3 ± 1.5</td>
</tr>
<tr>
<td>Th</td>
<td>A</td>
<td>5 26.9</td>
<td>6 41.4</td>
<td>5 29.1</td>
<td>6.1 ± 1.3</td>
</tr>
<tr>
<td>Ng</td>
<td>FA</td>
<td>5 26.8</td>
<td>7 47.4</td>
<td>3 21.1</td>
<td>6.4 ± 1.0</td>
</tr>
<tr>
<td>Rc</td>
<td>FA</td>
<td>4 21.8</td>
<td>5 38.2</td>
<td>4 26.5</td>
<td>6.6 ± 1.6</td>
</tr>
<tr>
<td>Pp</td>
<td>FA</td>
<td>4 23.5</td>
<td>4 30.9</td>
<td>4 27.7</td>
<td>6.8 ± 1.5</td>
</tr>
<tr>
<td>Ha</td>
<td>FA</td>
<td>4 22.8</td>
<td>4 29.9</td>
<td>3 18.6</td>
<td>6.5 ± 1.5</td>
</tr>
<tr>
<td>Bl</td>
<td>A</td>
<td>3 17.4</td>
<td>4 26</td>
<td>3 19.1</td>
<td>6.3 ± 0.9</td>
</tr>
<tr>
<td>Mk</td>
<td>A</td>
<td>2 12.3</td>
<td>3 20.8</td>
<td>4 28.1</td>
<td>6.8 ± 0.8</td>
</tr>
<tr>
<td>Rb</td>
<td>YA</td>
<td>2 11.3</td>
<td>3 23.1</td>
<td>3 18.6</td>
<td>6.6 ± 1.5</td>
</tr>
<tr>
<td>Mc</td>
<td>YA</td>
<td>2 12</td>
<td>3 19.5</td>
<td>2 11.7</td>
<td>6.2 ± 0.8</td>
</tr>
<tr>
<td>Co*</td>
<td>FA</td>
<td>0 -</td>
<td>0 -</td>
<td>4 24.9</td>
<td>6.2 ± 0.9</td>
</tr>
<tr>
<td>Tv*</td>
<td>FA</td>
<td>3 18.3</td>
<td>0 -</td>
<td>0 -</td>
<td>6.1 ± 0.5</td>
</tr>
</tbody>
</table>

*: Co and Tv were excluded from statistical analysis due to their short observation time.
**: FA: full adult males who were estimated more than 13 years old and 10–13 kg; A: adult males who were estimated 10–12 years old and 7–10 kg; YA: young adult males who were estimated 7–9 years old and 5–7 kg.
Table 2-2 Dataset of visual encounter ratio (VER), mean number of individuals within visual range, and proximity ratio entered into the principal component analysis

<table>
<thead>
<tr>
<th>Name</th>
<th>VER with males</th>
<th>VER with females</th>
<th>Number of individuals within visual range with males</th>
<th>Number of individuals within visual range with females</th>
<th>Proximity ratio with males</th>
<th>Proximity ratio with females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kl</td>
<td>0.9</td>
<td>0.86</td>
<td>2.51</td>
<td>3.54</td>
<td>0.69</td>
<td>0.29</td>
</tr>
<tr>
<td>Th</td>
<td>0.71</td>
<td>0.24</td>
<td>2.06</td>
<td>0.75</td>
<td>0.62</td>
<td>0</td>
</tr>
<tr>
<td>Ng</td>
<td>0.72</td>
<td>0.61</td>
<td>2.31</td>
<td>2.27</td>
<td>0.62</td>
<td>0.02</td>
</tr>
<tr>
<td>Rc</td>
<td>0.87</td>
<td>0.84</td>
<td>2.2</td>
<td>3.12</td>
<td>0.65</td>
<td>0.3</td>
</tr>
<tr>
<td>Pp</td>
<td>0.89</td>
<td>0.93</td>
<td>2.5</td>
<td>3.54</td>
<td>0.74</td>
<td>0.22</td>
</tr>
<tr>
<td>Ha</td>
<td>0.91</td>
<td>0.97</td>
<td>2.07</td>
<td>4</td>
<td>0.29</td>
<td>0.22</td>
</tr>
<tr>
<td>Bl</td>
<td>0.65</td>
<td>0.33</td>
<td>1.74</td>
<td>0.92</td>
<td>0.67</td>
<td>0</td>
</tr>
<tr>
<td>Mk</td>
<td>0.78</td>
<td>0.28</td>
<td>2.17</td>
<td>0.81</td>
<td>0.54</td>
<td>0</td>
</tr>
<tr>
<td>Rb</td>
<td>0.76</td>
<td>0.38</td>
<td>1.92</td>
<td>1.45</td>
<td>0.65</td>
<td>0</td>
</tr>
<tr>
<td>Mc</td>
<td>0.78</td>
<td>0.5</td>
<td>2.15</td>
<td>1.73</td>
<td>0.58</td>
<td>0</td>
</tr>
<tr>
<td>Co*</td>
<td>0.27</td>
<td>0.12</td>
<td>0.33</td>
<td>0.35</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tv*</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*: Co and Tv were excluded from principal component analysis due to their short observation time.
Table 2-3 Components, factor loadings, eigenvalues, and cumulative contributions in principal component analysis run on six variables

