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Sex, Rank and Age Differences in the Japanese Macaque (*Macaca fuscata yakui*) Participation in Inter-Group Encounters

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Abstract

In many species interactions among group are often characterized by agonistic behaviour. Although animals may participate in inter-group encounters in different ways, depending on their energetic requirements, reproductive tactics, and/or developmental stage, the proximate causes affecting an animal's participation in inter-group encounters are still poorly understood. Indeed, many studies have analysed the behaviour of males and females during inter-group encounters without considering the importance of additional factors (e.g. rank). This study focuses on wild non-provisioned Japanese macaques (*Macaca fuscata yakui*) living on Yakushima Island, Japan. It aims to determine how monkeys of different sex, age, and rank behave during inter-group encounters and it discusses the implications and consequences of their behaviour on group composition and male dispersal. Males participated significantly more than females in inter-group encounters, by displaying more aggressive or affiliative behaviour. High-ranking and/or adult males were more aggressive than low-ranking and/or subadult males during encounters occurring in the mating season and they also showed more herding behaviour. This trend was not found in inter-group encounters occurring during the non-mating season. Finally, males which then emigrated to new groups were low-ranking and/or subadult individuals. Those males displayed more affiliative behaviour towards foreign males than males which did emigrate. These data indicate that in non-territorial species with male dominance over female and high competition for mating partners males play an active, and often aggressive, role during inter-group encounter while female participation is scarce. Factors such as age, rank and period of the year (in seasonally breeding species) have to be taken into considerations when analysing interactions between groups and their effects on group composition and social behaviour.

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Introduction

Interactions among groups have been intensively studied by behavioural ecologists for the effects that they may have on group size, its composition, and the social structure of a species (e.g. Wrangham 1980; Cheney 1987; Cant et al. 2002). Sex, hierarchical status, and developmental stage are all factors that may affect the energetic requirement of an animal, its reproductive strategy, and its social relationships with the other group members. As such, these factors are expected to influence the way an animal participates in inter-group encounters. Trivers (1972) hypothesized that female reproductive fitness should be mostly limited by access to food sources whereas that of males should be limited by reproductive access to females. These assumptions imply that females should be aggressive during inter-group encounters, when direct inter-group food competition is high, in order to defend food sources (the resource-defence hypothesis: Wrangham 1980). Conversely, males may follow at least three strategies during inter-group encounters. First, they may defend females of their own group from extra-group mating by means of herding behaviour and aggression towards foreign males (the mate-defence hypothesis: Wrangham 1980; van Schaik et al. 1992). Secondly, males may defend food sources in order to indirectly defend females (the hired-guns hypothesis: Rubenstein 1986). Thirdly, males may use inter-group encounters to assess their chances to successfully transfer to new groups (Lazaro-Perea 2001). In some species (e.g. vervet monkeys, *Chlorocebus aethiops*: Cheney 1981), for example, young males often direct amicable behaviour towards foreign males during inter-group encounters and this probably affects their decision to transfer.

Although many studies have analysed inter-group encounters in a variety of social mammals, most of them have been focused on the different participation of males and females, given their different energetic requirements and/or reproductive tactics. However, this type of analysis gives an oversimplified picture of the topic. Playback experiments conducted on lions and chimpanzees (Heinsohn & Packer 1995; Wilson et al. 2001), for example, have demonstrated that an animal's decision to approach the recorded intruder is based on its rank and on the number of group companions which are nearby, and may ultimately be related to its personality traits. These observations clearly indicate that the behaviour of an animal during inter-group encounters cannot be simply predicted by its sex so that additional factors have to be taken into account. Indeed, the way animals participate in inter-group encounters is affected by the balance between benefits and costs that each individual may gain or lose, and by period of the year (e.g. mating vs. non-mating season in seasonal breeding animals; Heinsohn & Packer 1995). Although often only some animals actively participate in inter-group encounters, this participation may give collective benefits to all the group members (Nunn 2000). The animals which benefit more by collective acts are expected to have a more active role in these acts. In this situation, some group members may follow a 'free-rider' strategy, i.e. not participating in these collective acts while benefiting from them at low or no

