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ORIGINAL ARTICLE

Spatial position-associated mating strategies employed by male Japanese macaques (*Macaca fuscata yakui*) in Yakushima

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Abstract

In bisexual groups, dominant males occupy the central part of the group, which is advantageous because it is reproductively beneficial. However, high-ranking males do not necessarily monopolize reproductive success, which indicates that low-ranking males increase their reproductive success through alternative mating strategies. To reveal the effectiveness and cost of these strategies employed by group males, it is necessary to clarify the spatial configuration of males and their group, and show how males combine strategies in different situations. This study demonstrates the spatial configuration of male Japanese macaques (*Macaca fuscata yakui*) and their group when males adopt three mating strategies: mate guarding, sneak mating, and cross-boundary mating (mating with females of another group). High-ranking males tended to perform mate guarding, but they also mated with females in other groups when there were few sexually active females in their group. Low-ranking males performed sneak mating; they remained in the central part of the group to monitor sexually active females and moved toward the periphery for copulation but never completely left the group. In addition, males individually ventured outside the group's ranging area and succeeded in mating with females of other groups. The cross-boundary mating strategy has the advantage of increasing the number of potential mating partners, which is not present in the other two strategies. However, because of considerable costs and low contribution to mating frequency, this strategy is complementary and is employed when the expectation of mating success in their group is low.

Keywords Dominance hierarchy · Reproductive strategy · Seasonal variation · Social structure · Solitary

Introduction

Group-living primates compete for favorable spatial positions within their group (Janson 1990a), with dominant members occupying the advantageous central part and subordinates occurring at the periphery (Janson 1990b). With respect to reproduction, the basic strategy among males in bisexual groups is to remain close to females, thereby increasing mating chances (Berenstain and Wade 1983; Boyd et al. 2000). However, as not all males can occupy a favorable space to gain exclusive access to females in the group, some males may adopt alternative strategies (Ellis 1995).

One such strategy is sneak mating, whereby males hide from other males in order to mate with females of their group (Soltis 1999). This strategy is effective for low-ranking males to prevent monopolization of estrous females by high-ranking males. For example, Soltis (1999) and Hayakawa (2007) reported that low-ranking wild Japanese macaque males did not copulate within sight of other group members. However, those studies were based only on whether other members were in visual range, and the spatial configuration, or distance between individuals, was not quantified. Spatial configuration has substantial implications for elucidating the cost of sneak mating, because if individuals had to travel a long distance to hide from other group members, it would take a considerable amount of time to conduct sneak mating and catch up with their group after copulation; consequently, sneak mating could incur considerable travel costs.

Another alternative strategy would be for the males to leave their group temporarily to copulate with females of

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another group. This strategy was inferred from reports that group females also mate with males from outside the group (Ohsawa et al. 1993; Zhao et al. 2005); the sources of these males include other bisexual groups in addition to all-male groups and solitary males (Cords and Rowell 1986; Zhao et al. 2005). For group males, this strategy is worth noting, as it increases the number of potential mating partners to greater than the number of females in their group. Previous studies have speculated that Japanese macaques also adopt this strategy. Despite their group being generally cohesive (Sugiura et al. 2011), a considerable number of males were observed ranging individually (Otani et al. 2013). During mating season, researchers reported that males from outside the observed group succeeded in copulating with group females (Yamagiwa 1985; Okayasu 2001; Hayakawa 2008), and it was determined that these males included males from other bisexual groups (Fukuda 1989; Sprague 1991). These studies demonstrate that group males temporarily visit other groups for mating. However, the entire act of a male leaving a resident group and visiting a different group has never been documented. Therefore, the details of this strategy have remained unspecified, including its cost, the contribution to mating success, and the association with male social position.

As noted above, previous studies have shown three types of mating strategies for group males. However, although the spatial configuration of males and their group is clearly an important factor in these strategies, it remains unclear how males choose the spatial position in order to implement these strategies. For example, in the implementation of sneak mating, it has not been clarified whether males stay at the periphery and wait for a chance to mate, or move from the center of the population to the periphery only when copulating. Additionally, knowledge regarding the degree of separation of males from their group in order to carry out mating with females in another group is needed to assess the efficiency and cost of this strategy. Thus, to reveal the effectiveness and cost of each strategy employed by group males, the spatial configuration of males and their group during mating season should be clarified, and the details of sneak mating strategies and mating behavior in other groups need to be documented. Because researchers in many previous studies followed one individual at a time, it was difficult to quantify the relative distances between multiple individuals. In this study, the spatial configuration of males and their group is quantitatively clarified by parallel tracking of two individuals to reveal the effectiveness and cost of mating strategies employed by group males. In addition, we aimed to clarify how males choose which of the three mating strategies to employ, in order to show how they combine strategies in different situations.

Because our study subject, Japanese macaques, are strictly seasonal breeders, and mature individuals are not subject to predation (Takahata et al. 1998), the effect of reproduction on spatial arrangement could be confirmed. Furthermore, direct tracking of individuals moving among multiple groups was feasible in our study site, which was the western coastal area of Yakushima Island, because multiple neighboring groups were well habituated (Yamagiwa 2008), and the home range of each group was relatively small (Hanya et al. 2006). Therefore, the subjects were ideal for studying mating strategies associated with spatial positions.

Methods

Study site, subjects, and period

Our study subjects were from a group called AT that inhabits the western coastal area of Yakushima. We directly tracked males and females in parallel during two periods: from 9 September to 23 November 2009, and from 19 March to 10 June 2010. In addition, we tracked only females from 24 November 2009 to 24 January 2010 and males from 21 October to 10 November 2010. The periods from September 2009 to January 2010 and from October to November 2010 corresponded to the mating seasons (hereafter, mating seasons I and II, respectively), and the period from March to June 2010 corresponded to the non-mating season.

