CONFLICT MANAGEMENT IN WILD JAPANESE MACAQUES (*MACACA FUSCATA YAKUI*)

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A thesis submitted in fulfilment of the
requirements of Liverpool John Moores University
for the degree of Doctor of Philosophy

November 2003

List of Contents

Chapter 7

Causes and Consequences of Inter-Group Encounters in Nina A Group

Acknowledgements

It is usually "good practice" to have your supervisor as the first name in the Acknowledgements. Although I follow this rule here this is only because I believe she deserves it and not for convenience. Throughout the thesis Nicola Koyama has been a continuous source of scientific advice, support, kindness, friendship, and patience to correct my mistakes and my poor English, no matter how busy she was herself. Moreover, her quiet character has always represented a stable and valid support to me who too often fluctuate between depression and excitement. Nicola has got all the qualities a good supervisor should have.

I will be forever grateful to Filippo Aureli, my second supervisor, and Gabriele Schino. They have contributed to this thesis with many scientific comments, long discussions (as I need much time to understand new ideas), and various forms of help, friendship, and hospitality. Filippo and Gabriele are the ideal teachers for a young scientist who wants to "learn the job" and their bad result with me is only due to my scarce intelligence.

I would like to thank my Ph.D. examiners, Mark Feltham and Robin Dunbar, for an enjoyable and interesting "viva", and for many useful comments that greatly improved my thesis.

Many people have contributed to this thesis in different ways. First of all, I would like to thank the Yakushima District Forestry Office for permission to carry out the study. While in Japan, Naoki Agetsuma, Shigeru Suzuki, David Hill, and all the students at the Kyoto University Yakushima Station (Syuhei Hayaishi, Sachiko Hayakawa, Shiro Horiuchi, Taketoshi Teramura, Riyon Tsujino, and Peter Winn-Brown) kindly helped me in many ways and for that I am extremely grateful. Without their help I would probably not have been able to live and carry on with my research in Japan. All people living on Yakushima were always extremely friendly and kind and I will never forget them. Finally, I would like to thank Naoki Agetsuma, Louise Barrett, Matthew Cooper, Goro Hanya, Marc Hauser, David Hill, Nobuyuki Kutsukake, Peter Nonacs, David Sprague, Josef Soltis, Hideki Sugiura, and Shigeru Suzuki for useful discussion, comments, and/or papers that I could not find.

This research was funded by a Liverpool John Moores University studentship and for that I am exceedingly grateful. Many thanks to all the technical and administrative staff for their assistance, in particular Jim McCloskey and Jill Beesley.

For their help I thank with all my heart Hannah Buchanan-Smith, Laura Bishop, Spartaco Gippoliti, Scott Hardie, Tomoko and Masao Kishi, Angela Lamb, Barbara and Valentina Majolo, Armando and Daniela Pagliari, Giuseppe Russo, Stella Shackel, Colleen Schaffner, Livia Speranza, Federica Ventura, Umberto Zanghieri, and all my relatives and friends.

A particular "*mille grazie*" goes to Patrizia and Francesco Ventura. They have given me an incredible amount of practical and financial help, kindness, friendship, and support. Moreover, Patrizia has spoiled me with large quantities of delicious food every time I was nearby. She is the only human being I know who seriously thinks that there is no food in her house while serving on the table large quantities of *prosciutto* and *bresaola*, different cheeses, at least two types of pasta, half a chicken, some *polpettone* and a bottle of good wine. Finally, Francesco kept me fit with fantastic tennis matches every time I was in Rome. Those matches also helped me to improve my ability to collect behavioural data: for each match I like recording the latency of the first time Francesco says "*sempre sul nastro*!" and "*quanto corri figlio mio*"!.

I will be forever grateful to my parents, Francesco and Emilia, for their financial and practical support, for the wonderful Sunday lunches, for all the good food they sent me while in Japan, and for a fantastic *pastiera* that my wife and I ate on a staircase at the Fukuoka train station, with great surprise of the Japanese

people there. Most of all, I thank them for having created, since I was a child, a friendly and stimulating environment in our home where frank and open-minded discussions were always welcome, and where topics ranged from Dostoevsky's novels to the high frequency with which my mother cooks *pasta alla puttanesca* or to why I do not like the way my father cooks *pasta e fagioli.* I believe such an environment to be essential for the moral and cultural development of a child. As a father, I really hope to be able to recreate such an environment for my daughter and to have with her the same type of relationship I have with my parents.

During the course of my Ph.D. two wonderful events happened to me: my wedding and the birth of my first daughter. Without the moral strength and enthusiasm of Raffaella, my wife, I would have left Japan after only one week. She has been a constant source of support, helpful discussion, scientific advice, and good humour. I thank her for a funny *frittata* with raw potatoes, for our periodical trips to Miyanoura to get enough ice cream for the whole week (while in Japan) and for our expeditions to the best pizzerias or patisseries (while in Italy), for many political discussions (that always ended with me as the winner), for having shared a wonderful Easter with the macaques and their new-born infants, for her fantastic maternal style that helped me to finish my thesis (despite all the efforts made by our baby), and for many other reasons that I do not want to mention here. This thesis (and my happiness) owes a great debt to her.

Few experiences are more wonderful than spending a long period of time with animals as intelligent as the Japanese macaques, for one may feel emotions like peace, love, fear, aggression in a pure and unconstrained way. I strongly believe that being with the monkeys has even improved my appreciation for life in all its expressions and increased my desire to become a father. Moreover, the feeling of being completely accepted and trusted by the monkeys so that they allowed me and Raffaella playing with their infants is so powerful that it would require a poet to describe it, not an animal behaviour student. However, even if I was a poet able to describe all the wonderful moments that I had with the monkeys, this description would constrain my feelings into the boundaries of the words and reduce their strength. Therefore, here I just want to say thank you to all the macaques I had the pleasure to meet and spend my time with in Japan; they know why.

Thesis Abstract

Food quality and distribution, presence of predators, and mating strategies of the two sexes are all factors that may affect social behaviour in primate and non-primate species. Competition for valuable resources (e.g. food or allies) is one of the main potential costs of group-living and its importance depends on the availability of such resources. Given the detrimental effects that competition may have on the fitness of an animal, mechanisms have evolved to keep aggression and conflicts between group members under control. In social primates the occurrence of aggression is reduced among animals maintaining good relationships with one another (mainly through grooming exchange). When a conflict cannot be avoided, reconciliation may take place to restore the social relationships between former opponents damaged by the conflict. Studies analysing the effect of ecological factors on how animals manage conflicts are scarce despite the importance that these studies may have for behavioural ecologists, social psychologists, and anthropologists. The aims of this thesis, therefore, were to analyse conflict management in two groups, of different size (N = 8 and N = 20 females), of wild Japanese macaques (*Macaca fuscata yakui*) living on Yakushima Island, Japan.

Seasonal variations in activity budgets and diet composition had no evident effect on grooming distribution and frequency of reconciliation among females. Conversely, group size had many significant effects on the behavioural ecology of this species. Females living in the large group spent more time grooming and less time resting than females in the small group. However, grooming inequality was higher and frequency of reconciliation lower among females in the large group. This indicates that the social costs of group-living increase together with group size so that both social constraints and non-social factors (e.g. food abundance) can limit group size and/or lead to fission. Moreover, this thesis also showed that male Japanese macaques may exchange amicable interactions and reconciliation at a level similar to females. This finding shed new light on the social behaviour of this species as previous studies have usually considered interactions among

males to be mostly aggressive. This result may be related to the particular habitat conditions of Yakushima Island. Finally, data on inter-group encounters showed that other factors than sex (i.e. age, rank, and period of year) may explain the different participation of group members in inter-group encounters.

Chapter 1

General Introduction

1.1 Brief Overview of the Thesis.

Aggression and competition between group members are two of the main potential costs associated with group-living as they may reduce the survival rate and reproductive success of an animal. In order to reduce these detrimental effects social animals try to maintain amicable relationships with some group members (e.g. closely-related individuals). Amicable social relationships help to keep competition under control as the occurrence of aggressive interactions is lower among animals who exchange amicable interactions with one another than among animals who do not. When competition cannot be avoided, post-aggression mechanisms (reconciliation) have evolved to restore the social relationships between former opponents that were damaged by the occurrence of conflict.

This thesis analyses conflict management in two groups of Japanese macaques (*Macaca fuscata yakui*) living on Yakushima Island, Japan. It aims to determine the effect of different ecological factors (e.g. diet composition, group size, or frequency of inter-group encounters) on the quality of social interactions and on the occurrence of reconciliation among group members. The following sections of this chapter contain overviews of factors affecting group living, social behaviour, and conflict management, information on the behavioural ecology of Yakushima macaques, and the specific aims of this thesis. Chapter 2 provides details on the study site and on the methods of data collection used in this thesis. Chapters 3 to 7 contain the results, and Chapter 8 the discussion and possible further lines of research.

1.2 Costs and Benefits of Group-Living.

Although many animal species live in groups, a single explanation for the evolution of sociality is still far from being found (Clutton-Brock and Harvey, 1976; Trivers, 1985). Primates represent one of the most social groups of animals showing high social complexity comparable to only a few other species (e.g. marine mammals or elephants; Mann *et al.*, 2000; Moss, 1988). Early attempts to formulate a general theory for the evolution of primate societies (Crook and Gartlan, 1966) were based on scarce data and concentrated on few species. With the increasing amount of data collected on different primate species it has become possible to have a clearer picture of the factors affecting primate social behaviour.

a) Wrangham's and van Schaik's theories on the evolution of group-living.

Males and females are thought to differ with respect to the factors that may affect their fitness (Trivers, 1972). Given the energetic costs of lactation and long parental care the reproductive success of female primates is mostly affected by food quality and abundance. Conversely, male reproductive success mostly depends on competition for mating partners. Therefore, female behaviour and grouping patterns are a direct consequence of many habitat characteristics while male behaviour depends on the number and distribution of females in a given area. Based on these considerations the two main theories proposed for the evolution of group-living both paid particular attention to female relationships. These theories differ from one another in the relative importance that the authors attribute to the two main ecological factors that shape social groups: food and predators. The first theory (Wrangham, 1980) postulates that feeding advantages alone promote group living in primates, as larger groups defend food sources from foreign groups better than smaller ones or single individuals. The theory also states that predation pressure is a relatively irrelevant factor. When food is clumped (i.e. defensible) and of high energetic value groups should be characterised by female philopatry and matrilines, as females should form coalitions against foreign groups and/or within the single matriline in order to defend food sources. Conversely, when food is dispersed and of low quality female transfer may appear and coalitions among females and inter-group food competition should be low. The second theory (van Schaik, 1983, 1989; see also Sterck *et al.*, 1997) argues that group living evolved mainly as a response to predation pressure as large groups should pinpoint predators or defend themselves from them more easily than small groups or individuals alone (e.g. Dunbar, 2002). This theory also recognises the importance of intra- and inter-group food competition as an important factor (although secondary with respect to predation pressure) affecting social behaviour.

The relative importance of factors shaping social groups is still unresolved and thus a matter of great debate (Johnson *et al*, 2002; Kappeler and van Schaik, 2002). This is essentially caused by three main problems: first, all these factors interplay with one another and their importance is a direct consequence of many ecological characteristics; secondly, there is not always agreement about how to measure the importance of each factor; third, factors other than food and predation may influence social behaviour.

b) The effect of predation pressure on social behaviour.

Group size, its composition, and social interactions between group members may clearly be affected by predation pressure (e.g. Isbell *et al.*, 2003). For example, ill, young, or animals with most evident ornamentation usually are more at risk of predation (Cheney and Wrangham, 1987; Huhta *et al.*, 2003). Moreover, groups are more cohesive and inter-individual distances shorter when predation pressure is high (Barton *et al.*, 1996; Hamilton, 1971). Short inter-individual distances, however, also increase the potential risk of contest competition. This is probably the reason why inter-individual distance during foraging is related to both predation pressure and food distribution (Fairbanks and Bird, 1978).

However, in a recent review on the effect of predation pressure on group size in the primate order Hill and Dunbar (1998) found that the reproductive rate of a species or population was the main factor predicting predation rate (a positive relationship was found between these two variables). When this factor was removed from the analysis no relationship between predation rate and group size was found. Therefore, predation pressure seems to be a secondary factor shaping social behaviour, at least for the primate populations studied by Hill and Dunbar.

c) The effect of food competition on social behaviour.

Although with different emphasis, all theories proposed so far recognise that food competition is an important factor shaping social behaviour. However, many authors also evidence that assessing the relative importance of this factor for social behaviour is a complex matter. It is generally thought that access to food sources is one of the main reasons animals compete as it has fitness effects on individual survival rate and reproductive success (Janson, 1988; Whitten, 1988). Food competition is usually distinguished as indirect (scramble) competition, when some animals remove limited food supplies from an area before other group members can feed, and direct (contest) competition, when high-ranking individuals monopolise access to food or when animals fight over a food item (van Schaik and van Noordwijk, 1988). These two types of competition (both intra- and inter-group) are often found together and their relative importance varies across species and even among populations. It is hypothesised that competition should increase as food becomes less abundant, slowly renewed or depleted (Pruetz and Isbell, 2000; van Schaik, 1989) and under high population densities (Isbell and Young, 2002). Food sources that are more spatially clumped or less divisible can easily be monopolised by dominant individuals (Janson and van Schaik, 1988; Mathy and Isbell, 2001). Moreover, a positive relationship is found between size of food and frequency of aggression (Mathy and Isbell, 2001). Finally, some ecological conditions have to be met for competition over food to take place (Janson, 1988). Firstly, food patch size must be neither so small as to allow only one animal to feed, nor so large as to allow all group members to feed on it. Secondly, inter-patch distance must be greater than the maximum distance individuals are willing to feed apart. Thirdly, if alternative/lower energy food sources are available, subordinate animals will prefer to feed on those (increasing their foraging effort) in order to avoid competition. One problem rises, however, when one has to assess the relative importance of all these factors. For example, imagine a species that affords a period of low food availability (which should result in high food competition) but that this food is dispersed and of low energetic value (e.g. leaves), a situation which should maintain low food competition. Which one of these two factors is most important in affecting the level of food competition? Furthermore, it is still unclear exactly what it is meant by "clumped" or "dispersed" food and how it can be measured (Isbell and Young, 2002; Janson and van Schaik, 1988). This consideration led Isbell and Young (2002) to propose that behavioural interactions between animals (e.g. frequency of aggression during foraging) rather than ecological measures (e.g. patch size) are the easiest data to collect and the most reliable measures of food competition.

d) Additional factors affecting social behaviour.

Many factors other than food or predators may potentially affect social behaviour. Dunbar (1988) proposed that increased foraging efficiency (as groups have more chances to detect clumped and/or concealed food than single individuals) and improved care-giving opportunities (as related individuals may help each other in the care of the infants) are two additional factors that may have favoured the evolution of groups.

Recently, male behaviour and reproductive strategy have been clearly recognised as important factors, particularly in relation to male ability to commit infanticide (Nunn and van Schaik 2000; van Schaik *et al.*, 1999; van Schaik and Janson, 2000). Males of many primate species (especially langurs; Blaffer-Hrdy, 1979) often attempt to kill infants of lactating females in order to stimulate the resumption of oestrus in those females. Infanticidal males are usually foreign and/or subordinate animals who have attained the alpha position in a group (e.g. Soltis *et al.*, 2000). Large groups containing many lactating females attract more infanticidal males than small groups. As a consequence of this, it is hypothesised that female langurs may try to exclude other females from the group or transfer to small groups to reduce the risk of infanticide (Steenbeek and van Schaik, 2001). Moreover, given that transferring into new groups is risky (e.g. Cheney and Seyfarth, 1990b) males (but also females in species with female or no sex-biased dispersal) may prefer to remain in their natal group longer after they reach sexual maturity. These observations indicate that male behaviour is an important, although often ignored, factor that may affect sex ratio, level of competition, and type of social interactions within a group.

Finally, the maximum tolerable group size for a species may also depend on its cognitive capacities (Barton, 1996; Dunbar, 1996). In stable social groups animals need to have some knowledge not only of the type of interactions they exchange with the other group members but also of the type of interactions the other members maintain with one another (Cheney and Seyfarth, 1990a, b; van Schaik and Deaner, 2003). This is crucial information in order to follow effective social strategies such as choosing the best possible group member with whom to form an alliance. In this view, each species has an upper limit of group size, related to its cognitive capacities, beyond which animals are not capable of gathering and memorising sufficient information on the social interactions of all group members (Barton and Dunbar, 1997). Other things being equal (i.e. ecological variables) this limit can affect group size and type of social interaction within a group as non-social factors do.

1.3 Conflict Management.

Conflicts are observable at every biological level, from those occurring between genes to conflicts between parents and offspring, group members or societies (Clutton-Brock, 1991; Keller, 1999). Conflicts are typical of social animals (Lorenz, 1966; Mc Donald and Potts 1994; Neumann, 1999; Peterson and Wrangham, 1996; Preuschoft and Paul, 2000). Indeed, all the theories proposed for the evolution of sociality in primates recognise that there are potential costs associated to group-living (Dunbar, 1988). These costs are related to the risk of conflict between two or more group members for every limited resource, be it food, grooming or mating partner, play companion, or resting place. Group living, however, has to give some benefits to group members (as the vast majority of primate species live in groups; Smuts *et al.*, 1987) and its benefits have to exceed its costs. One way of reducing the costs of group-living would be the evolution of mechanisms that keep situations that increase agonistic behaviour and social tension under control (such as competition over food or mating partners). In fact, social primates utilise different pre- and post-aggression mechanisms to limit the occurrence of conflicts among group members or restore their damage on group cohesiveness (Aureli and de Waal, 2000).

a) Pre-aggression mechanisms.

Studying how primates try to avoid or limit the occurrence of situations that may lead to aggression is a difficult task to deal with as many subtle displays may be used by animals to spot a dangerous situation, the hierarchical status and/or the behaviour of a potential rival (Humphrey, 1976). It is usually thought that primates establish and maintain good relationships with some group members in order to limit the occurrence of conflicts with those animals with whom they share such amicable relationships (Hinde, 1976; Kummer, 1978). In order to form such relationships among group members some conditions have to be met (Cheney and Seyfarth, 1999; Hinde, 1976). First, animals have to individually recognise each group member and remember the quality of their relationships with them (i.e. aggressive or amicable). Secondly, they should be in the same group long enough to form and maintain stable and amicable relationships (see below). However, social interactions among group members occur throughout the day, thus making it difficult to prove a cause-effect relationship between amicable interactions and reduced occurrence of conflicts. This relationship is made more difficult to detect by the fact that behaviours preventing the occurrence of aggressive interactions are also used as post-aggression mechanisms of conflict management (see below).

An effective method to study the type of pre-aggression mechanisms used by primates is to observe animals immediately before or during contexts that are thought to increase social tension (Judge, 2000), such as crowded conditions and feeding time. These studies usually concentrate on grooming exchange as allo-grooming (hereafter grooming) is the main affiliative behaviour that primates use to form or maintain amicable relationships (e.g. Dunbar, 1991). Although many studies indicate that high population density promotes aggression and other behavioural pathologies, "such a density-aggression relationship is overly simplistic" (Judge and de Waal, 1997: p. 643). At least in some primate species (e.g., rhesus macaque, *Macaca mulatta*; Judge and de Waal, 1997) aggression does not increase under crowding conditions whereas rates of affiliative behaviours (i.e. grooming) do so. These behaviours, therefore, may serve to keep aggression under control when risk of conflicts should increase as a consequence of reduced inter-individual distance. These mechanisms, however, differ across experimental situation and individuals within a group (Judge, 2000). For example, tolerance over food is greater the higher the degree of kinship between Japanese macaques (Belisle and Chapais, 2001; but see Ihobe, 1989 for a different result in wild Japanese macaques). Grooming also increases in the minutes before feeding in captive chimpanzees, *Pan troglodytes* (Koyama and Dunbar, 1996), and especially when food is clumped, suggesting that this species is able to foresee and limit the potential risk, on group stability, of conflicts caused by food competition. Moreover, groomees (i.e. animals receiving grooming) were more willing to share food with groomers (i.e. animals giving grooming) if a grooming session preceded food provisioning in captive chimpanzees (de Waal, 1989).

b) Post-aggression mechanisms.

In comparison to mechanisms involved in controlling aggression before it takes place many more researchers have focused their attention on what happens in the minutes following conflicts between group members. De Waal and van Roosmalen (1979) were the first to observe, in a captive group of chimpanzees (*Pan troglodytes*), that former opponents often tend to contact each other in an amicable way in the first minutes after a conflict, and they called this type of interaction "reconciliation". Reconciliation is now defined, in direct relation to the "good relationship hypothesis" (see below), as the "post-conflict friendly reunion of former opponents that restores their social relationship disturbed by the conflict" (Aureli and de Waal, 2000: p. 387). Since it was first observed, many studies have recognised the occurrence of reconciliation in many social primates and other mammals (e.g. marine mammals: Samuels and Flaherty, 2000; domestic goat: Schino, 1998; spotted hyena: Wahaj *et al.*, 2001) and its importance for stable social relationships (see for reviews Aureli and de Waal, 2000; Aureli *et al.*, 2002).

Four hypotheses, not mutually exclusive, have been proposed for the evolution of reconciliation (Kappeler and van Schaik, 1992): 1) the "reconciled hierarchy hypothesis" (de Waal, 1986) predicts that reconciliation is granted by dominant animals in exchange for the formal acceptance of their higher status; 2) the "good relationship hypothesis" (Aureli *et al.*, 1989) states that reconciliation evolved to restore tolerance and the relationship between former opponents, and thus it exists whenever the social relationships is important for the fitness of the animals (e.g., two animals may support each other in agonistic conflicts or may share food sources); 3) the "minimum cognitive capacity hypothesis" (Cheney and Seyfarth, 1990a) states that reconciliation occurs only in those species that have a minimum cognitive capacity; 4) the "benign intention hypothesis" (Silk, 1997) proposes that peaceful post-conflict interactions between former opponents are honest signals evolved to indicate that both the opponents have now benign intentions. Data currently available clearly support the "good relationship hypothesis" (Aureli and de Waal, 2000; Kappeler and van Schaik, 1992). This hypothesis is based on the idea that in social primates, and maybe in other social mammals, each animal establishes and maintains, during the course of his/her life, social relationships with the other group members which differ from one another in quality and intensity (Hinde, 1976; Kummer, 1978). The quality of a relationship is usually characterised by its value ("what the subject gains from her/his relationship with a partner"), its security ("the perceived probability that the relationship with the partner will change"), and its compatibility ("the general tenor of social interactions in a dyad"; all quotations after Cords and Aureli, 2000: p. 178). As a consequence of this, one would expect that former opponents from reconciled conflicts should gain, or re-gain, some benefits (e.g., reduced risk of renewed aggression, tolerance over food sources or access to a grooming partner) that should be precluded to those from non-reconciled conflicts. Moreover, the conciliatory tendency should vary within groups, namely a higher percentage of reconciliation should be found after conflicts between opponents with a "good relationship".

Cords and Thurnheer (1993) set up a series of experiments, using long-tailed macaque pairs (*Macaca fascicularis*), to test these hypotheses. They artificially increased the value of a relationship between two monkeys, training them to perform a cooperative task in which the animals had access to food only if they were simultaneously feeding close to each other. Then, the reconciliation rate for each pair was measured and compared with the baseline rate (in both the cases the conflicts were experimenter-induced). The reconciliation rate after training was three times higher than the baseline. This result shows that monkeys gain some benefit by reconciling as the victim of the conflict was allowed by the aggressor to access the same food source (see also Cords, 1992). Moreover, it indicates that the occurrence of reconciliation is greatly affected by the quality of the relationship between two animals (measured by the amount of cooperative tasks performed in the training sessions).

Many studies have determined that victims of aggression, after a conflict, show an increase of self-grooming and scratching, behaviours that indicate distress and anxiety in primates (Maestripieri *et al.*, 1992; Schino *et al.*, 1996). The rate of these behaviours remains high if a conflict is not reconciled, whereas it drops almost immediately to baseline levels when reconciliation occurs (Aureli and van Schaik, 1991; Kutsukake and Castles, 2001). This is due to the fact that reconciliation reduces the chances of future conflicts and restores the tolerance between former opponents, thus reducing their anxiety (Aureli, 1997; Kappeler and van Schaik, 1992).

Clearly, animals establish and maintain good relationships especially with certain group members, such as relatives, allies, and potential mates (Kappeler and van Schaik, 1992). Many studies have shown that the conciliatory tendency is higher after conflicts among kin than between non-kin (Aureli *et al.*, 1997; Schino *et al.*, 1998) and when social relationships and alliance partners are well-established (Castles *et al.*, 1996). Regardless of the quality of the relationship between two opponents, conciliatory tendency may also vary depending on the context of the conflict. For example, Aureli (1992) found that in wild long-tailed macaques (*Macaca fascicularis*) the rate of occurrence of reconciliation was considerably lower following conflicts over food than those occurring in other contexts. To explain these results, he suggested that social relationships might not be endangered by food competition as food-related aggressions would be limited to the displacement from the food sources, not disrupting the relationship between the opponents.

In some primate species conflict resolution follows more complex patterns (Judge, 1991). Third parties may play a major role in the occurrence and resolution of conflicts as they may reassure and console the victim (e.g., reduce his/her anxiety by means of affiliative behaviours; de Waal and van Roosmalen, 1979; de Waal and Yoshihara, 1983), or function as allies, thus supporting the aggressor during the conflict or helping the victim to avoid further aggression (Bernstein and Erhardt, 1985). Moreover, victims of aggression may redirect aggression against the aggressor kin, functioning as a "revenge" system, or against a third, usually subordinate, individual to divert the attention of the former aggressor (Aureli *et al.*, 1993; Cheney and Seyfarth, 1989).

The "good relationship hypothesis" provides a framework where the species-specific differences in ecology, sex-biased philopatry, genetic relationship, and social structure can be combined to predict the occurrence and distribution of reconciliation and vice-versa, (Aureli *et al.*, 2002; Thierry, 2000). Stable relationships, and thus high reconciliation tendencies, are more easily established and maintained by animals who remain in the same social group for long periods than by animal who move from one group to another many times during their lifetime. Moreover, closely-related individuals usually exchange higher frequencies of amicable interactions, cooperate, and reconcile more often than unrelated animals (e.g. Schino *et al.*, 1998). Finally, the occurrence of reconciliation is affected by the species-specific pattern of competition observed (van Schaik, 1989). Overall, species with a strict and linear dominance hierarchy (i.e. despotic species) have a lower frequency of reconciliation than species with less defined dominance-subordinance relationships among group members (i.e. egalitarian species).

Macaques are the perfect animals on which to test these predictions as they form large multi-male/multi-female groups, females are usually philopatric and often have some closely-related female in their group, and their dominance hierarchy is nepotistic and based on matrilines (Melnick and Pearl, 1987). Moreover, differences exist among species in dominance gradient and rigidity of the hierarchy (Petit *et al.*, 1997; Thierry, 2000). As predicted by the "good relationship hypothesis", reconciliation tendency in macaques is higher for kin than for non-kin (this effect being stronger the more despotic the species is; Aureli *et al.*, 1997), after conflicts among females than among males (Kappeler and van Schaik, 1992), and for species with a higher social tolerance over food sources (Thierry, 2000).

1.4 Ecology and Social Behaviour of Japanese Macaques Living on Yakushima Island, Japan.

Yakushima Island (see Chapter 2 for details on the study site) is inhabited by an endemic sub-species of Japanese macaque (*Macaca fuscata yakui*). Since 1973 different groups of macaques living in the lowland forest of the western slope of the Island have been habituated and studied by Japanese researchers (Yamagiwa *et al.*, 1998). Yakushima macaques differ from the other sub-species living on the mainland (*Macaca fuscata fuscata*) as they have slightly smaller body size and different behavioural ecology (Yamagiwa *et al.*, 1998).

a) Ecology.

Yakushima macaques are generalist foragers, feeding on fruits, seeds, and leaves in different proportions throughout the year (Agetsuma, 1995a,b; Hill, 1997; Maruhashi, 1980). Small animals (mainly insects and spiders), fungi, and other plant parts (e.g. flowers) are also eaten when available. Previous studies have shown that foraging effort is greatest and time spent moving least when monkeys are feeding on leaves and when temperatures are low (Agetsuma, 1995a).

Because of the peculiar habitat characteristics found in Yakushima (i.e. sub-tropical ever-green forest vs. temperate deciduous forest on the mainland; Yamagiwa *et al.*, 1998), the ecology and social behaviour of Japanese macaques living on the coastal area of the island are different from those of northern populations (Nakagawa, 1998). Home ranges are smaller in Yakushima, they overlap with those of neighbouring groups (up to 50% of the area), and, as a consequence of this and of the high population density found on the island, inter-group encounters are frequently observed (Maruhashi *et al.*, 1998). The high frequency of inter-group encounters and the fact that they are usually characterised by aggressive interactions has led some authors to postulate that inter-group contest food competition is high on the island (Maruhashi *et al.*, 1998; Sugiura *et al.*, 2000). However, the large overlap between neighbouring home ranges (which implies that groups do not actively defend their home range's boundaries) would suggest that competition is more scramble than contest (e.g. Janson and van Schaik, 1988). Moreover, a high level of contest inter-group food competition should in theory favour large groups as they should be more able to defend food sources than small groups (Wrangham, 1980). In support of the view that inter-group competition for food is more scramble than contest is the observation that the average group size is small in Yakushima (26.6 animals, in comparison to 37.7 animals for groups living on Kinkazan Island; Sprague *et al.*, 1998) and large groups tend to fission when they reach around 50 units (Maruhashi, 1982). Group fission, however, may also be due to a high level of intra-group direct food competition (Nakagawa, 1998). Therefore, at the present stage of our knowledge we cannot give a definitive answer on the type of food competition among Yakushima macaques and on its importance for group size.

b) Social behaviour.

Japanese macaques belong to the Cercopithecidae family (Melnick and Pearl, 1987). Males usually leave their natal group when they reach adulthood and may move from one group to another several times during their lifetime (Muroyama *et al.*, 2000; Yoshimi and Takasaki, 2003). Conversely, females are philopatric and rarely disperse. However, when group size decreases dramatically (e.g. N = 1-3 adult females) females have been observed to successfully join larger groups in Yakushima (Sugiura *et al.*, 2002; Takahata *et al.*, 1994). Both male and female Japanese macaques show a strict and linear dominance hierarchy (Alexander and Bowers, 1967; Chapais *et al.*, 1991). Previous studies have never observed a percentage of reconciled conflicts greater than approximately 20-30% of total conflicts (Aureli and de Waal, 2000). As a consequence of these observations, Japanese macaques (together with rhesus macaques) are considered to be the most despotic macaque species (Chaffin *et al.*, 1995; Thierry, 2000). Fully-adult males are usually dominant over females although coalitions among females may outrank them as the two sexes do not considerably differ in size or canine length (Watanabe, 1979).

Females are organised into matrilines composed of closely related individuals (Chapais *et al.*, 1995; Melnick and Pearl, 1987). In Japanese macaques dominance relationships between females belonging to the same matriline follow the youngest ascendancy rule (also known as the Kawamura's rule; Kawamura, 1958): the youngest daughter of a female ranks immediately after her mother and above all her older sisters (Hill and Okayasu, 1996; Koyama, 2003). However, this is not the case of Yakushima macaques where the oldest female is usually dominant over her younger sisters. This is probably due to the fact that agonistic support among females is rarely observed in Yakushima and thus youngest daughters do not receive any help from their mothers during agonistic interactions with their older sisters (Hill and Okayasu, 1995). Hill and Okayasu argue that high agonistic support and youngest ascendancy typically occur when resources are concentrated and agonistic interactions over these resources frequent. This conclusion represents additional support for the view that direct food competition is not particularly high in Yakushima (see above).

Given that females are the philopatric sex in this species and that, unlike males, they often have some related animal in the group, amicable interactions (mainly through grooming exchange), reconciliation, and coalitions occur with higher frequency among females than among males (although this may not apply to Yakushima macaques; see above), and especially among females belonging to the same kin-group (e.g. Nakamichi and Shizawa, 2003). Indeed, amicable interactions are rarely observed among male Japanese macaques. Conversely, males compete for the highest-ranking positions in the group and high-ranking monkeys aggressively attempt to exclude lower-ranking males from access to oestrous females (Soltis *et al.*, 2001; Takahashi, 2002).