costs. Inter-group encounters are ideal situations where the benefits of collective acts and the possibility for 'free-rider' strategies may be analysed (van Schaik 1996). In multi-male, multi-female groups with a high level of competition for mating partners fully adult/high-ranking males are expected to defend their group females from foreign males. If this happens, females may avoid participating in the encounters (thus reducing the risk of aggression from foreign animals) but still gain many benefits from the behaviour of their group males (i.e. defence of food sources and/or protection from infanticidal males). Subadult/low-ranking males may also benefit from the active participation of adult/dominant males in the encounters as this may discourage the immigration of foreign males. The active participation of fully adult/high-ranking males in the encounters, however, and thus the possibility for females and/or subadult/low-ranking males to follow a 'free-rider' strategy, may only be restricted to encounters occurring when oestrous females or dependent infants are present. As such, the decision to participate in an inter-group encounter is a complex consequence of many factors. Unfortunately, studies on the factors that may affect the participation of an animal in inter-group encounters are still scarce, although such data may clarify the different strategies that group members follow during inter-group encounters and their associated benefits and costs. Here, we analyse the importance of sex, age, rank, and period of the year (mating vs. non-mating season) as factors affecting an animal's participation in inter-group encounters and the fitness consequences that this participation may have in a wild non-provisioned group of Japanese macaques (*Macaca fuscata yakui*) living on Yakushima Island, Japan.

The Japanese macaque is a female-bonded species, living in multi-male, multi-female groups with female philopatry and male dispersal (Melnick & Pearl 1987). The average group size is 20–30 animals in Yakushima macaques (Maruhashi 1982; Sprague et al. 1998) and home ranges largely overlap with those of neighbouring groups (up to 50% of the total area: Maruhashi et al. 1998). See Nakagawa (1998) for further details on the ecology and social behaviour of Yakushima macaques.

Methods

Study Area and Subjects

Yakushima is a volcanic island of around 500 km^2 located 60 km south of Kyushu, Japan (31°N, 131°E). Subjects of this study were 21 monkeys (13 males and eight females, aged ≥4 yr), members of a non-provisioned troop (Nina A), living along the coast. At the beginning of the study, the group consisted of 25 individuals (the study subjects plus three yearlings and one infant). The monkeys living in the neighbouring groups and the study group were habituated to human beings and thus their behaviour during inter-group encounters was not affected by our presence.

Data Collection

This study is part of a larger project on conflict management in the Japanese macaque. Data were collected continually from 15 Jun. 2001 to 30 Apr. 2002, between 7:00 and 18:00 h each day. There were only two intervals without data collection longer than 3 d in this period: from 2 to 10 Sep. 2001, and from 20 Dec. 2001 to 23 Jan. 2002. In this study, an inter-group encounter was considered to occur when two groups were in visual contact, inter-group distance was shorter than 50 m, and at least 50% of our study animals were present in the group. During the whole duration of each inter-group encounter, we recorded all the occurrences of aggressive or affiliative behaviour displayed by our study animals (Altmann 1974). This type of data collection was made possible by the nature of the inter-group encounters observed. Encounters often lasted many minutes (see below), during which few monkeys (i.e. ≤4) from each group actively interacted one another at the same time in a restricted area, while the remaining group members were involved in other activities, showing no evident participation in the encounter. As such, the monkeys which actively participated in inter-group encounters were visible and their behaviour easily detectable. However, we decided to consider all the behaviours recorded as events (i.e. behavioural patterns of short duration; Martin & Bateson 1993) to avoid problems related to reliability of the data. Moreover, to avoid the two observers collecting data on the same animal at the same time, when an inter-group encounter was detected one of us (BM) observed the study troop and communicated the occurrence of all the behaviours to be recorded to the other observer (RV), who then completed check-sheets. Whenever contact with the monkeys could not be maintained, the data collection was stopped and the inter-group encounter was considered to be finished. We considered threat, chase, bite and slap as aggressive behaviour, while we considered allo-grooming, social play, genital inspection, lip-smacking, and affiliative mount as affiliative behaviour (see Enomoto 1974 and Kurland 1977 for definitions). Herding behaviour was defined as any aggressive act displayed by a study male towards its group females when these approached or attempted to interact with foreign males during encounters. Data on avoidances (one animal avoids or is displaced by another one in a non-agonistic context) and dyadic conflicts, with a clear-cut result and not involving third parties, were collected ad libitum throughout the study period in order to assess the rank of the study animals. The duration of contact between the observers and the study group was recorded every day in which the study troop was found.