The group included eight, seven, and seven mature males during mating season I, mating season II, and the non-mating season, respectively, and nine mature females throughout the three periods. Our study subjects included seven, five, and six mature males during mating season I, mating season II, and the non-mating season, respectively, and the nine mature females throughout the three periods. According to the criteria of previous studies (Suzuki et al. 1998; Soltis 1999; Okayasu 2001), all subject males were confirmed to be group male by the following criteria: were included in this group as of at least 2008; included in the group during the non-mating season of our study period; and their grooming with group females was observed. One mature male emigrated to another group between mating season I (autumn 2009) and the non-mating season (spring 2010). Throughout the three periods, we excluded one male (ranked 8th), as he had only joined the group during mating season I. During mating season II, another male was excluded, as he was absent from the group most of the time. Based on agonistic interactions, the subject males were ranked from 1st to 7th, 1st to 2nd and 4th to 6th, and 1st to 6th during mating seasons I and II and the non-mating season, respectively (Table 1). All males had immigrated from other groups. Males were divided into high-ranking (1–3rd) and low-ranking males (4th–7th) to analyze the effect of male rank on separate ranging, presence rate (PR), and copulation frequency.

Table 1 Rank and estimated age of subject males

Mating season I		Non-mating season		Mating season II	
September 2009–January 2010		March–June 2010		October–November 2010	
Rank	Estimated age	Rank	Estimated age	Rank	Estimated age
1st	Over 13 years old	1st	Over 13 years old	1st	Over 13 years old
2nd	Over 13 years old	2nd	Over 13 years old	2nd	Over 13 years old
3rd	Over 10 years old	3rd	Over 10 years old	*3rd*	*Not subject*
4th	Over 10 years old	4th	Over 10 years old	4th	Over 10 years old
5th	Over 10 years old	5th	Over 10 years old	5th	Over 10 years old
6th	Over 7 years old	6th	Over 7 years old	6th	Over 7 years old
7th	Over 10 years old	*7th*	*Emigrated*	*7th*	*Emigrated*
8th	*Not subject*	*8th*	*Not subject*	*8th*	*Not subject*

Presence rate

By collecting PR, which is the percentage of mature animals in the vicinity of the focal animal, we measured the aggregation of animals based on visual observation. Two researchers independently recorded all other mature individuals that were visually detected throughout each hour of the day (e.g., 6:00 AM–6:59 AM). The male- and female-following researchers recorded data for 63 and 77 days, respectively, during mating seasons I and II and the non-mating season. We defined PR as the percentage of individuals that were visible to the researcher following a focal animal for each 1-h period. For example, if nine of 15 individuals in the group were observed in the vicinity of a focal male, the PR of mature individuals from the focal male during that hour would be 60%. In this manner, we calculated the PRs of mature individuals from the focal male, females from the focal male, males from focal females, and females from focal females. These calculations were used to determine whether males and females were aggregating.

Male–female distance

We quantitatively calculated the relative distance between males and females. The absence of particular individuals from the sight of the focal individual did not indicate how far they were, because the visibility in the current study site was restricted to approximately 20 m (Koda et al. 2008). The distance of males from their group was needed to clarify the mating strategy used and the associated costs.

To measure the relative distance of males and females, we conducted parallel tracking during two periods: 16 days during mating season I and 35 days during the non-mating season. Two researchers simultaneously tracked one male and one female (99 h and 263 h during mating season I and the non-mating season, respectively) using GPS devices (Garmin 60CSx) to record their locations every 30 s. During the parallel tracking, we switched from one female to another every 3 h, whereas the same male was tracked throughout the day. We refer to the tracking of a particular male and female pair during the day as a bout. Each male was tracked for 2.4 days (± 0.49 SD) and 5.8 days (± 0.37 SD) on average during mating season I and the non-mating season, respectively. The spatial position of males and a group was approximated by measuring the relative distance of the focal female's position, which was considered the central part of the group (Otani et al. 2014). In addition, we determined whether males ranged with their group by setting an operational definition (see "Analysis" below).

To avoid bias caused by focusing on a particular combination of males and females, we selected the focal animals in advance to ensure equal sample sizes among individuals. We also recorded each location where focal group members exhibited some response to the presence of another group as a site of an intergroup encounter (Saito et al. 1998).

Mating behavior within and outside the group

The number of sexually active females observed was recorded daily. We judged sexual activeness of females based on copulation and male sexual behaviors, such as sexual attack, hindquarter displays, and hand-on-back behaviors (Takahata 1980). A copulation bout was defined as a male/female mounting series accompanied by ejaculation. The number of copulation bouts of focal males was recorded. In addition, we calculated the male–female distance at the onset of a copulation event between the focal male and a non-focal female of the group, and compared this information with other distance data.

A visit of one male to another group was assumed to have occurred when at least one individual from another group was observed and the distance from the focal female exceeded the criteria of separate ranging (see "Analysis" below). Mating with females of other groups was defined as a copulation bout during the focal males' visitation to another group.

Analysis

Based on male–female distance, we standardized a definition to compare separate ranging among the multiple periods. Following Otani et al. (2014), we operationally defined separation from the group as a distance of > 100 m between the focal male and female for more than 10 min. To calculate the duration of separation bouts, we discarded instances where the observers required > 20 min to change focal females. If changing focal females required < 20 min and the distance between the focal male and female remained > 100 m, we considered separate ranging to have continued throughout the period.

To distinguish the spatial positions of males within their group (the central part and periphery), we divided male–female distance data into 5-m classes and calculated the percentages of each class for data points < 100 m. Because the visibility in the current study site was restricted to approximately 20 m (Koda et al. 2008) and cohesiveness among females in the group was strong (Otani et al. 2014), we considered a male to have remained in the central part of the group when the male–female distance was < 20 m. For this analysis, we applied the hours when more than half of the other eight group females were in the vicinity of the focal female (PR of females from the focal female > 0.5) to ensure that focal females were in the central part of the group.