It is usually though that grooming gives some benefits to animals exchanging this behaviour. These benefits may be agonistic support, tolerance over food sources, and/or grooming *per se* (as grooming also contribute to the care of the pelage; Zamma, 2002). If this is true, the benefits gained by a female are greater the higher the rank of her grooming partner (as, for example, high-ranking animals are more valuable allies than low-ranking animals). This is the reason why primates compete for access to preferable grooming partners (e.g. Palombit *et al.*, 2001; Watts, 2000). Competition for grooming partners, therefore, results in the fact that high-ranking females receive more grooming than low-ranking females (Seyfarth, 1977, 1980). At the same time, high-ranking females are less constrained by this competition than low-ranking females. As a consequence of these considerations, matrilines formed by high-ranking females are expected to be more cohesive (as measured by the amount of grooming exchanged) than matrilines formed by low-ranking females (Barrett and Henzi, 2001, 2002; Schino *et al.*, in press).

1.5 Aims.

Even though most of the studies on conflict management have focused on primate species, very few of them have been conducted in the field. It is still largely unclear how primates manage conflict occurrence and resolution in their natural habitat, and especially in contexts (e.g., while feeding) where social tension and risk of conflict is high. Data are also scarce on how variations in activity budgets and/or group size affect conflict management. Moreover, studies have often neglected to analyse in depth how affiliative behaviour and reconciliation occur among male macaques. This is because males are expected to compete for mating partners and do not maintain amicable relationships with the other group males.

The current study, therefore, focuses on wild, non-provisioned Japanese macaques (*Macaca fuscata yakui*) living at Yakushima Island, Japan, and analyses different aspects of conflict management in this species. Chapters 3 to 7 will specifically aim to determine if and how:

1. Activity budgets, diet composition, and home range size vary across the months and in relation to group size (Chapter 3).
2. Grooming distribution, frequency of aggression and reconciliation, and level of direct intra-group food competition are affected by variations, discussed in Chapter 3, in activity budgets and diet composition (Chapter 4).
3. Group size influences grooming distribution, frequency of aggression and reconciliation, and food competition (Chapter 5).
4. Reconciliation among males occurs with similar frequencies and following similar patterns to those observed among females. The relationship between frequency of reconciliation and inter-group encounters will also be analysed (Chapter 6).
5. Frequency and type of inter-group encounters are related to food abundance. Moreover, the effect of sex, age, rank, and period of the year (i.e. mating vs. non-mating season) on monkey participation in inter-group encounters, and their consequences on male transfer will be analysed (Chapter 7).

Chapter 2

General Methods

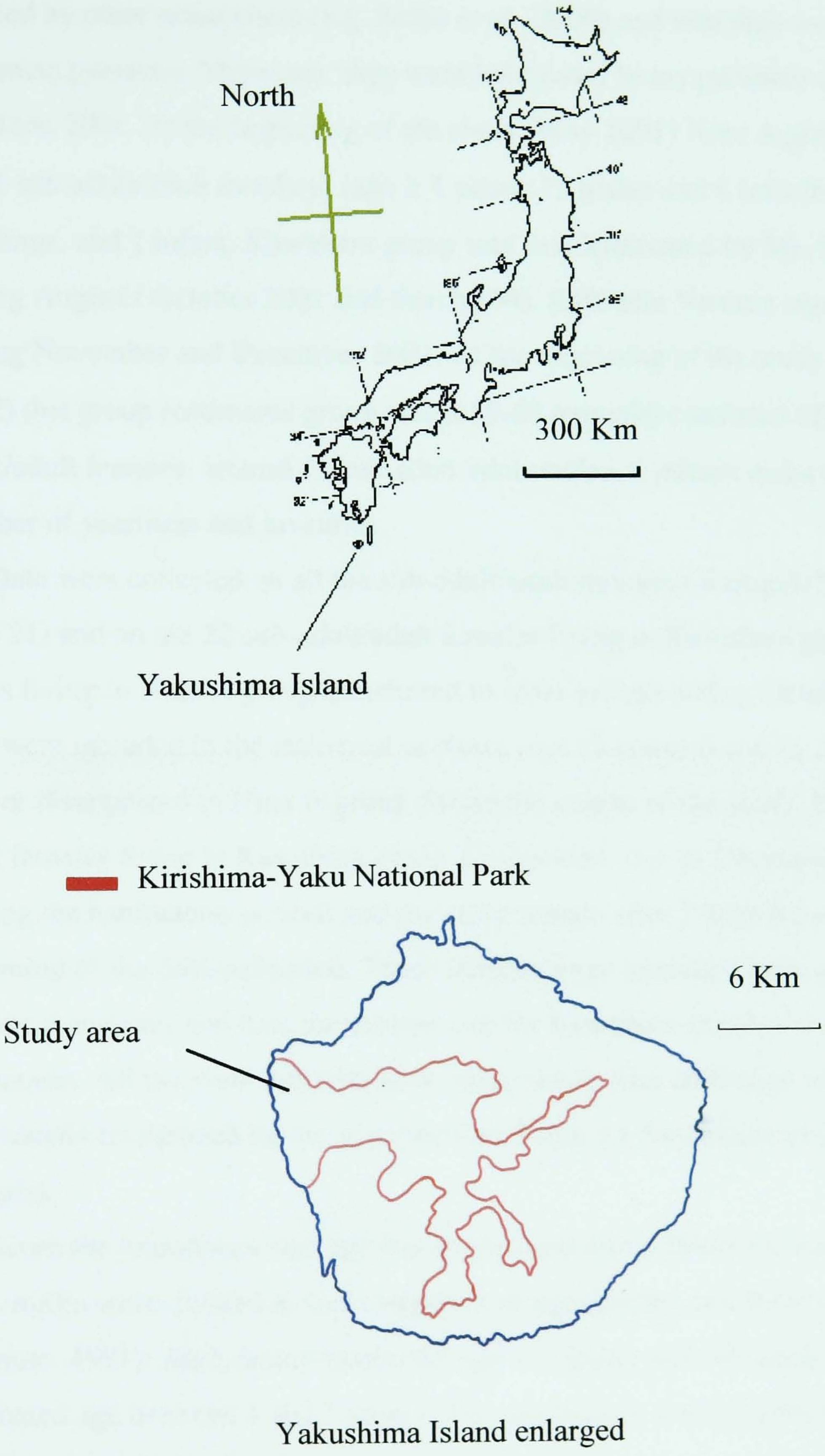
2.1 Study Area and Subjects.

a) Study area.

Yakushima is a volcanic Island of around 500 km^2 located 60 km south of Kyushu, Japan (31°N, 131°E; see Figure 2.1). The Island is covered with a warm temperate evergreen forest on the coast (where the study area is), approximately up to 400 m above sea level, and with a deciduous forest on the mountains. The highest peak of the Island is 1,935 m a.s.l. The coastal forest is part of the Kirishima-Yaku National Park that covers most of the mountains of the Island. Although a road crosses the western slope of the Island, human activities (e.g. logging or tourist access to the area) and food provisioning to macaques are prohibited in the study area. As such, Yakushima represents one of the few areas of Japan where ranging patters and social behaviour of Japanese macaques is scarcely affected by human presence.

Dominant tree species on the coastal forest are *Distylium racemosus*, *Ficus superba*, *Ficus microcarpa, Camelia japonica*, and *Ardisia sieboldii* (Yamagiwa *et al.*, 1998). Temperature ranges from a minimum of about 3°C to a maximum of about 32°C, rainfall is between 100 and 400 mm each month but it is higher than 400 mm in June, which is the peak of the rainy season (Hill, 1997). Japanese macaques and sika deer (*Cervus nippon*) are the only large mammals living on the Island and no natural predators are present (Agetsuma *et al.*, 2003).

Figure 2.1: Map of Japan; Yakushima Island is enlarged and the approximate position of the study area is indicated.



b) Study subjects.

Subjects of this study were two groups of Japanese macaques living in two neighbouring valleys around 1 Km apart. One group (Nina A) was previously studied by other researchers (e.g. Soltis *et al.*, 2000) and was thus well-habituated to human presence. Moreover, they were habituated to my presence during May and June 2001. At the beginning of the study (May 2001) Nina A group consisted of 21 sub-adult/adult monkeys (age $\geq$ 4 years; 13 males and 8 females), 3 yearlings, and 1 infant. Kawahara group was first habituated by Mr. Hiroki Koda during August / October 2001 and then by Ms. Raffaella Ventura and myself during November and December 2001. At the beginning of the study (January 2002) this group (estimated group size $\cong$ 55-60 animals) consisted of 22 sub-adult/adult females, around 15 sub-adult/adult males, 3 infants and a not definite number of yearlings and juveniles.

Data were collected on all the sub-adult/adult monkeys living in Nina A group (N = 21) and on the 22 sub-adult/adult females living in Kawahara group. Seven males living in Nina A group transferred to other groups during October 2001 but they were included in the statistical analyses (see Chapters 6 and 7). No monkey died or disappeared in Nina A group during the course of the study. However, 2 adult females living in Kawahara group disappeared: one in December 2001 (during the habituation period) and the other female after 7 days from the beginning of the data collection. These females were excluded from all the statistical analyses and thus the sample size for Kawahara females was reduced to 20 females. All the monkeys who were subjected to data collection were individually recognised by the observer (see Table 2.1 for details on the study animals).

Given the importance that age has on size and social status for male macaques, study males were divided in two categories of age (Hanby and Brown, 1974, Enomoto, 1981): adult males (estimated age > 7 years) and sub-adult males (estimated age between 4 and 7 years). This distinction was not considered to be important for females and thus it was not used for statistical analyses (Enomoto, 1974). Back-record information, grooming interactions between males and females, and age were used to assign Nina A males to one of the two categories:

natal male (i.e. male born in the study group, see Table 2.1) and non-natal male (i.e. male born in an unknown group and transferred to one of the study groups). Females were all considered to be born in the study groups. In this thesis, the mating season was considered to last from the first to the last recorded consortship in which sexual mounts were observed (Hanby and Brown, 1974).

Table 2.1: Details of the study animals (* males who left Nina A group during the course of the study; see below for explanations).

Nina A females (data collected from June 2001 to May 2002)

Monkey	Hrs of focal data / Hrs from Jan to May 2002	Rank
Syako	18.4 / 8.9	1
Shijimi	17.5 / 8.8	2
Hanabi	18.8 / 8.1	3
Yamaimo	18.4 / 9.3	4
Yamayuri	18.7 / 8.4	5
Ramu	18.3 / 8.0	6
Hotate	18.3 / 8.9	7

Hotaru	17.5 / 8.7	8

Kawahara females (data collected from January to May 2002)

Monkey	Hrs of focal data	Rank
Zina	7.4	1
June	7.3	2
Livia	7.7	3
Doris	7.7	4
Zazie	7.3	5
Blanche	6.9	6
Hannah	6.4	7
Nobuko	7.1	8
Fumiko	7.5	9
Miyo	6.5	10
Chichi	4.1	11

Chocolat	7.1	12
Anie	7.5	13
Kiki	7.0	14
Anne	7.1	15
Olive	6.9	16
Sara	7.3	17
Raffi	7.0	18
Eli	7.0	19
Eliza	7.1	20

Nina A males (data collected from June 2001 to May 2002)

Monkey	Hrs of focal data	Rank	Age	Origin
Shark	14.4	1	Adult	Non-natal
India	16.0	2	Adult	Non-natal
Momo *	7.9	3	Adult	Non-natal

Babe	11.8	4	Adult	Non-natal
Syachihoko *	7.2	5	Sub-adult	Natal
Jacknife	12.8	6	Adult	Non-natal
Shishi *	6.3	6	Sub-adult	Natal
Noritama	11.9	8	Sub-adult	Non-natal
Roku	13.0	9	Sub-adult	Non-natal
Byakko *	5.9	10	Sub-adult	Non-natal
Rakko *	7.3	11	Sub-adult	Natal
Josif *	6.1	12	Sub-adult	Non-natal
Bino *	8.5	13	Sub-adult	Non-natal

2.2 Data Collection.

Data on social interactions (see Section 2.2c) were collected by two observers: myself and Ms. Raffaella Ventura. Data collection began when inter-observer agreement was over 95%. In order to avoid repetitions, the Methods sections of Chapters 3 to 7 will only contain specific details not given here in Chapter 2.

Data on Nina A were collected from the 22nd June 2001 to the 4th May 2002 whereas data on Kawahara group were collected from the 24th January to the 4th May 2002. During the data collection, there were only two intervals longer than 3 days: from the 2nd to the 10th of September 2001, and from December 20th 2001 to January 23rd 2002.

This study covers different aspects of the behavioural ecology of the Japanese macaques. Therefore, data were collected following three different sampling methods (i.e. *ad libitum*, scan, and focal sampling) and three sampling rules (i.e. instantaneous, all occurrences, and one-zero; Altmann, 1974; Martin and Bateson, 1993). Observation sessions were grouped into five different categories in relation to the type of behaviour recorded (see below). All behaviours recorded in this study are defined in Table 2.2.

Table 2.2: Definitions of the behavioural categories recorded (S: behavioural state; E: behavioural event; * data collected only during scan-sampling sessions; ** data collected only during focal-sampling sessions and PCs-MCs; aggressive or submissive behaviour were also recorded *ad libitum*).

Behaviour	Definition
Moving (S)	The monkey is moving but is not engaged in other behaviours (e.g., foraging or agonistic behaviours)
Resting (S)	The monkey is not moving or feeding nor is it involved in social or agonistic behaviours
Foraging (S)	The monkey is gnawing, searching for food or is picking up food items, and this activity is not interrupted by pauses of longer than 1 minute (Whitten, 1988). During foraging, the food category (i.e. fruits, seeds, leaves and other plant parts, fungi, and animals) eaten by the monkey is recorded

Grooming (S) **	The monkey grooms (defined as picking through and/or slow brushing aside the fur of another individual with one or both hands), or is groomed by another individual and this activity is not interrupted by pauses longer than 30 seconds
Self-grooming (S) **	The monkey grooms itself and this activity is not interrupted by pauses longer than 30 seconds
Scratching (E) **	The monkey repeatedly and rapidly moves its hand or foot drawing its fingertips across its own fur (Schino *et al.*, 1988)
Yawning (E) **	The monkey opens its mouth for a few seconds with a movement closely resembling that by humans (Schino *et al.*, 1988)
Body-shake (E) **	The monkey shakes its entire body, similar to that of a wet dog (Schino *et al.*, 1988)
Aggressive behaviour (E) **	This category includes threat (the monkey opens its mouth without showing its teeth, flaps its ears, stares at its opponent, or slaps its hand on the ground), chase, and physical assault (the monkey attacks another animal biting, grabbing, or slapping him/her) towards another individual
Submissive behaviour (E) **	The monkey flees when approached by another individual or direct "bared-teeth display" to it (de Waal and Luttrell, 1985)
Sitting in contact (E) **	The monkey is embracing another individual or a significant portion of its body is in contact with the body of another individual

Social play (E) **	Highly active and non-aggressive social behaviour (including "rough and tumble" and chasing).
Lip-smacking (E) **	The monkey thrusts forward and purses its lips flat, sometimes with rapid movements of the lips. There is not tongue protrusion and this behaviour grades into chewing movements (Kurland, 1977)
Genital inspection (E) **	The monkey gentle touches with its hand, or directs its muzzle towards and smells, the genital area of another individual or receives this behaviour (Enomoto, 1974)
Muzzle contact (E) **	The monkey directs its muzzle towards, touches or smells, the muzzle of another individual, and/or receives this behaviour (Enomoto, 1974)
Socialising (S) *	The monkey grooms another individual (see above for definition), receives grooming, is sitting in contact with another individual, or is engaged in social play, lip-smacking, genital inspection, or muzzle contact
Other (S) *	The monkey is involved in sexual or agonistic interactions with other individuals

a) Dominance/subordinance relationships.

Data on the dominance/subordinance relationships among the study animals were recorded *ad libitum* every time one monkey avoided or was displaced by another monkey in a non-agonistic context. Moreover, data on conflicts between two monkeys, not involving third parties, and with a clear-cut result (i.e. decided: one of the opponents showed clear signs of submission) were used for the same purpose. The hierarchical status of the monkeys was analysed separately for Nina A males and females. All the agonistic interactions observed were entered into matrices (see Tables 2.3 to 2.5) and analysed using MatMan 1.0 that assigned a hierarchical rank to each animal. The value one was given to the highest-ranking male/female, two to the beta individual, and consequently to the following monkeys. The percentage of decided agonistic interactions for Nina A females was 99.5% and it was 100% for both Kawahara female and Nina A males.

b) Activity budgets and diet composition.

Scan sampling was used to analyse activity budgets and diet composition of the study animals. Every hour the activity of all the visible study animals (i.e. foraging, moving, socialising, resting, or other; see Table 2.2 for definitions) was recorded using instantaneous sampling. When monkeys were observed foraging, the food category eaten by each monkey was recorded. Five food categories were considered: fruits, seeds, leaves and other plant parts (e.g. flowers, bark, or sap), fungi, and animals (Agetsuma, 1995a). For each monkey, data collected on activity budgets and diet composition were transformed into percentages of time spent displaying each behaviour using the formula:

(N of scans for each behaviour / Total N of scans for each monkey) x 100

When data were analysed using monthly scores, data collected on the study monkeys on each month were pooled together and percentages of sample points obtained accordingly.

Table 2.3: Dominance matrix for Nina A females (N = 8) showing the number of aggressive interactions with a clear-cut result per dyad.

Aggressor	Victim							
	Syako	Shijimi	Hanabi	Yamaimo	Yamayuri	Ramu	Hotate	Hotaru
Syako		1	7	24	11	9	7	13
Shijimi			14	19	15	1	1	8
Hanabi				25	25	22	15	17
Yamaimo					32	12	13	22
Yamayuri						17	6	13
Ramu							1	25
Hotate								17
Hotaru								

Table 2.4: Dominance matrix for Kawahara females (N = 20) showing the number of aggressive interactions with a clear-cut result per dyad (the Table continues on the next page).

Aggressor	Victim																			
	Zina	June	Livia	Doris	Zazie	Blanche	Hannah	Nobuko	Fumiko	Mijo	Chichi	Sara	Anie	Kiki	Anne	Olive	Chocolat	Raffi	Eliza	Eli
Zina		1	5	2	1	1		1	3		2	3	6	2	1	3	1	2	1	1
June			1	6	9	1	1	2		1		4	8	1	1	1	5	2	2	3
Livia				1	7	1	2	2				3	6	1			3	2	1	
Doris					8	1		4	2	4			2	4	3	1	4	4		1
Zazie							8	2	1	3	1	7	3	3	3		5	4		2
Blanche							4		1	1	1		3	2	1		3	3		
Hannah									3	1		1	1		1	1		2		2
Nobuko									3			2	2	4		1				
Fumiko												1	7	3	1	3	2	1	2	1
Mijo													1					3		2
Chichi												1								
Sara																	1	1	4	7
Anie														2	2	3				2

Kiki	5	7				
Anne		1	1	1		
Olive			1			2
Chocolat					2	6
Raffi					1	2
Eliza						
Eli						

Table 2.5: Dominance matrix for Nina A males (N = 13) showing the number of aggressive interactions with a clear-cut result per dyad.

Aggressor	Victim												
	Shark	India	Momo	Syachihoko	Babe	Jacknife	Shishi	Noritama	Roku	Byakko	Josif	Rakko	Bino
Shark		56	14	9	22	18	21	15	44	9	1	4	2
India			5	4	12	6	8	8	21	2	2	1	3
Momo				1	7	4				1	4		2
Syachihoko						2	8	2	1	2		3	
Babe						23	3	4	16				2
Jacknife								2	32			1	6
Shishi										1	2	4	
Noritama									11			1	2
Roku										1	1		9
Byakko											5	6	1
Josif													5
Rakko													
Bino													

c) Social interactions.

Focal animal sampling was used to record social interactions among the study animals. Observation sessions lasted 10 minutes and between 3 and 6 sessions per week were collected on each monkey. Observation sessions were distributed approximately equally from 8.00 to 19.00 for each monkey (see Table 2.1 for the amount of hours collected on each study animal). All occurrences sampling was used to obtain the frequency of behavioural events (i.e. events / hr; see Table 2.2) and the duration of behavioural states. For each monkey, behavioural states were then transformed into percentages of time spent displaying each behaviour following the formula:

$$(\text{Total minutes for each behaviour} / \text{Total minutes collected on each monkey}) \times 100$$

In case the focal animal could not be followed for the whole duration of the session, all the observation sessions lasting 6 minutes or more were retained while the others were discarded. If the focal animal was involved in an agonistic interaction within the last 5 minutes of the session, the session was continued for an additional 5 minutes after the occurrence of the conflict and these data were considered as a post-conflict session (see below).

d) Post-conflict behaviour.

Post-conflict-matched-control (PC-MC) observations were collected following the method used by de Waal and Yoshihara (1983) to analyse the occurrence of reconciliation, and of other post-conflict behaviours. Post-conflict sessions started within 30 seconds after an agonistic interaction (but the session was stopped if the conflict started again within 30 seconds) on the victim or the aggressor, lasting 5 minutes. For each aggressive interaction, the identity of the animals involved, the intensity of the attack (i.e. threat, chase, slap, or bite), the distance between former opponents at the beginning of the session, the cause or context of conflict (i.e. foraging, grooming, mating partner, or other: play, moving, resting) were recorded. For conflicts occurring during foraging, data were collected on whether the victim and/or aggressor left the food patch immediately after the conflict. A food patch was defined as a discrete area within which individuals were able to collect food continuously as they moved within it (therefore, a patch could contain more than one food type; White and Wrangham, 1988; Whitten, 1988). In addition, the outcome of the conflict was recorded: a conflict was decided only if one monkey displayed a clear submissive behaviour towards the other individual involved. All the behaviours recorded in c) were collected with the same sampling techniques. Moreover, time elapsed (seconds) from the end of the conflict to the first affiliative contact between former opponents was recorded. On the next possible day, a matched-control observation was made on the same animal (victim or aggressor) using the same sampling methods. The session was postponed for at least 10 minutes if the focal-animal was involved in an agonistic interaction within 3 minutes before a planned MC (Aureli *et al.*, 1993). The session only started when the activity of the focal animal was similar to that of the PC and his/her former opponent was visible and at the same distance as when the PC was started. If these conditions were not met within 2 weeks, the PC was discarded. Observation session c) was stopped if a conflict between two animals (not involving the focal animal) was observed meanwhile or the conditions for an MC occurred. PCs-MCs were collected on either the victim or the aggressor, with care taken to collect data evenly on both. Moreover, PC-MCs were collected for as many different dyads as possible. Each PC-MC pair was assigned to one of the following three groups according to the timing of the first affiliative interaction between former opponents in the two observation sessions: 1) "Attracted" pair: affiliative interaction between former opponents was observed earlier in the PC than in the MC, or only in the PC; 2) "Dispersed" pair: affiliative interaction between former opponents was observed later in the PC than in the MC, or only in the MC; 3) "Neutral" pair: affiliative interaction between former opponents was observed at the same time in the PC and the MC, or was never observed in the two sessions. Once all the PC-MC pairs were divided into these three groups conciliatory tendency per individual or per dyad was measured following the formula (Veenema *et al.*, 1994):

(Number of "attracted" pairs – Number of "dispersed" pairs) /
Total number of PC-MC pairs

This formula controls for the baseline level of affiliation between former opponents and is independent of the length of the observation (Veenema, 2000). Therefore, it is an appropriate measure to compare reconciliation between different individuals, dyads, or groups. Conciliatory tendency was only measured when at least two PCs-MCs pairs were available for each monkey or dyad.

e) Inter-group encounters.

An inter-group encounter was considered to occur when monkeys from different troops were in visual contact. Frequency of inter-group encounters (i.e. N of encounters / hr) was obtained by dividing the number of encounters observed by contact time with the study group. Contact time was recorded every day in which the study groups were found (see Chapter 7 for details on the data collected during inter-group-encounters). The monkeys living in the neighbouring groups were well-habituated to human beings. As such, our presence did not affect their behaviour during inter-group encounters. Observation sessions 2.2a, b, c, and d collected within one hour before or after the occurrence of an encounter were discarded to avoid any effect of inter-group encounter on social interactions within the study groups.

2.3 Data Analysis.

Data were analysed using non-parametric statistics (Siegel and Castellan, 1988; Everitt, 1996; Howell, 1999), even when sample size and normality of data allowed the use of parametric tests, in order to have comparable results throughout the thesis. All the tests were two-tailed and significance was set at $p < 0.05$. The particular statistical tests used in this thesis will be discussed in the Methods Section of each of the following chapters.

Chapter 3

Activity Budgets and Diet Composition in Nina A and Kawahara Females

This chapter focuses on the females (age ≥ 4 years old) living in Nina A and Kawahara group. For the study year as a whole, activity budgets and diet composition of Nina A females (N = 8) were analysed across the months. Data collected from January to May 2002, on Nina A and Kawahara (N = 20) females, were used to determine if activity budgets, diet composition, and home range size were affected by group size.

3.1 Introduction.

Access to food sources is one of the main reasons for animals to compete (Janson, 1988) as it affects an individual's survival rate and reproductive success (e.g. Barton *et al.*, 1996; Cheney and Seyfarth, 1987; Whitten, 1988). The level and type of food competition within a group, however, is related to habitat characteristics such as food abundance and distribution (Janson and van Schaik, 1988; Johnson *et al*, 2002; White and Wrangham, 1988; see Chapter 1). At the same time, the level and type of food competition has important effects on group size, activity budget, day range, and social behaviour of a species (Gartlan, 1968; van Schaik, 1983; Wrangham, 1980). For this reason, many studies have attempted to analyse the relationship between all of these factors (e.g. Wrangham *et al.*, 1993). One consistent finding of these studies appears to be the observation that the relationship between ecological factors and social behaviour is different for frugivorous and for folivorous species (Janson and Goldsmith, 1995). This result is due to the difference between fruits and leaves in terms of their energetic value, digestion speed, availability and distribution in a given area (Dunbar, 1988). These differences clearly have profound effects on the movements, activity budgets and social behaviour of a species. In this view, the Japanese macaques living in the coastal forest of Yakushima represent a good opportunity to analyse how variations in diet composition and activity budgets affect food competition and social behaviour. Yakushima macaques show seasonal variations in the use of different food categories, feeding especially on leaves from February to April, on fruits from May to August, and on seeds in September and October (Hill, 1997). Moreover, ecological surveys conducted on the island have shown that food abundance is high in the study area (i.e. 2.417 trees / ha; Maruhashi *et al.*, 1998; see also Agetsuma and Nakagawa, 1998) and that fruit- and seed-food trees are more clumped than leaf-food trees (Agetsuma, 1995a). In light of the difference between fruits and seeds and leaves in terms of distribution and of consumption rate by the monkeys the aims of the first part of this chapter was to determine the relationship existing between day-range, activity budgets, and diet composition among Nina A females. Moreover, it aimed to identify two periods of the year that differed in activity budgets and diet composition in order to analyse (in Chapter 4) how these differences affected the level of within-group contest food competition and the quality and quantity of social relationships among females.

Living in large groups has associated benefits and costs for animals. The benefits are: 1) That animals living in large groups may monopolise food sources better than those living in small groups when between-group food competition is high, and 2) That they should detect predators more easily (although this factors does not apply to Japanese macaques as no predators live on Yakushima; see Chapter 1). However, the costs are that the depletion rate of a given area is higher for large groups than for small groups, if food abundance and distribution are similar (van Schaik *et al.*, 1983). Within-group food competition, therefore, increases as group size increases. This results in larger home ranges, longer day-range, and greater foraging effort (i.e. time spent actively searching for food and feeding) for animals living in large groups compared to those in small groups (Chapman and Chapman, 2000). The relationship between foraging effort and group size, however, in still unclear as some studies found a positive correlation between these two variables while others found that foraging effort was unaffected by group size (Henzi *et al.*, 1997b; Mc Farland Symington, 1988; Stacey, 1986). Beside these observations, time is an important constraint for wild primates and it has profound effects on their activity budgets (Dunbar, 1992). Even if two groups do not differ in the time they devote to foraging and thus in the time left for other activities (e.g. grooming exchange), for a given amount of time one monkey in a small group has more opportunities to groom all the potential grooming partners than one female in a large group. Indeed, female baboons have been observed to concentrate their grooming effort towards few grooming partners when group size reaches a given size rather than try to exchange short grooming bouts with as many partners as possible (Henzi *et al.*, 1997b). Given the importance that grooming has as a means to keep competition and aggression under control (e.g. Dunbar, 1991) small groups are expected to be more cohesive than large groups. Therefore, the aims of the second part of this Chapter were to analyse how activity budgets, diet composition, and day range differed between a large and a small troop of Japanese macaques. Based on these comparisons, Chapter 5 will analyse how social behaviour and conflict management are affected by group size.

3.2 Methods.

a) Study subjects and data collection.

Subjects of this study were all the females living in Nina A and Kawahara troops (N = 8 and N = 20, respectively; see Chapter 2). Data collected on females from Nina A troop were used to analyse seasonal variations in activity budgets and diet composition (from June 2001 to May 2002). In these analyses, data collected each month were pooled together. However, data collected in June 2001 and in January and May 2002 were excluded because of the small amount of data collected in those months (see Chapter 2). Females living in the two troops were used to determine the effects of group size on activity budgets and diet composition. To this end, the data collected from January to May 2002 on each study troop were pooled together. Data on activity budgets and diet composition were obtained from scan sampling while frequencies of female-female aggression were obtained from focal sampling (see Chapter 2).

Home range size may be measured with many different methods (Singleton and van Schaik, 2001). In this study, the method used by Stoner (1996), among others, was followed (Powell, 2000). That is, all the movements of a group were plotted as lines on a 1:10.000 map. Then, a grid, comprising cells of 0.25 ha (50 x 50 metres), was superimposed on the map and all the quadrats that were entered by the monkeys were considered to be part of the group's home range. The size of these quadrats was considered to yield reliable data and the best approximation of the real home range size (in comparison, for example, to 100 x 100 metres cells; Palacios and Rodriguez, 2001). Day-range (expressed as metres travelled by the monkey per hour) was obtained by measuring the length of each line plotted on the map, representing the group's movements (Defler, 1996). One-zero sampling was used to calculate the dispersion of the study females. Data were collected on the identity of all the females seen, at least once, during each observation day. These data were then divided by the total group size of each group to obtain the relative party size. When analysing day-range and relative party size, days in which the study troops were not followed for at least four consecutive hours were discarded.

b) Data analysis.

Scores per individual were used to obtain percentages of the main activities and of diet composition (see Chapter 2). Scores per day were used for day range and party size. Spearman rank-correlation was run to analyse the relation between activity budgets and diet composition using monthly percentages whereas partial correlation was used to correlate these variables to home range size. Monthly variations of activity budgets and diet composition were analysed using percentages per monkey and running a series of Friedman tests. Wilcoxon signed-rank test was used when activity budgets and diet composition were compared between the period July-August and February-April at the individual level. A series of Mann-Whitney tests was run to compare activity budgets, diet composition, day-range, and relative party size between the two study troops using scores per monkey. The Bonferroni correction (Howell, 1999) was applied when the same variables were repeatedly correlated with each other. Following the Bonferroni correction, the new p-value was obtained by dividing 0.05 (the p-value limit for significance) by the number of tests run using the same variables.

3.3 Results.

a) Variations in activity budgets and diet composition in relation to season.

Overall, monkeys devoted the vast majority of their time to foraging and to social behaviour (i.e. grooming; see Table 3.1). The food category eaten by the monkeys often could not be determined given that monkeys usually foraged in trees where vegetation was dense (see Table 3.1). However, diet composition was highly diversified with fruits, seeds, and leaves accounting for the majority of food consumed. Fruit- and seed-food tree species had a similar distribution in the study area and were more clumped than leaf-food tree species (Agetsuma, 1995a). Moreover, for a given amount of food, fruits and seeds give an animal a higher net energetic gain than leaves (Dunbar, 1988; Stephens and Krebs, 1986). For this reason, scores of time spent foraging on fruits and on seeds were pooled together and the following analyses were based on two food categories only (i.e. time spent foraging on fruits / seeds and time spent foraging on leaves). Activity budgets and consumption of fruits / seeds, and leaves differed significantly among the months (see Figures 3.1 and 3.2, and Table 3.2). Time spent foraging was negatively related to time spent resting (see Table 3.3) and a similar relation (although not significant following the Bonferroni correction) was found between grooming and moving. Given that both activity budgets and diet composition differed over the months (Figures 3.1 and 3.2) a series of Spearman rank correlations were run to analyse how the time that the monkeys spent foraging on fruits / seeds and on leaves was related to the time spent foraging and grooming. Time spent foraging on fruits / seeds was positively related to time spent grooming and negatively to time spent foraging, but both the correlations only approached statistical significance (see Table 3.4). All the other tests gave non-significant results.

Table 3.1: Overall activity budgets and diet composition of Nina A females (N = 8) using percentages of sample points per monkey (N = 8; see Chapter 2 for definitions).

Activity		Percentage
Foraging (total)		42.2%
	Food category	
	Fruits	39.8%
	Seeds	22.7%
	Leaves	9.9%
	Flowers	0.8%
	Fungi	1.7%
	Animals	5.3%
	Unknown	19.8%
Moving		7.9%
Grooming		31.4%
Resting		9.6%
Other		8.9%

Figure 3.1: Monthly variations of the four activity budgets of Nina A females (N = 8; mean percentage of sample points).