<table>
<thead>
<tr>
<th>Variables</th>
<th>Component 1</th>
<th>Component 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. VER with males</td>
<td>-0.94</td>
<td>0.07</td>
</tr>
<tr>
<td>2. VER with females</td>
<td>-0.97</td>
<td>0.1</td>
</tr>
<tr>
<td>3. Number of males within visual range</td>
<td>-0.74</td>
<td>-0.4</td>
</tr>
<tr>
<td>4. Number of females within visual range</td>
<td>-0.97</td>
<td>0.13</td>
</tr>
<tr>
<td>5. Proximity ratio with males</td>
<td>0.09</td>
<td>-0.97</td>
</tr>
<tr>
<td>6. Proximity ratio with females</td>
<td>-0.94</td>
<td>-0.1</td>
</tr>
<tr>
<td>Eigenvalue</td>
<td>4.19</td>
<td>1.13</td>
</tr>
<tr>
<td>Cumulative contribution</td>
<td>0.7</td>
<td>0.89</td>
</tr>
</tbody>
</table>

VER: visual encounter ratio
High loadings (absolute value > 0.5) are underlined.
Table 2-4 Mean ± SD of daily visual encounter ratio (VER), VER and mean number of males within visual range in the absence of females, proximity ratio, and grooming frequency at individual level