Using the kernel method (Worton 1989) with Hawth's tool in ArcGIS 9.3 (ESRI, Inc.), we estimated the ranging area (95%) of the females and males who ranged separately from their group. We set 10 m as the raster size and 50 m as the smoothing factor.

We built a general linear model (Mundry and Nunn 2009) that included study periods (non-mating season and mating season I) as a predictor variable and the duration of each separate ranging bout as a response variable. We examined the effect of study period on separate ranging duration by conducting a likelihood ratio test between the models with and without the study period. We log-transformed the duration of separate ranging to achieve an approximation of normality. For other analyses, we used nonparametric statistical tests (Wilcoxon signed-rank test, Mann–Whitney *U* test, χ^2 test, and Steel–Dwass test) combined with the Bonferroni adjustment for multiple comparisons (Rice 1989) to examine associations among variables. All models and tests were conducted using R 2.13 (R Development Core Team 2012). We used the LM function to construct the general linear model.

Results

Separate ranging definition validation

The distance between males and females sometimes exceeded several hundreds of meters during mating season I and the non-mating season (Fig. 1). The median and maximum distances between focal males and females during

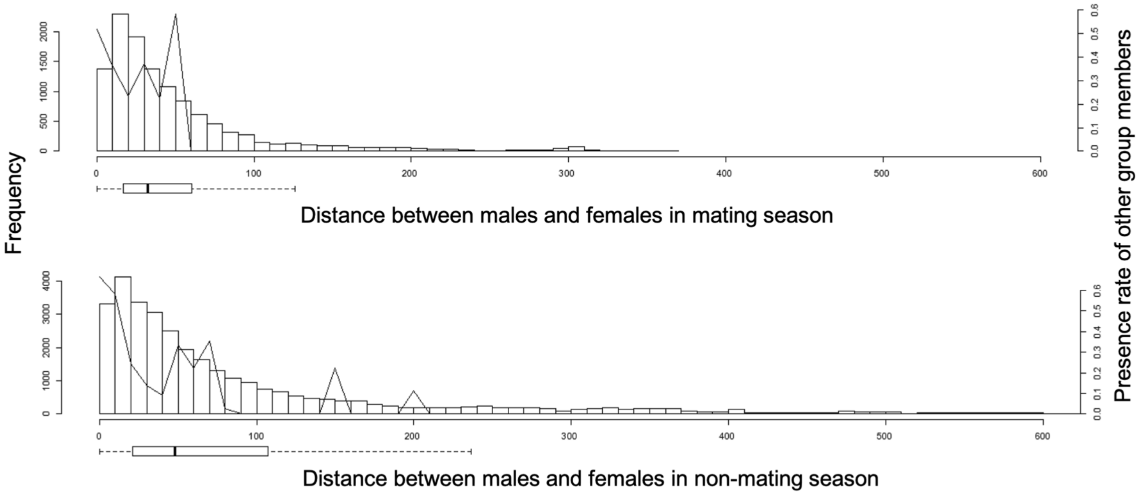

Fig. 1 Histograms of distance between focal animals. The upper and lower histograms indicate distances between focal males and females during mating season I and the non-mating season, respectively. Distances were calculated every 30 s. Samples that exceeded 600 m were omitted from the graphs because they were outliers. The boxplots under the histograms indicate the degree of dispersion of the distances. The left side, band, and right side of the box indicate the lower quartile (Q1), median (Q2), and upper quartile (Q3) of the distances, respectively. The left and right ends of the whiskers indicate the lowest and highest distances within 1.5 × of the ranges of the lower and upper quartiles, respectively. The line plot indicates variations in the mean presence rate of mature individuals in the vicinity of focal males

mating season I and the non-mating season were 32.4 m and 48.0 m, and 365 m and 632 m, respectively.

When the minimum male–female distance for 1 h exceeded 100 m, the PR of mature individuals from focal males was greater than zero in only two cases ($n = 12$, Fig. 1). In these two cases, two and four individuals appeared near the focal male that hour. These findings indicate that when distance exceeded 100 m, the male separated from most of the group members (separate ranging).

Spatial position of males within their group

Differences in spatial positions of males within the group based on the social position were observed only in the non-mating season. When males ranged with their group (male–female distance < 100 m), the percentage of male–female distance < 20 m was higher in high-ranking males than in low-ranking males only during the non-mating season (χ^2 test, mating season I, $\chi^2 = 2.18$, $P = 0.139$; non-mating season, $\chi^2 = 690.62$, $P < 0.0001$, Fig. 2). PR data showed a similar trend. When males ranged with their group, the PR of females from the focal male was lower for low-ranking males (mean ± SD, 36.3 ± 34.8%) than high-ranking males (55.4 ± 34.6%) during the non-mating season (Steel–Dwass, $P < 0.05$), whereas no difference was observed between high- and low-ranking males during mating seasons I (high-ranking, 48.9 ± 27.5%; low-ranking, 46.3 ± 27.0%; Steel–Dwass, $P > 0.1$) and II (high-ranking, 76.3 ± 20.7%; low-ranking, 59.1 ± 27.5%; Steel–Dwass, $P > 0.1$).

Spatial position of males relative to their group

The duration of time spent within the group differed among differently ranked males. Over the entire observation time, the PR of males from the focal female was greater in high- than low-ranking males during both mating season I (high-ranking, 47.0 ± 31.4%; low-ranking, 18.8 ± 25.3%; Steel–Dwass, $t = 10.4$, $P < 0.001$) and the non-mating season (high-ranking, 49.5 ± 30.2%; low-ranking, 16.8 ± 23.8%; Steel–Dwass, $t = 12.6$, $P < 0.001$, Fig. 3).

Males ranged separately from their group for a shorter time during mating season I compared with the non-mating season. The duration of a separate ranging bout was longer during the non-mating season than mating season I (GLM, $P < 0.05$, Tables 2, 3). The percentage of time spent in separate ranging relative to observation time was higher during the non-mating season than the mating season I (χ]] ><![CDATA[^{2} test, $P < 0.01$, Table 2).