Data Analysis

The rate of inter-group encounters was obtained dividing the number of encounters observed by contact time with the troop. Rates of aggressive and affiliative behaviour per individual were obtained by dividing the occurrence of all the behaviours recorded for each monkey by the amount of time that monkey was observed to participate in the encounters.

During the course of the study seven males emigrated from the group (see below). This factor could clearly affect the behaviour of monkeys which remained in the group. As preliminary analyses, the behaviour of those monkeys before and after the emigration of the seven males was compared. No difference was found in the frequency of inter-group encounters before and after the emigration of the seven males from the group (before: 0.053 mean encounters per hour; after: 0.043). Moreover, rate of aggressive or affiliative behaviour displayed by males which remained in the group did not significantly differ between the two periods (Wilcoxon test, aggressive behaviour: before, 0.71 ± 0.07 events per hour ± SE; after: 0.89 ± 0.12; $T = 17$, $N = 6$, ns; affiliative behaviour: before, 0 events per hour ± SE, after: 0.12 ± 0.08; $T = 3$, $N = 6$, ns). Therefore, all the 13 males were considered in the following analyses to have a larger sample size.

In order to analyse the effect of age on male participation in inter-group encounters males were divided into two categories: adult males (estimated age >7 yr) and subadult males (estimated age between 4 and 7 yr). Finally, the following independent variables were used to analyse male emigration, which was the dependent variable (i.e. yes or no): frequencies of aggressive and affiliative behaviour displayed by males during inter-group encounters; age (i.e. adult or subadult); origin (non-natal males or natal males); rank. Mann–Whitney test was used for independent samples when the test variable was continuous, and chi-square test was used when the test variable was categorical. Wilcoxon test was used for paired samples while Spearman correlation was used to analyse relationships among variables. The mating season was considered to last from the first to the last recorded consortship in which sexual mounts were observed (Hanby & Brown 1974). All the tests were two-tailed and the alpha level was set at $p < 0.05$. Data are presented as $\bar{x}$ ± SE throughout the text and in the figures.

Results

The Effects of Sex, Age and Rank on Monkey Participation in Inter-Group Encounters

During the course of the study a total of 28 inter-group encounters were observed, one every 5.13 ± 0.91 observation days. The mean frequency of encounters per hour was 0.045 and their duration was 1 h 21 ± 11 min. The study females (eight) were always present in the group during the inter-group encounters. On average, male presence in the group during the inter-group encounters was 84.6 ± 7.7 and 83.3 ± 6.4% of total males, for encounters occurring before and after the emigration of seven males from the group respectively. Only two encounters were clearly elicited by defence of food sources: when the two groups met near a big fig tree and tried to displace each other from it. All the other encounters did not occur near conspicuous food sources. In 28.6% (eight) of encounters, one of the groups changed travel direction following the inter-group encounter. Overall, aggressive behaviour towards monkeys of the neighbouring troops was observed in every inter-group encounter while affiliative behaviour was observed in 21.4% (six) of the encounters. Aggressive behaviour

consisted of threats at a distance and brief chases (1–2 m) while in one inter-group encounter (occurring during the mating season) an adult male was caught by our study group and repeatedly bitten by the 13 males and the alpha female. After a couple of minutes that male managed to escape but we were unable to assess how badly he was injured. Overall, all the males directed at least one aggressive act towards foreign monkeys but only 61.5% (eight) of males directed affiliative behaviour. Conversely, 37.5% of females (i.e. three; ranking first, second and forth respectively) displayed aggressive behaviour during the encounters observed and 50% of females (i.e. four; ranking forth, fifth, sixth and eighth respectively) showed affiliative behaviour. Males always displayed aggressive or affiliative behaviour towards foreign males and never to foreign females. Among the three females which participated in the encounters, the alpha female was the only female which was aggressive towards a foreign female, during one encounter. The remaining two females directed aggressive behaviour towards foreign males in order to support their siblings which were participating in the encounter. Moreover, the four females which displayed affiliative behaviour always did so towards foreign adult males and never to foreign subadult males. The study females were never observed attempting to, or mating with foreign males.