<table>
<thead>
<tr>
<th>Name</th>
<th>Daily VER* with males</th>
<th>Daily VER* with females</th>
<th>Absence of females VER only with males</th>
<th>Absence of females No. males</th>
<th>Proximity ratio with males</th>
<th>Proximity ratio with females</th>
<th>Grooming frequency with males</th>
<th>Grooming frequency with females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cluster 1</td>
<td><strong>Ha</strong></td>
<td>0.91 ± 0.04 (0/11)</td>
<td>0.97 ± 0.01 (0/11)</td>
<td>0.005</td>
<td>0.4 ± 0.9</td>
<td>0.29</td>
<td>0.218</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td><strong>Pp</strong></td>
<td>0.89 ± 0.07 (0/12)</td>
<td>0.93 ± 0.08 (0/12)</td>
<td>0.003</td>
<td>0.1 ± 0.7</td>
<td>0.74</td>
<td>0.223</td>
<td>11.9</td>
</tr>
<tr>
<td></td>
<td><strong>Kl</strong></td>
<td>0.91 ± 0.10 (0/18)</td>
<td>0.86 ± 0.08 (0/18)</td>
<td>0.072</td>
<td>1.7 ± 1.9</td>
<td>0.69</td>
<td>0.294</td>
<td>14.4</td>
</tr>
<tr>
<td></td>
<td><strong>Rc</strong></td>
<td>0.87 ± 0.03 (0/13)</td>
<td>0.84 ± 0.03 (0/13)</td>
<td>0.070</td>
<td>1.1 ± 1.5</td>
<td>0.65</td>
<td>0.298</td>
<td>12.2</td>
</tr>
<tr>
<td>Mean</td>
<td>0.89 ± 0.07 (0/54)</td>
<td>0.90 ± 0.08 (0/54)</td>
<td>0.042</td>
<td>1.1 ± 1.6</td>
<td>0.59</td>
<td>0.261</td>
<td>9.8</td>
<td>18.8</td>
</tr>
<tr>
<td>Cluster 2</td>
<td><strong>Ng</strong></td>
<td>0.72 ± 0.05 (0/15)</td>
<td>0.61 ± 0.40 (0/15)</td>
<td>0.274</td>
<td>2.3 ± 2.0</td>
<td>0.52</td>
<td>0.023</td>
<td>21.9</td>
</tr>
<tr>
<td></td>
<td><strong>Mc</strong></td>
<td>0.78 ± 0.04 (0/7)</td>
<td>0.48 ± 0.22 (0/7)</td>
<td>0.392</td>
<td>2.3 ± 1.7</td>
<td>0.58</td>
<td>0.003</td>
<td>9.3</td>
</tr>
<tr>
<td></td>
<td><strong>Rb</strong></td>
<td>0.76 ± 0.04 (0/8)</td>
<td>0.36 ± 0.36 (2/8)</td>
<td>0.461</td>
<td>1.9 ± 1.7</td>
<td>0.65</td>
<td>0</td>
<td>20.6</td>
</tr>
<tr>
<td></td>
<td><strong>Bl</strong></td>
<td>0.65 ± 0.07 (0/10)</td>
<td>0.36 ± 0.38 (2/10)</td>
<td>0.438</td>
<td>1.7 ± 1.8</td>
<td>0.67</td>
<td>0</td>
<td>17.4</td>
</tr>
<tr>
<td></td>
<td><strong>Mk</strong></td>
<td>0.78 ± 0.04 (0/9)</td>
<td>0.31 ± 0.31 (1/9)</td>
<td>0.559</td>
<td>2.2 ± 1.9</td>
<td>0.54</td>
<td>0.003</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td><strong>Th</strong></td>
<td>0.71 ± 0.06 (0/16)</td>
<td>0.24 ± 0.29 (6/16)</td>
<td>0.538</td>
<td>2.0 ± 1.8</td>
<td>0.62</td>
<td>0.004</td>
<td>21.5</td>
</tr>
<tr>
<td>Mean</td>
<td>0.73 ± 0.07 (0/65)</td>
<td>0.39 ± 0.35 (11/65)</td>
<td>0.430</td>
<td>2.1 ± 1.8</td>
<td>0.59</td>
<td>0.006</td>
<td>17.8</td>
<td>0</td>
</tr>
</tbody>
</table>

* The numbers in the first half of the parentheses show the number of days in which the focal animal did not visually encounter with any other males (or females). The numbers in the latter half of the parentheses show the number of observation days.
**Table 2-5 Matrix of dyadic proximity ratios among focal males and adult females in the subject troop**

<table>
<thead>
<tr>
<th></th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Exception*</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ha</td>
<td>Pp</td>
<td>Kl</td>
<td>Rc</td>
</tr>
<tr>
<td>Cluster 1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ha</td>
<td>-</td>
<td>0.0032</td>
<td>0.0232</td>
<td>0.0067</td>
</tr>
<tr>
<td>Pp</td>
<td>-</td>
<td>0.0336</td>
<td>0.0325</td>
<td>0.0073</td>
</tr>
<tr>
<td>Kl</td>
<td>-</td>
<td>0.0333</td>
<td>0.0016</td>
<td>0.0075</td>
</tr>
<tr>
<td>Rc</td>
<td>-</td>
<td>0.0124</td>
<td>0.0031</td>
<td>0.0025</td>
</tr>
<tr>
<td>Cluster 2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ng</td>
<td>-</td>
<td>0.0069</td>
<td>0.0051</td>
<td>0.0118</td>
</tr>
<tr>
<td>Mc</td>
<td>-</td>
<td>0.0165</td>
<td>0.0048</td>
<td>0.0196</td>
</tr>
<tr>
<td>Rb</td>
<td>-</td>
<td>0.0013</td>
<td>0.0059</td>
<td>0.0145</td>
</tr>
<tr>
<td>Bl</td>
<td>-</td>
<td>0.0098</td>
<td>0.0006</td>
<td>0.0026</td>
</tr>
<tr>
<td>Exception*</td>
<td>Co*</td>
<td>-</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Tv*</td>
<td>-</td>
<td>0</td>
<td></td>
</tr>
</tbody>
</table>

*: two focal males (Co and Tv) were not classified into clusters because they were excluded from principal component analysis.
Table 2-6 Matrix of dyadic grooming frequencies among focal males and adult females in the subject troop