Low-ranking males ranged separately more often than high-ranking males during all seasons. The percentage of time spent in separate ranging relative to observation time each day was greater for low- than high-ranking males during both mating season I and the non-mating season (Steel–Dwass test, $t = 2.78$, 2.52, respectively, $P < 0.05$, Fig. 4). The percentages of time spent in separate ranging

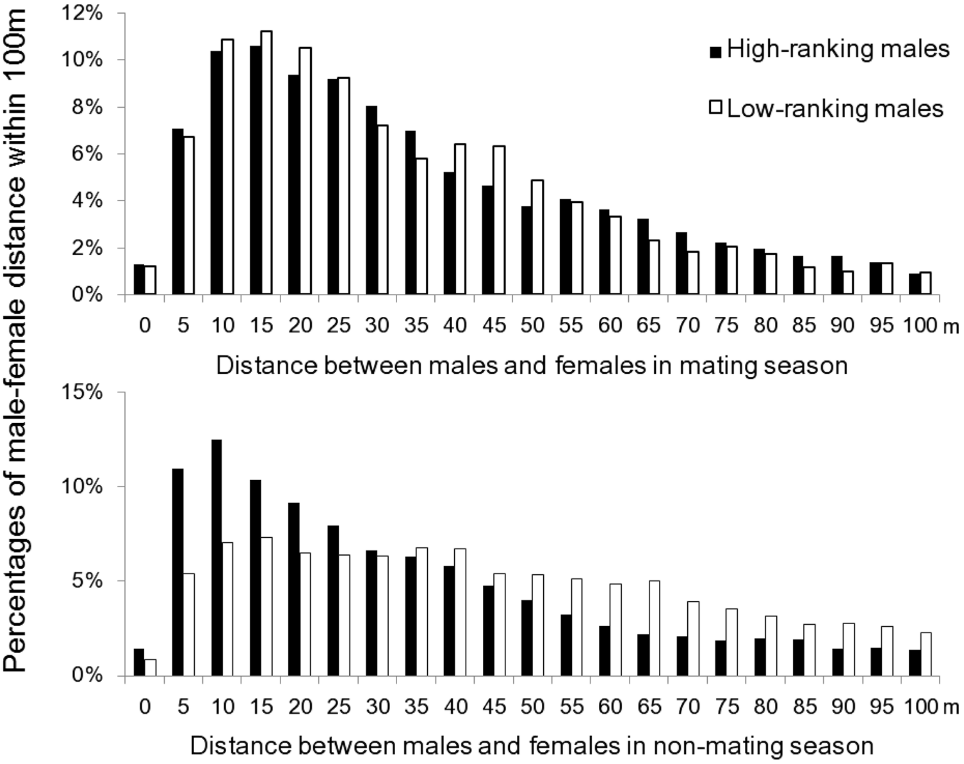

Fig. 2 Percentages of male–female distances within 100 m. Black and white bars indicate the percentage of male–female distances in each distance class

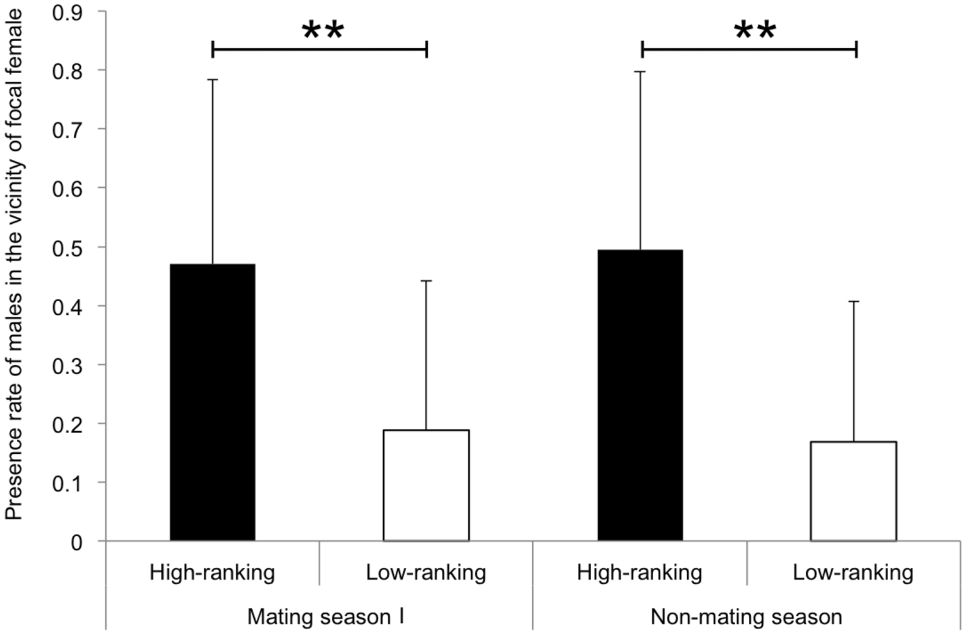

Fig. 3 Presence rate of males in the mating and non-mating seasons. High- and low-ranking indicate high- and low-ranking males, respectively. We discarded the hours when the presence rate of females in the vicinity of the focal female was < 0.5. **Indicates $P < 0.001$ (Steel–Dwass test). Vertical bars indicate SEM

Table 2 Number, duration, and percentage of separate ranging during mating and non-mating seasons

	Number of separate ranging	Mean duration (min)	Percentage of separate ranging (%)	Total observation time (h)
Mating season I	15	35.7	9.01	99
Non-mating season	76	68.0	32.7	263

Table 3 General linear model results for separate ranging duration

	Coefficients	SE	95% CI
(intercept)	3.74	0.102	3.54–3.95
Mating season I	-0.71	0.252	− 1.21 to − 0.204

by low- and high-ranking males were greater during the non-mating season than during mating season I (Steel–Dwass test, $t = 2.65$, 2.88, respectively, $P < 0.05$, Fig. 4).