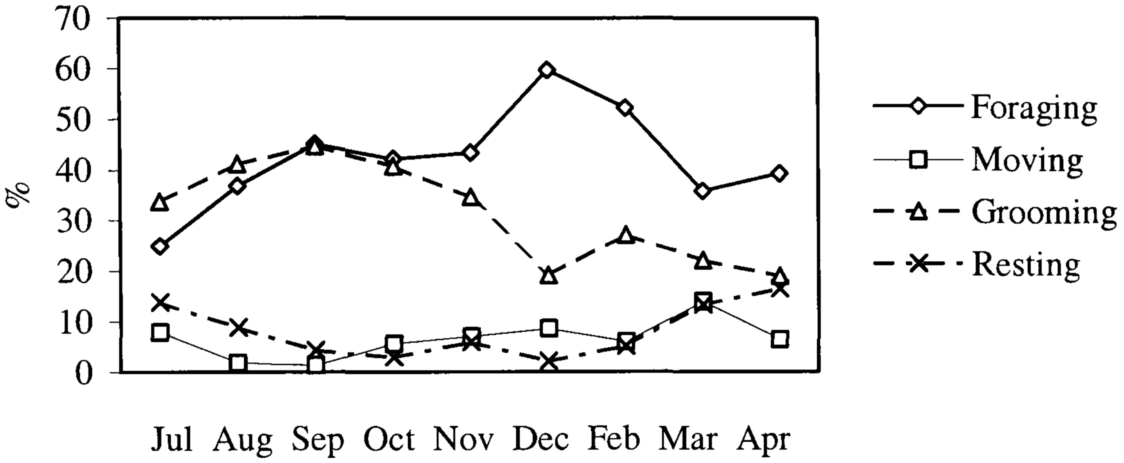


Figure 3.2: Monthly consumption of the three main food categories eaten by Nina A females (N = 8; mean percentage of sample points).

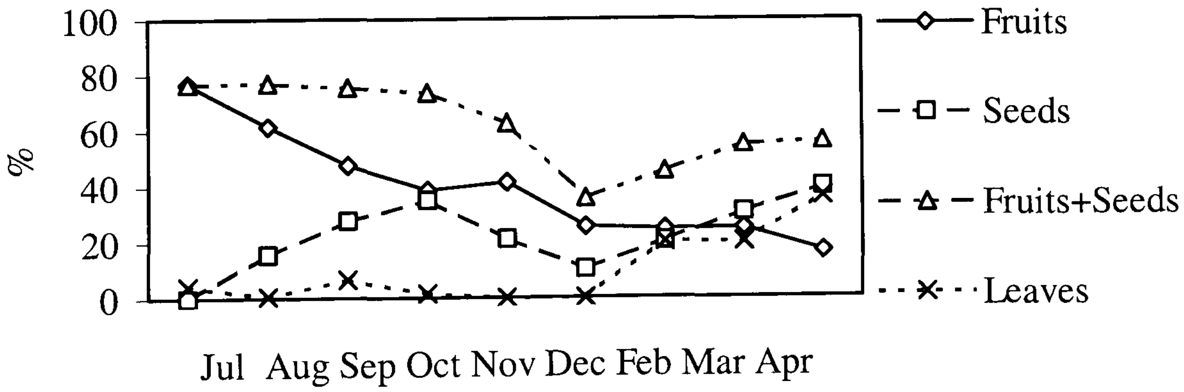


Table 3.2: Results of the Friedman tests on the monthly variations of the four activities and of the two main food categories eaten by Nina A females using percentages of sample points per monkey (N = 8, *** $p < 0.001$).

Variable		χ^2
Foraging		57.08 ***
	Foraging on fruits / seeds	53.14 ***
	Foraging on leaves	60.00 ***
Moving		41.59 ***
Grooming		70.77 ***
Resting		49.31 ***

Table 3.3: Results of the Spearman rank correlations among the four main activities of Nina A females using percentages of sample points per month (N = 9, Bonferroni correction: * $p < 0.017$).

Variables	r_S and p values
Foraging x Moving	$r_S = -0.20$, $p > 0.1$
Foraging x Grooming	$r_S = -0.33$, $p > 0.1$
Foraging x Resting	$r_S = -0.78$, $p = 0.013$ *
Grooming x Moving	$r_S = -0.73$, $p = 0.025$
Grooming x Resting	$r_S = -0.30$, $p > 0.1$
Moving x Resting	$r_S = 0.23$, $p > 0.1$

Table 3.4: Results of the Spearman rank correlations between the four activities and the three main food categories eaten by Nina A females using percentages of sample points per month (N = 9, Bonferroni correction: * $p < 0.0125$).

Variables	r_S and p values
Foraging x Foraging on fruits / seeds	$r_S = -0.67, p = 0.050$
Foraging x Foraging on leaves	$r_S = -0.21, p > 0.1$
Moving x Foraging on fruits / seeds	$r_S = -0.43, p > 0.1$
Moving x Foraging on leaves	$r_S = -0.08, p > 0.1$
Grooming x Foraging on fruits / seeds	$r_S = 0.73, p = 0.025$
Grooming x Foraging on leaves	$r_S = -0.34, p > 0.1$
Resting x Foraging on fruits / seeds	$r_S = 0.28, p > 0.1$
Resting x Foraging on leaves	$r_S = 0.50, p > 0.1$

Home range size was positively correlated with contact time with the study group each month ($r_S = 0.68$, N = 9, $p < 0.05$). Therefore, partial correlation (using contact time as the controlling factor) was used to analyse the relationship between home range size, activity budgets and diet composition. The only significant result was the positive relationship between home range size and time spent grooming (see Table 3.5) although correlations between home range size and time spent resting or foraging on leaves, respectively, approached significance.

Table 3.5: Results of the partial correlations (with contact time with the group as the controlling factor) between home range size and activity budgets or the two main food categories eaten by Nina A females using percentages of sample points per month ($N = 9$).

Variables	Coefficient and significance
Home range x Foraging	0.38, $p > 0.1$
Home range x Foraging on fruits / seeds	0.37, $p > 0.1$
Home range x Foraging on leaves	-0.65, $p = 0.083$
Home range x Moving	-0.27, $p > 0.1$
Home range x Grooming	0.78, $p < 0.05$
Home range x Resting	-0.70, $p = 0.055$

In order to analyse how monthly variations of activity budgets and diet composition affected within-group food competition, social behaviour, and reconciliation (these topics will be analysed in Chapter 4) two different methods could be used. One method would be to run a series of correlations using monthly scores of activity budgets, diet composition, and social interactions. The other method would consist in identifying different, longer than one month, time windows and analysing how ecological and social data differed among these time windows. This second solution is the most feasible method. Variations of group movements and of home range size greatly affected contact time with the study troop each month, which in turn affected the amount of data that could be collected on each study female. Therefore, using monthly scores to analyse how variations of activity budgets affected social behaviour would reduce the sample size given that many data would be lacking (as, for example, post-conflict observations are not be available for all the study females each month). This problem is, at least partially, prevented by collapsing data collected during longer time windows.

Summer and autumn months represent the peak of fruits and seeds production and consequently of consumption by the monkeys while winter and spring months represent the highest level of leaf consumption (Hill, 1997; Maruhashi, 1980; Nakagawa, 1989, 1990; Nakagawa *et al.*, 1997; Noma, 1997). The mating season corresponded to months from late August to December during the study year (see Chapter 6). The mating season represents a confounding factor when analysing seasonal variations of social behaviour given the effects that it may have on grooming distribution and competition (D'Amato *et al.*, 1982; Mehlman and Chapais, 1988; Schino *et al.*, 1998). Taking together all these considerations two periods of the year were identified and compared: the period comprising July and the first part of August (hereafter, July - August), corresponding to the summer months, and the period from February to April, corresponding approximately to the winter and spring months.

Monkeys spent significantly less time foraging and moving in the periods July - August than in the period February- April (time spent foraging: $T = 36$, $N = 8$, $p < 0.05$; time spent moving: $T = 37$, $N = 8$, $p < 0.05$; see Figure 3.3). Moreover, time spent grooming was higher in the period July – August than in the period February – April ($T = 37$, $N = 8$, $p < 0.05$) while time spent resting did not significantly differ ($T = 27$, $N = 8$, NS). Finally, the two periods also differed in the consumption of the main food categories. Monkeys spent more time foraging on fruits / seeds and less time foraging on leaves in the period July - August than in the period February - April (time spent foraging on fruits / seeds: $T = 35$, $N = 8$, $p < 0.05$; time spent foraging on leaves: $T = 36$, $N = 8$, $p < 0.05$; see Figure 3.4). Home range size was 34.5 ha during July - August and 29.4 during February-April. Given that contact time with the study troop differed between the two periods (i.e. 178.1 hrs in July - August and 135.2 hrs in February - April) home range size was divided by contact time. Following this method the value for the two periods was very similar (i.e. 0.20 and 0.22, respectively).

Figure 3.3: Activity budgets of Nina A females (N = 8) in the periods July-August and February-April (mean percentage of sample points ± SE; * $p < 0.05$).

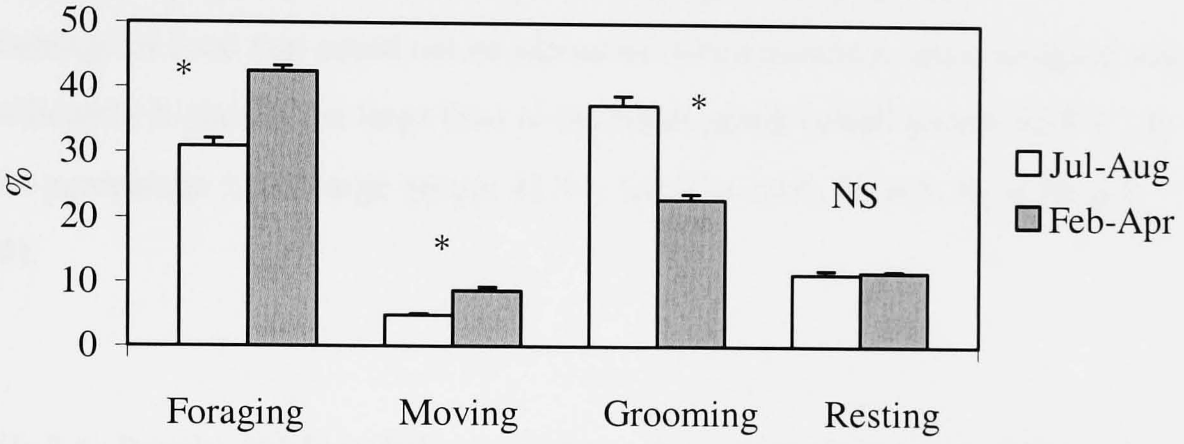
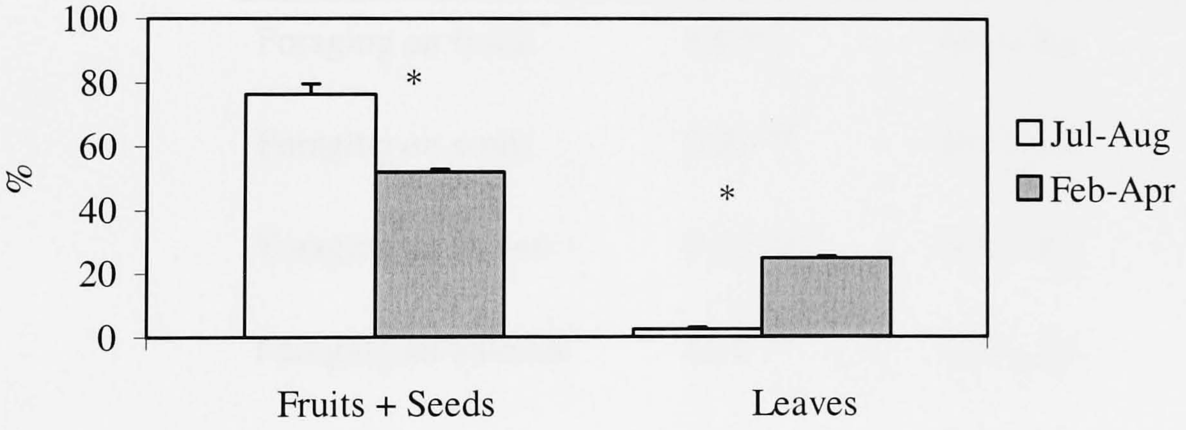


Figure 3.4: Diet composition of Nina A females (N = 8) in the periods July-August and February-April (mean percentage of sample points ± SE; * $p < 0.05$).



b) Variations in activity budgets and diet composition in relation to group size.

No significant difference was found between the two troops either in time spent foraging and moving (see Table 3.6 and Figure 3.5). However, females living in the large troop devoted significantly more time to grooming and less time to resting than females in the small troop. Moreover, the two groups differed considerably in their diet composition. Females in the small group spent more time foraging on seeds and on leaves but spent less time foraging on fruits and on animals (see Table 3.6 and Figure 3.6). No significant difference was found between the two groups in the time spent foraging on fungi. Finally, the percentage of food that could not be identified when monkeys were foraging was significantly higher in the large than in the small group (small group: 25.8 ± 1.0, mean percentage ± SE; large group: 41.4 ± 1.0; $U = 0.01$, $N_1 = 8$, $N_2 = 20$, $p < 0.01$).

Table 3.6: Results of Mann-Whitney tests on the activity budgets and diet composition of Nina A (N = 8) and Kawahara (N = 20) females using percentages of sample points per monkey (** $p < 0.01$).

Variable		U value and significance	Direction of difference
Foraging		62.5	NA = Ka
	Foraging on fruits	4.0 **	NA < Ka
	Foraging on seeds	0.01 **	NA > Ka
	Foraging on leaves	0.01 **	NA > Ka
	Foraging on animals	10.0 **	NA < Ka
	Foraging on fungi	53.5	NA = Ka
Moving		60.0	NA = Ka
Grooming		0.01 **	NA < Ka
Resting		0.02 **	NA > Ka

Figure 3.5: Activity budgets of Nina A (N = 8) and Kawahara (N = 20) females (mean percentage of sample points ± SE; ** p < 0.01).

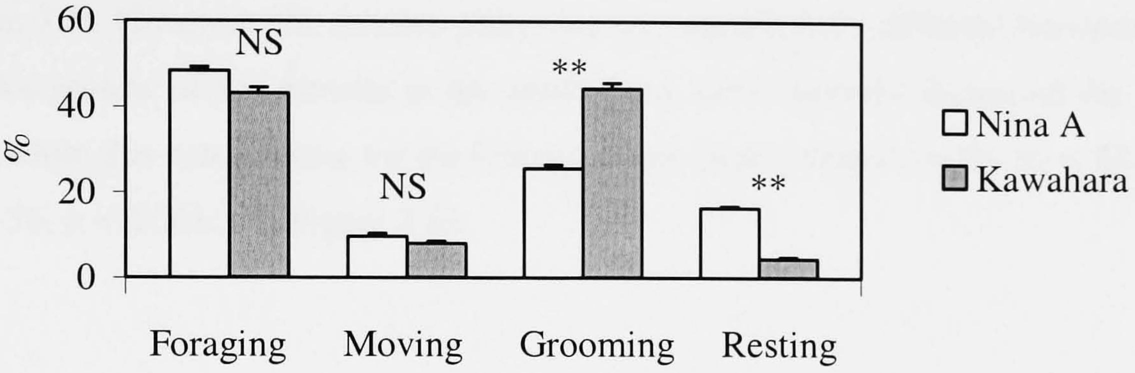
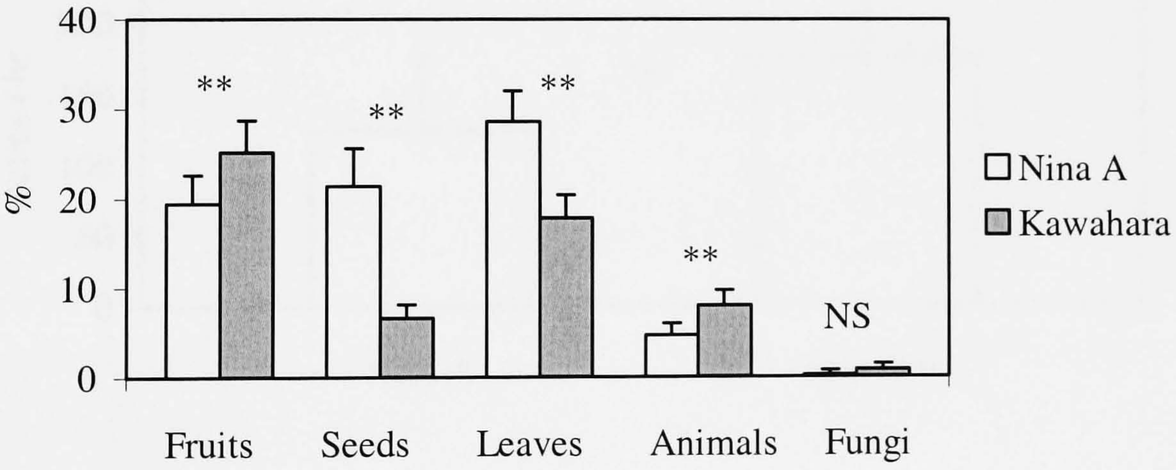


Figure 3.6: Diet composition of Nina A (N = 8) and Kawahara (N = 20) females (mean percentage of sample points ± SE; ** p < 0.01).



The size of the Nina A troop home range was 29.8 ha while that of Kawahara troop was 59.3 ha. Time spent in contact differed between the two troops (i.e. 162.9 hrs for Nina A troop and 200.1 hrs for Kawahara troop). When home range size was divided by contact time the difference between the two groups was reduced but still evident (i.e. 0.18 for Nina A troop and 0.30 for Kawahara troop).

At the end of the study, a total of 55 days that could be used for analysing day-range was obtained, 26 on Nina A troop and 29 on Kawahara troop. Moreover, 32 observation days were used for Nina A troop and 36 for Kawahara to calculate the relative party size. Females in the large troop travelled significantly more each day than females in the small troop ($U = 183.5$, $N_1 = 26$, $N_2 = 29$, $p < 0.01$; see Figure 3.7). However, the relative party size was significantly different between the two groups: all the females in the small group were observed almost all the days while this was not true for the females in the large group ($U = 79$, $N_1 = 32$, $N_2 = 36$, $p < 0.001$; see Figure 3.8).

Figure 3.7: Day-range of Nina A (N = 8) and Kawahara (N = 20) females (mean metres / hr ± SE; ** p < 0.01).

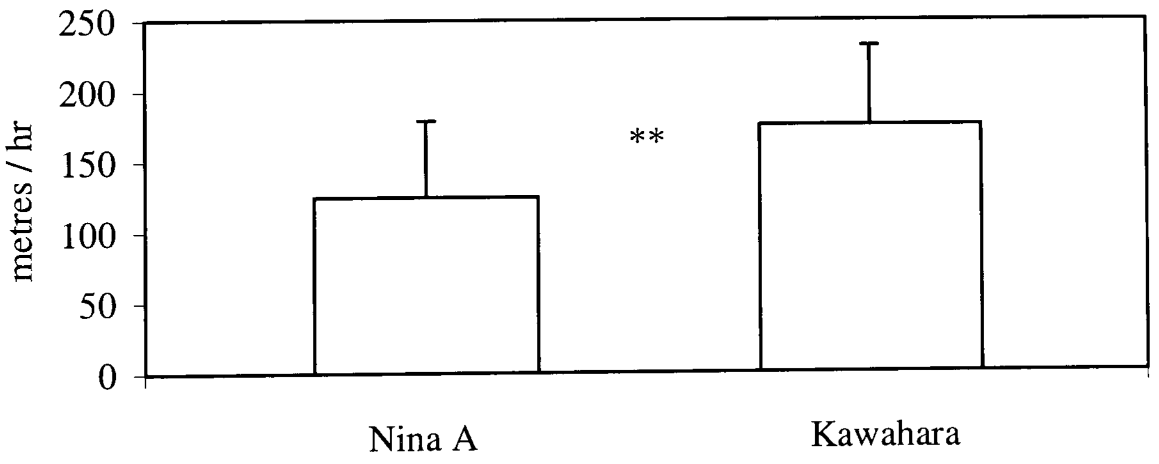
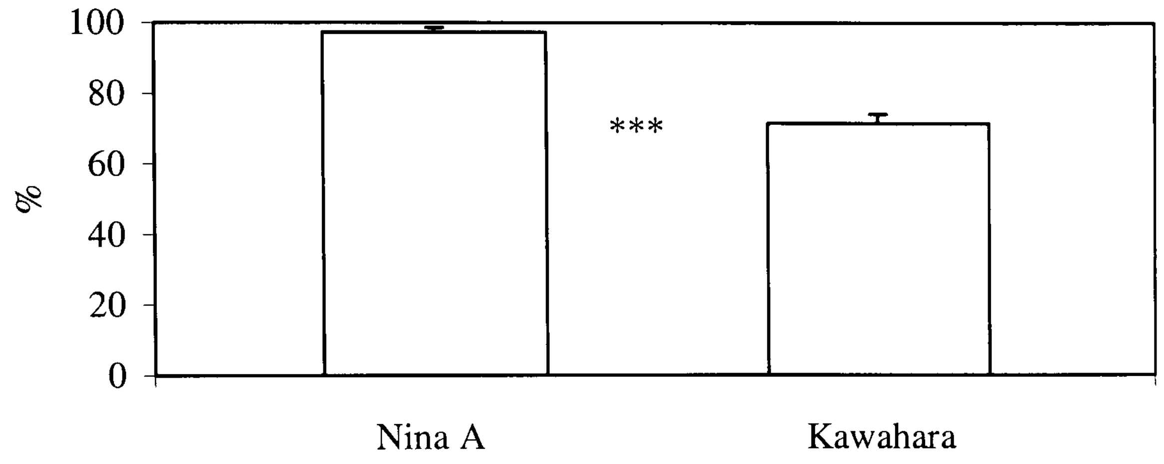


Figure 3.8: Relative party size of Nina A (N = 8) and Kawahara (N = 20) females (mean percentage of females seen / total number of females in a group ± SE; *** $p < 0.001$).



In order to analyse how time spent foraging and moving was affected by social status, females in each group were divided into three rank classes, namely high-, middle-, and low-ranking females. To have a sufficient sample size the upper and lower bound was set at the 40% of the females in a group. That is, the upper and lower 40% of females in the hierarchy of a group were considered to belong to the high-ranking and low-ranking classes, respectively. Therefore, for the smaller group the first three females were considered to represent the high-ranking class, the last three females as the low-ranking class, and the two remaining females (ranking 4 and 5 in the hierarchy) as the middle-ranking class. This meant that for the larger group the first 8 females in the hierarchy represented the high-ranking class, the last 8 females represented the low-ranking class, while the remaining 4 females represented the middle-ranking class. The middle-ranking class was not considered in the following analysis to have a clear distinction between females of different rank.

No significant difference was found either when time spent foraging was compared between females of the two groups but belonging to the same ranking-class and when this variable was compared between females belonging to different ranking-classes but of the same group (see Table 3.7 and Figure 3.9). The same non-significant results were found for time spent moving (see Table 3.7 and Figure 3.10).

Table 3.7: Results of Mann Whitney tests on time spent foraging or moving by females belonging to different rank-classes.

Comparison	Sample size	U value and significance
Time spent foraging		
High-rank Nina A vs. High-rank Kawahara	$N_1 = 3$ $N_2 = 8$	11.0, NS
Low-rank Nina A vs. Low-rank Kawahara	$N_1 = 3$ $N_2 = 8$	11.0, NS
High-rank Nina A vs. Low-rank Nina A	$N_1 = 3$ $N_2 = 3$	2.0, NS
High-rank Kawahara vs. Low-rank Kawahara	$N_1 = 8$ $N_2 = 8$	28.5, NS
Time spent moving		
High-rank Nina A vs. High-rank Kawahara	$N_1 = 3$ $N_2 = 8$	10.0, NS
Low-rank Nina A vs. Low-rank Kawahara	$N_1 = 3$ $N_2 = 8$	6.0, NS
High-rank Nina A vs. Low-rank Nina A	$N_1 = 3$ $N_2 = 3$	2.0, NS
High-rank Kawahara vs. Low-rank Kawahara	$N_1 = 8$ $N_2 = 8$	31.0, NS

Figure 3.9: Time spent foraging by Nina A (N = 8) and Kawahara (N = 20) females belonging to the two rank classes (mean percentage of sample points ± SE).

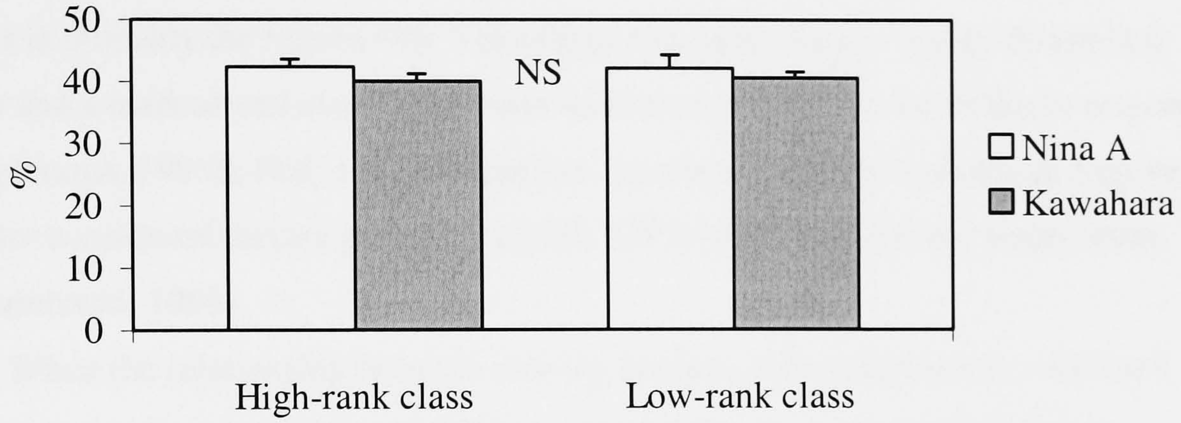
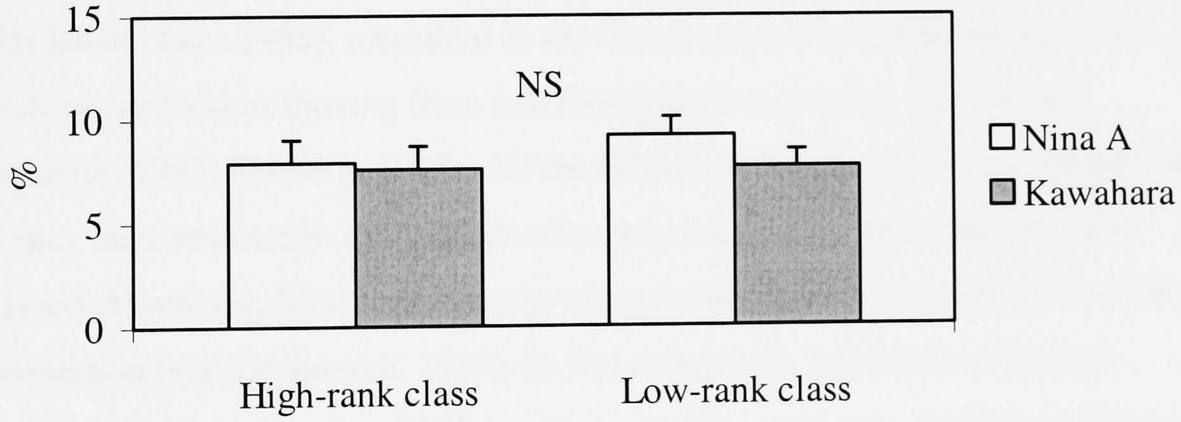


Figure 3.10: Time spent moving by Nina A (N = 8) and Kawahara (N = 20) females belonging to the two rank classes (mean percentage of sample points ± SE).



3.4 Discussion.

a) Variations in activity budgets and diet composition in relation season.

In this study Japanese macaques showed a large variation in the activity budgets and diet composition among the months. As such, these results confirmed what has been found in other studies (e.g. Domingo-Roura and Yamagiwa, 1999; Hanya *et al.*, 2003). Indeed, if one excludes mature leaves, that are always available throughout the year in evergreen forests, all the other food sources show clear seasonal patterns in terms of abundance on the Island (Agetsuma, 1995b). This is probably the reason why Yakushima macaques have a highly diversified diet and a marked variation in the main food sources eaten in the different seasons (Agetsuma, 1995b; Hill, 1997). Therefore, monkeys living in Yakushima may be better considered dietary generalists (Hill, 1997) rather than simply frugivorous (Maruhashi, 1980).

When the relationship between activity budgets, diet composition, and home range size was analysed few significant correlations were obtained. No clear pattern was evident from these correlations so that no definitive answer may be given on how all these factors are related one another. This result may be due to many different reasons. Food abundance, its dispersion, its quality in terms of energetic intake, the presence of other groups that may monopolise food sources (see Chapter 7), and the ambient temperature are all factors that have profound effects on the foraging effort of a monkey (Agetsuma, 2000, Dunbar 1988; Isbell, 1991; Isbell *et al.*, 1988), measured as the time that an animal spends actively searching for food or moving from one food source to another (Janson and Goldsmith, 1995; Norberg, 1977). All these factors interplay with one another and this may have resulted in the absence of a clear relation between the variables analysed. Moreover, food abundance is often positively related to the amount of precipitation (e.g. Deshmukh, 1984). In Yakushima the rainy season usually represents an increment in rainfall but does not allow the clear distinction of a wet from a dry season. This is an additional factor that may affect the relationship existing between activity budgets, diet composition and home range size. This is not to say that Yakushima may be considered a stable habitat. Indeed, food abundance may vary dramatically within a short period of time (e.g. from one week to another; Hill and Agetsuma, 1995). These fluctuations, however, are difficult to detect when data are collapsed using arbitrary delimitations such as months or seasons. For example, fruit productivity may be very high in the first part of a given month and significantly decrease in the following weeks as a consequence of intense foraging by the monkeys. This pattern is unlikely to be detected when data for that month are pooled together. Unfortunately, an amount of data larger than that available for this study would be necessary in order to run more fine-tuned analyses that could detect such variations.

Beside these considerations, the important finding of this study was that two periods of the year were identified that differed in the amount of time that monkeys spent foraging, moving, and grooming. Moreover, these two periods also differed in the consumption of the two main food categories.

The time that birds and mammals spend looking for food and moving is often considered to be a reliable measure of food availability and dispersion, respectively (Norberg, 1977; Pyke *et al.*, 1977). Previous studies conducted on Yakushima have shown that macaques spend more time moving and less time foraging when they are searching for fruits, seeds and animals, whereas the reverse trend is found when they are searching for leaves (Agetsuma, 1995a; Nakagawa, 1989). Agetsuma (1995a) explained these findings by stating that monkeys follow a "high-cost high-yield" strategy when foraging on highly energetic, easy to process, clumped, and/or difficult to find food sources such as fruits, seeds, and animals, and a "low-cost low-yield" strategy when foraging on leaves, that are easy to find and require much time to be processed. That is, animals increase the costs associated with searching for food (i.e. more time spent moving) when the benefits, in terms of energetic intake, are high (e.g. insects) and/or food is easy to process (e.g. ripe fruits) whereas they minimise the costs of moving from one food source to another when food is of low quality and difficult to process (as it is the case of leaves). Other studies have shown that this strategy is followed by many primate species (e.g. green monkey: Harrison, 1985; titi monkey: Heiduck, 2002).

The comparison of the periods July – August and February – April partly supports this picture. When fruits and seeds are abundant Japanese macaques prefer to forage on them while increasing the time spent foraging on leaves when their availability is not sufficient to fulfil the energetic requirements of the monkeys (Hanya *et al.*, 2003). The summer months represent the peak of fruit production and possibly of overall food abundance as shown by the low time spent foraging. Therefore, when easy to process food is abundant monkeys spend relatively less time foraging (Agetsuma, 1995a) and thus have more time available for social activities (i.e. grooming). Indeed, time spent foraging on fruits / seeds was the only variable that was significantly related (or approached significance) to both overall time spent foraging and grooming (through a negative and a positive correlation, respectively). This result indicates that the amount of fruits and seeds consumption has important effects on how monkeys distribute their time among the different daily activities. On the contrary, when the energetic value of food is reduced (as fruits and seeds are less abundant) monkeys have to spend more time foraging to gain an equal amount of energy. In contrast with what has been found by Agetsuma (1995a), time spent moving was lower when highly-energetic food was abundant. This result may indicate that time spent moving is more related to the overall food abundance than to the distribution of the different food sources (Isbell *et al.*, 1998).