<table>
<thead>
<tr>
<th>Groomee</th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Exception*</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ha</td>
<td>Pp</td>
<td>Kl</td>
<td>Re</td>
</tr>
<tr>
<td>Groomer</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cluster 1</td>
<td>-</td>
<td>1.2</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>1.8</td>
<td>-</td>
<td>6.3</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>7.7</td>
<td>-</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>2.3</td>
<td>1.8</td>
<td>-</td>
</tr>
<tr>
<td>Cluster 2</td>
<td>0.0</td>
<td>7.6</td>
<td>11.6</td>
<td>10.1</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>0.0</td>
<td>3.6</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>3.2</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>0.0</td>
<td>1.6</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>1.6</td>
<td>9.7</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>4.8</td>
<td>9.6</td>
<td>0.0</td>
</tr>
<tr>
<td>Exception*</td>
<td>Co*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ty*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>Tu</td>
<td>0.0</td>
<td>10.3</td>
<td>9.4</td>
</tr>
<tr>
<td></td>
<td>Kr</td>
<td>0.0</td>
<td>7.9</td>
<td>7.6</td>
</tr>
<tr>
<td></td>
<td>Um</td>
<td>7.3</td>
<td>0.0</td>
<td>7.3</td>
</tr>
<tr>
<td></td>
<td>Sk</td>
<td>9.3</td>
<td>6.1</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>AR</td>
<td>0.0</td>
<td>0.0</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>NN</td>
<td>0.0</td>
<td>13.3</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>YM</td>
<td>0.9</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

*: two focal males (Co and Ty) were not classified into clusters because they were excluded from principal component analysis.
Blank cells indicate that proximity was not observed in the dyad, and cells with 0.0 indicate that grooming was not observed even though proximity was observed in the dyad. Coloured cells indicate female–female grooming. Values for female–female proximity and grooming was lacking in this study because of no focal data on females.
Table 3-1 Dataset of visual encounter ratio (VER), mean number of individuals within visual range, and proximity ratio in the non-mating season 209 entered into the principal component analysis

<table>
<thead>
<tr>
<th>Name</th>
<th>VER</th>
<th>Number of individuals within visual range</th>
<th>Proximity ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>with males</td>
<td>with females</td>
<td>with males</td>
</tr>
<tr>
<td>Kl</td>
<td>0.90</td>
<td>0.86</td>
<td>2.54</td>
</tr>
<tr>
<td>Ha</td>
<td>0.91</td>
<td>0.98</td>
<td>2.07</td>
</tr>
<tr>
<td>Rc</td>
<td>0.89</td>
<td>0.85</td>
<td>2.25</td>
</tr>
<tr>
<td>Th</td>
<td>0.71</td>
<td>0.13</td>
<td>2.07</td>
</tr>
<tr>
<td>Mc</td>
<td>0.76</td>
<td>0.17</td>
<td>2.13</td>
</tr>
<tr>
<td>Rb</td>
<td>0.76</td>
<td>0.18</td>
<td>1.94</td>
</tr>
<tr>
<td>Ga</td>
<td>0.54</td>
<td>0.10</td>
<td>1.37</td>
</tr>
</tbody>
</table>
Table 3-2 Names, age classes, number of observation days (N), and observation time in each focal male

<table>
<thead>
<tr>
<th>Name</th>
<th>Age class*</th>
<th>Non-mating season</th>
<th>Mating season</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>N</td>
<td>Observation time (h: min)</td>
</tr>
<tr>
<td>Troop males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kl</td>
<td>FA</td>
<td>8</td>
<td>57:20</td>
</tr>
<tr>
<td>Ha</td>
<td>FA</td>
<td>8</td>
<td>52:55</td>
</tr>
<tr>
<td>Rc</td>
<td>FA</td>
<td>8</td>
<td>51:20</td>
</tr>
<tr>
<td>Non-troop males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Th</td>
<td>A</td>
<td>8</td>
<td>65:45</td>
</tr>
<tr>
<td>Mc</td>
<td>YA</td>
<td>8</td>
<td>50:55</td>
</tr>
<tr>
<td>Rb</td>
<td>A</td>
<td>7</td>
<td>37:40</td>
</tr>
<tr>
<td>Ga</td>
<td>FA</td>
<td>7</td>
<td>37:20</td>
</tr>
</tbody>
</table>