Estrous status and mating frequency

The number of sexually active females was greater during mating season I than mating season II; however, the copulation frequency of the focal males did not differ between the two seasons. During mating seasons I and II, 0/9 and 7/9 group females had infants, respectively. The mean number of sexually active females in the group was 3.14 females/day ± 0.81 SD and 2.08 females/day ± 1.14 SD during mating seasons I and II, respectively. During both periods, all females except an elderly female exhibited signs of sexually active behavior. The number of births in the following spring was seven and one in mating seasons I and II, respectively. The mean copulation frequency of the focal males with group females per day did not differ between the two mating seasons (34 and 29 copulation events in mating seasons I and II, respectively, Mann–Whitney U test, $P = 0.309$).

Copulation frequency did not differ among differently ranked males. The copulation frequency of the focal males with group females did not differ between high- and low-ranking males during either mating season I or II (Mann–Whitney U test, mating season I, $P = 0.7$, $n = 34$; mating season II, $P = 0.2$, $n = 29$, Table 4).

Mating behavior associated with spatial position

In 34 bouts of parallel tracking of males and females during mating season I, there were two cases in which the distance between males and females was 20 m or less in 80% or more of the bouts (Fig. 5; Cases 1, 2). In these two cases, the focal males were the 1st- and 2nd-ranked males, who continuously threatened the approach of the other males. Grooming and mating with ejaculation with focal females were observed in both cases. These results suggest that the focal males performed mate guarding of the focal females in these two cases. In the parallel tracking, we selected the focal animals in advance to avoid bias caused by focusing on a particular combination of males and females, so there were only two cases where the combination was coincidentally involved in mate guarding.

High-ranking males copulated in the central part of the group, whereas low-ranking males did so in the peripheral

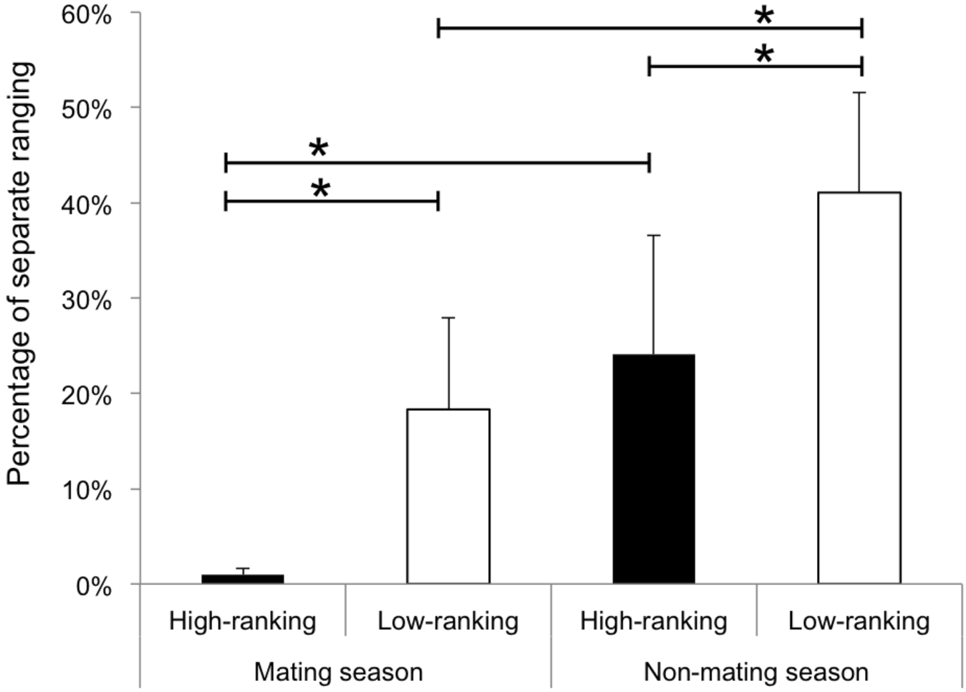

Fig. 4 Percentage of time spent ranging separately and males' rank. High-ranking and low-ranking indicate high-ranking males and low-ranking males, respectively. *Indicates $P < 0.05$ (Steel–Dwass test). Vertical bars indicate SEM

Table 4 Copulation frequency of the focal males with their group females

Social position of males	Frequency of copulation with their group females	
	Mating season I	Mating season II
High-ranking males		
1st	0.39	0.12
2nd	0.11	0.25
3rd	0.28	
Low-ranking males		
4th	0.20	0.35
5th	0.23	0.65
6th	0.21	0.33
7th	0.10	

part. During mating seasons I and II, the PR of females from low-ranking males during the hours that included copulation events with group females was smaller than that from high-ranking males (low-ranking, 40.1 ± 26.7%; high-ranking, 69.5 ± 25.9%; Mann–Whitney *U* test, $P < 0.001$). Moreover, for low-ranking males, the male–female distance was greater when the focal male copulated with a non-focal female of the group than when they exhibited other behaviors (Wilcoxon signed-rank test, $P < 0.05$ after Bonferroni correction, Fig. 6), whereas high-ranking males maintained the same level of distance, regardless of whether they copulated (Wilcoxon signed-rank test, $P > 0.05$ after Bonferroni correction). The sum of the changes in male–female distance (/30 s) during the 10 min before the onset of copulation with a non-focal female of the group was higher in low-ranking males than in high-ranking males (low-ranking, 24.6 ± 60.1 m; high-ranking, 6.4 ± 21.2 m; Mann–Whitney *U* test, $P < 0.005$), which indicated that during the 10 min before copulation, the position of the low-ranking males shifted from the center of the group to the periphery. When the focal male copulated with a non-focal female of the group, the distance between the focal male and focal female was < 100 m in all cases; these findings indicate that the low-ranking males moved to the periphery to copulate, but did not leave the group when they copulated with a group female. Cases 3 and 4 of Fig. 5 show examples of the density distribution of the male–female distance when such sneak mating was adopted.