The different participation of males and females in inter-group encounters is reflected in the rate of aggressive or affiliative behaviour displayed by the two sexes. Males showed significantly more aggressive behaviour towards foreign monkeys (Mann–Whitney U test, $U = 10.0$, $N_1 = 13$, $N_2 = 8$, $p < 0.01$; Fig. 1) and also more affiliative behaviour than females ($U = 30.0$, $N_1 = 13$, $N_2 = 8$, $p < 0.05$). Given their rare participation in the encounters females were excluded from the following analyses.

No significant difference was found in the occurrence of aggressive behaviour between adult males and subadult males ($U = 11.0$, $N_1 = 5$, $N_2 = 8$, ns; Fig. 2), but subadult males displayed significantly more affiliative behaviour towards foreign monkeys than did adult males ($U = 0.0$, $N_1 = 5$, $N_2 = 8$, $p < 0.01$).

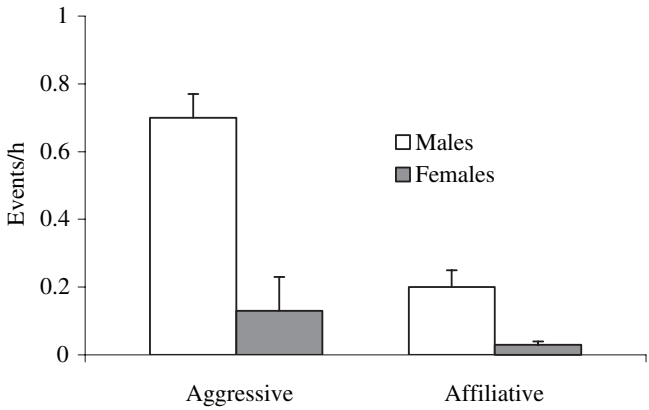

Fig. 1: Rate of aggressive and affiliative behaviour displayed by males and females ($\bar{x} \pm SE$)

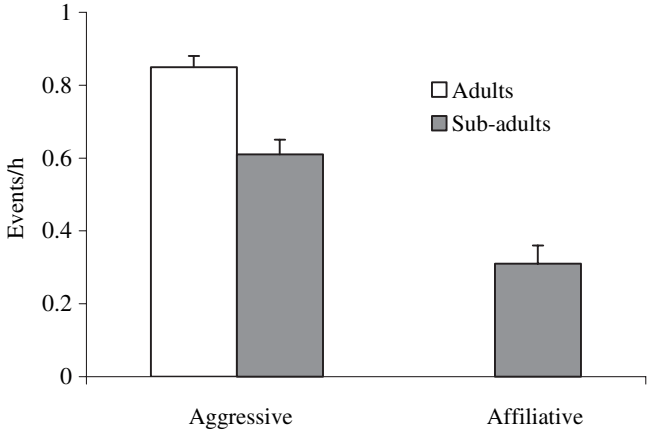

Fig. 2: Rate of aggressive and affiliative behaviour displayed by adult and subadult males ($\bar{x} \pm SE$)

There was no significant correlation between rank and aggressive behaviour (Spearman correlation, $r_s = -0.46$, $n = 13$, ns) but low-ranking males showed more affiliative behaviour towards foreign monkeys than high-ranking males ($r_s = 0.81$, $n = 13$, $p < 0.01$). Finally, a positive correlation was found between rank and age ($r_s = 0.78$, $n = 13$, $p < 0.01$).

The Effects of the Mating Season on Monkey Participation in Inter-Group Encounters

The mating season began on 18 Aug. and was finished by the time the data collection began again in Jan. (see Methods). All 13 males were observed to ejaculate during the 2001 mating season and thus they were all considered to be sexually mature. Frequency of inter-group encounters was similar during the mating and the non-mating season (0.05 and 0.04 mean encounters per hour respectively). Male aggressive behaviour did not differ between the two periods (Wilcoxon test, $T = 56$, $N = 13$, ns; see Fig. 3) while male herding behaviour was significantly more frequent during the mating than the non-mating season ($T = 21$, $N = 13$, $p < 0.05$).