These observed differences between the two periods in the activity budgets and diet composition of Nina A females are likely to have significant effects on the social behaviour of the monkeys. Therefore, the next Chapter will aim to analyse how grooming distribution, the quality of social relationships and conflict management are affected by these differences.

b) Variations in activity budgets and diet composition in relation to group size.

In this study, the large group had a larger home range than the small group but no difference in time spent foraging between the two troops was found. It is possible that this result was due to differences in terms of food abundance and/or distribution between the areas inhabited by the two troops as large groups are usually able to supplant small groups from more productive areas (Isbell *et al.*, 1998; Koganezawa and Imaki, 1999; Takasaki, 1981; Wranham *et al.*, 1993). In Yakushima, habitat quality is strongly affected by the logging history of an area as large trees, bearing high quantities of food items, are more frequent in areas where logging was prohibited or stopped many years ago (Hill *et al.*, 1994). Unfortunately, no map showing the logging history of the study areas is available

(Hill, pers. comm.) and no detailed phenological data were collected in this study. As such, possible differences in habitat quality cannot be clarified. Moreover, the differences found between the two groups in diet composition may be indicative of different availability of the food categories. However, given that other studies have not found an increase in time spent foraging as group size increases (e.g. Henzi *et al.*, 1997b; Stacey, 1986) probably no linear relationship exists between these two variables.

Home range was larger for the large group compared to the small group and day range was also greater in the large group. No difference was found between the two groups in time spent moving. However, monkeys in the large group were more dispersed than monkeys in the small group as measured by the different relative party size of the two groups. This probably means that females in the small group moved between different food patches as a single unit while this was less true for females in the large group who moved in different sub-units. Indeed, small groups of Japanese macaques show more synchrony of movements during foraging than large groups (Agetsuma, 1995c). Other things being equal, one of the main costs of increased group size is the increased time monkeys have to spend moving from one food patch to the other (as depletion rate per hour and home range size both increase as group size increases). The results of this study indicate that monkeys in the large group followed two non-mutually exclusive strategies to avoid or limit this potential cost. First, they increased the travel speed so that the time spent moving remained similar to that of monkeys living in the small group. Moreover, they were more dispersed than females in the small group. These solutions have clear advantages. The difference in the relative party size between the two groups may be a means to increase inter-individual distance during foraging and thus reduce the level of within-group food competition (Furuichi, 1983). Moreover, by maintaining stable the time spent moving females are able to not give up some time for social activities (i.e. grooming exchange). Finally, monkeys often travel longer distances to reach an abundant patch of food and shorter distances when patches are small (Chapman *et al.*, 1995). Therefore, the difference in day-range may be a consequence of the different distribution of resources in the home ranges of the two groups.

When time spent foraging and moving was compared between females belonging to the high- and low-classes of the two groups no difference was found. Taking together all these observations, this study has not presented supporting evidence for increased costs associated with increased group size. Within the range of the group size considered, monkeys are capable of following strategies (i.e. increased dispersion) that maintain a stable foraging effort as group size increases. Moreover, the large group had a frequency of inter-group encounters much lower that the small group. Therefore, females probably benefit from living in large groups through a decrease in the level of between-group food competition.

Finally, one interesting result of this study is that monkeys in the large group reduced the time devoted to resting and spent significantly more time exchanging grooming than monkeys in the small group. An increase in time spent grooming as group size increases has been predicted by theoretical models (Dunbar, 1988) and by observation in the field (Henzi *et al.*, 1997). This is due to the higher number of grooming partners potentially available in large groups than in small groups. Within-group competition should increase as group size increases. Moreover, the amount of time spent grooming observed in the large group may not be sufficient to establish good relationships with all the group members and thus to keep competition under control. How quality of social relationships, grooming distribution and conflict management are affected by group size will be explored in Chapter 5.

Chapter 4

Seasonal Effects on Grooming Distribution and Conflict Management in Nina A Females

Nina A females (N = 8) spent less time foraging and moving, and more time grooming in the period July-August than in February-April (see Chapter 3). Moreover, monkeys consumed more fruits and seeds, and less leaves in July-August than in February-April. This chapter analyses if and how these differences in activity budgets and diet composition affect grooming distribution and reconciliation in the two periods.

4.1 Introduction.

Ecological variables greatly affect the social behaviour of animals (e.g. Krebs and Davies, 1997; Fleagle *et al.*, 1999). Food is probably the main factor in this respect as it has direct and indirect effects on social behaviour. The direct effects are mainly related to the quantity and distribution of resources. Data from field and captive studies agree in showing that when food is less available and/or clumped aggression and competition for resources increases while tolerance at feeding sites decreases (Barton *et al.*, 1996; Boccia *et al.*, 1988; Mathy and Isbell, 2001; Saito, 1996). When this happens low-ranking individuals are forced to feed far from high-ranking animals in order to reduce competition and/or to maintain their foraging effort stable (van Schaik and van Noordwijk, 1986). Moreover, size of food predicts frequency of aggression in rhesus macaques (Mathy and Isbell, 2001) while food quality does not have any effect on rate of aggression in baboons (Shopland, 1987). It is the type of food competition (see Chapter 1) that determines the nature of social interactions within a group. When food sources can be monopolised strict dominant hierarchies are likely to evolve whereas when food can be shared more "egalitarian" societies should be favoured (Matsumura, 1996; Sterck *et al.*, 1997; van Schaik, 1989; Vehrencamp, 1983).

Time necessary to find, consume, and digest food sources are the most salient indirect factors affecting social behaviour (e.g. Dunbar, 1988). The time that animals have to devote to foraging clearly influences how much time is left each day for social interactions. The exchange of amicable behaviour is extremely important for social animals as it helps to maintain good relationships with some other group members and to keep competition under control (see Chapter 1). The effects of diet and time spent foraging on quality and quantity of social interactions within a group have been clearly recognised for social primates. All things being equal, folivorous species usually spend more time resting or being inactive during the day (given the long time required to digest leaves and other plant parts; Kirkpatrick *et al.*, 2001) while frugivorous species are more active and often exchange grooming when not foraging (Janson and Chapman, 1999; Janson and Goldsmith, 1995).

The relationship between habitat type, diet, and social behaviour is not only evident when comparing different species but also among populations of species inhabiting different habitats. For example, as a consequence of the different habitat type baboons living at climatic extremes (i.e. high altitudes) often form one-male groups while populations living in more productive areas usually live in multi-male groups (Byrne *et al.*, 1993).

Although many ecological variables may affect activity budgets and thus social behaviour, the importance that seasonal or monthly variations in activity budgets and diet composition may have on social behaviour has rarely been analysed. Indeed, studies have usually identified the effect that the mating season has on grooming distribution and/or reconciliation (D'Amato *et al.*, 1982; Mehlman and Chapais, 1988; Schino *et al.*, 1998) but rarely focused the attention on seasonal variations outside the mating season. However, Barrett and colleagues (2002) have shown that grooming reciprocity increases when within-group direct food competition increases. This study indicates that social groups often have to cope with long- or short-term variations in competition that may dramatically affect social interactions. With this in mind, the aims of this Chapter were to analyse how differences in activity budgets and diet composition (see Chapter 3) affect grooming distribution, reconciliation, and food competition among female Japanese macaques.

4.2 Methods.

a) Study subjects and data collection.

Subjects of this study were all the eight adult/sub-adult females living in Nina A troop. Data were collected from June 22nd 2001 to May 4th 2002. However, only data collected in July and August 2001 and from February to April 2002 were used for this study (see Chapter 3). Focal animal sampling was used to obtain percentages of time spent grooming and frequency of aggression (Altmann, 1974; Martin and Bateson, 1993) while post-conflict behaviour was recorded using the post-conflict / matched-control method (de Waal and Yoshihara, 1983; see Chapter 2 for details).

b) Data analysis.

Two different indices were used to compare inequality in grooming distribution in the two periods: the Shannon-Wiener diversity index, which was developed by communication theory studies (Shannon and Wiener, 1949), and the B index, which comes from studies on social behaviour (Nonacs, 2000). The Shannon-Wiener diversity index has been frequently used in ecology and in population biology (Wilson and Bossert, 1971) but, recently, also in studies on social behaviour (Cheney, 1992; Henzi *et al.*, 1997b; Nakamichi and Shizawa 2003; Watts, 2000). Information on the number of females in a group and the frequency of grooming given to all the available partners is incorporated in the index in the formula:

$$H = -\Sigma p_i (\ln p_i)$$

p_i is the frequency of grooming given by the i^{th} female to each grooming partner (i.e. total grooming given to each female divided by total grooming given by the i^{th} female). A female achieves the maximum diversity when she grooms all the available partners equally. In order to determine how evenly each female groomed all potential partners I divided the actual diversity index (H_s) of each female by the theoretical maximum diversity for a group of a given size, which is calculated using the formula (Henzi *et al.*, 1997b):

$$H_{max} = ln\ N$$

where N is the number of potential grooming partners for a group (and thus $N = 7$ in this study). This ratio is called the grooming diversity ratio (DGR; Cheney, 1992; Di Bitetti, 2000). If a female grooms all the potential partners about equally her DGR approaches 1 while her DGR is considerably less than 1 if she grooms only some potential partners or grooms some individuals considerably more than others.

In the last few years, more than 20 indices have been used to analyse inequalities in the acquisition of food sources or mating partners, and in particular in studies of lekking animals (e.g. Blanckenhorn *et al.*, 1998; Ruzzante *et al*, 1995; Tsuji and Kasuya, 2001; Tsuji and Tsuji, 1998). Apparently, no single index is completely independent from factors that may affect its value (e.g. number of competitors or quantity of resource available). This consideration has led some authors to postulate that the whole range of indices should be used in studies on inequalities of resource acquisition (Galimberti *et al.*, 2002; Kokko *et al.*, 1999). This conclusion is clearly not feasible as it is time-consuming and, most importantly, as different indices may give contrasting results, thus making difficult to give a rationale biological explanation of the phenomenon under study (Kokko *et al.*, 1999; Nonacs, 2003). In a recent review on the reliability of these indices Nonacs (2003) has shown that a new index, the B index (Nonacs, 2000), could become the "benchmark" index as it better controls for factors that may affect its value (namely, number of competitors in a group, group productivity, and differential survival of group members). As such, the B index may have many applications in ecology and animal behaviour studies. Given the benefits that grooming can give to an animal (e.g. tolerance over food sources or agonistic support; see Chapter 1) this behaviour can be considered a resource, as food or mating partners, to compete for. Therefore, the B index was used to determine how females distributed their time available for social interactions to all the potentially available partners in the two periods under study. To my knowledge, this is the first time that such an inequality index has been used to measure grooming distribution.

The B index for each female can be calculated using the formula (Nonacs, 2000):

$$B = \sum_{i=1}^{N} (p_i - n_i / N)^2 - (1 - 1 / \bar{N}) / K$$

p_i is the frequency of grooming given by the i^{th} female to each grooming partner (i.e. total grooming given to each female divided by total grooming given by the i^{th} female), K is the total grooming given by the i^{th} female, n_i is the time that the i^{th} female has spent in the group, and N is the total number of females in a group. No female left the group or died during the course of the study and this results in $n_i / N = 1 / N$ and $\bar{N} = N$. The B index may range from $(1 / \bar{N} - 1) / K$, which corresponds to equal distribution of resources, to zero (i.e. random distribution), and to $1 - 2n / N + \sum_{i+1}^{N} n_i^2 / N^2 + (1 / \bar{N} - 1) / K$, which corresponds to complete inequality. This means that, unlike the Shannon-Wiener diversity index, lower values of the B index correspond to higher equality of grooming distribution.

The maximum number of grooming partners per female was obtained from focal data. For each female I counted the number of females she groomed when she was the focal animal, regardless of the duration of the grooming bouts. Conciliatory tendency per individual or per dyad was measured following the formula used by Veenema and colleagues (1994; see Chapter 2).

A strong relationship exists between grooming and conciliatory tendency while these factors are often loosely related to the level of food competition (see Chapter 1). I analysed separately conflicts occurring during foraging and those occurring during grooming/resting sessions as the former are more closely related to the level of food competition in a group and the latter to grooming exchange. Some monkeys or dyads were not represented in some of the following analyses and the sample size was reduced accordingly. Wilcoxon test was used for comparisons between the two periods at the individual or dyadic level. Spearman rank correlation was used to analyse the relationship between social interactions, rank distance, and conciliatory tendency.

4.3 Results.

a) Grooming distribution and post-conflict behaviour.

At the end of the study period, a total of 101.7 hrs of focal observation was collected, 43.2 hrs during July-August (5.4 ± 0.2 mean hrs of observation per female ± SE) and 58.5 hrs during February-April (7.3 ± 0.2 hrs per female).

Di Bitetti (2000) has recently criticised the use of the Shannon-Wiener index as a means to measure grooming distribution (see Chapter 5) on the basis that this index does not control for group size and/or differences in sampling effort. While this factor clearly does not apply to this study, the different sampling effort per female in the two periods could affect grooming distribution. However, no significant correlation was found between sampling effort and number of grooming partners per female in the two periods (July-August: rho = -0.66, N = 8, NS; February-April: rho = -0.13, N = 8, NS). Therefore, data on grooming distribution were independent from differences in sampling effort.

No difference was found between the two periods in the mean number of grooming partners per females (T = 9.0, N = 8, NS; see Figure 4.1). Moreover, grooming distribution between the two periods did not differ either when using the Shannon-Wiener index (T = 22.0, N = 8, NS; see Figure 4.2) and the B index (T = 22.0, N = 8, NS; see Figure 4.3).

Overall frequency of aggression among females was significantly greater during the period July-August than during February-April (T = 28.0, N = 7, $p < 0.01$; see Figure 4.4). A total of 143 PC-MC pairs was collected in the two periods: 95 in July-August and 48 in February-April. Mean number of PC-MC pairs per female was 11.9 ± 2.0 (SE) in July-August and 6.0 ± 1.1 in February-April. Among these PC-MC pairs, 90.5% (i.e. 86/95) of conflicts occurred in a grooming/resting context in July-August and 70.8% (i.e. 34/48) during February-

April (PC-MC pairs occurring in a foraging context will be analysed in Section 4.3b).

Figure 4.1: Number of grooming partners for Nina A females (N = 8) in the two study periods (mean number of partners ± SE).

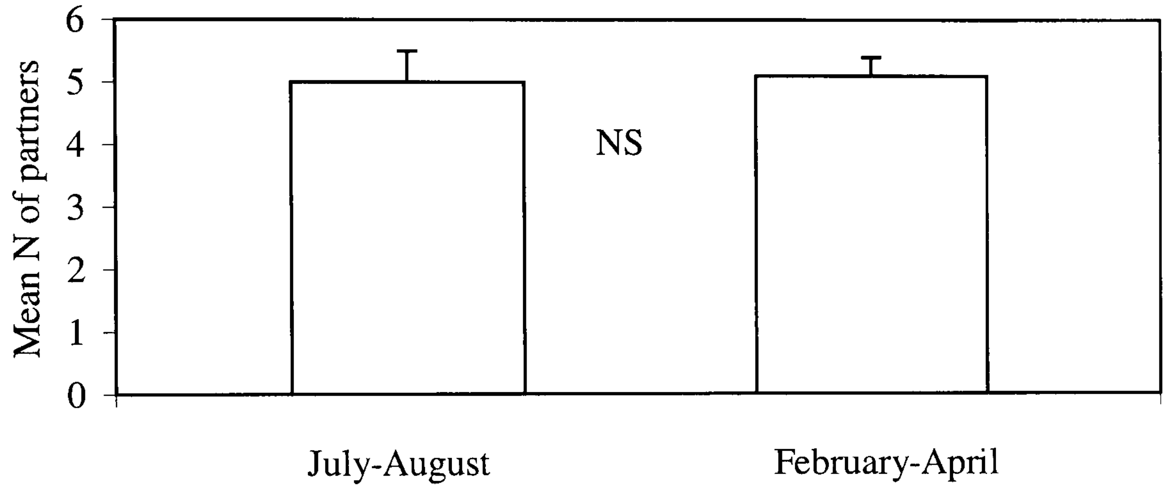


Figure 4.2: Shannon-Wiener diversity index for Nina A females (N = 8) in the two study periods (mean grooming diversity ratio ± SE).

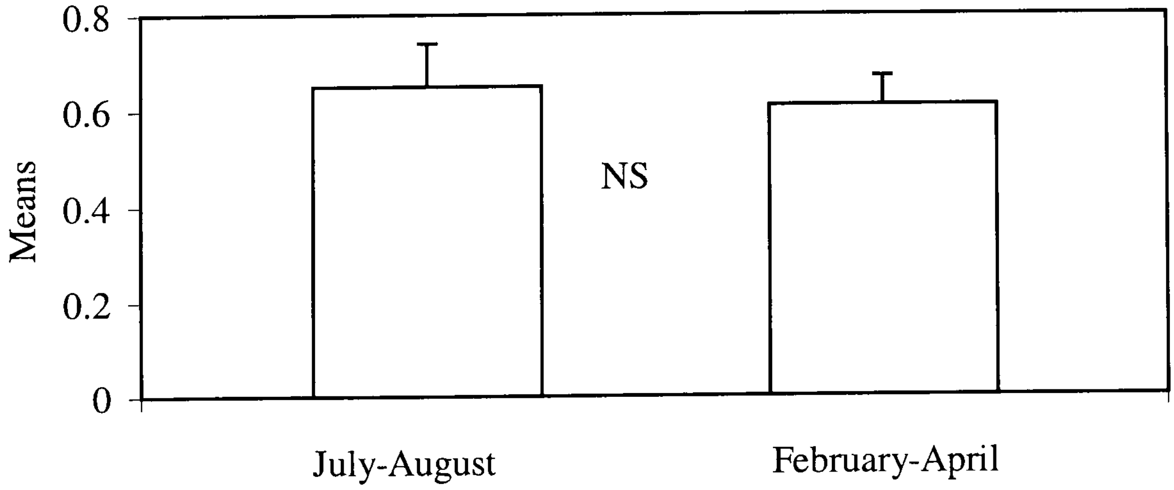


Figure 4.3: B index for Nina A females (N = 8) in the two study periods (mean B value ± SE).

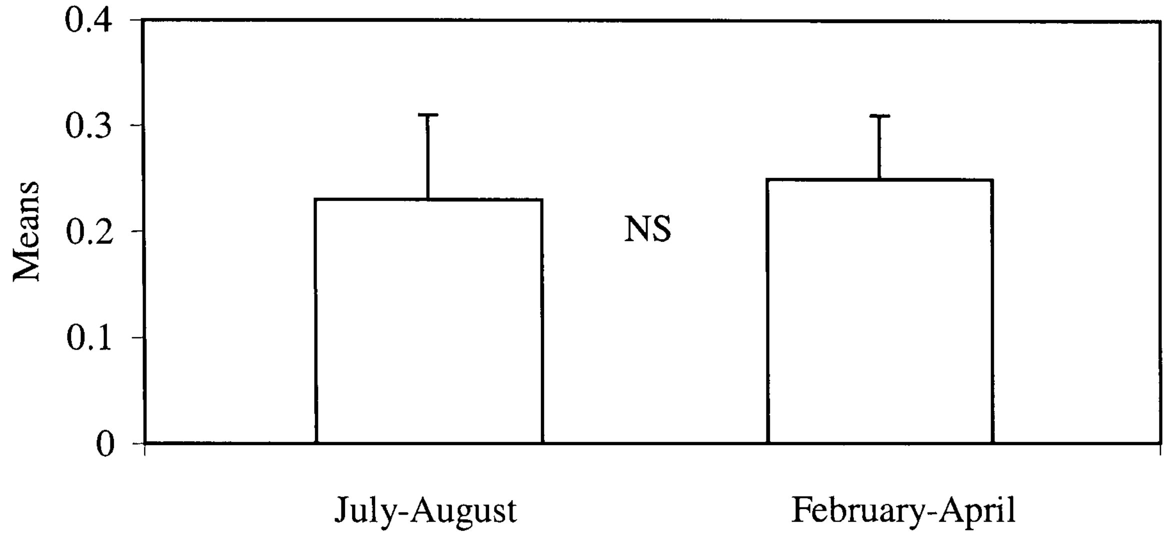
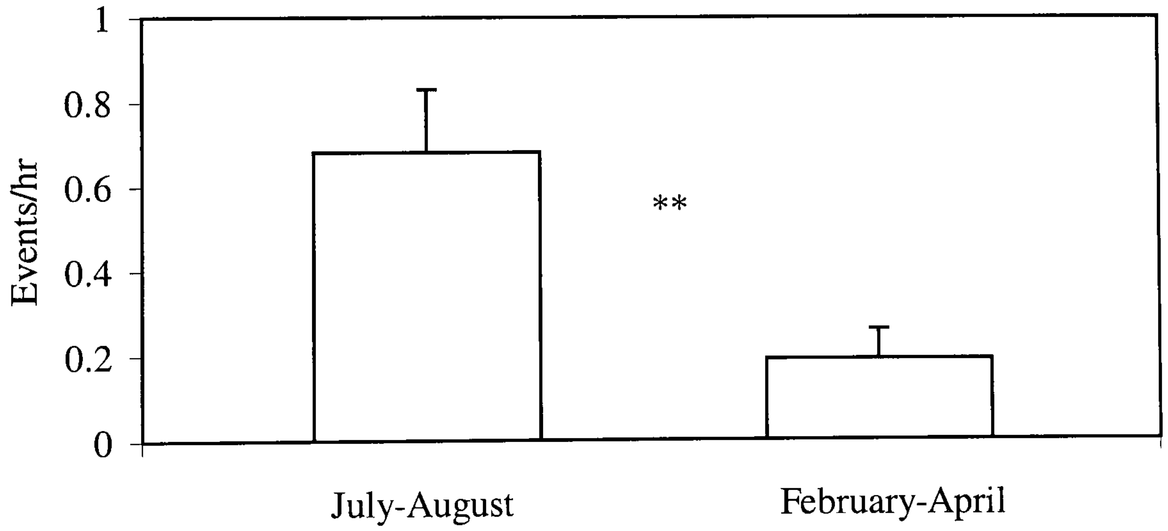
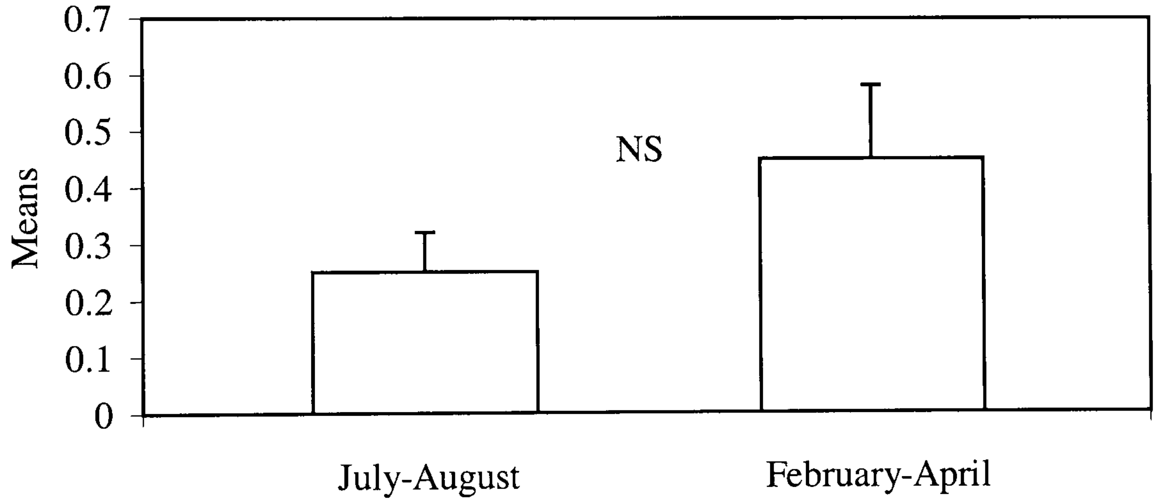


Figure 4.4: Frequency of aggression for Nina A females (N = 8) in the two study periods (mean events / hr ± SE; ** $p < 0.01$).



Conciliatory tendency was lower during July-August than during February-April but the difference was not significant (T = 12.0, N = 6, NS; see Figure 4.5). All the conflicts had a clear-cut result but two, in the period February-April, when none of the opponents showed any sign of submission. Only 4 conflicts, occurring in July-August, involved more than two females while all the other conflicts were dyadic. Victims of aggression were the subjects of further aggression from the former opponents in only 7.4% (i.e. 7/95) of post-conflict observations occurring in the period July-August and in 2.1% (i.e. 1/48) of conflicts during February-April. During post-conflict observations victims were rarely observed to be aggressive towards group members other than the former opponents: redirection was observed in 3.2% (i.e. 3/95) of post-conflict observations in the period July-August and in 4.2% (i.e. 2/48) during February-April. Given the rarity of these events, no further analyses could be run on alliance formation, agonistic support, retaliation, and redirection.

Figure 4.5: Conciliatory tendency (see formula in Chapter 2) for Nina A females (N = 8) in the two study periods (mean conciliatory tendency ± SE).



b) Conflicts over food.

Reconciliation was never observed following conflicts occurring during foraging. Conflicts over food were very rarely observed during focal sampling, making any analysis at the individual level impossible. Therefore, the level of food competition in the two periods was measured by using conflicts over food collected *ad libitum* and divided by contact time. During the period July-August 9 conflicts over food were observed whereas 14 conflicts were observed in February-April. When data were divided by contact time it was evident that conflicts over food doubled during February-April in comparison to July-August (February-April: 0.10 events/hr; July-August: 0.05 events/hr). Conflicts over food occurred with different percentages in relation to the food sources eaten by the monkeys (see Table 4.1). Overall, most of the conflicts over food occurred when monkeys were foraging on fruits. However, the different percentages of conflicts in relation to food source probably reflected the diet composition in the two periods.

Table 4.1: Percentages of conflicts over food and of food consumption for Nina A females (N = 8) in relation to the different food sources in the two study periods.

Food source	Period			
	July-August		February-April	
	% of conflicts	% of food consumed	% of conflicts	% of food consumed
Fruits + Seeds	57.1%	73.6%	33.3%	52.0%
Leaves	14.3%	2.4%	25.0%	24.9%
Animals	28.6%	4.8%	25.0%	4.0%
Fungi	0	0.9%	16.7%	0.8%
Unknown	0	18.3%	0	18.3%

4.4 Discussion.

a) Grooming distribution and post-conflict behaviour.

The two periods under study significantly differed in the time the monkeys spent foraging and grooming and in the consumption of the main food categories (see Chapter 3). However, no difference was found for number of grooming partners per female between the period July-August and February-April. The Shannon-Wiener diversity index and the B index both showed that there was no difference between the two periods in terms of grooming distribution. The same result was obtained when conciliatory tendency was compared, although the absence of significance could be due to the small sample size (conciliatory tendency could be calculated for only 6 females). Finally, frequency of aggression was the only variable that differed between the two periods.

Many studies have shown that habitat quality (measured as type, abundance, and distribution of food sources) has profound effects on the activity budgets of social animals that in turn affect the type and quality of social interactions among group members (e.g. Janson and Chapman, 1999; Mc Farland Symington, 1988; Pruetz and Isbell, 2000; Sterck *et al.*, 1997). Moreover, an increasing number of studies is showing that species which inhabit a wide range of habitats, such as baboons, may present large variations in ecology and social behaviour among populations (Byrne *et al.*, 1993). Conversely, this study suggests that, at least in Yakushima, ecological differences among seasons are too short or mild to affect social behaviour within a group. Indeed, the absence of variation in number of grooming partners, in grooming distribution, and in conciliatory tendency has two explanations that are not mutually exclusive. First, although significant, the differences in the activity budgets and diet composition between the two periods may not be of sufficient amplitude to affect social interactions among females. Indeed, the variation of time spent grooming in the two periods ranged from 37.4% of time in July-April to 22.4% of time in February-April. Moreover, time spent foraging on fruits and seeds never accounted for less than 50% of total time spent foraging while time spent foraging on leaves barely exceeded 20% of time in February-April. Such observations indicate that females were never forced by ecological constraints to significantly limit the time devoted to social activities during the study periods nor did they completely switch from an essentially frugivorous diet in the summer months to a folivorous diet in winter and early spring. A second explanation is related to the importance of social grooming for philopatric females as a means to keep competition under control, to recruit allies, and to increase tolerance between individuals (Barret and Henzi, 2001; Dunbar, 1991; Seyfarth, 1977). With the exception of periods of extreme crisis in terms of food availability, when animals are forced to dramatically increase their foraging effort at the expenses of other activities, monkeys try to maintain a certain amount of time for social interactions. Lactating female gelada baboons, for example, reduce the length of their resting bouts during the day in favour of grooming exchange when maternal care and/or foraging effort increase (Dunbar and Dunbar, 1988). Therefore, when monkeys have less time for social activities they simply reduce the amount of grooming given to each partner rather then increase inequality of grooming distribution (by, for example, keeping stable the grooming given to certain preferable partners while reducing or avoiding to groom the other usual partners). This strategy probably reduces the risk of deterioration of some amicable relationships and thus helps to maintain a stable conciliatory tendency between females.

Former opponents that reconcile after a conflict also restore the type of relationship they had before the conflict (see Chapter 1). On the contrary, former opponents from not-reconciled conflicts avoid each other and may significantly reduce the frequency of grooming exchange for several weeks (Koyama, 2001). These observations, together with the results of this study, indicate that social relationships may be deteriorated by other factors (e.g. the absence of reconciliation) than short-term variations in activity budgets (Barrett and Henzi, 2002).

Clearly, the stability of social relationships has positive effects on group cohesion and on the fitness of each group member (Pusey and Packer, 1997; Van Hooff, 2001). In this view, it is important to consider that the study group consisted of relatively few females. Although they were representative of the situation found in Yakushima, where groups are relatively small (see Chapter 1), such small sample size may have affected the results of this study. Seasonal variations in activity budgets and diet composition may not affect social behaviour in a small group as females may easily maintain grooming interactions with most of the other group females even when time for social activities is shorter. However, females living in large groups, who have a large number of potential partners for grooming exchange, may be less cohesive than females in small groups (see Chapter 5). As a consequence of this, they might be forced to reduce the number of grooming partners during periods of low food availability.

Interestingly, the variation in the frequency of aggression between the two periods followed the opposite trend in comparison to conflicts over food (see below). This was due to the fact that aggressive acts were almost always collected during grooming sessions. It is well known that animals that spend a lot of time in close proximity and/or in interaction have more opportunities to exchange agonistic behaviours than those who rarely interact (this is the reason why aggression is usually more frequent among kin than among unrelated animals; see Chapter 5). As a consequence of this, when monkeys spend more time grooming then the frequency of aggression increases accordingly.

b) Conflicts over food.

As already noted in previous studies (e.g. Aureli, 1992; Koyama, 2001; Verbeek and de Waal, 1997) and in post-conflict behaviour among males (see Chapter 6) reconciliation is never, or rarely observed when conflicts occur in a foraging context. One possible explanation is that social relationships might not be endangered by food competition as food-related aggression would be limited to the displacement from the food sources, not disrupting the relationship between the opponents (Aureli, 1992). This view would probably need to be confirmed by further research on the topic. Indeed, the main consequence of food competition is that a dominant animal has a higher foraging efficiency than a subordinate animal. This means that an animal being aggressively displaced from a food source or item will incur in considerable costs in terms of reduced time available for social behaviour (as he/she will need more time to obtain the daily energetic requirement) and/or reduced reproductive success (Dunbar, 1988). If this is true, a social relationship between two animals is likely to be greatly damaged by conflicts over food given the costs that one of these animals inflicts on the other (i.e. reduced foraging efficiency and increased level of stress for the absence of reconciliation and for the displacement from the food source). At the present state of research we cannot give a definitive answer about the effect that food competition has on social relationships.

Data on the occurrence of conflicts over food per female were too scarce to permit analyses on the level of food competition between the two periods. However, the higher frequency of conflicts over food observed in February-April in comparison to July-August suggests that food competition was lower in the summer months. This result supports the view that time spent foraging is a reliable indicator of food abundance in Yakushima (see Chapter 3). However, given that diet composition varied between the two periods, the possibility exists that the increase in food competition in February-April was due to the lower abundance of highly palatable/energetic food sources (i.e. fruits and animals; Hanya *et al.*, 2003), that are likely to elicit most competition, rather than to the lower overall food availability. Unfortunately, *ad libitum* observations provide measures that are not completely reliable as conflicts over food sources that are easier to be detected (for example, fungi on the ground) are likely to be over-represented. This factor, together with the scarcity of data on conflicts over food does not allow a clear picture of how food competition differed in the two periods.