*: FA: full adult males who were estimated more than 13 years old and 10–13 kg; A: adult males who were estimated 10–12 years old and 7–10 kg; YA: young adult males who were estimated 7–9 years old and 5–7 kg.
Table 3-3 Matrix of grooming indices in two seasons (non-mating season / mating season) among focal males

<table>
<thead>
<tr>
<th>Groomee</th>
<th>Groomer Troop males</th>
<th>Groomer Non-troop males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kl</td>
<td>0.60 / 0.037</td>
<td>2.29 / 0.122</td>
</tr>
<tr>
<td>Ha</td>
<td>0.35 / 0.013</td>
<td>5.6 / 0.148</td>
</tr>
<tr>
<td>Rc</td>
<td>1.41 / 0.061</td>
<td>2.32 / 0.172</td>
</tr>
<tr>
<td>Th</td>
<td>0 / 0</td>
<td>0 / 0</td>
</tr>
<tr>
<td>Ga</td>
<td>0.55 / 0</td>
<td>1.22 / 0.133</td>
</tr>
<tr>
<td>Rb</td>
<td>0.68 / 0</td>
<td>0.62 / 0.154</td>
</tr>
<tr>
<td>Mc</td>
<td>0.037</td>
<td>0.57 / 0.032</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Groomee</th>
<th>Groomer Troop males</th>
<th>Groomer Non-troop males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kl</td>
<td>-</td>
<td>2.21 / 0.225</td>
</tr>
<tr>
<td>Ha</td>
<td>0.93 / 0.200</td>
<td>0.64 / 0</td>
</tr>
<tr>
<td>Rc</td>
<td>1.29 / 0.103</td>
<td>1.36 / 0.117</td>
</tr>
<tr>
<td>Th</td>
<td>-</td>
<td>1.75 / 0.208</td>
</tr>
<tr>
<td>Ga</td>
<td>0.81 / 0</td>
<td>1.33 / 0.426</td>
</tr>
<tr>
<td>Rb</td>
<td>0</td>
<td>1.02 / 0.362</td>
</tr>
<tr>
<td>Mc</td>
<td>0.047</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3-4 Matrix of aggression indices in two seasons (non-mating season / mating season) among focal males and dominance rank in the mating season

<table>
<thead>
<tr>
<th>Rank*</th>
<th>Aggressor</th>
<th>Troop males</th>
<th>KI</th>
<th>Ha</th>
<th>Re</th>
<th>Th</th>
<th>Ga</th>
<th>Rb</th>
<th>Mc</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Troop males</td>
<td>(1) KI</td>
<td>-</td>
<td>0.022 / 0.075</td>
<td>0 / 0.039</td>
<td>0 / 0.041</td>
<td>0 / 2.769</td>
<td>0 / 0.345</td>
<td>0 / 0.250</td>
</tr>
<tr>
<td></td>
<td>Troop males</td>
<td>(2) Ha</td>
<td>0 / 0.009</td>
<td>-</td>
<td>0 / 0.05</td>
<td>0 / 0</td>
<td>1.000 / 0.462</td>
<td>0 / 3.500</td>
<td>0 / 1.000</td>
</tr>
<tr>
<td></td>
<td>Troop males</td>
<td>(3) Re</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>-</td>
<td>0 / 0.069</td>
<td>0 / 1.500</td>
<td>0 / 0.308</td>
<td>0.167 / 0.750</td>
</tr>
<tr>
<td>Non-troop males</td>
<td>(4) Th</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>-</td>
<td>0 / 1.333</td>
<td>0 / 0.033</td>
<td>0 / 0.026</td>
<td></td>
</tr>
<tr>
<td>Non-troop males</td>
<td>(5) Ga</td>
<td>0 / 0.615</td>
<td>0 / 0.769</td>
<td>0 / 0.75</td>
<td>0 / 0.5</td>
<td>-</td>
<td>0 / 0.25</td>
<td>0 / 0</td>
<td></td>
</tr>
<tr>
<td>Non-troop males</td>
<td>(6) Rb</td>
<td>0 / 0.207</td>
<td>0 / 1</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0.05 / 0.083</td>
<td>-</td>
<td>0 / 0</td>
<td></td>
</tr>
<tr>
<td>Non-troop males</td>
<td>(7) Mc</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>0 / 0</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

*: Numbers in the parentheses indicate the dominance rank in the mating season.
**Table 3-5** Observed and expected frequencies of aggression in each activity