Adult males displayed more aggressive behaviour than subadult males during the mating season ($U = 8.0$, $N_1 = 5$, $N_2 = 8$, $p < 0.05$; see Fig. 4). This difference disappeared during the non-mating season ($U = 12.0$, $N_1 = 5$, $N_2 = 8$, ns) and the same happened with herding behaviour (see Fig. 5): adult males herded females more than subadult males during the mating season ($U = 1.0$, $N_1 = 5$, $N_2 = 8$, $p < 0.01$) but no difference was found during the non-mating season ($U = 16.0$, $N_1 = 5$, $N_2 = 8$, ns).

Higher-ranking males were more aggressive than lower-ranking males during the mating season ($r_s = -0.64$, $n = 13$, $p < 0.05$) but not during the non-mating season ($r_s = -0.46$, $n = 13$, ns). Male herding behaviour during the mating season was also significantly related to hierarchical rank: high-ranking males displayed more herding behaviour towards females of their own group than

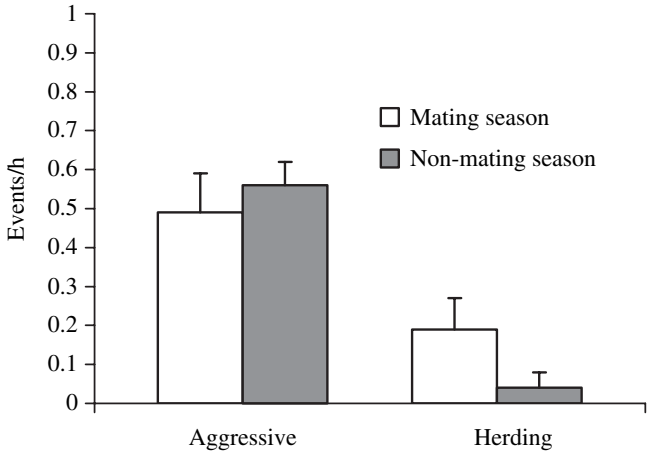

Fig. 3: Rate of aggressive and herding behaviour displayed by males during the mating and the non-mating season ($\bar{x} \pm SE$)

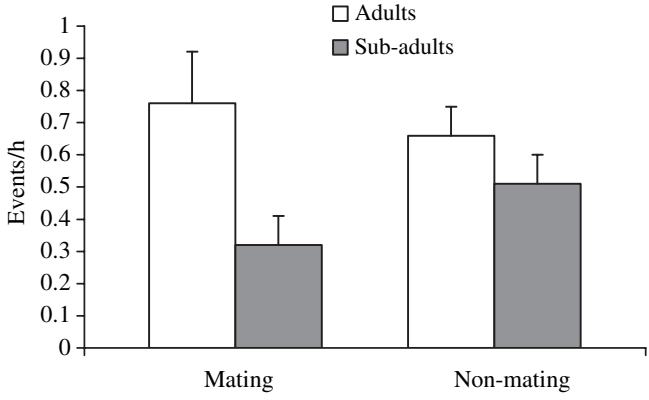

Fig. 4: Rate of aggressive behaviour displayed by adult and subadult males during the mating and the non-mating season ($\bar{x} \pm SE$)

low-ranking males ($r_s = -0.73$, $n = 13$, $p < 0.01$). Finally, the correlation between male rank and herding behaviour during the non-mating season was not significant ($r_s = -0.46$, $n = 13$, ns).

The Relationship between Participation in Inter-Group Encounters and Male Dispersal

During Oct. 2001 seven males independently emigrated to neighbouring groups (three of those males were born in the group). Males which did not emigrate were more aggressive than males which emigrated but the difference only approached significance ($U = 11.0$, $N_1 = 6$, $N_2 = 7$, $p = 0.068$; see Fig. 6). Conversely, males which emigrated displayed more affiliative behaviour than

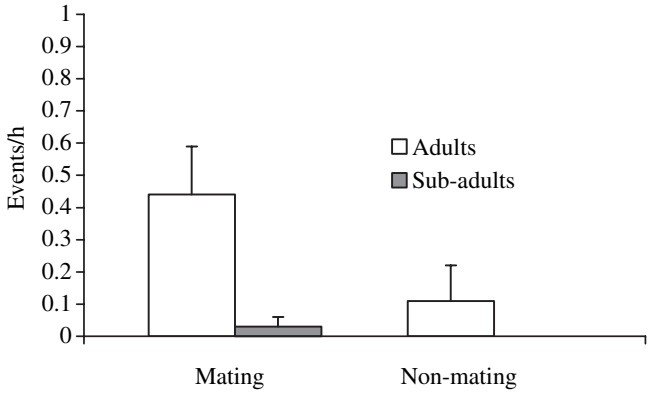

Fig. 5: Rate of herding behaviour displayed by adult and subadult males during the mating and the non-mating season ($\bar{x} \pm SE$)