Beside this consideration, the results of this study clearly indicate that, at least in small groups of Japanese macaques, seasonal variations in activity budgets, diet composition, and food competition do not apparently affect social interactions and conflict management within the group. Group size is an additional factor that may potentially have dramatic effects on social interactions within the group. The next Chapter will thus analyse how female Japanese macaques exchange grooming and manage conflicts in two groups of different size.

Chapter 5

Group Size Effects on Grooming Distribution and Post-Conflict Behaviour in Nina A and Kawahara Females

In Chapter 3 it was shown that females living in the two groups of different size (Nina A: N = 8, and Kawahara: N = 20) devoted a similar amount of time to foraging and moving but Kawahara females moved faster and were more dispersed than Nina A females. Moreover, females living in the large group spent more time grooming and consequently less time resting than females in the small group. Based on these differences, this chapter analyses how grooming distribution and agonistic interactions are affected by group size. Moreover, it analyses how frequency of reconciliation differs between the two groups and in relation to hierarchical rank.

5.1 Introduction.

The balance between benefits and costs of group living is affected by many ecological and social factors. Habitat characteristics, quantity and distribution of food sources, presence of potential predators, and level of between-group food competition are all important factors that can influence ranging patterns, intra-group food competition, and group cohesion (see Chapter 1). However, size of a group is another factor that may determine the benefits gained by social animals (Isbell and Young, 2002; van Schaik *et al.*, 1983). Depletion rate for a given area is shorter the higher the number of animals foraging in that area. As a consequence of this, animals living in large groups should increase their foraging effort in comparison to animals in small groups at the expense of other activities. However, this positive relation between foraging effort and group size is not always found: the two Japanese macaque groups of this study did not differ in percentage of time spent foraging (see Chapter 3), a finding also obtained among baboons (Henzi *et al.*, 1997b). This may be due to the fact that large groups occupy more productive areas than small groups.

Time is another, "hidden", factor that may interact with group size to impose severe limitations on the time budget and social "choices" of an animal (Cuthill and Houston, 1997; Dunbar, 1992; Dunbar and Dunbar, 1988). Among diurnal animals, such as the Japanese macaque, activities are concentrated during daylight hours (while the reverse is true for nocturnal species). These animals thus have a limited amount of time (which may vary considerably among seasons) to fulfil their daily energetic requirement and to exchange amicable social interactions with the other group members. The time devoted to social activities has important fitness consequences for social animals (e.g. Dunbar, 1988). As group size increases so does the number of potential partners with whom an animal may exchange social interactions. Therefore, time devoted to social activities should rise proportionately as group size increases up to a certain limit (determined by the time devoted to essential activities such as foraging). Given that a minimum amount of time must be devoted to foraging, animals in large groups may reduce, or ultimately sacrifice, less important activities in order to have more time available for solving this social problem. For example, baboons living in large groups spend more time grooming than baboons in small groups, by reducing resting time during the day (Dunbar, 1988). However, a problem arises with increasing group size. Although it would be important for a monkey to maintain amicable relationships (mainly through grooming exchange) with all the group members, there comes to a point when the time available for social activities is not enough for such widespread relationships. Moreover, some group members are more important as social partners than others (e.g. close kin). Therefore, when group size grows beyond a certain point monkeys will preferentially groom some partners and not interact with others at all. Consequently, inequality in grooming distribution is expected to increase. Indeed, Henzi and colleagues (1997b) showed that, in baboons, number of grooming partners increased and grooming became more evenly distributed as group size grew up to a certain point, beyond which the two variables began to decrease. They argued that this relation between group size and inequality of grooming distribution deteriorates group cohesion so that it may lead to fission.

It is unclear whether this pattern of grooming distribution is typical of baboons or if other primates show the same variation in social interactions as group size changes. Moreover, Henzi and colleagues used the Shannon-Wiener diversity index to measure grooming distribution. The use of this index has been recently criticised (Di Bitetti, 2000). Therefore, the aims of this Chapter were: to analyse how grooming distribution and inequality differed between a large and a small group, to compare the results of the Shannon-Wiener diversity index with a new index, to determine whether differences in grooming distribution between the two groups affect post-conflict behaviour and conciliatory tendency, and to discuss how grooming inequality and/or variation in conciliatory tendency may lead to fission in Japanese macaques.

5.2 Methods.

a) Study subjects and data collection.

Subjects of this study were females living in Nina A (small group: N = 8) and Kawahara (large group: N = 20) troops. Data were collected from January 24th to May 4th 2002. At the end of the study period, a total of 69.06 hrs of observation was collected on Nina A females (8.63 ± 0.15 mean hrs of observation per female ± SE; see Table 2.1) and 139.76 hrs on Kawahara females (6.99 ± 0.17 hrs per female). See Chapter 2 for details of data collected on post-conflict behaviour and on frequency of inter-group encounters.

b) Data analysis.

Data were analysed following the same methodology used in Chapter 4. Mann-Whitney test was used for comparisons between the two groups at the individual or dyadic level. Spearman rank correlation was used to analyse the relationship between social interactions, rank distance, and conciliatory tendency.

Contact time was 162.9 hrs with the small group and 200.1 hrs with the large group.

5.3 Results.

a) Grooming distribution.

The use of the Shannon-Wiener index as a means to compare grooming distribution in groups of different size has been recently criticised (Di Bitetti, 2000). These critics postulate that the number of grooming partners that an observer is able to detect for each female partly depends on the sampling effort on a group. That is, the higher the amount of data collected on a monkey the higher is the probability to observe all the grooming partners of that monkey. This problem is not solved if one uses the same amount of observations for each monkey as different groups may have different amounts of time available for social activities. These criticisms do not apply to this study on the grounds of three observations. First, if the number of grooming partners depends on sampling effort we would expect to find a positive correlation between these two variables. Contrary to this prediction the sampling effort was not significantly related to the number of grooming partners ($r_s = -0.03$, $N = 28$, NS). Secondly, the two troops did not differ in the time they spent foraging or moving (see Chapter 3) and thus could potentially devote a similar amount of time to social activities. However, females in the large troop exchanged more grooming than those in the small troop by reducing the time spent resting. Finally, sampling effort per female was rather similar for the two troops (see Section 5.2).

Kawahara females had a higher number of grooming partners than Nina A females although this difference did not reach significance ($T = 325.0$, $N_1 = 8$, $N_2 = 20$, $p = 0.069$; see Figure 5.1). However, on average females in the small group did not exchange any grooming with only 21.9% of females in that group whereas females in the large group did not groom 62.3% of potential partners. Inequality in grooming distribution was significantly greater in the large group than in the small group when using the Shannon-Wiener diversity index ($T = 248.0$, $N_1 = 8$,

$N_2 = 20$, $p < 0.05$; see Figure 5.2), This result indicates that females in the small group groomed more evenly all the available partners than females in the large group. However, when grooming distribution was compared between the two groups using the B index the difference was not significant, although grooming was still more equally distributed in the small group ($T = 301.0$, $N_1 = 8$, $N_2 = 20$, NS; see Figure 5.3).

Figure 5.1: Number of grooming partners in Nina A (N = 8) and Kawahara (N = 20) females (mean number of partners ± SE).

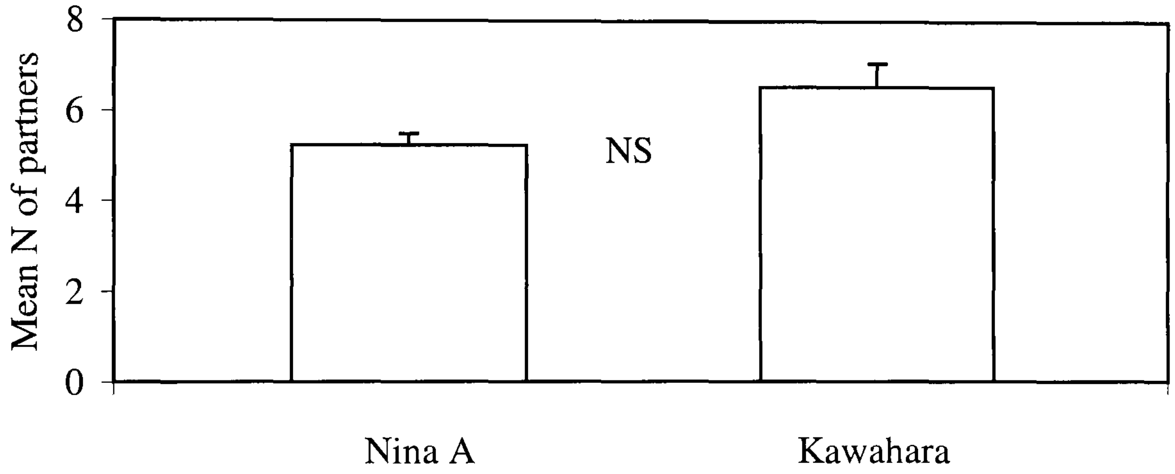


Figure 5.2: Shannon-Wiener diversity index for Nina A (N = 8) and Kawahara (N = 20) females (mean grooming diversity ratio ± SE; * p < 0.05).

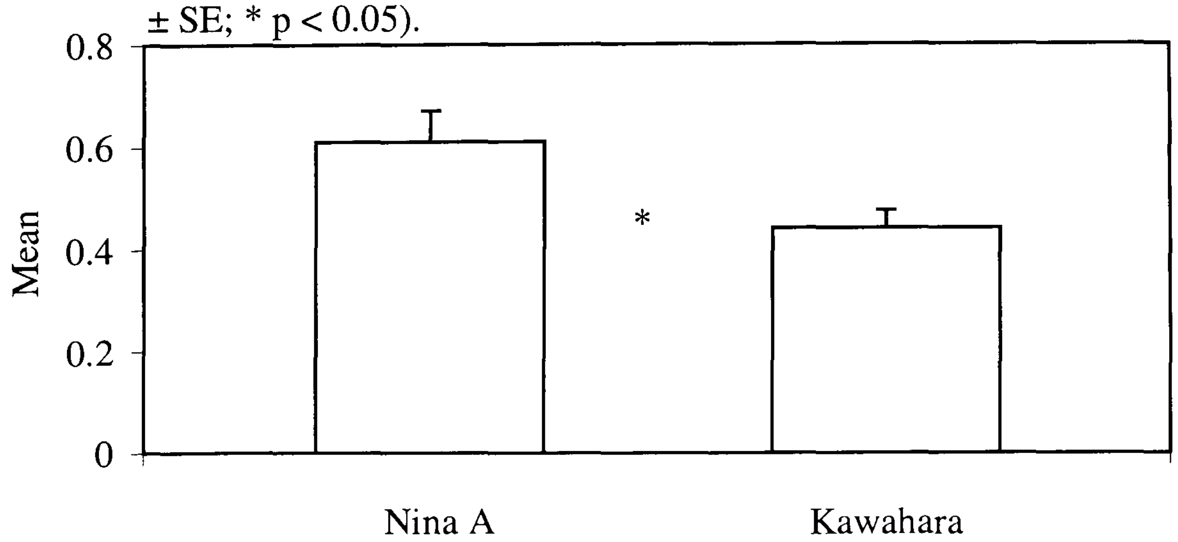
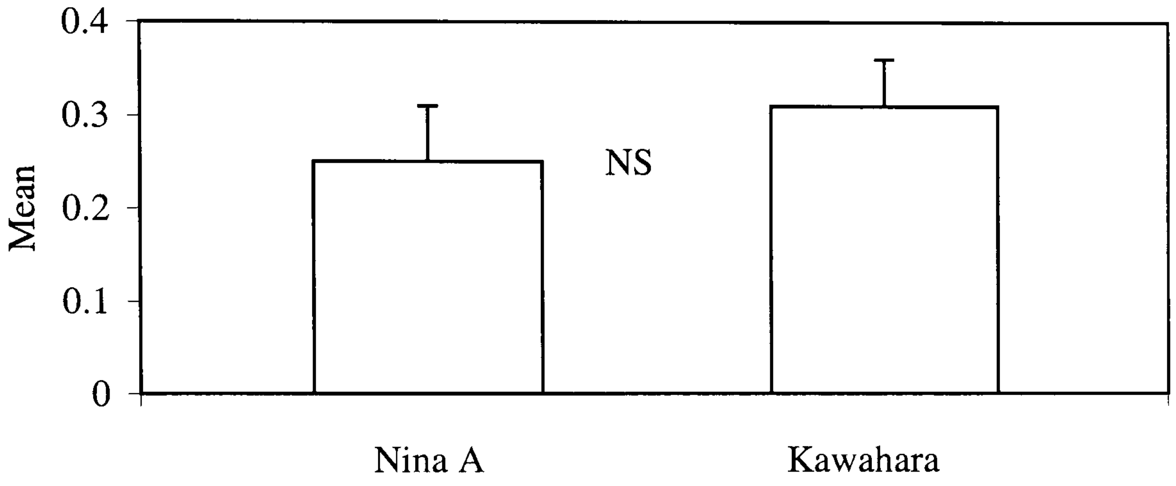


Figure 5.3: B index for Nina A (N = 8) and Kawahara (N = 20) females (mean B lavue ± SE).

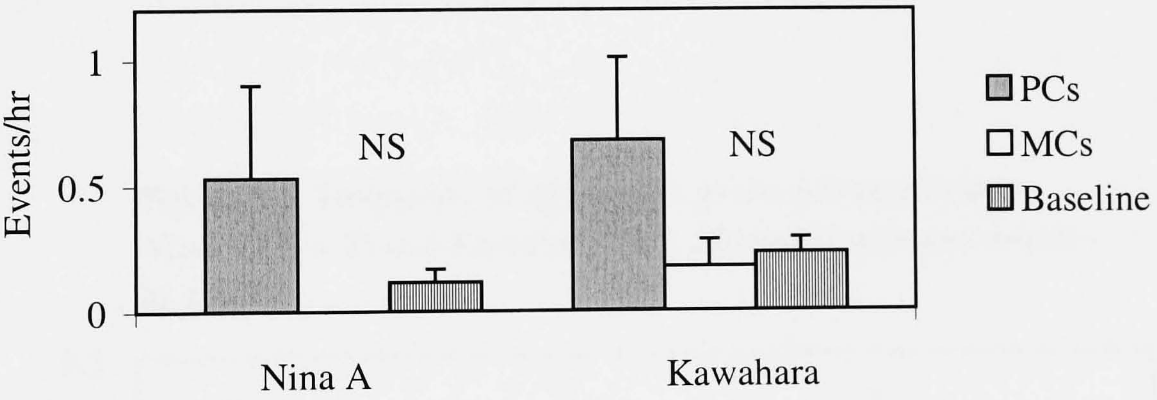


In order to analyse how grooming was related to rank distance and rate of aggression two Spearman rank correlations were run on each group. Grooming was negatively related to rank distance in both groups (Nina A: $r_s = -0.48$, $N = 28$, $p < 0.01$; Kawahara: $r_s = -0.20$, $N = 190$, $p < 0.01$), indicating that closely-ranked females exchanged more grooming with one another than distantly-ranked females. Moreover, grooming was not related to rate of aggression in the small group (Nina A: $r_s = 0.05$, $N = 28$, NS) while a positive correlation was found in the large group (Kawahara: rho = 0.23, $N = 190$, $p < 0.01$).

b) Post-conflict behaviour.

At the end of the study period 58 PC-MC pairs were obtained for the small group and 157 PC-MC pairs for the large groups. Polyadic conflicts (i.e. conflicts involving more than two females) were never observed to occur among females living in the small group. However, they constituted 5.1% (i.e. 8 / 157) of conflicts observed in the large group. All the conflicts observed except six (one in the small group and five in the large group) had a clear-cut result. During post-conflicts observations, aggressors received aggression from group members other than the former opponent in only two cases (one in the small and one in the large group). On the contrary, victims of aggression often received further aggression from the former opponent or from other group members. The two most dominant females in the small group and the alpha female in the large group were never victims of aggression from other females and thus were excluded from the following analyses. A Mann-Whitney test showed that frequency of aggression received during post-conflict observations was not significantly different between the two groups ($T = 296.0$, $N_1 = 6$, $N_2 = 19$, NS; see Figure 5.4). Moreover, frequency of aggression received during post-conflict, matched-control, and baseline observations did not significantly differ either for the small group (Friedman test: $\chi(2) = 4.00$, $N = 6$, NS; see Figure 4) and for the large group ($\chi(2) = 4.31$, $N = 19$, NS).

Figure 5.4: Frequency of aggression received observed during post-conflict (PCs), matched-control (MCs), and focal (baseline) observations for Nina A (N = 8) and Kawahara (N = 20) females (mean events / hr ± SE).



Victims of aggression were rarely observed to be aggressive towards group members other than the former opponents during post-conflict observations (i.e. 2 observations in the small group and four in the large group). Therefore, no statistical test was run to determine the occurrence of redirection after conflicts in the two groups. Finally, overall frequency of aggression (i.e. aggression given and received by each female) during baseline observations was compared between the two groups but the difference was not significant ($T = 322.5$, $N_1 = 8$, $N_2 = 20$, $p = 0.095$; see Figure 5.5).

During grooming/resting sessions a total of 41 PC-MC pairs were observed for Nina A and of 113 PC-MC pairs for Kawahara. This restricted data set was used for the following analyses (see Section 5.3c for analyses of conflicts occurring during foraging). As predicted by the "good relationship hypothesis" (see Chapter 1) grooming was positively related to conciliatory tendency in the small group as well as in the large group (Nina A: $r_s = 0.73$, $N = 15$, $p < 0.01$; Kawahara: $r_s = 0.49$, $N = 31$, $p < 0.01$). Conciliatory tendency was significantly higher in the small group than in the large group when data were analysed at the individual level ($T = 174$, $N_1 = 6$, $N_2 = 17$, $p < 0.05$; see Figure 5.6). Given that grooming exchanged among dyads was negatively correlated to rank distance and positively to conciliatory tendency (see above), a series of analyses was run to determine whether the different conciliatory tendencies observed in the two groups were due to differences in reconciliation rate in relation to rank of the opponents. A significant negative correlation was found between conciliatory tendency and rank distance for the small group ($r_s = -0.53$, $N = 15$, $p < 0.05$) while the test did not reach significance for the large group ($r_s = -0.22$, $N = 31$, NS).

Figure 5.5: Frequency of aggression given and received for Nina A (N = 8) and Kawahara (N = 20) females (mean events / hr ± SE).

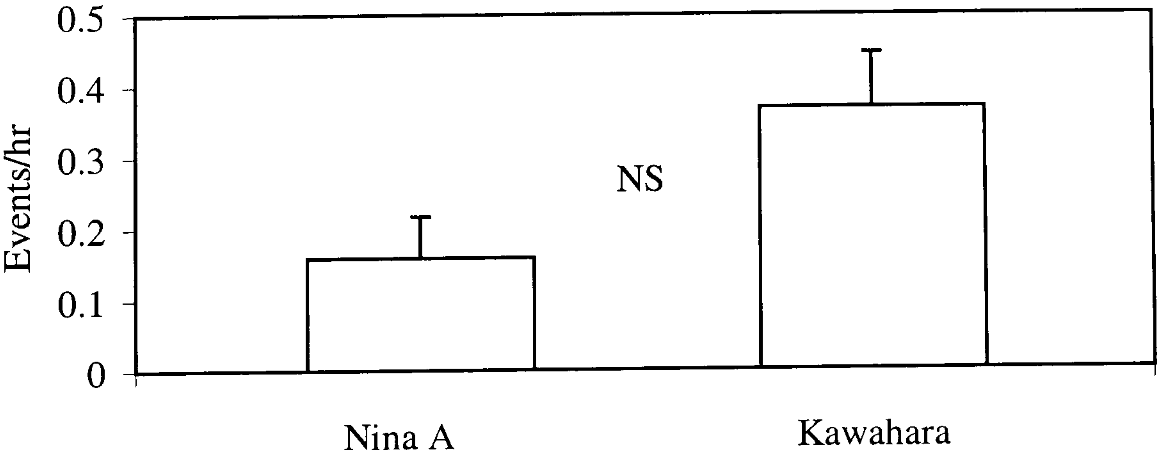
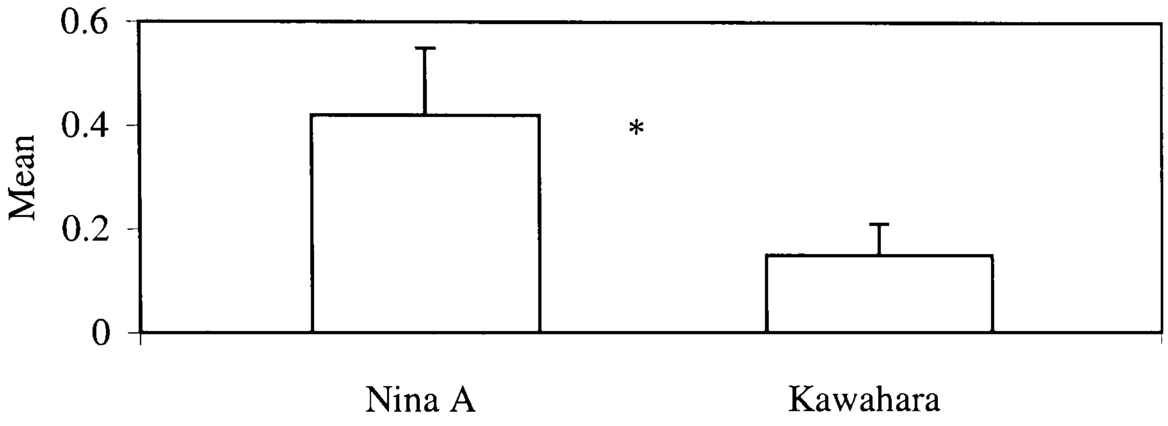


Figure 5.6: Conciliatory tendency (see formula in Chapter 2) for Nina A (N = 8) and Kawahara (N = 20) females (mean conciliatory tendency ± SE; * $p < 0.05$).

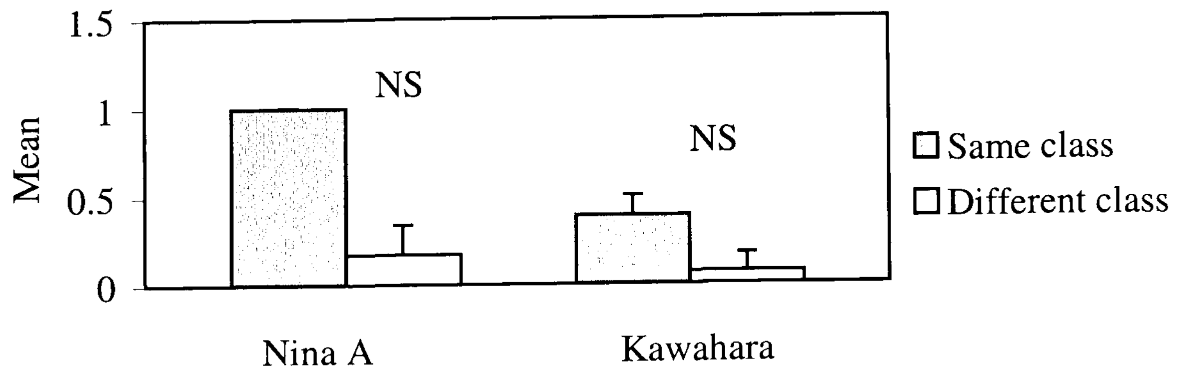


Finally, conciliatory tendency was compared between the different rank-classes of the two groups. Females in each group were divided into three rank classes, namely high-, middle-, and low-ranking females following the same procedure used in Chapter 3. For the large group the first 8 females in the hierarchy represented the high-ranking class, the last 8 females represented the low-ranking class, while the remaining 4 females represented the middle-ranking class. Dyads for whom conciliatory tendency could be measured (see above) were divided into two classes for each group: 1) dyads composed of females belonging to different rank-classes, and 2) dyads composed of females belong to the same rank-classes. No further division was done (e.g. dyads composed of females belonging to the high rank-class vs. those belonging to the low-rank class) as the sample size was too small for statistical analyses. In order to have clearly distinguished classes, the middle-ranking females were excluded from this analysis. A series of Mann Whitney tests showed that no significant result was found following the Bonferroni correction when comparing the conciliatory tendency of the four rank-classes, although some differences approached significance (see Table 5.1 and Figure 5.7).

Table 5.1: Results of Mann Whitney tests on conciliatory tendency (see formula in Chapter 2) for Nina A (N = 8) and Kawahara (N = 20) belonging to different rank-classes (Bonferroni correction: * p = 0.0125).

Comparison	Sample size	U value and significance
Same rank-class NA vs. Different rank-class NA	$N_1 = 3$ $N_2 = 6$	U = 1.5, p = 0.025
Same rank-class Ka vs. Different rank-class Ka	$N_1 = 20$ $N_2 = 20$	U = 163.5, p > 0.1
Same rank-class NA vs. Same rank-class Ka	$N_1 = 3$ $N_2 = 20$	U = 6.0, p = 0.020
Different rank-class NA vs. Different rank-class Ka	$N_1 = 6$ $N_2 = 20$	U = 58.5, p > 0.1

Figure 5.7: Conciliatory tendency (see formula in Chapter 2) for Nina A (N = 8) and Kawahara (N = 20) females belonging to different rank-classe(mean conciliatory tendency ± SE; see text for details).



c) Conflicts over food.

Aggressive behaviour was rarely observed during focal animal sampling when the monkeys were foraging and thus no clear picture about the level of food competition in the two groups can be drawn. Percentage of PC-MC pairs occurring during foraging was rather similar for the two groups (i.e. number of PC-MC pairs collected during foraging divided by the total number of PC-MC pairs for each group; Nina A: 29.3%, i.e. 17 / 58; Kawahara: 28.0%, i.e. 44 / 157). However, when these PC-MC pairs were divided by contact time frequency of aggression during foraging was rather different for the two groups (Nina A: 0.10 events per hr; Kawahara: 0.22 events per hr). Percentage of conflicts during foraging largely differed between the two groups in relation to the food category eaten by the monkeys (see Table 5.2). When a food patch (i.e. a discrete area within which individuals were able to collect food continuously as they moved within it) was clearly recognisable and a conflict was observed I recorded whether the former opponents left the patch after the conflict. A total of nine observations was obtained for the small group and eleven for the large group. In the small group the aggressor was never observed to leave the patch, but the victim left the patch after two conflicts (i.e. 22.2%) while in the remaining seven observations (i.e. 77.8%) both the former opponents remained foraging on the patch. In the large group, both former opponents left the patch after one conflict (i.e. 9.0%), the victim left the patch in five observations (i.e. 45.5%), and both former opponents remained on the patch after five conflicts (i.e. 45.5%). Given the scarce amount of data available for conflicts over food no other analysis could be run.

Table 5.2: Percentage of conflicts over food and of food consumption for Nina A (N = 8) and Kawahara (N = 20) females.

	Study group			
Food source	Nina A		Kawahara	
	% of conflicts	% of food consumed	% of conflicts	% of food consumed
Fruits	0	19.4%	16.7%	25.2%
Seeds	31.3%	21.4%	40.4%	6.8%
Leaves	25.0%	28.6%	4.8%	17.8%
Animals	25.0%	4.6%	21.4%	8%
Fungi	12.5%	0.2%	2.4%	0.8%
Unknown	6.2%	25.8%	14.3%	41.4%

d) Inter-group encounters.

During the course of the study, 7 inter-group encounters were observed for the small group and 2 encounters for the large group. Frequency of inter-group encounter per hour of contact with each group was higher for the small group than for the large group (i.e. 0.043 vs. 0.009). For the two groups, inter-group encounters were characterised by scarce female participation (see Chapter 7). However, the small sample size did not allow any further analysis.

5.4 Discussion.

a) Grooming distribution and post-conflict behaviour.

Two different indices have been used in this study to analyse variation of grooming distribution in relation to group size. The Shannon-Wiener index was chosen in order to have comparable data with those of previous studies on this topic (e.g. Cheney, 1992; Di Bitetti, 2000; Henzi *et al.*, 1997b). The B index was used as there is mathematical evidence that this index controls, better than all the other proposed indices, for factors that may affect its value, namely, group size, quantity of resource available, and presence of each individual in a group (Nonacs, 2003). In order to decide which index is best to use in a study the important problem to consider is which biological aspect one wants to analyse (Nonacs, pers. comm.). When one is interested in comparing resource monopolisation in different populations then group size is an important factor that one wants to control in order to have more reliable data as, for example, for comparisons within- or between-species. However, when one is analysing how group size affects the distribution of a resource (grooming, in this study) among all the group members, group size is the factor under study and thus an index that controls for it would eliminate useful biological information. Therefore, given the aims of this study and as the sampling effort did not affect the amount of data under analysis (see above) the Shannon-Wiener index gives more biological meaningful results.

Given a certain amount of time available for social activities, monkeys may follow two alternative strategies: they may try to exchange a limited amount of grooming with all, or with as many as possible, potential partners or they may concentrate their grooming effort towards few partners while exchanging a small amount of grooming, or no grooming at all, with the other partners. Data presented in this study indicate that females in the two groups followed the second strategy as values of the two indices were relatively far from those predicted for complete random distribution of grooming. However, a question arises as group size increases. Females living in a relatively small group may groom almost all the available grooming partners even though they devote a considerable higher proportion of their total grooming time to only some preferred partners. This option is difficult to achieve for females living in a large group. If they preferentially groom some partners not much time is left to groom, even briefly, all the other potential partners. Indeed, females living in the large group had a higher number of grooming partners than females in the small group. However, on average each female in the large group exchanged grooming with less than half of females in that group while this proportion was considerably higher for females in the small group. This means that the effort to groom all the available partners is more effectively constrained as group size increases. Moreover, the two indices used in this study showed, although with differing strength, that inequality in grooming distribution was higher in the large group. One important consideration here is that percentage of time spent grooming was significantly higher in the large group than in the small group (as they cut back resting time; see Chapter 3). Therefore, females in the large group could potentially compensate for the higher number of partners by having more time available for social activities. These observations evidence that grooming inequality was greater for females in the large group concentrated than for females in the small group.

Henzi and colleagues (1997b), in their study on five baboon groups of different size, showed that while foraging time was unaffected by group size grooming time increased as group size increased. Moreover, number of grooming partners and grooming distribution plotted against group size formed an inverted U-shaped curve (see Section 5.1). Interestingly, the inversion point corresponds to a group composed of 9 females and thus very close to the small group of Japanese macaques of this study. Henzi and colleagues argued that as group size grows it becomes more difficult for a female to exchange reciprocated grooming with all the potential partners. This social dilemma is resolved in favour of an increase in inequality of grooming distribution. However, this solution weakens the social network of a group and, eventually, forces females to fission (Henzi *et al.*, 1997a).

The results of this study support what has been found in baboons. Foraging time was unaffected by group size (see Chapter 3) and, as expected (Dunbar, 1991) grooming time was higher in the large group. Moreover, grooming inequality was higher in the large group than in the small group. However, data presented here are only from two groups and thus it cannot be clarified how grooming distribution and group size vary together. One important consideration here is that monkeys seem to follow particular social strategies depending on group size but that these are independent from habitat characteristics and from time available for social activities. Indeed, Japanese macaques and baboons live in largely different habitats (i.e. sub-tropical forest versus montane grassland, respectively) and consequently can devote different amounts of time to social interactions (i.e. 40% of total time versus 20%). This observation, together with the importance of social behaviour for group cohesion and individual fitness (Dunbar, 1988), supports the view that social constraints alone may lead to group fission (Henzi *et al.*, 1997a).

Japanese macaques and baboons differ in their social relationships with the other group members and probably in the pattern of group fission. Female Japanese macaques form strong grooming relationships with close maternal kin who usually rank close together in the hierarchy (Mehlman and Chapais, 1988; Muroyama, 1996). This results in a negative correlation between grooming exchanged among dyads and rank distance (de Waal, 1991; de Waal and Luttrell, 1986). Moreover, females rarely exchange grooming with resident males (with the exception of siblings or during consortship; D'Amato *et al.*, 1982; Mehlman and Chapais, 1988). On the contrary, kinship is still an important factor that regulates the quality of social relationships among female baboons (Seyfarth, 1976; Sambrook *et al.*, 1995; Silk *et al.*, 1999) but, at the same time, females form amicable relationships with some group males that may lead to preferential mating and agonistic support (Palombit *et al.*, 1997, 2001; Smuts, 1985). Moreover, Japanese macaques females of the same matriline rarely split up during fission but tend to join the same newly-formed group (Maruhashi, 1982). In baboons, females tend to join the group that has not been joined by the female who rank immediately before them (as, by doing so, they gain at least one position in the hierarchy; Ron *et al.*, 1994) or to follow the male with whom they have an amicable relationship (Smuts, 1985). Unfortunately, data currently available cannot confirm whether grooming inequality may be a factor that elicits group fission in Japanese macaques.