Males visited other groups and copulated with the females of other groups during each mating season. During mating season I, both 5th and 6th males were observed visiting other groups (E and Nina-A2) once each during 99 h of observation, and copulated with females of those groups in both instances. Cases 5 and 6 of Fig. 5 show the density distribution of the male–female distance when such cross-boundary mating (mating with females of another group) was adopted. Male–female distances when the copulation bouts were initiated were 298 m and 350 m, respectively. During mating season II, five males were each observed visiting another group (E, Nina-A2, or Kw-z) during 95 h of observation, and copulation with females of these groups was observed twice (by the 1st- and 6th-ranked

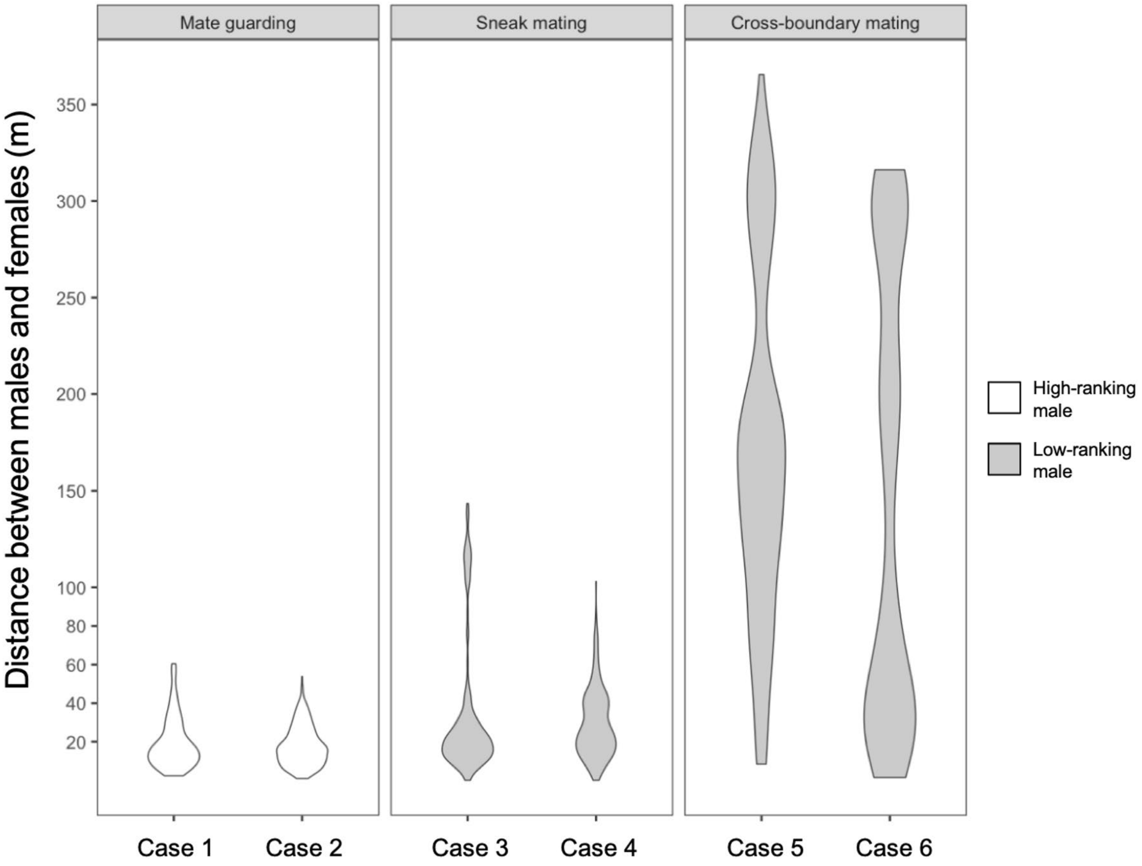

Fig. 5 Typical density distribution of male–female distance when three mating strategies were employed. The outlines of violin plots indicate the distribution space of the distances, in which violin widths show data frequency. The white and gray areas show the distribution of the male–female distance of the high-ranking male and low-ranking male, respectively. The "male–female distance" in this study was strictly the distance between the two researchers, so even if the distance between the two individuals was 0 m, the "male–female distance" would not be 0 m