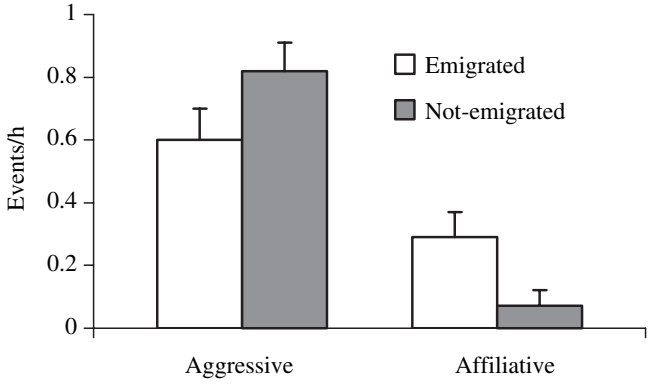

Fig. 6: Rate of aggressive and affiliative behaviour displayed by males which emigrated and by those which did not emigrate ($\bar{x} \pm SE$)

those which did not ($U = 6.0$, $N_1 = 6$, $N_2 = 7$, $p < 0.05$; see Fig. 6). There was a non-significant tendency for emigrating males to be low ranking rather than high ranking ($U = 9.50$, $N_1 = 6$, $N_2 = 6$, $p = 0.057$). Emigrating males were more likely to be subadult than adult (chi-square test, $\chi_1^2 = 3.75$, $p < 0.05$). However, emigrating and non-emigrating males did not differ in origin (i.e. natal or non-natal: $\chi_1^2 = 1.04$, ns).

Discussion

The Effects of Sex, Age and Rank on Monkey Participation in Inter-Group Encounters

All the females and almost all the males were present in the group during inter-group encounters. This suggests that the different participation of the study

animals did not depend on the different probability to be in the group when an encounter occurred. Rather, the presence of most of the group members indicates that the 'decision' to actively participate in the encounters depended on the benefits and costs for each animal and on the behaviour of the other group members (see below).

A high frequency of aggression between groups is typical of animals that aggressively defend food sources (Rubenstein 1986; Cheney 1987; Saito et al. 1998; van Schaik & van Noordwijk 1988; Sugiura et al. 2000; Gray et al. 2002). However, the low female participation in inter-group encounters does not support the resource defence hypothesis (Wrangham 1980; van Schaik 1989). This result may have two alternative explanations. First, it might be the consequence of a low level of direct inter-group food competition. Alternatively, males may gain many benefits by being aggressive during inter-group encounters (see below), regardless to the level of food competition (Rubenstein 1986), so that female participation becomes unnecessary. Females may thus follow a 'free-rider' strategy by gaining benefits from male aggressive behaviour towards foreign groups at no costs. The high overlap between home ranges of neighbouring groups (Maruhashi et al. 1998) and the observation that inter-group encounters almost never occurred near food sources suggest that male behaviour during inter-group encounters is more directly related to defence of mating partners and avoidance of male immigration than to food competition. Indeed, in species such as the Japanese macaque with high male competition for mating partners, high risk of extra-group mating, and male dominance over females, males may potentially gain more benefits than females by being active during inter-group encounters. First, males may directly defend their mating partners (see below) and/or they may attempt to mate with foreign females (although extra-group copulations were never observed in this study). Moreover, males may establish dominance/subordinance relationships with foreign males (Kawanaka 1973) that may discourage transfers into their own group (thus limiting intra-group competition for mating partners) or that may increase their chances of successfully joining a new group at the high-ranking position. Finally, in periods of low food availability, males may gain access to limited and/or highly palatable food sources for their group females and for themselves. Moreover, high group densities (i.e. number of groups per unit area, as it is the case of Yakushima Island; Nakagawa 1998) often correlate with high socionomic sex ratio and frequent male aggressive behaviour during inter-group encounters (Ridley 1986; S. Horiuchi, unpubl. data) as the risk of extra-group mating increases. These considerations explain why a higher participation of males than of females in inter-group encounters has been reported in some social mammals (e.g. horses and zebras: Rubenstein 1986; guerezas, *Colobus guereza*: Fashing 2001; bonnet macaques, *M. radiata*: M. Cooper et al., 2004).