The absence of grooming interactions between two females may have profound consequences on their social relationships and is likely to be the primary social factor favouring group fission. One such consequence may be reconciliation. The absence of reconciliation has fitness effects on a monkey as it may affect grooming interactions between former opponents on a long period of time, the probability of receiving further attacks and social distress both increase (see Chapter 1). Therefore, females that have no grooming interaction and do not reconcile when a conflict occurs will tend to avoid one another. Moreover, the significant difference in conciliatory tendency in the two groups was due to the lower level of reconciliation found among females close in rank (who are usually grooming partners) in the large group compared to the small group. Inequality of grooming distribution increased in the large group (or at least remained similar) as did the number of grooming partners. Evidently, females in the large group were not as able as females in the small group to groom all their partners for a sufficient amount of time to secure a certain level of reconciliation. These factors have detrimental effects on the cohesion of females belonging to the same grooming network and in general of the group, and they may possibly elicit fission. Finally, the large group had a considerably lower frequency of inter-group encounters than the small group. Usually a large group is noisier than a small group and thus more detectable from neighbouring groups, this resulting in low frequencies of encounters. Yet, large groups are more successful at displacing small groups (Wrangham, 1980). One may speculate that fission is avoided until the foraging benefits of group living (i.e. reduced direct between-group food competition) outweigh the social costs. When group size increases above a certain point, within-group food competition and social constraints may then become important factors affecting group size in macaques.

One final consideration to make is that grooming distribution is affected by kinship, as grooming exchange within kin is much higher than between kin (e.g. Call *et al.*, 1996; Defler, 1978; Dunbar, 1991). It is possible that the size of kin-groups was proportionately different in the two groups, this resulting in different inequality of grooming distribution (Silk *et al.*, 1999) and different conciliatory tendency. Unfortunately, no data are available on the genetic relatedness of females and thus this factor cannot be ruled out.

b) Conflicts over food.

Data available on aggression rate and on post-conflict behaviour during foraging were too scarce to have a clear picture on the level of food competition in the two groups. However, rate of conflicts occurring during foraging was apparently higher in the large group than in the small group. Moreover, data available on the consequences of these conflicts indicate that victims in the small group were less likely to leave the food patch than victims in the large group. This would indicate that tolerance over food sources was higher in the small group than in the large group. One may speculate that this tolerance is a consequence of the higher cohesion of the small group but this consideration is supported by no data. Finally, as observed in other studies (e.g. Aureli, 1992) and among male Japanese macaques (see Chapter 6) reconciliation was basically never observed after conflicts over food (the possible reasons for this are discusses in Chapter 4).

Chapter 6

Post-conflict behaviour among Nina A males

Amicable social interactions among males have rarely been analysed in detail in Japanese macaques. Chapter 6 thus aims to analyse the occurrence of reconciliation among male macaques living in Nina A group (N = 13) in relation to period of year (i.e. mating vs. non-mating season) and age of the monkeys. Moreover, it aims to determine if and how grooming and reconciliation are affected by frequency of inter-group encounters.

6.1 Introduction.

The idea that males and females of human-beings and of other animals differ for many psychological and behavioural aspects other than the anatomical ones has been the general view of science for centuries. For example, Aristotle [1994] thought that males were more intelligent than females and thus more adapted for "higher" activities such as politics. Darwin (1871) supported this view and he also considered the two sexes to differ considerably for males have an aggressive nature while females are less egoistic. Early primatologists emphasised this hypothesised difference in the aggressive tendency between the two sexes. Zuckermann (1932) thought that relationships among males are characterised by high levels of aggression and competition for females whereas females are more likely to exchange amicable behaviour with one another. With the increasing number of studies on primates and other animals this picture has changed considerably in the last few decades. For example, Small (1993) showed that a certain level of competition for mating partners exists among barbary macaque females and it is thus not exclusive of males. However, the two sexes are still thought to differ in the strategies they follow for maximising their inclusive fitness, to a point where Trivers (1972) considered males and females as being two different "species". In order to obtain the maximum reproductive success during her lifetime, female behaviour is directed to achieve safety for her and her offspring and the food sources necessary for her survival and reproduction. On the contrary, male reproductive success is mainly determined by the number of females he is able to mate with during his life. As a consequence of this, relationships among females are predicted to vary from overly agonistic to cooperative and/or amicable (as, under certain circumstances, food source may be shared) whereas relationships among males are mostly agonistic (as mating partners are resources that cannot be shared and thus no room is left for cooperation).

Overall, inclusive fitness and/or reciprocal altruism are the main factors that favour cooperation among animals (Hamilton, 1964; Trivers, 1971) and indeed, these factors effectively explain why males cooperate and have good relationships in some primate species (de Waal, 1998; Hill and van Hooff, 1994; Nunn, 2000, 2001; van Hooff, 2000). All things being equal (e.g. sex-biased dispersal), related individuals are more likely to maintain amicable relationships regardless of their sex or age (Silk, 2002). This is one reason why female cercopithecines establish good relationships with one another through affiliative interactions (mainly grooming) and show cooperative acts more often than males (Melnick and Pearl, 1987). Male dispersal, female philopatry, multi-male/multi-female groups that elicit competition among males for fertile females, and the presence of matrilines composed of related females are all factors that favour the occurrence of amicable relationships among females more than among males in this group of primates (see Chapter 1). Moreover, Japanese macaque males living in the same group are usually unrelated to one another (Kurland, 1977; Melnick and Hoelzer, 1996), show low levels of amicable interactions and a strict dominance hierarchy (Matsumura, 1996; Muroyama, 1991), and, unlike other species (e.g. baboons; Noë, 1994), rarely show coalitions (Watanabe, 1979). Based on these assumptions, the "good relationship hypothesis" predicts that reconciliation is expected to occur more often among females than among males and this is indeed what has been found so far (see Chapter 1). These considerations have lead students of primate behaviour to give less consideration to analyses of post-conflict behaviour among males because the majority of species studied were social groups based on matrilines. Although reconciliation has been first described more than 30 years ago (de Waal and van Roosmalen, 1979), to my knowledge, no single study has been specifically focused on reconciliation among males.

With this background in mind, one would expect to find low frequencies of grooming and reconciliation among males of this species. Indeed, the scarce occurrence of reconciliation following conflicts among males has been observed in captive and free-ranging troops of Japanese macaques (Kutsukake and Castles, 2001; Schino *et al.*, 1998). However, affiliative interactions and/or cooperative acts among males have been predicted to occur when group males have some similarity of intent under certain circumstances (van Hooff, 2001). One of these circumstances is when group males defend their females and/or food sources from foreign males. Although there may not necessarily be a cause-effect relationship between similarity of intents and affiliative interactions among males (van Hooff, 2001), it is possible that particular conditions (i.e. high competition with extra-group males) may favour the establishment of good relationships and consequently a high level of reconciliation among same-group males. Yakushima macaques show higher frequency of inter-group encounters than populations living on the mainland (Saito *et al.*, 1998; Sugiura, 2000) and males actively participate in these encounters (see Chapter 5). These factors may have favoured amicable relationships among group males and indeed grooming among males is frequently observed (Takahashi and Furuichi, 1998). Therefore, the aim of this Chapter was to analyse post-conflict behaviour among males, the occurrence of reconciliation in relation to context of conflict, and to discuss the possible consequences that grooming and reconciliation may have on male relationship and competition within and between groups. To this end, data were collected on post-conflict behaviour, social interactions (i.e. grooming and aggression), and male behaviour during inter-group encounters.

6.2 Methods.

a) Study subjects and data collection.

Subjects of this study were 13 adult/sub-adult males living in Nina A troop (see Chapter 2 for details on the study animals, on the sampling methods used, and on the behavioural categories recorded).

b) Data analysis.

The method developed by Aureli and colleagues (1989), defined as the "time-rule", was used here to determine the occurrence of reconciliation. First, it was determined for each PC and MC the minute in which the first affiliative contact between former opponents was observed. Then, the distribution over time of these affiliative contacts was compared between PCs and MCs using the Kolmogorov-Smirnov test. To check for the possibility that the different distribution of affiliative contact between PCs and MCs was due to the extreme behaviour of some animals, data were analysed at the individual level. To this end, the "PC-MC method", developed by de Waal and Yoshihara (1983), was used (see Chapter 2). A Wilcoxon matched-pairs signed-rank test was then run to compare the percentage of "attracted" versus "dispersed" pairs for each animal (i.e. number of "attracted", or "dispersed", pairs divided by the total number of pairs for each female and multiplied by 100; see Chapter 2 for definitions). The same procedure was used to determine the occurrence of consolation (i.e. the occurrence of an affiliative contact between the focal animal and a group member other that the former opponent earlier in the PCs than in the MCs) and the distribution and occurrence of stress-related behaviours in PCs and MCs. A series of non-parametric tests were used to analyse post-conflict behaviour at the individual level. In order to analyse the effect of age males were divided in adult (estimated age > 7 years) and sub-adult males (estimated age between 4 and 7 years; see Chapter 2).

6.3 Results.

At the end of the study 155.3 hrs of complete record using focal animal sampling were collected. Moreover, a total of 128 PC-MC pairs was obtained, 79 in the mating season and 49 in the non-mating season. Among these PC-MC pairs, 15 (i.e. 11.7%) involved more than two males while the remaining 113 (i.e. 88.3%) were dyadic conflicts, yet 89.1% (i.e. 114 / 128) of conflicts had a clear-cut result whereas 10.9% (i.e. 14) of conflicts were undecided. Finally, 52.3% (i.e. 67) of conflicts were characterised by a threat directed from the aggressor to the victim, 38.4% (i.e. 49) by a chase, 7.0% (i.e. 9) by a slap, and 2.3% (i.e. 3) by a bite.

a) The occurrence of reconciliation.

The distribution of the first affiliative contact between former opponents was compared between PCs and MCs. Affiliative contacts were more frequent in the first minute of the post-conflict observations than in the matched-control observations ($D = 1.27$, $p < 0.05$; see Figure 6.1). When data were analysed at the individual level the percentage of attracted pairs was significantly greater than that of dispersed pairs ($T = 66$, $N = 11$, $p < 0.01$; see Figure 6.2), indicating that affiliative contacts between former opponents did not occur by chance but were due to selective attraction (i.e. reconciliation).

Figure 6.1: Number of PCs and MCs with an affiliative contact between former opponents in each minute (N = 5; * p < 0.05).

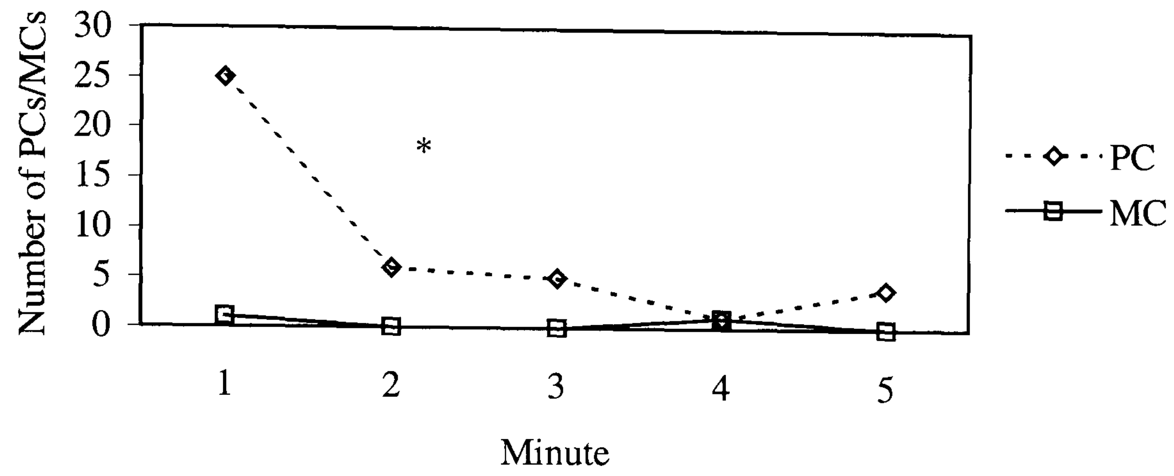
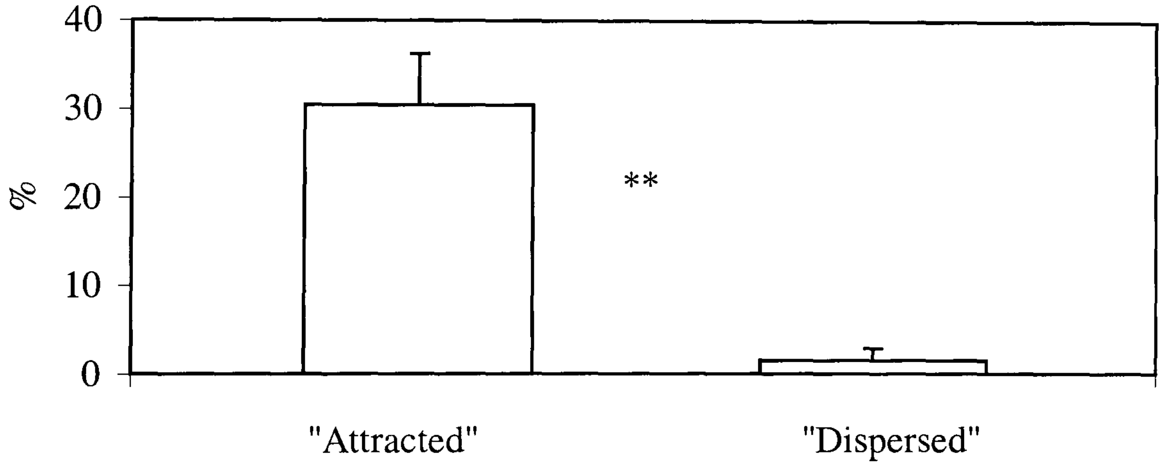


Figure 6.2: Percentage of "attracted" and "dispersed" PC-MC pairs (N = 11; mean percentage ± SE; ** p < 0.01; see Chapter 2 for definitions).



All the affiliative behaviours considered in this study were displayed by males, although in different proportions, as the first affiliative behaviour exchanged between former opponents (i.e. grooming = 61.0%; mounting = 21.9%; sitting in contact = 7.3%; playing = 4.9%; muzzle-contact = 2.5%; bi-directional lip-smacking = 2.4%). The aggressors took the initiative to reconcile in 29.3% (i.e. 12 / 41) of the attracted PCs-MCs, the victim in 51.2% (i.e. 21 / 41), while in 19.5% (i.e. 8 / 41) of attracted pairs both the former opponents took the initiative to reconcile. Finally, the intensity of aggression in the 41 "attracted pairs" was analysed. A simple threat characterised 58.2% of the "attracted pairs", the aggressor chased the victim in 34.5% of conflicts, a slap was observed in 4.9% of conflicts, and a bite in 2.4%.

b) The occurrence of consolation.

The distribution over time of first affiliative contacts between the focal animal and group members other than the former opponent did not significantly differ between PCs and MCs (D = 0.63, NS; see Figure 6.3). The percentage of PCs and MCs showing an affiliative contact between the focal animal and group members other than the former opponent was also analysed at the individual level using two Wilcoxon matched-pairs signed-rank tests. No significant difference was found between PCs and MCs (T = 43.5, N = 11, NS; see Figure 6.4) and the result remained basically unchanged (T = 43.0, N = 11, NS) when MCs, in which the focal animal was already involved in affiliative contact from the beginning, were excluded from the analysis.

Figure 6.3: Number of PCs and MCs with an affiliative contact between the focal animal and group members other than the former opponent in each minute (N = 5).

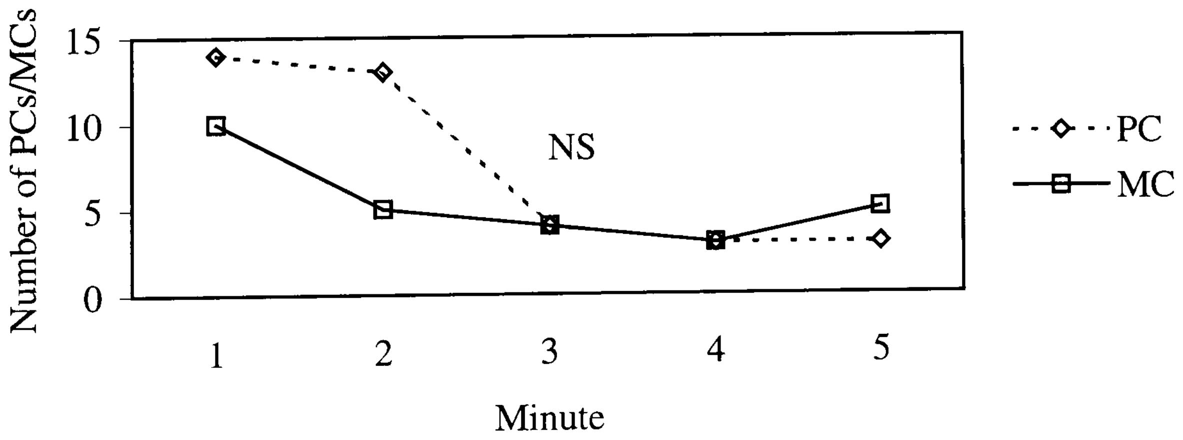
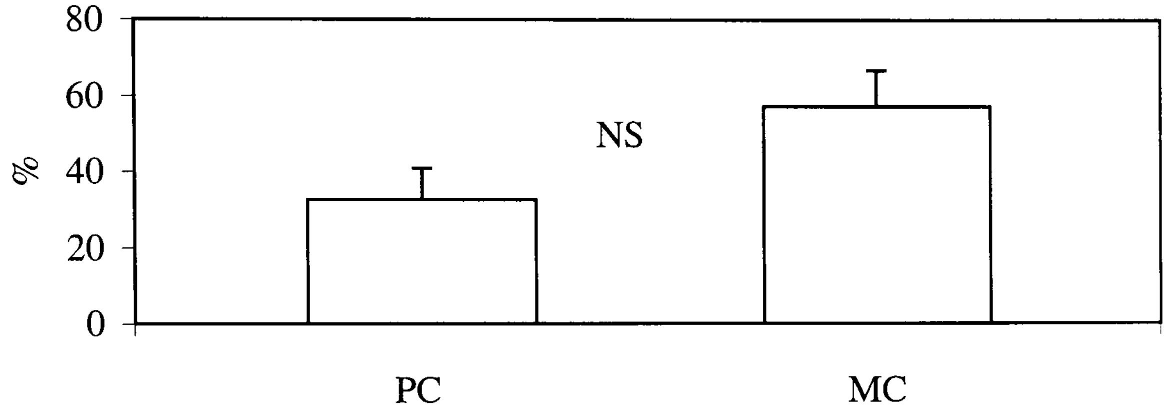


Figure 6.4: Percentage of PCs and MCs showing an affiliative interaction between the focal animal and group members other than the former opponent (N = 11; mean percentage ± SE).



c) Redirection, retaliation and stress-related behaviours.

The victim of aggression was observed to be aggressive towards group members other than the former aggressor in 4.7% of PCs (i.e. 6 / 128) and 0.8% of MCs (i.e. 1 / 128). Moreover, the victim of aggression was observed to be the subject of further aggression from the former aggressor or from other group members in 12 PCs (i.e. 9.4%) and 3 MCs (i.e. 2.3%). The small sample size did not allow establishing whether redirection and retaliation took place following conflicts among males.

In order to test whether the frequency of stress-related behaviours increased in the minutes after conflicts all the neutral and decided PCs-MCs pairs were selected in which redirection and retaliation did not occur, as these factors may have profound effects on the occurrence of stress-related behaviours (see Chapter 1). A total of 63 PCs-MCs pairs was obtained, 26 pairs where the aggressor was the focal animal and 37 pairs where the victim was the focal animal. First, the distribution over time of the frequency of scratching was compared between PCs and MCs, but no difference was found (D = 0.95, NS; see Figure 6.5). The frequency of scratching in PCs and MCs was also compared at the individual level but still the difference was not significant (PCs: 0.52 ± 0.11 mean events per minute ± SE; MCs: 0.43 ± 0.09; T = 27.5, N = 9, NS). Given that reconciliation took place more often during the first minute after the conflict (see Figure 6.1) the frequency of scratching per monkey was compared only considering the first minute of observation. Frequency of scratching was higher during the first minute of PCs than during the first minute of MCs but the difference only approached significance (T = 44, N = 10, p = 0.053). Finally, the PC-MC pairs were divided according to the role of the focal animal (i.e. aggressor or victim) and scratching rate in PCs and MCs was compared at the individual level. No difference was found between PCs and MCs for aggressor (T = 5.0, N = 7, NS; see Figure 6.6) nor was it found for victim (T = 39.5, N = 10, NS).

Figure 6.5: Frequency of scratching in each minute (N = 5; mean events / minute).

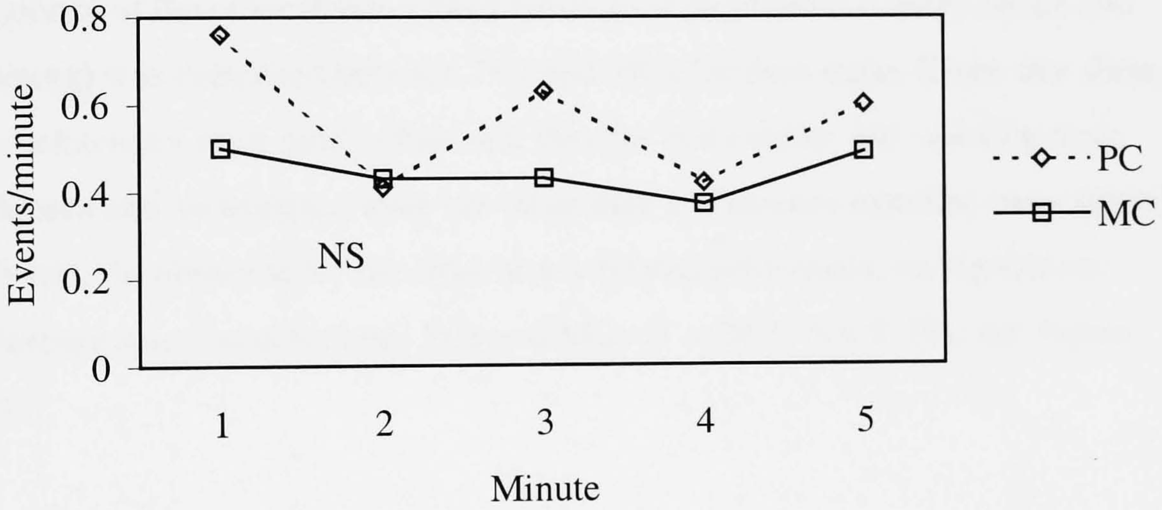
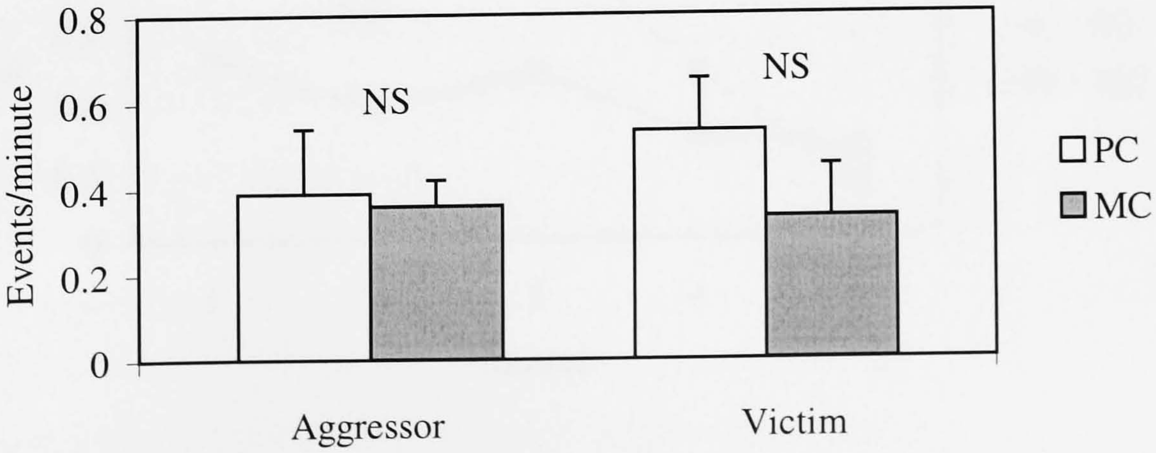


Figure 6.6: Frequency of scratching during PCs and MCs for aggressor (N = 7) and victim (N = 10) of conflicts (mean events / minute ± SE).



The same analyses were run on the percentage of time that the monkeys spent self-grooming. No difference was found in the distribution of self-grooming over time in PCs and MCs (D = 0.95, NS; see Figure 6.7). Self-grooming was higher during neutral PC observations than during MCs when data were analysed at the individual level (PCs: 6.21 ± 1.52 mean percentage ± SE; MCs: 2.99 ± 1.06; T = 38.0, N = 9, $p < 0.05$). However, this difference between PCs and MCs was not confirmed when only the first minute of observation was compared (T = 10.0, N = 10, NS). PCs and MCs had a similar amount of self-grooming for aggressor (T = 21, N = 7, NS; see Figure 6.8) whereas victims showed a higher amount of self-grooming during PCs than during MCs (T = 48.0, N = 10, $p < 0.05$). Finally, the frequency of the other stress-related behaviours recorded (i.e. body-shake and yawning) was compared between PCs and MCs for each male. Given that these two behaviours were rarely observed, data for body-shake and yawning were collapsed and no analyses were run other than a Wilcoxon matched-pairs signed-rank test. As observed for the other stress-related behaviours, no significant difference was found between PCs and MCs (T = 24.5, N = 9, NS; see Figure 6.9).

Figure 6.7: Mean percentage of time spent self-grooming in each minute (N = 5).

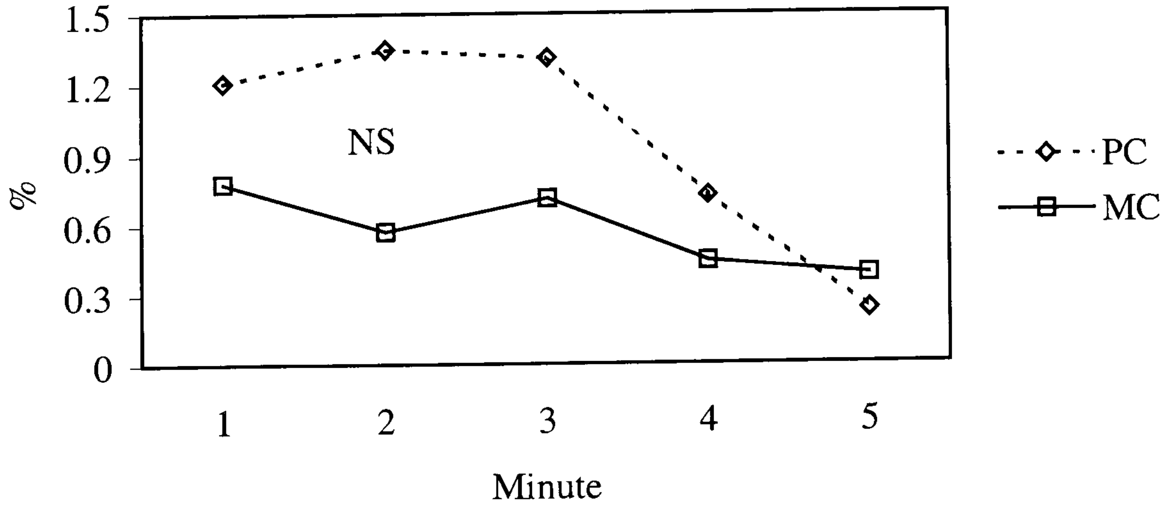


Figure 6.8: Percentage of self-grooming during PCs and MCs for aggressor (N = 7) and victim (N = 10) of conflicts (mean percentage ± SE; * $p < 0.05$).

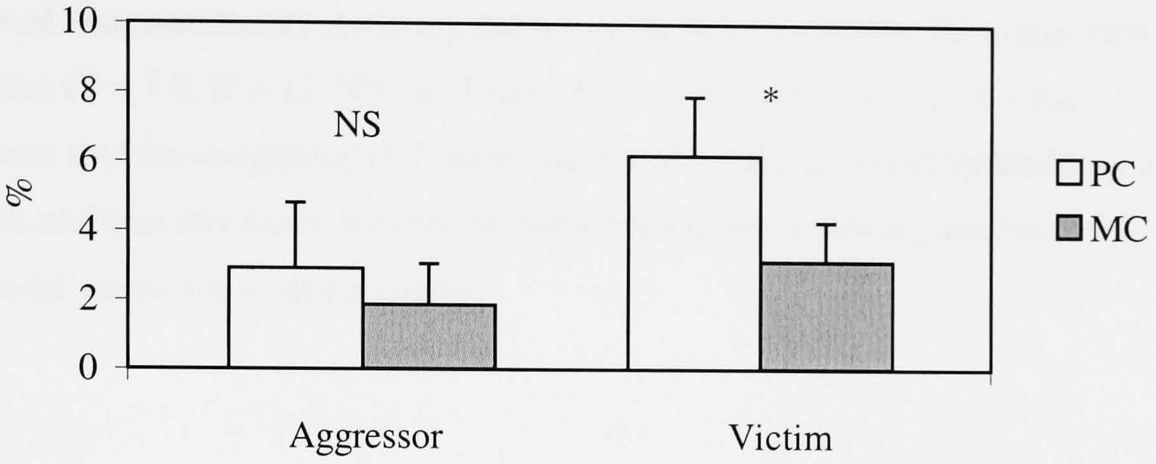
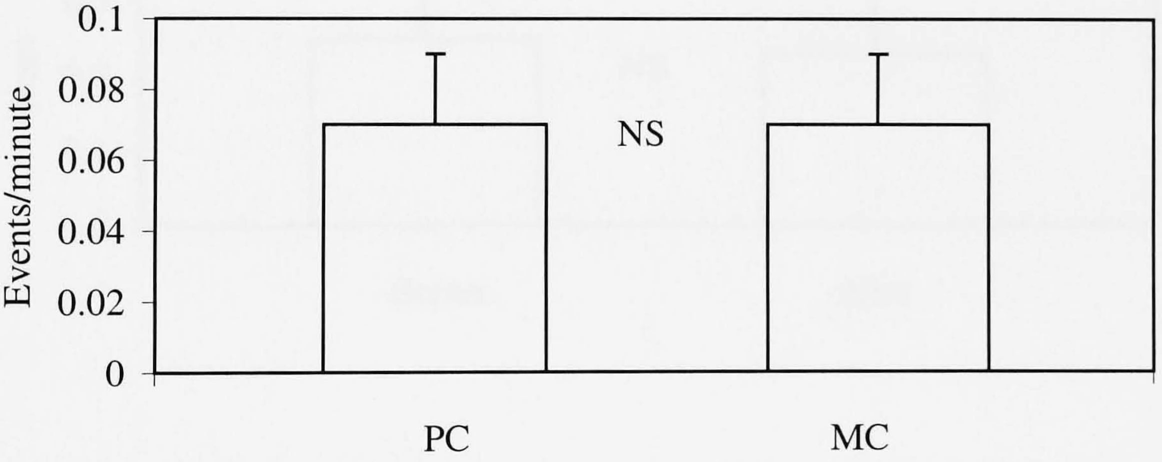


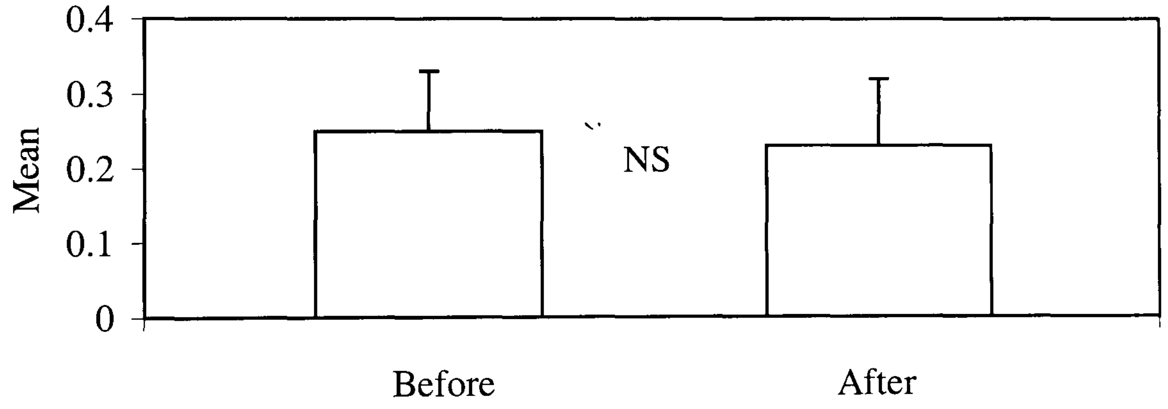
Figure 6.9: Frequency of body-shake+yawning during PCs and MCs (N = 9; mean events / minute ± SE).



d) Variation in conciliatory tendency in relation to context of the conflict, season, and among dyads.