<table>
<thead>
<tr>
<th></th>
<th>Feeding</th>
<th>Moving</th>
<th>Resting</th>
<th>Mating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-mating season</td>
<td>6</td>
<td>0</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(3.2)</td>
<td>(2.0)</td>
<td>(2.9)</td>
<td></td>
</tr>
<tr>
<td>Mating season</td>
<td>17</td>
<td>19</td>
<td>84</td>
<td>77</td>
</tr>
<tr>
<td></td>
<td>(65.6)</td>
<td>(82.1)</td>
<td>(16.4)</td>
<td>(32.9)</td>
</tr>
</tbody>
</table>

Values in the parentheses indicate the expected values in each activity.
### Table 3-6 Matrix of coalition indices among focal males in the mating season

<table>
<thead>
<tr>
<th>Rank*</th>
<th>Supported</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kl</td>
</tr>
<tr>
<td>Troop males</td>
<td></td>
</tr>
<tr>
<td>(1) Kl</td>
<td>-</td>
</tr>
<tr>
<td>(2) Ha</td>
<td>0</td>
</tr>
<tr>
<td>(3) Rc</td>
<td>0</td>
</tr>
<tr>
<td>Non-troop males</td>
<td></td>
</tr>
<tr>
<td>(4) Th</td>
<td>0.0051</td>
</tr>
<tr>
<td>(5) Ga</td>
<td>0</td>
</tr>
<tr>
<td>(6) Rb</td>
<td>0.0051</td>
</tr>
<tr>
<td>(7) Mc</td>
<td>0</td>
</tr>
</tbody>
</table>

*: Numbers in the parentheses indicate the dominance rank in the mating season.
Table 3-7 Distribution of coalitions according to patterns of coalition, initial aggression dyad, supporter, being supported male, common target, and the number of each instance

<table>
<thead>
<tr>
<th>Patterns of coalition</th>
<th>Initial aggression</th>
<th>Coalition formation</th>
<th>Target</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Supporter</td>
<td>Being supported</td>
<td></td>
</tr>
<tr>
<td>All-down coalition</td>
<td>Troop male vs. Non-troop male</td>
<td>Troop male</td>
<td>Troop male</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-troop male</td>
<td>Non-troop male</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Non-troop male vs. Non-troop male</td>
<td>Troop male</td>
<td>Non-troop male</td>
<td>2</td>
</tr>
<tr>
<td>Bridging coalition</td>
<td>Troop male vs. Non-troop male</td>
<td>Troop male</td>
<td>Non-troop male</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Non-troop male vs. Non-troop male</td>
<td>Non-troop male</td>
<td>Non-troop male</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Non-troop male</td>
<td>Non-troop male</td>
<td>4 (2)</td>
</tr>
</tbody>
</table>

Number in the parentheses indicates the internal number of looser support coalitions.
Fig. 2-1 Principal component analysis (PCA) of focal males runs on six variables. See Table 2-3 for explanations of variables and loadings.
Fig. 2-2 Dyadic proximity ratios and results of multiple comparisons according to groups based on the combination of male attributes. P values were adjusted using the Holm’s method.*: P < 0.05.
**Fig. 2-3** Dyadic grooming frequencies per duration of proximity and results of multiple comparisons according to groups based on the combination of male attributes. P values were adjusted using the Holm’s method. *: P < 0.05.
Fig. 2-4 Comparison of the direction in grooming frequencies between C1 males and C2 males. *: P < 0.05.
Fig. 3-1 Principal component analysis of focal males for the classification of troop males and non-troop males run on six valuable in the non-mating season. See Table 2-1 for the data set of these six valuables.
Fig. 3-2 Seasonal difference of dyadic interaction of (a) grooming rates and (b) aggression rates between non-mating season (NMS) and mating season (MS).
Fig. 3-3 Number of coalitionary supports every three patterns according to dominance hierarchy. See methods for detail explanation of coalition patterns.
**Fig. 3-4** Results of partial tau $\tau_r$ test in grooming, aggression, and coalition in two seasons. (a) Results of grooming given in the non-mating (NMS), grooming given in the mating season (MS), and aggression received in MS. (b) Results of grooming given in NMS, grooming given in MS, and coalition received in MS. Solid lines indicate significant correlation, and dotted lines indicate non-significant correlation.