The Effects of the Mating Season on Monkey Participation in Inter-Group Encounters

The effects on male aggressive or herding behaviour of rank, age, or period of the year support the mate defence hypothesis (Wrangham 1980; van Schaik et al.

1992), which predicts that males should guard females of their own group and should also be particularly aggressive during inter-group encounters in order to prevent mating between foreign males and females of their own group. Extra-group copulations are frequently observed during encounters in a variety of mammals (e.g. Japanese macaque, *M. fuscata*: Sprague 1991; banded mongoose, *Mungos mungo*: Cant et al. 2002) and high-ranking/adult males usually have more chances to sire the infants of their own group (Cowlishaw & Dunbar 1991; but see also Takahata et al. 1999). Therefore, for high-ranking males the benefits of mate defence (i.e. reduced frequency of female extra-group copulations) might exceed the costs associated with aggressively defending mating partners, a situation that may result in severe injury. The difference between benefits and costs is expected to increase with male rank. Indeed, low-ranking/subadult males, which are usually less able to compete for oestrous females effectively, are expected to gain lower net benefits from mate defence. In seasonally breeding species, such as the Japanese macaque, the different benefits that males may gain depending on their social status and/or age become evident during the mating season but may be reduced outside the mating season (Cowlishaw 1995).

The Relationship Between Participation in Inter-Group Encounters and Male Dispersal

In many social species, individuals entering a new group often suffer from aggression by resident males that may result in loss of weight and even death of the animal (Pusey & Packer 1987). Therefore, the decision to transfer into a new group has important consequences on male reproductive success, and indeed monkeys show complex assessment and decision-making in this process (Lazaro-Perea 2001; van Noordwijk & van Schaik 2001). Group size and composition, age, maternal rank and presence/absence of peers are all factors that may affect the decision to emigrate and the target group of a male (Sprague et al. 1998; van Noordwijk & van Schaik 2001). Overall, males which are about to transfer may follow two different strategies. They may join a new group by aggressively attempting to outrank the dominant individuals. Such a strategy would be more likely to succeed if attempted by fully grown males, which are often high-ranking animals, but it has high potential costs and indeed is not frequently observed in Yakushima (Suzuki et al. 1998). Alternatively, males may reduce the risk of aggression by exchanging affiliative behaviours with dominant individuals and enter a new group at the bottom of the hierarchy. This option may be particularly effective for subordinate/young males which still have to reach their full size and strength. Indeed, subadult males were more likely to emigrate than adult males (there was also a non-significant tendency for low-ranking males to emigrate more than high-ranking males). Moreover, low-ranking/subadult males displayed more affiliative behaviour during the encounters. Males often rise in rank following the emigration or death of higher-ranking monkeys (Suzuki et al. 1998). As such, these results indicate that low-ranking/subadult males follow a low risk strategy in order to enter a new group: they exchange affiliative behaviours

with foreign males to reduce the risk of aggression and, subsequently, they may attempt to rise in rank. This strategy may be particularly effective for species with high competition among males. The cause–effect relationship between behaviour displayed during inter-group encounters and future transfers has often been predicted but not frequently observed in field studies (Cheney 1981; Hamilton & Bulger 1990; Sprague 1992; Lazaro-Perea 2001). In this view, inter-group encounters represent a good opportunity for these males as they can easily monitor composition and size of foreign groups, assess the potential risks of the transfer, and decide on the target group.

Conclusions

This study has shown that Japanese macaque's participation in encounters varied with their sex, rank, age and period of the year (i.e. mating vs. non-mating season). These results indicate that the balance between benefits and costs affects the strategies that social animal follow during inter-group encounters and it may change during the course of the year and during an animal's lifetime. This study thus supports the view that many factors, and not only sex, may affect the behaviour of an animal during inter-group encounters. These factors have to be taken into account by future studies trying to analyse inter-group interactions and the decision-making process of social animals.

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