During the course of this study (i.e. October 2001), 7 males left the troop (see Chapter 7). As this emigration could have had profound effects on the quality of social relationships among males, the conciliatory tendency before and after this emigration was analysed. The overall conciliatory tendency was equal in the two periods (conciliatory tendency before = 0.31, from 75 PC-MC pairs; conciliatory tendency after = 0.31, from 53 PC-MC pairs). Moreover, the conciliatory tendency among dyads of males who remained in the troop was compared between the two periods. This analysis was run using dyads instead of individuals in order to have a sufficient sample. A Wilcoxon matched-pairs signed-rank test showed that conciliatory tendency did not differ before and after the emigration of 7 males ($T = 7.0$, $N = 13$, NS; see Figure 6.10). Taken together, these results indicate that the emigration of 7 males did not affect the conciliatory tendency of males and thus this factor will not be considered in the following analyses on seasonal variations in reconciliation.

Figure 6.10: Conciliatory tendency (see formula in Chapter 2) for dyads of males who remained in the group, before and after the emigration of 7 males ($N = 13$; mean consiliatory tendency ± SE).

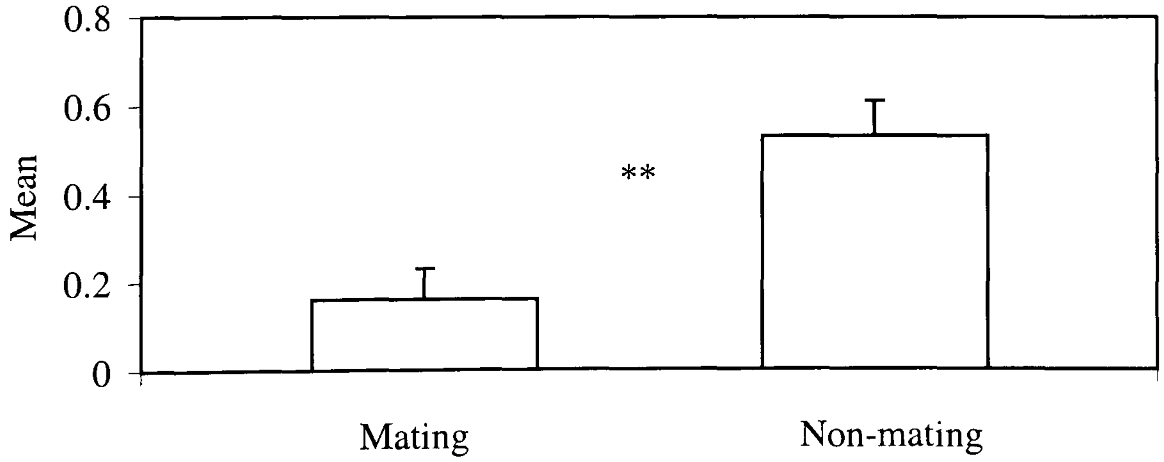


In this study the overall conciliatory tendency (Veenema *et al.*, 1994) was 0.305. A large variation in conciliatory tendency was found in relation to context of conflict (see Table 6.1). Reconciliation was relatively rare following conflicts over mating partners and over food but it was more frequent after conflicts occurring during grooming sessions. Conciliatory tendency was significantly lower during the mating season than during the non-mating season (see Chapter 2 for criteria used to define the mating season) when data were analysed at the individual level ($T = 54.0$, $N = 10$, $p < 0.01$; see Figure 6.11).

Table 6.1: Variation of conciliatory tendency (see formula in Chapter 2) in relation to context of conflict.

Context	Number of conflicts	Conciliatory tendency
Food	8	0.13
Mating partner	27	0.04
Grooming	80	0.38
Other (i.e. play, moving, resting)	13	0.46

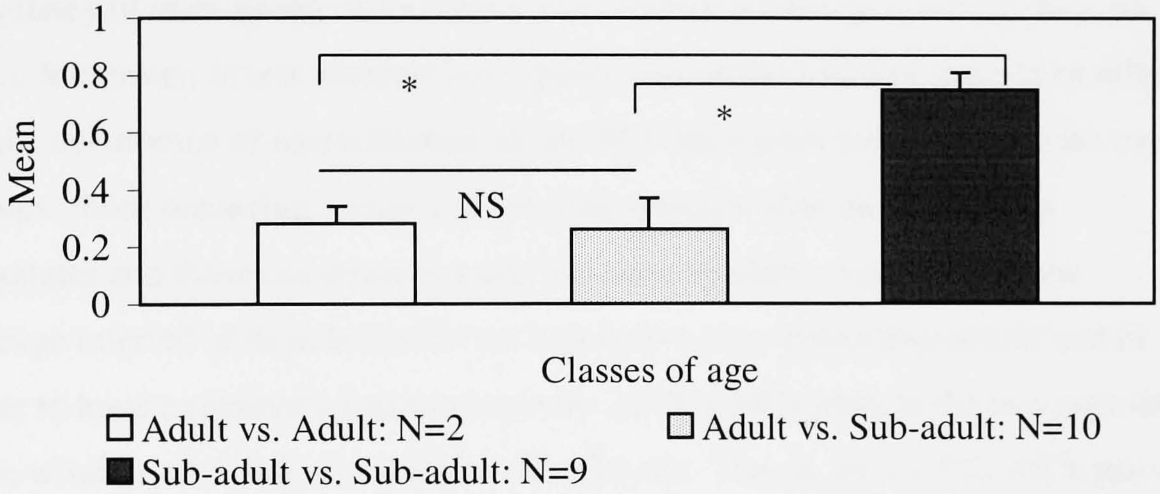
Figure 6.11: Conciliatory tendency (see formula in Chapter 2) during the mating and the non-mating season (N = 10; mean conciliatory tendency ± SE; ** $p < 0.01$).



Previous studies have shown that reconciliation occurs more often after conflicts between sub-adult males than between adult males or between the two classes of age (Schino *et al.*, 1998). To test this, a series of Mann-Whitney tests were run. Conciliatory tendency after conflicts among sub-adult males was significantly higher than that after conflicts among adult males ($U = 47$, $N_1 = 2$,

$N_2 = 9$, $p < 0.05$; see Figure 6.12) and that between the two classes ($U = 57.5$, $N_1 = 2$, $N_2 = 10$, $p < 0.05$). Conversely, conciliatory tendency did not differ for conflicts between adult males and those occurring between the two classes of age ($U = 102$, $N_1 = 2$, $N_2 = 10$, NS).

Figure 6.12: Conciliatory tendency (see formula in Chapter 2) in relation to age-class of the opponents (mean conciliatory tendency ± SE; * $p < 0.05$).



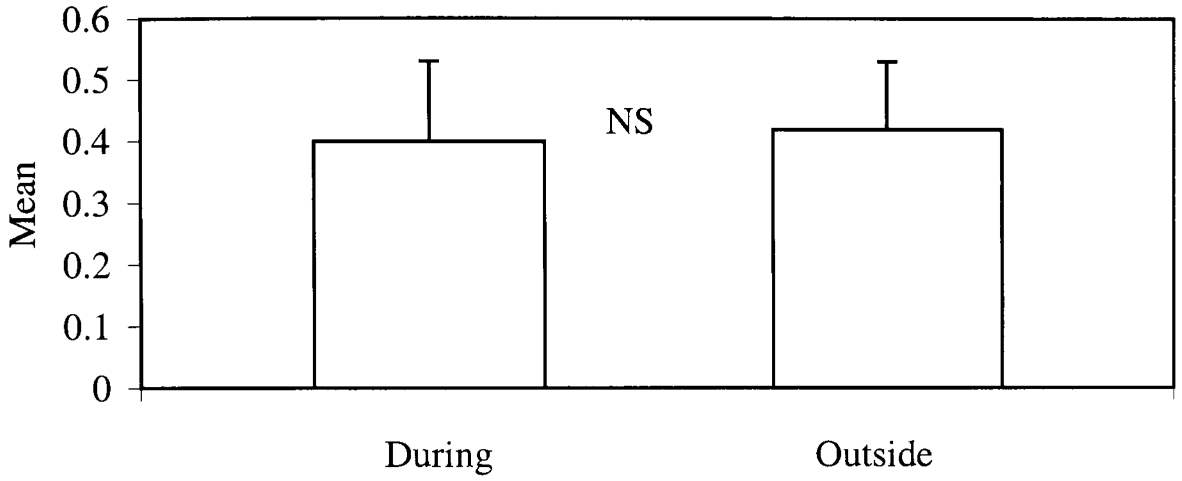
The "good relationship hypothesis" predicts that conciliatory tendency should be higher among monkeys who frequently exchange affiliative behaviours (mainly grooming) than among those who rarely do so. In order to test whether this hypothesis applies to Japanese macaque males a Spearman rank correlation was run to analyse the relationship between conciliatory tendency and grooming exchanged per dyad. Conciliatory tendency was positively correlated to the quality of the relationship existing between former opponents ($r_s = 0.52$, $N = 22$, $p < 0.05$).

e) The effects of inter-group encounters on grooming and reconciliation.

The possible effects that interactions between primate groups may have on the social relationships among members of the same group have been analysed in other primate species (see Section 6.1). Inter-group encounters are relatively frequent in Yakushima macaques and they are often characterised by the aggressive participation of males (see Chapter 7). In this study, 28 inter-group encounters were observed, on average one every 5.13 observation days. With this background in mind, a series of analyses was run to determine the relationship between inter-group encounters and the frequency of grooming and reconciliation among males.

First, two Spearman rank correlations showed that no significant relationship existed between frequency of inter-group encounters, grooming, and conciliatory tendency (frequency of inter-group encounters x grooming: $r_s = -0.5$, $N = 10$, NS; frequency of inter-group encounters x conciliatory tendency: $r_s = 0.12$, $N = 10$, NS.). Moreover, to test whether inter-group encounters had any short-term effects on the occurrence of reconciliation all the PCs-MCs pairs were divided into two groups: those occurring within a given time-window after an inter-group encounter and those occurring outside this time-window. According to the average interval of days between two successive inter-group encounters and in order to have a relatively balanced number of PCs-MCs pairs in the two periods, a time-window of 3 days was used in this analysis. That is, all the PCs-MCs pairs occurring within three days following an inter-group encounters were compared to all the PCs-MCs pairs occurring outside this time-window. Following this method, a total of 12 dyads was obtained for which at least 2 PCs-MCs pairs were available for each period. The analysis was based on 30 PCs-MCs pairs for the period after the inter-group encounters and 63 PCs-MCs pairs for the period outside it. A Wilcoxon matched-pairs signed-rank test showed that conciliatory tendency in the two periods was very similar ($T = 8.0$, $N = 12$, NS; see Figure 6.13).

Figure 6.13: Conciliatory tendency (see formula in Chapter 2) during the first 3 days after an inter-group encounter and outside this period (N = 12; mean conciliatory tendency ± SE).



6.4 Discussion.

a) The occurrence of reconciliation.

In this study two different methodological approaches have been used to analyse post-conflict behaviour (the "time-rule" and the "PCs-MCs" methods; see Section 6.2). Both the distribution over time of the first affiliative contact between former opponents in PCs and MCs and the analysis conducted at the individual level clearly demonstrated the occurrence of reconciliation. This study also showed that post-conflict behaviour among Japanese macaque males follow similar patterns to that among females, as affiliative contacts between former opponents occurred mostly during the first minute after conflicts and grooming was the most used behaviour for reconciliation (Schino *et al.*, 1998). The percentage of "attracted" pairs after conflicts characterised by mild aggression (i.e. threat) was higher than that after conflicts characterised by more intense forms of aggression. This result might suggest that reconciliation is related to the intensity of conflict but is more likely to be due to the fact that conflicts characterised by mild aggression were more frequent than others. Finally, victims took the initiative to reconcile more often than aggressors. This result may be related to the low percentage of PCs in which the victim received further aggression, suggesting that the low risk of being attacked may make it easier for victims to approach the former aggressor in order to reconcile. However, the possibility that aggressors vocally communicated the intention to reconcile favouring the victims' approach cannot be completely ruled out.

Post-conflict behaviour has been the subject of intense research over the last three decades (Aureli and de Waal, 2000) but most of these studies have been conducted in captivity. Inter-individual distance between former opponents in PCs and MCs is a factor that may affect the percentage of "attracted" and "dispersed" pairs, as two monkeys are more likely to interact the smaller the distance that separates them (Call, 1999; Call *et al.*, 1999). These results have led some authors (Sommer *et al.*, 2002) to postulate that reconciliation is more an artefact of the reduced inter-individual distance among animals due to captivity (as animals often live in dense groups and/or in small compounds where the possibility to flee for victims of aggressions are reduced) than a functional behaviour that may follow conflicts. Indeed, the results of this study, together with many others on the same topic, support the view that reconciliation is a widespread phenomenon among mammalian species with particular social characteristics (see Section 6.1 and Chapter 1), regardless to the setting or the group size and composition of the species on which the study is conducted.

b) The occurrence of consolation.

This study failed to demonstrate the occurrence of consolation but this result is not surprising. The other studies that have investigated this phenomenon in different macaque species (including Japanese macaques: Aureli *et al.*, 1993; *Macaca fascicularis*: Aureli and van Schaik, 1991; *M. nemestrina*: Judge, 1991; *M. sylvanus*: Aureli *et al.*, 1994) did not provide evidence for the occurrence of consolation, indicating that consolation may not occur in any macaque species. This may be due to the structure of macaque societies as hypothesised by Aureli and his co-workers (1994). They suggested that in macaque societies, characterised by a strict dominance hierarchy and a kin-based alliance system, the victim's allies usually are subordinate to the aggressor and thus cannot effectively help the victim. Given that the victim of attacks may be the subject of further aggression from the former aggressor or from other group members, associating with him/her may be risky for the victim's allies and thus consolation is not observed. The consideration that Japanese macaque males living in the same group are usually unrelated (Melnick and Pearl, 1987) and thus the kin-based alliance system is lacking (Watanabe, 1979; see below), provide a further explanation for why consolation did not occur in this study.

c) Redirection, retaliation and stress-related behaviours.

Analyses on the occurrence of stress-related behaviour following non-reconciled conflicts in comparison to MCs gave contrasting results. Almost all the studies on this topic (on Japanese macaques as well as on other primate species) have demonstrated that stress-related behaviour increases in non-reconciled conflicts whereas it drops almost immediately to baseline levels when reconciliation occurs (Aureli, 1992a, 1997; Aureli and van Schaik, 1991; Maestripieri *et al.*, 1992; Schino *et al.*, 1996). This is most likely due to the fact that reconciliation reduces the chances of further aggression from the former aggressor or other group members and restores the tolerance between former opponents, all factors that lower the level of anxiety of animals (Aureli, 1992; Kappeler and van Schaik, 1992). Redirection is also a factor that may help stress-related behaviour to go back to baseline levels after conflicts (Aureli, 1992b). In light of these observations the absence of a clear increase of stress-related behaviour is not surprising. If one excludes the youngest and/or lowest-ranking individuals, Japanese macaque males are rarely attacked by females (this is especially true when the number of females and the size of kin-groups is small as it is the case of this study troop; see Chapter 2). Yet, males do not frequently support other males fighting (Watanabe, 1979) and indeed the percentage of polyadic conflicts in this study was low. Finally, former opponents were rarely subject of aggression from the other group members. The low risk of receiving further aggression observed in this study was probably the main factor why the frequency of stress-related behaviour did not clearly increase after conflicts. However, the relatively small number of neutral PC-MC pairs on which the analyses were based could be an additional factor that caused the contrasting results obtained.

d) Variation in conciliatory tendency in relation to context of the conflict, season, and among dyads.

Reconciliation was more frequent following conflicts occurring in a grooming context than those over mating partners or food. This result supports the view that reconciliation is rarely observed when primates are competing over food (Aureli, 1992; Koyama, 2001; see Chapter 4 for discussion on the possible explanations of this result). It is clear that reconciliation rarely occurs after conflicts over resources that cannot be shared by the two contestants, be these food items or mating partners. This is confirmed by the lower conciliatory tendency observed during the mating season than during the non-mating season. Clearly, conflicts over these primary resources can only have two distinct results (i.e. "win" or "lose") whereas no room is left for negotiation (van Hooff, 2001). An exception to this picture is when reciprocal altruism or inclusive fitness is at work (Hamilton, 1964; Trivers, 1971) but these factors usually do not apply to Japanese macaque males (Kurland, 1977). In this species, males do not form coalitions in order to outrank a third dominant male who would otherwise monopolise the receptive females as it happens, for example, in baboons and in bonnet macaques (Noë, 1994; Silk, 1992). Therefore, the mating season represents a period of intense male competition during which social relationships with other males become less important and consequently reconciliation occurs at low rates. This conclusion has also been drawn from a study in captivity (Schino *et al.*, 1998).

Conflicts among sub-adult monkeys were reconciled more often than those among fully-adult monkeys. Juvenile Japanese macaques have been observed to reconcile more often in one captive study (Schino *et al.*, 1998) whereas no difference has been found in a provisioned troop (Kutsukake and Castles, 2001) or among long-tailed macaques (Cords and Aureli, 1993). The result obtained in this study was based on only two dyads of sub-adult monkeys (data coming from four different individuals) and thus a larger sample is required to clarify if sub-adult and/or juvenile Japanese macaques show higher rates of reconciliation than fully-adult animals.

Although most of the studies on post-conflict behaviour have been conducted on cercopithecines (and on macaques in particular; Aureli and de Waal, 2000), data on reconciliation among males are rare. This is because macaque males are usually unrelated one another, do not remain in their natal group, and often move from one group to another many times during their lives. Moreover, Japanese macaque males rarely form coalitions (Watanabe, 1979). These observations would suggest (van Hooff, 2000) that, unlike females, males have no particular reason or time for establishing good relationships with their same-sex companions, thus resulting in low rates of grooming and reconciliation (Soltis *et al.*, 1997). The results presented in this study contradict this prediction, as reconciliation was relatively high among males even if one compares it with the frequency of reconciliation observed among females in this and in other studies (see Table 8.1). Yet, conciliatory tendency was positively correlated to the quality of the relationship existing among opponents. As such, the results of this study raise two considerations. First, these data support the "good relationship hypothesis" and confirm that reconciliation may be predicted to occur among animals that maintain amicable relationships (Aureli *et al.*, 2002). Moreover, the case of the Yakushima macaque largely contrasts with what has been observed in the other sub-species (see above). A possible explanation to this result may be based on a comparison of the behavioural ecology of the two sub-species which differs in many characteristics (Nakagawa, 1998). First, the number of males per female in a group is higher in Yakushima macaques than in those living on the mainland (Sprague *et al.*, 1998). Moreover, grooming among males is more frequent in Yakushima as is the occurrence of inter-group encounters (see Section 6.1 and Chapter 1). Although it remains unresolved if the different sex ratio found in the two sub-species has a genetic basis or is due to different mortality of the two sexes, it is clear that males gain some benefits by establishing good relationships with some other group males. Such relationships cannot be long-lasting as they are among females, who remain in their natal group for their whole lives, but they may still give some benefits to males. These possible benefits will be discussed in the next section.

e) The effects of inter-group encounters on grooming and reconciliation.

The number of males per female is high in Yakushima macaques and thus one would expect to find high levels of aggression and low frequency of affiliation among males as observed in other species (e.g. Grant and Foam, 2002). Contrary to this prediction, males established good relationships with some other group males that affected the frequency of reconciliation among dyads (see above). At the same time, inter-group encounters are relatively frequent in Yakushima in comparison to Japanese macaque groups living on the mainland (Saito, 1998). Males aggressively participated in inter-group encounters more often than females (see Chapter 7). This would suggest that the "hired-guns" hypothesis (Rubenstein, 1986) may apply to Yakushima macaques. That is, during inter-group encounters males indirectly defended mating partners by directly defending food sources from other groups. The absence of any relationship between male behaviour during encounters and food abundance, however, indicates that this is not the case (see Chapter 7). Furthermore, during such encounters males may attempt to join a foreign troop (Sprague, 1991; 1992). When fully-adult males join a troop as the new alpha male this may also result in infanticide of the infants (Soltis *et al.*, 2000). Taking together all these observations, we may hypothesise the following scenario. Given the frequency of inter-group encounters troops with more resident males are favoured over those with a lower number of males as they are more able to defend mating partners and food sources. Moreover, males can more easily avoid new males from joining the troop. From such behaviour males may gain different benefits (see Chapter 7 for further discussion on this topic). Dominant males may defend their mating partners and the infants that they are likely to have sired from foreign troops/males. Yet, they may avoid or limit male transfer to their troop as the absence of new group males may increase the length of their tenure as dominant individuals. Subordinate males also gain some benefits by being aggressive during inter-group encounters, although they rarely have access to fertile females. They may avoid the transfer of foreign males who might join the troop at a rank higher than that of subordinate resident males. Moreover, they might obtain tolerance over food sources and reduce the chances of being attacked by the most-dominant individuals. Therefore, this similarity of intents among group males may favour the establishment of good relationships and the occurrence of reconciliation. Such relationships are also favoured by the high number of males who are present in a group (Horiuchi, submitted), a factor that otherwise would have disruptive effects on group cohesion. Contrary to this picture, no significant relationship was found between the occurrence of inter-group encounters, grooming among males, and the frequency of reconciliation. However, these results may be due to the lack of variation in the data as the intervals between two successive encounters may be too small to affect the quality of social relationships among males in a short period of time. In this view, the relationship between social behaviour and inter-group encounters remains a hypothesis to be tested with additional data. Indeed, a comparison of grooming distribution, frequency of reconciliation and of inter-group encounters in groups with different numbers of males would clarify if conflict management is related to the type of interactions among groups. In this view, analysing the costs and benefits of grooming exchange among males is essential for understanding the strategies that males follow.

Chapter 7

Causes and Consequences of Inter-Group Encounters in Nina A group

This chapter aims to investigate the relationship between frequency of inter-group encounters and food abundance in Nina A group (N = 21 adult/sub-adult males or females). Furthermore, the effect of sex, age, hierarchical rank, and period of year on monkey participation in the encounters is considered. Finally, this chapter analyses the relationship between male participation in the encounters and migration to foreign groups.

7.1 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 (Cant *et al.*, 2002; Cheney, 1987; Wrangham, 1980). The reasons why inter-group encounters occur may be summarised into three different categories: food defence, mating partner defence/access, and migration to and from other groups. Aggressive interactions are typical of species with a high level of inter-group competition for food and/or for mating partners. Inter-group food competition should increase as food becomes less abundant, slowly renewed or depleted, of high energetic value, and/or clumped (Janson and van Schaik, 1988; Pruetz and Isbell, 2000; Sterck *et al.* 1997; van Schaik, 1989). Moreover, direct competition is more often found in ungulates and carnivores living in small home ranges than in larger ones, although this relationship may not apply to primate species (Grant *et al.*, 1992).

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 the strategy that females and males follow during inter-group encounters should differ between the sexes. Females should aggressively participate in the encounters when direct inter-group food competition is high, in order to defend food sources (the resource-defence hypothesis: Wrangham, 1980). Moreover, in species where the risk of infanticide is high (e.g. *Presbytis thomasi*: Steenbeek, 1999) females with dependent infants are expected to be aggressive towards foreign males as they have been observed while attempting to kill infants during inter-group encounters in order to attract females in their own group. Yet, female aggressive behaviour should prevent foreign males from entering their group, as dominance reversal following male transfer increases the risk of infanticide (Hrdy, 1979; Soltis *et al.*, 2000).

Males may follow various non-alternative 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: van Schaik *et al.*, 1992; Wrangham, 1980). Moreover, males may defend food sources in order to indirectly defend females (the hired-guns hypothesis: Rubenstein, 1986). Finally, monkeys may use inter-group encounters to test their chances to successfully transfer to new groups (Lazaro-Perea, 2001). For example, young males often direct amicable behaviour towards foreign males during inter-group encounters and this probably affects their decision to transfer (Cheney, 1981; Matsumura, 1993).

Although many studies have analysed inter-group encounters in many 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. This type of analysis, however, gives an oversimplified picture of the topic. Playback experiments conducted on lions and chimpanzees (Heinsohn and 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, on the number of group companions who 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. This balance may change in different periods of the year (e.g. mating vs. non-mating season in seasonal breeding animals) and is expected to be different for each group member. Unfortunately, studies on the factors that may affect the type of participation of an animal in inter-group encounters are still scarce, although these data are urgently required to clarify the nature of interactions between groups and to test their theoretical implications on the evolution of social groups. Here, I analyse if and how inter-group encounters are related to inter-group food competition; 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 group of Japanese macaques.

A negative correlation exists between food availability and time spent foraging in Yakushima macaques (Agetsuma, 1995; Nakagawa, 1989) as is also the case in many birds and mammals (Norberg, 1977; Pyke *et al.*, 1977). Therefore, I used the proportion of time spent foraging each month as an index of food availability. If contest competition among groups is high in Yakushima then two predictions can be made: 1) Inter-group encounters are likely to be more frequent when food is scarce (i.e. when proportion of time spent foraging is high) as groups should be more active in detecting foreign monkeys in order to defend limited resources (Sugiura *et al.*, 2000); 2) Inter-group encounters are likely to be characterised by aggressive behaviours especially when food is scarce. I tested these predictions in order to determine the importance of inter-group direct competition for food on frequency and type of inter-group encounters. I also tested the predictions of Sugiura *et al.* (2000) that if aggressive behaviours are associated with resource defence then a positive relationship should exists between the agonistic nature of the encounters, their frequency, and the frequency of the encounters resulting in displacements.

7.2 Methods.

a) Study subjects and data collection.

Subjects of this study were 13 males and 8 females (age ≥ 4 years), members of Nina A group (see Chapter 2 for details on the study animals). Data were collected from 15th June 2001 to 30th April 2002. Whenever an inter-group encounter was detected the following data were recorded: location and duration of the encounter; presence/absence of our study animals; number, estimated age, and sex of the monkeys of the neighbouring troop; result of the encounter (i.e. won or lost: the study troop displaced or it was displaced by its opponent, respectively; undecided: neither the study troop nor its opponent were displaced by the other group). Moreover, during the whole duration of each encounter, data were collected on all the affiliative/sexual and aggressive behaviours displayed by our study animals using all occurrences sampling (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 faced one another in a restricted area while the remaining group members were involved in other activities. As such, the monkeys who actively participated in inter-group encounters were usually visible. However, given the large number of monkeys to be observed at the same time, all behaviours recorded were considered as events to avoid problems related to reliability of the data. Whenever contact with the monkeys could not be maintained, the data collection was stopped and the inter-group encounter was considered to be finished. I considered grooming, social play, genital inspection, lip-smacking, and affiliative/sexual mounts as affiliative/sexual behaviours, while all the behaviours ranging from threat at a distance to bite and slap were considered as aggressive acts. Data on size, composition, and home range of the neighbouring groups were obtained from Kyoto University Yakushima field station. Moreover, the study area was surveyed fortnightly to record the location of the neighbouring groups.

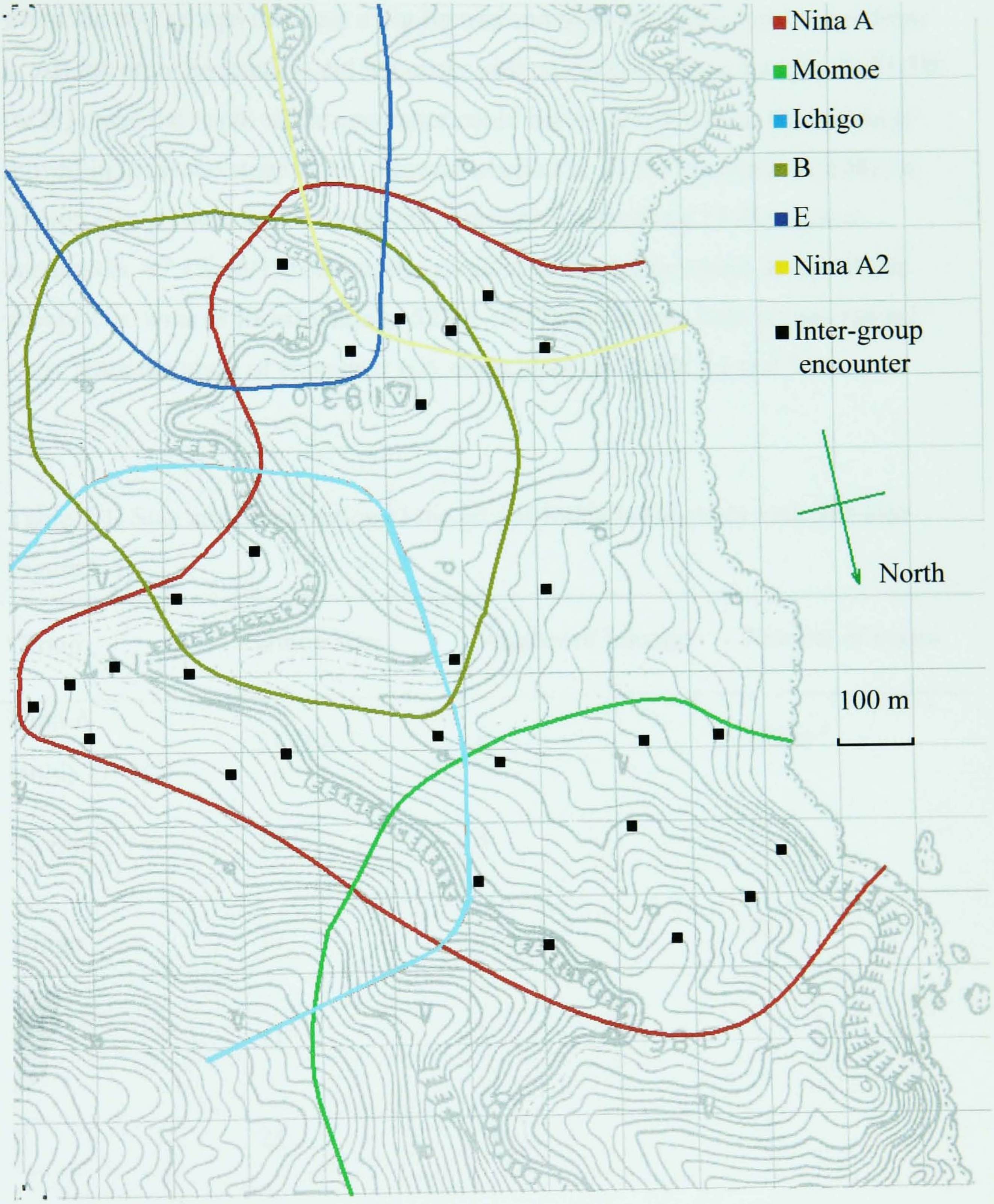
b) Data analysis.

Scan sampling was used to measure time spent foraging each month (see Chapter 2). June 2001 and January 2002 were excluded from the analyses of monthly variations given the small number of observation days. Moreover, no encounter was observed in July and November and thus the sample size for some correlations was reduced accordingly. Individual frequencies have been obtained dividing the occurrence of all the behaviours recorded per animal by the amount of time that each monkey was observed to participate to the encounters. Scores per individual were averaged for the total number of monkeys to obtain mean monthly frequency of aggressive behaviours displayed during the encounters. The data shown are means per hours of observation per individual or per month. Spearman rank correlations were used to test the importance of direct inter-group food competition in Yakushima macaques, and to analyse rank-related effects on the behaviour of the monkeys. Mann-Whitney tests were used for comparisons between individuals of different sexes or ages. Males were divided in two categories of age: adult males and sub-adult males (see Chapter 2). Wilcoxon matched-pairs signed-rank tests were used to compare the behaviour of males during and outside the mating season (see Chapter 2 for criteria used to define the mating season). In order to analyse male emigration a series of χ^2 and Mann-Whitney tests were run depending on whether the dependent variables were categorical or not. Male emigration was the independent variable (i.e. yes or no) while frequencies of aggressive and affiliative/sexual behaviour displayed by males during inter-group encounters; age (see above); origin (see Chapter 2); and rank were the dependent variables.

7.3 Results.

In this study a total of 28 inter-group encounters were observed (see Figure 7.1). The mean frequency of encounters per hour was 0.045 ± 0.011 (SE) and their mean duration was 1 hr 21’ ± 11’ (SE). Overall, aggressive behaviours towards monkeys of the neighbouring troops were observed in every inter-group encounter

Figure 7.1: Approximate home ranges of the groups living in the study area (see Table 7.1 for details on size and composition of the groups).