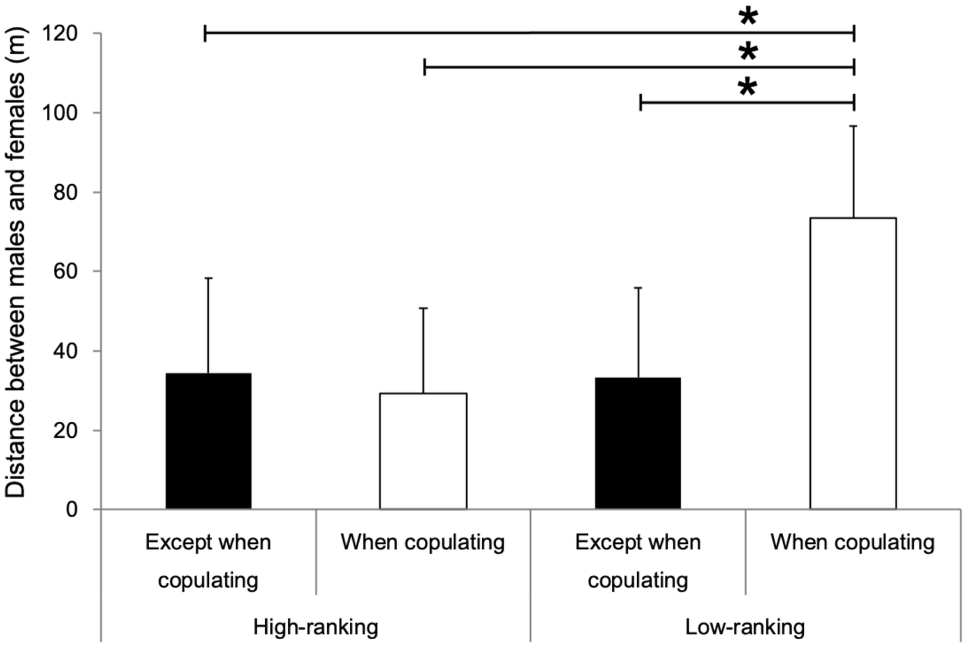

Fig. 6 Distances between the focal male and focal female when a focal male copulated with a non-focal female of the group (when copulating) and when males ranged with the group and did anything other than copulation during mating seasons I and II (when exhibiting other behaviors). *Indicates $P < 0.005$ (Wilcoxon signed-rank test with Bonferroni correction, significance level = 0.05/6). Vertical bars indicate SEM

males). Every female that engaged in the copulation bouts appeared to be different. In all cases, the females of other groups approached the focal males, and the males of other groups responded aggressively. During mating season I, the copulation frequency with the females of other groups during separate ranging was 0.22 times/h, whereas the copulation frequency with the females of their group during ranging with their group was 0.38 times/h.

Ranging behavior

During the non-mating season, males ranged separately from other group members but did not venture outside their group's home range, whereas they ventured outside the home range during the mating season. During mating season I, the ranging area of the separated males (37.9 ha) spread outside the ranging area of the group (48.1 ha, 21.3% of separated males' ranging area was outside the group's ranging area); alternatively, during the non-mating season, the ranging area of the group (53.0 ha) included almost the entire ranging area of the separated males (42.6 ha). These findings reveal that males hardly ever ranged outside their group's ranging area (2.00% of the ranging area of separated males was outside the group's ranging area; Fig. 7).

In contrast to mating season I, the core ranging area of separated males included a smaller number of intergroup encounter points than that of males in the group during the non-mating season. The group's core ranging area (50% kernel estimate) during mating season I and the non-mating season included two out of four and six out of nine locations, respectively, where intergroup encounters occurred. The core ranging area of separated males during mating season I and the non-mating season included two out of four and one out of nine locations of intergroup encounters, respectively (Fig. 7).

Discussion

This study demonstrated the spatial configuration of males and their group when males adopt three mating strategies: mate guarding, sneak mating, and cross-boundary mating (mating with females of another group). Males spent more time in their group during the mating season than during the non-mating season, because one of the advantages of being in a group is increased mating success during mating season. Despite these trends, males are flexible in their choice of strategy based on their social position and the estrous status of the females in their group.

Mate guarding

During the mating season, high-ranking males tended to remain in their group and perform mate guarding, and the percentage of time spent ranging separately by high-ranking males was substantially lower than that spent by low-ranking males (Fig. 4). In addition, high-ranking males remained in the central part of their group when they copulated, in contrast to low-ranking males (Fig. 6). Compared with low-ranking males, high-ranking males were less likely to range separately, as they experience greater benefits and fewer costs through group living (receiving more grooming and less contest competition) (Otani et al. 2014); this was observed during mating season. For reproduction, dominant males performed mate guarding within their group and therefore ranged with the sexually active females for a greater amount of time than low-ranking males. However, high-ranking males applying this strategy spend less time feeding than subordinate males (Matsubara 2003) and do not necessarily have high reproductive success (Hayakawa 2008). In addition, because of the Westermarck effect (Westermarck 1921; Takahata 1982), males who are present over a long period of time become less acceptable as copulation partners (Inoue and Takenaka 2008), and it may become more difficult for them to succeed in copulation using mate-guarding behavior.

Sneak mating

During the non-mating season, low-ranking males spent most of their time in the periphery when ranging with the group (Fig. 2). In contrast, during the mating season, when males ranged with their group, both high- and low-ranking males remained in a similar position within the group (Fig. 2), and only low-ranking males moved more to the periphery to copulate with their group females (Fig. 5, 6). The present data indicate that low-ranking males remained in the central part of the group in preparation for sneak mating, and moved more to the periphery with females only when copulating.

The entire process of sneak mating is described below. Low-ranking males usually remained in a position similar to that occupied by high-ranking males within the group, after which they moved more toward the periphery only for copulation, but never farther than 100 m from the group. Low-ranking males remained in the central part of the group during the mating seasons, probably to monitor sexually active females, and they escaped from other members to avoid disturbance only for copulation. Sneak mating was conducted relatively nearby (< 100 m), as the visibility in this study site was restricted to approximately 20 m (Koda et al. 2008). This ease in hiding would minimize the cost of returning to the central part of the group. Moreover, as the

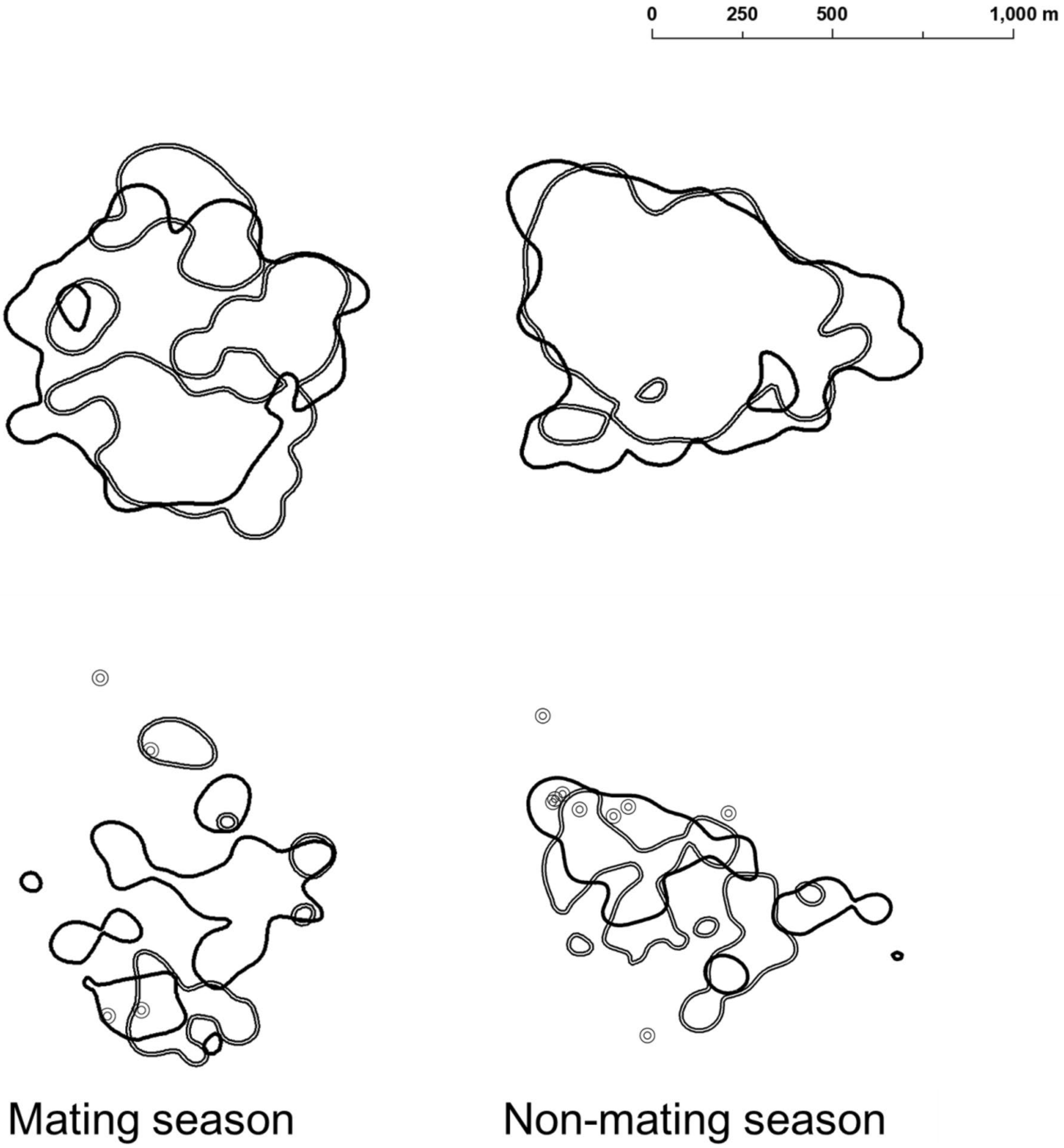

Fig. 7 Ranging area of the group and separated males. The upper and lower maps show ranging areas (95% kernel estimate) and core ranging areas (50% kernel estimate), respectively. The single and double lines on each map indicate the group's ranging area and separated males' ranging area, respectively. The double circles indicate locations of intergroup encounters

copulation frequency did not differ between high- and low-ranking males, sneak mating was as effective as the mate-guarding strategy.

Cross-boundary mating

During the mating season, males reduced the frequency and time spent ranging separately (Table 2). However, once they separated, males individually ventured outside the group's ranging area (upper part of Fig. 7). Because of their vulnerability to intergroup competition (Otani et al. 2014), separately ranging males tended to avoid places where they could encounter other groups during the non-mating season, but not during the mating season (lower part of Fig. 7). During the mating seasons, separately ranging males appeared to actively search for other groups. Consequently, they succeeded in mating with females of other groups (cross-boundary mating), although less frequently. Because of the higher frequency of separate ranging during mating season and cross-boundary mating in low-ranking males, we inferred that this strategy tends to be primarily adopted by low-ranking males. This strategy was highly feasible in the study site, as group density is high (Yoshihiro et al. 1999). This finding is consistent with those of previous studies in this area. In Yakushima, non-troop males, which include males from other groups, males from male groups, and solitary males, are reported to account for 41% of copulations (Sprague 1991) and sire 56% of offspring (Hayakawa 2008).

Males applying this strategy incur travel costs and risk of attack by the resident males in the group they visit (Boggess 1980). During the mating seasons, males visited other groups seven times in total, and succeeded in cross-boundary mating four times. Attacks by the resident males were observed in all seven visits. The copulation frequency with females of other groups during separate ranging was less than that with the females of their group while ranging with their group. Thus, this strategy is complementary and employed when the expectation of mating success in their group is low, such as when the number of sexually active females in the group is low; we inferred this, because males visited other groups more frequently, and even the 1st-ranked male also mated with females in other groups during mating season II, when there were fewer sexually active females in their own group compared with mating season I.

In conclusion, differently ranked males achieved the same level of mating frequency by employing different combinations of mating strategies associated with their spatial position. The mate-guarding strategy does not involve travel costs but can only be employed if the males are highly ranked, and this strategy limits feeding behavior. The sneak mating strategy was associated with less travel cost and contributed to increased mating frequency of low-ranking males. The cross-boundary mating strategy has an advantage compared with the other two strategies: there is an increased number of potential mating partners. However, this strategy incurs considerable travel costs and risk of attack by resident males in the group they visit; therefore, this strategy is infrequently adopted and plays a complementary role.

Further progress in this study requires that the adaptive significance of each strategy be clarified by paternity testing. This is because the number of copulations is not correlated with the number of offspring fathered by males (Inoue et al. 1993). Additionally, since the subjects of this study are group males, male mating strategies are not comprehensively clarified. Previous studies have reported that non-group males approach groups during mating season (Nishida 1966; Okayasu 2001). In addition to males from other groups shown in this study, non-group males include solitaries that do not belong to any group and males that belong to male groups. Further study is needed to clarify the overall male mating strategy, as it requires research on solitaries and male groups.

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