(28/28) while affiliative/sexual behaviours were observed in 21.4% (6/28) of the encounters. 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 21.5% (6/28) cases the result of the encounter could not be determined as the monkeys moved in areas too steep to be followed whereas in 17.8% encounters (5/28) the foreign group could not be identified. Among the remaining 17 inter-group encounters, 47.1% (8/17) encounters resulted in the displacement of one of the groups (i.e. wins or loses) while in 52.9% (9/17) encounters both groups moved away from the place of encounter (i.e. undecided; see Table 7.1 and 7.2).

Table 7.1: Size and composition of the groups living in the study area (see also Figure 7.1).

Group	Group size	Number of females	Number of males
Nina A (study group)	21 (14) [a]	8	13 (6) [a]
Momoe	15	8	7
Ichigo	27	16	11
B	11	5	6
E	21	10	11
Nina A_2	14	8	6

a: Numbers in parentheses refers to group size and number of males following male transfer.

Table 7.2: Result of the inter-group encounters with a known result (N = 17) between the study group and its opponents (see Section 7.2 for definitions).

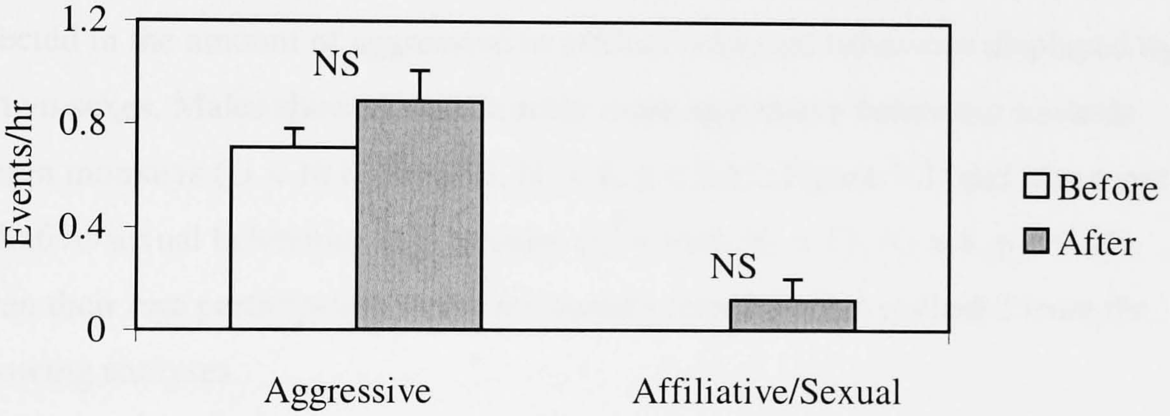
Group	Result		
	Won	Lost	Undecided
Momoe	3	0	2
Ichigo	2	1	4
B	1	0	0
E	0	1	3
Total	6	2	9

During the course of the study 7 males left the group (see below). This factor could clearly affect the behaviour of the males who remained in the group. As preliminary analyses, the effect of male emigration on inter-group encounters was analysed. No large difference was found in the frequency of inter-group encounters before and after the emigration of the 7 males (before: 0.053 mean encounters per hr; after: 0.043). Moreover, frequency of aggressive or affiliative/sexual behaviour displayed by males who remained in the group did not significantly differ before and after the emigration of the 7 males (aggressive behaviour: T = 17, N = 6, NS; affiliative/sexual behaviour: T = 3, N = 6, NS; see Figure 7.2). Therefore, all 13 males were considered in the following analyses to have a larger sample size.

a) The effect of food competition on inter-group encounters.

No significant correlation was found between frequency of inter-group encounters and time spent foraging per month ($r_s = -0.15$, N = 9, NS), nor between this last measure and frequency of aggressive behaviours displayed during the encounters (r_s = -0.39, N = 7, NS). Furthermore, time spent foraging was not correlated to the proportion of encounters resulting in displacements (r_s = 0.11, N = 7, NS). No significant relation was found between rates of aggressive behaviours and frequency of encounters (r_s = -0.11, N = 7, NS), nor between rates of aggressive behaviours and proportion of encounters resulting in displacements (r_s = -0.40, N = 8, NS).

Figure 7.2: Frequency of aggressive and affiliative/sexual behaviour before and after the emigration of 7 males displayed by males who remained in the group (N = 6; mean events / hr ± SE).



The same analyses were run using frequency of aggressive behaviours displayed by males alone, in order to test the "hired guns" hypothesis (see Section 7.1). No significant correlation was found between this measure and time spent foraging (r_s = 0.07, N = 7, NS), frequency of encounters (r_s = -0.54, N = 7, NS) or frequency of encounters resulting in displacement (r_s = -0.49, N = 7, NS).

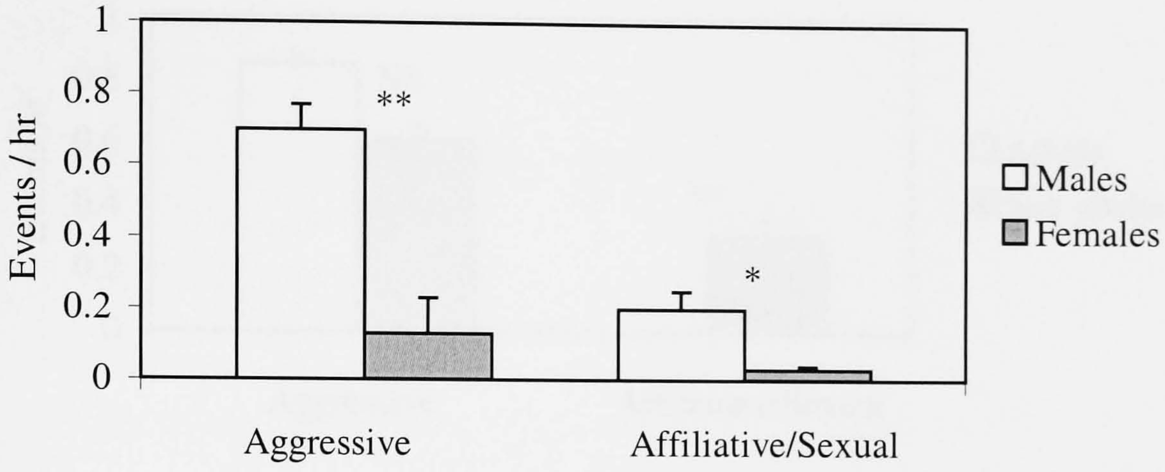
b) The effect of sex, age, and rank on participation in inter-group encounters.

Overall, aggressive behaviour towards monkeys of the neighbouring troops was observed in every inter-group encounter (28/28) while affiliative/sexual behaviour in 21.4% (6/28) of the encounters. Aggressive behaviour consisted of threats at a distance and brief chases (i.e. 1-2 metres) while in only one inter-group encounter an adult male was caught by our study group and repeatedly bitten. Overall, all the males directed at least one aggressive act towards foreign monkeys but only 61.5% (8/13) of males directed affiliative/sexual behaviour. Conversely, 37.5% (3/8) of females displayed aggressive behaviour during the encounters observed and 50% (4/8) of females showed affiliative/sexual behaviour. Males displayed aggressive or affiliative/sexual behaviour always towards foreign males. During only one encounter a female was aggressive towards a foreign female while in all the other cases females directed aggressive behaviour towards males in order to support their siblings who were participating in the encounter. Finally, females displayed affiliative/sexual behaviour always towards foreign adult males.

The different participation of males and females in inter-group encounters is reflected in the amount of aggressive or affiliative/sexual behaviour displayed by the two sexes. Males showed significantly more aggressive behaviour towards foreign monkeys ($U = 10.0$, $N_1 = 13$, $N_2 = 8$, $p < 0.01$; Figure 7.3) and also more affiliative/sexual 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 sub-adult males ($U = 11.0$, $N_1 = 5$, $N_2 = 8$, NS; Figure 7.4), but sub-adult males displayed significantly more affiliative/sexual behaviour towards foreign monkeys than did adult males ($U = 0.0$, $N_1 = 5$, $N_2 = 8$, $p < 0.01$). Finally, Spearman rank correlation was used to analyse the relationship between male hierarchical rank and their behaviour during inter-group encounters. There was no significant correlation between rank and aggressive behaviour ($r_s = -0.46$, $n = 13$, NS) but low-ranking males showed more affiliative/sexual behaviour towards foreign monkeys than high-ranking males ($r_s = 0.81$, $n = 13$, $p < 0.01$). A positive correlation was found between rank and age ($r_s = 0.78$, $n = 13$, $p < 0.01$).

Figure 7.3: Frequency of aggressive and affiliative/sexual behaviour displayed by males (N = 13) and females (N = 8; mean events / hr ± SE; * $p < 0.05$; ** $p < 0.01$).



c) The effect of the mating season on participation in inter-group encounters.

The mating season began on 18th August and was finished by the time the data collection began again in January. All 13 males were observed to ejaculate during the 2001 mating season and they were thus 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 hr, respectively). Male aggressive behaviour did not differ between the two periods (T = 56, N = 13, NS; see Figure 7.5) while male herding behaviour was significantly more frequent during the mating than the non-mating season (T = 21, N = 13, $p < 0.05$).

Figure 7.4: Frequency of aggressive and affiliative/sexual behaviour displayed by adult (N = 5) and sub-adult males (N = 8; mean events / hr ± SE; ** $p < 0.01$).

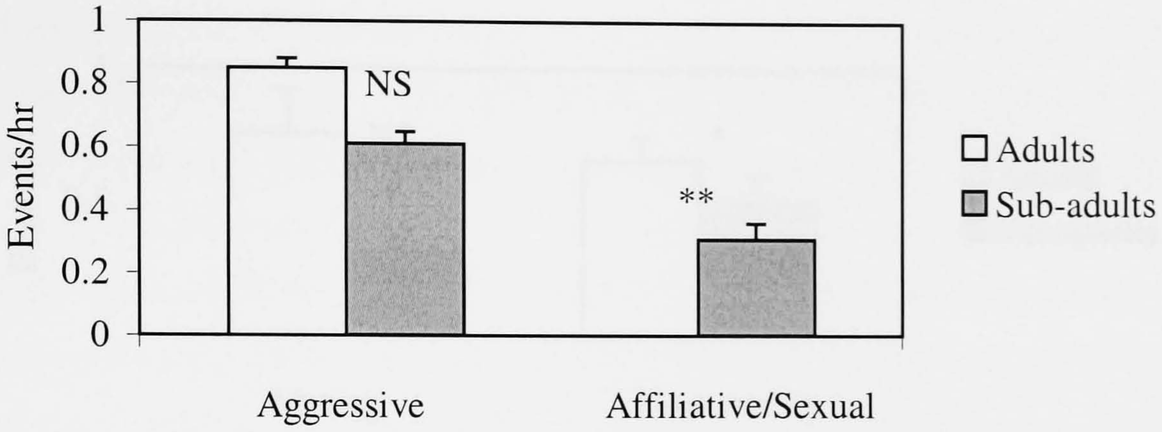
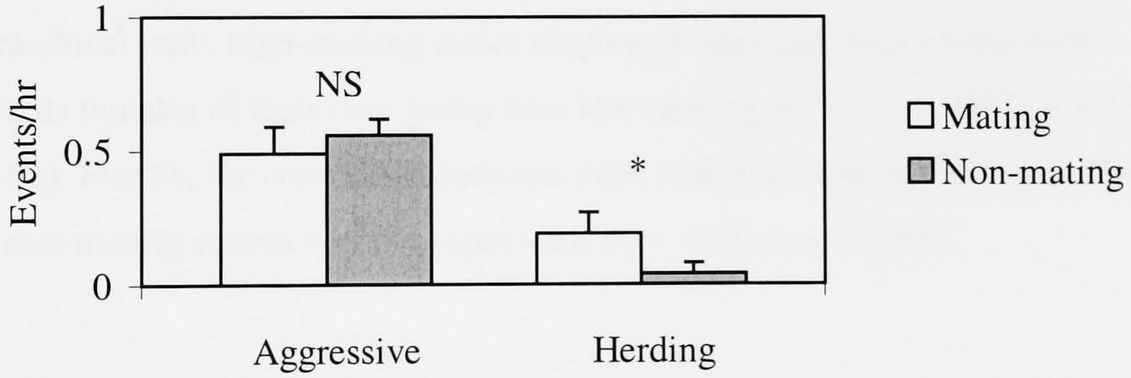
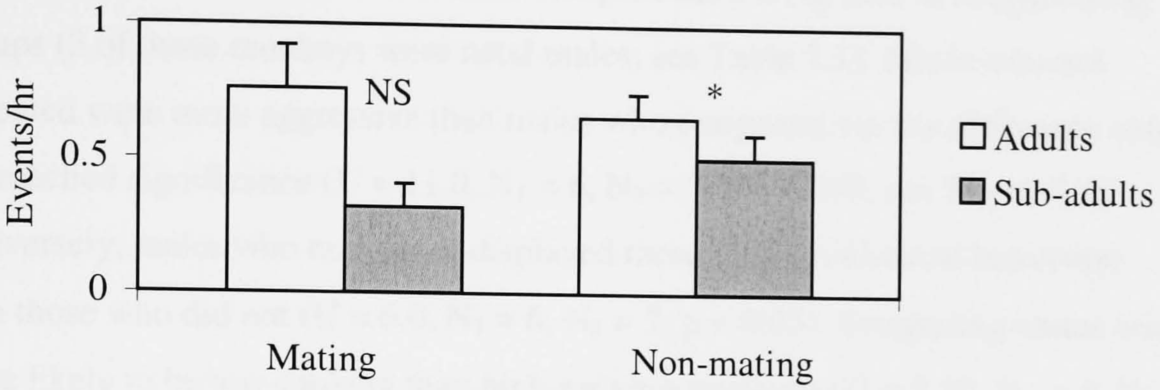


Figure 7.5: Frequency of aggressive and herding behaviour displayed by males (N = 13) during the mating and the non-mating season (mean events/ hr ± SE; * $p < 0.05$).



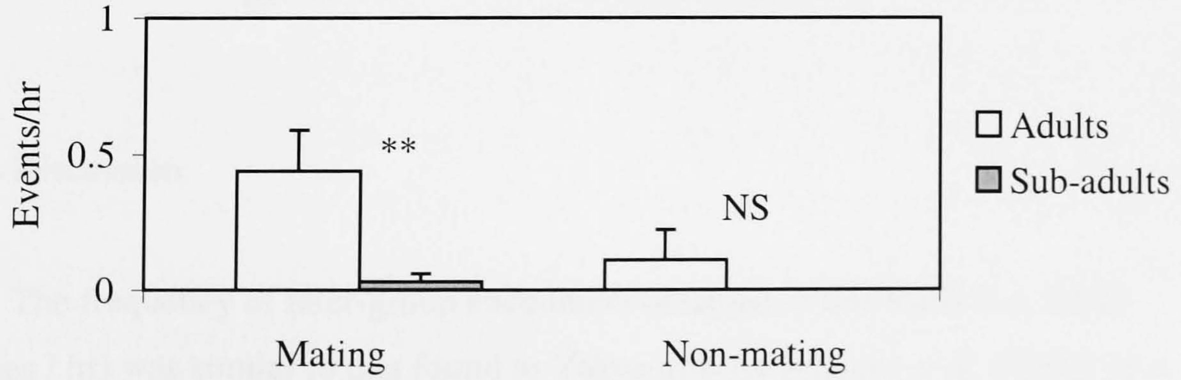
Adult males displayed more aggressive behaviour than sub-adult males during the mating season ($U = 8.0$, $N_1 = 5$, $N_2 = 8$, $p < 0.05$; see Figure 7.6). This difference disappeared during the non-mating season ($U = 12.0$, $N_1 = 5$, $N_2 = 8$, NS) and the same result was found with herding behaviour (see Figure 7.7): adult males herded females more than sub-adult 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).

Figure 7.6: Frequency of aggressive behaviour displayed by adult (N =5) and sub-adult (N = 8) males during the mating and the non-mating season (mean events / hr ± SE; * p < 0.05).



High-ranking males were more aggressive than low-ranking males during the mating season ($r_s = -0.64$, $n = 13$, $p < 0.05$) whereas no significant result was found for aggression outside the 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 aggressive behaviour towards females of their own group than 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).

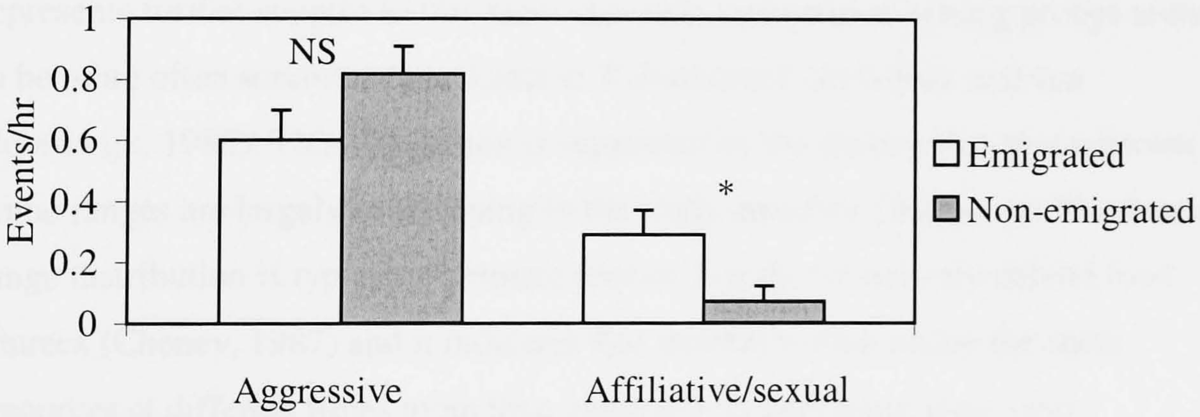
Figure 7.7: Frequency of herding behaviour displayed by adult (N = 5) and sub-adult (N = 8) males during the mating and the non-mating season (mean events / hr ± SE; ** p < 0.01).



d) The relationship between participation in inter-group encounters and male transfer.

During October 2001 seven males independently emigrated to neighbouring groups (3 of those monkeys were natal males; see Table 2.1). Males who not migrated were more aggressive than males who emigrated but the difference only approached significance ($U = 11.0$, $N_1 = 6$, $N_2 = 7$, $p = 0.068$; see Figure 7.8). Conversely, males who emigrated displayed more affiliative/sexual behaviour than those who did not ($U = 6.0$, $N_1 = 6$, $N_2 = 7$, $p < 0.05$). Emigrating males were more likely to be low-ranking than high-ranking monkeys ($U = 9.50$, $N_1 = 6$, $N_2 = 6$, $p = 0.057$), and sub-adult monkeys rather than adult monkeys ($\chi^2(1) = 3.75$, $p < 0.05$) whereas male origin (i.e. natal or not-natal) did not differ ($\chi^2(1) = 1.04$, NS).

Figure 7.8: Frequency of aggressive and affiliative/sexual behaviour displayed by males who emigrated (N = 7) and those who did not (N = 6; mean events / hr ± SE; * $p < 0.05$).



7.4 Discussion.

The frequency of inter-group encounters obtained in this study (i.e. 0.045 times / hr) was similar to that found in Yakushima by Sugiura *et al.* (2000) on a larger data set: 0.039 times / hr (151 encounters observed, data collected on 7 groups). Moreover, the percentage of inter-group encounters resulting in displacements in this study (i.e. 59.1%) is in line with the frequency found by the same authors (i.e. 66.2%). Finally, frequency of inter-group encounters, frequency and type of participation of the two sexes observed in this study were also very similar to that found in previous studies (Maruhashi *et al.*, 1998; Saito *et al.*, 1998; Sugiura *et al.*, 2000). These comparisons indicate that the results of this study may be representative of Yakushima macaques and are not due to the unusually skewed socionomic sex ratio of the study group (see Chapter 2).

a) The effect of food competition on inter-group encounters.

A high frequency of aggression between groups is typical of animals that aggressively defend food sources (Cheney, 1987; Gray *et al.*, 2002; Rubenstein, 1986; van Schaik and van Noordwijk, 1988). However, no strong evidence of direct inter-group competition for food was found: inter-group encounters were not related to time spent foraging and the same result was obtained when only male behaviour during the encounters was considered in the analyses. Moreover, the low female participation in inter-group encounters does not support the resource defence hypothesis (van Schaik, 1989; Wrangham, 1980). Finally, the observation that inter-group encounters rarely occurred near food sources represents further support to this view. As such, competition among groups seems to be more often scramble than direct in Yakushima (van Schaik and van Noordwijk, 1988). This conclusion is supported by the observation that adjacent home ranges are largely overlapping in the study area (see Chapter 1). This home range distribution is typical of primate species that do not actively defend food sources (Cheney, 1987) and it indicates that monkeys often utilise the same resources at different times more than aggressively defending them from neighbouring groups. Moreover, the high food-tree density in the study area (Maruhashi *et al.*, 1998) should favour a high level of scramble competition.

Many factors should be taken into account when analysing interactions and food competition among groups (Janson and van Schaik, 1988). Indeed, focusing the attention on inter-group encounters alone can give misleading results on the relative importance of direct and scramble food competition. Inter-group encounters may frequently be characterised by agonistic displays (as it is the case of Yakushima macaques) but still direct inter-group food competition may be relatively low. For example, two or more groups may spend a large amount of time foraging on the same resource at different times (e.g. a fruit tree in the overlapping area) and only seldom (relatively to this amount of time) encounter one another whilst foraging on these resources. Therefore, no definitive conclusion can be drawn on the type of food competition of a species without a wide range of measures (e.g. comparing the foraging effort of a group in the exclusive area of its home range with that in the area overlapping with neighbouring groups: Janson and van Schaik, 1988). Moreover, many studies have shown that clear and stable dominance/sub-ordinance relationships often exist among neighbouring groups (see for Japanese macaques: Kawanaka, 1973; Maruhashi and Takasaki, 1996). These relationships are likely to affect not only the foraging behaviour of monkeys (e.g. one group may change its original direction in order to avoid another, dominant one once detected) but also the frequency and type of inter-group encounters. In this study, vocalisations of foreign groups elicited variable responses in the monkeys: in some cases they quickly moved towards the other group, resulting in an inter-group encounter, whereas in others their behaviour remained apparently unaffected. The type of response to a foreign group may be affected by many factors. For example, wild chimpanzees respond to playback vocalisations of extra-group males (i.e. pant-hoot vocalisations) by approaching the speaker or by remaining silent, depending on party size and range location (Wilson *et al.*, 2001). It is possible that macaques remember some characteristics of the neighbouring groups (e.g. group size and number of adult females), the dominance/sub-ordinance relationship they have with them, and that they can recognise these groups by their vocalisations. Thus, the decision about whether to move towards a foreign group may be due to many factors (e.g. period of the year: mating vs. non-mating season), some of them not strongly related to resource defence. This decision may well affect the frequency and type of inter-group encounters observed. For example, inter-group encounters may be frequent and characterised by agonistic behaviours when no clear dominance/subordinance relationships exist amongst neighbouring groups whereas the reverse trend may be found when one group outranks the others (as the subordinate groups avoid the dominant one). Indeed, I observed only one inter-group encounter between the study group and B troop, which was the smallest group living in the study area, although their home ranges were largely overlapping (see Table 7.1 and Figure 7.1).

b) The effect of sex, age, and rank on participation in inter-group encounters.

The results of this study indicate that male behaviour during inter-group encounters was more related to defence of mating partners and avoidance of male transfer 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 female, males may potentially gain more benefits than females by being active during inter-group encounters: they may directly defend their mating partners (see below); they may attempt to mate with foreign females; they may establish dominance/subordinance relationships with foreign males (Kawanaka, 1973) that may discourage transfers in 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 top-ranking position; and, in periods of low food availability, they may gain access to limited and/or highly palatable food sources for their group females and for themselves. Moreover, high group densities favour a high socionomic sex ratio and male aggressive behaviour during inter-group encounters (Horiuchi, submitted; Ridley, 1986) 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 recently reported in some social mammals (e.g. horses and zebras: Rubenstein, 1986; *Colobus guereza*: Fashing, 2001; *Macaca radiata*: Cooper *et al.*, submitted).

This study has clearly shown that males' participation in the encounters differed in relation to their social status and/or age, and also in relation to period of the year (i.e. mating vs. non-mating season; see below). These results indicate that a monkey can change its frequency and type of participation in the encounters during the course of the year and during its lifetime. Indeed, social mammals present a complex behavioural plasticity and decision-making (van Noordwijk and van Schaik, 2001). Therefore, during inter-group encounters monkeys are probably able to assess their strength and that of their counterparts, and to "weigh", at least to a certain limit, the consequences of their behaviour. 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 their consequences on social behaviour.

c) The effect of the mating season on participation in inter-group encounters.

High-ranking/adult males were significantly more aggressive towards foreign males during the mating season than low-ranking/sub-adult males. Moreover, they also displayed more herding behaviour towards their group females. However, these differences were not found for inter-group encounters occurring outside the mating season. Overall, these results support the mate defence hypothesis (van Schaik *et al.*, 1992; Wrangham, 1980), that 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 (e.g. Cant *et al.*, 2002; Sprague, 1991) and high-ranking/adult males usually have more chances to sire the infants of their own group (Cowlishaw and Dunbar, 1991; but see also Takahata *et al.*, 1999). In addition to this, Takahata *et al.* (1998) suggested that resident males might even increase their chances of sneaky copulation with other group females by either guarding females of their own group and exchanging aggressive behaviour with foreign males. Therefore, for high-ranking males the benefits of mate defence (i.e. reduced frequency of female extra-group copulations) exceed the costs associated with aggressively defending mating partners, a situation that may result in severe injury. The discrepancy between benefits and costs is expected to increase the higher a male is up the hierarchy. These considerations weakly apply to low-ranking/sub-adult males, who usually are less able to effectively compete for oestrous females. 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).

d) The relationship between participation in inter-group encounters and male transfer.

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 and 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 and 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 and van Schaik, 2001). Overall, males who are about to transfer may follow two different strategies. They may join a new group by aggressively attempting to outrank the dominant individuals. This strategy is likely to be achieved by fully-adult males, who 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 amicable 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 who still have to reach their full size and strength (Matsumura, 1993). Indeed, in this study low-ranking/sub-adult males emigrated more than high-ranking/adult males and those males also displayed more affiliative/sexual 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/sub-adult 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 been often predicted but not frequently observed in field studies (Cheney, 1981; Hamilton and Bulger, 1990; Lazaro-Perea, 2001; Sprague, 1992). 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 the target group. These considerations may explain why males who then emigrated, were often the first ones to move towards foreign groups. The hypothesis that monkeys may influence inter-group distance and interactions in order to achieve their aims is sound but not unexpected in animals with complex cognitive abilities as the Japanese macaque.

Chapter 8

General Discussion

8.1 Conflict Management in Wild Japanese Macaques.

This study covered different aspects of conflict management in the Japanese macaque. Chapter 3 showed that Yakushima macaques show large variations in activity budgets and diet composition across the year. Moreover, it evidenced that group size affects many aspects of the behavioural ecology of this sub-species. Females in the large group (N = 20) had a larger home range and travelled more per hour than females in the small group (N = 8). They also spent more time grooming by reducing the time devoted to rest during daylights. Although time spent grooming significantly differed between the summer and the winter/early-spring months, this difference did not result in any evident seasonal variation in grooming distribution and reconciliation among females (Chapter 4). Conversely, group size did affect conflict management as grooming inequality was higher and conciliatory tendency lower among females living in the large group in comparison to females in the small group (Chapter 5). Post-conflict behaviour by male Japanese macaques (Chapter 6) showed that reconciliation follows similar patterns and occurs with comparable frequency with that found among females. The high conciliatory tendency found among males was analysed in relation to frequency of inter-group encounters but no significant result was obtained. Inter-group encounters were relatively frequent in Yakushima and they were characterised by the different participation of males and females (Chapter 7). Females rarely intervened in the encounters while males displayed aggressive or affiliative/sexual behaviour. Male behaviour during the encounters was affected by their rank, age, and/or period of the year (mating vs. non-mating season).

Many studies have hypothesised that variations in activity budgets and/or diet composition may have profound effects on social interactions within the group. However, this study demonstrated that short-term variations during the year do not have any significant effect on grooming distribution and conflict management. Conversely, grooming distribution and conflict management were both affected by variations in group size. Taken together, these results indicate that monkeys are relatively resilient to short-term (and/or of small amplitude) ecological variations while they are more strongly affected by variations in group size. Given the importance that amicable interactions and reconciliation have on individual fitness, this resilience possibly evolved to avoid the potential disruptive effects that constraining periods (with insufficient time available for social interaction) could have on individual relationships. In animals with good memory as the Old World monkeys (e.g. Cheney and Seyfarth, 1990b), social interactions may have long-term effects on the type of relationship that two monkeys share. As a consequence of this, social relationships may remain stable even though two monkeys cannot exchange amicable interactions every day. A different problem arises following social and/or non-social long-term variations, such as when group size increases above a certain point. When time constrains the number of group members with whom a monkey is able to maintain amicable relationships then monkeys would be forced to sacrifice some social relationships. This is why grooming inequality is higher the larger group size is in both baboons and Japanese macaques (Henzi *et al*, 1997b; see Chapter 5). In such situations seasonal variations in activity budgets may have a significant effect on grooming distribution and conflict management; an effect that it is not evident when group size is relatively small (Dunbar, 1996).

Male Japanese macaques have rarely been observed to exchange high levels of amicable behaviour or to reconcile with frequencies similar to, or even higher than females (see below). However, Yakushima macaques seem to represent an exception to this picture. Whether the results of this study were due to any particular characteristic of the study group (e.g. the unusually high socionomic sex ratio) or they evidence the behaviour of Yakushima male macaques it is not the main issue. What really matters here is the high variability at the population and group level that primates present. This variability has to be taken into account when we talk about species-specific behavioural patterns. Indeed, what we consider a species typical pattern is often only the result of few data concentrated on one or two populations, groups or few individuals. The same considerations apply to monkey participation in inter-group encounters. This study has demonstrated that the simple dichotomy between males and females does not explain the complex type of participation that monkeys show during inter-group encounters. Other factors (e.g. rank or age) may affect the behaviour of animals during inter-group encounters, although their importance has been often neglected.

An analysis of conciliatory tendency obtained in all the studies conducted so far on the Japanese macaque shows a large variation in the occurrence of reconciliation (see Table 8.1). This variation is partly due to the different genetic

Table 8.1: Conciliatory tendency in relation to sex of the opponents observed in this and in other studies on the Japanese macaque (sub-species: * *Macaca fuscata fuscata*; ** *Macaca fuscata yakui*).

Sex of the Opponents	Sample size	Condition of study	Conciliatory tendency	Reference
Female-Female *	8	Wild	0.38	Chapter 4
Female-Female *	20	Wild	0.16	Chapter 5
Female-Female **	8	Captivity	0.08	Petit *et al.*, 1997
Female-Female **	27	Provisioned	0.09	Schino *et al.*, 1998
Female-Female **	47	Provisioned	0.33	Koyama, pers. comm.
Male-Male *	13	Wild	0.31	Chapter 6

Male-Male **	6	Provisioned	0.00	Koyama, pers. comm.
Male-Male **	10	Provisioned	0.13	Kutsukake, pers. comm.
Male-Male **	6	Captivity	0.30	Petit *et al.*, 1997
Male-Male **	16	Captivity	0.10	Schino *et al.*, 1998
All **	35	Provisioned	0.14	Kutsukake and Castles, 2001
All **	20	Captivity	0.27	Aureli *et al.*, 1997

relatedness of the animals in the different studies. However, although the genetic relationship of the monkeys in this study was not available, conciliatory tendency for both females and males living in Nina A group (Chapters 4 and 6, respectively) was considerably higher than that observed in most of the other studies. The only studies obtaining comparable conciliatory tendencies are the study of Aureli and colleagues (1997) and of Koyama. Petit and co-workers (1997) also obtained a high conciliatory tendency for conflicts among males. However, this study was based on few individuals and few post-conflict observations. One possibility is that this result is due to differences (either genetic or ecological) between the two sub-species of Japanese macaques. Indeed, the sub-tropical, evergreen coastal forest of Yakushima has greater food abundance than the deciduous forests of northern Japan (Yamagiwa *et al.*, 1998). This results in a larger amount of time available for grooming exchange, which is likely to increase social cohesion and the frequency of reconciliation. However, conciliatory tendency among females living in the large group (Chapter 5) was lower than in the small group and similar to what has been found in other studies. Unfortunately, all the studies conducted on the northern sub-species of Japanese macaque (i.e. *Macaca fuscata fuscata*) have been done in captivity or on provisioned groups. Data gathered on the two sub-species, in groups of different size and living in different conditions would allow multiple comparisons. However, at the present state of our knowledge we cannot give a definitive answer to the relative importance of philogenetic and ecological factors in affecting conciliatory tendency and conflict management in this species. In an era where social instability and conflicts among and within human societies are a widespread phenomenon (Hobsbawm, 1994) data on how primates manage conflicts would not only deepen our understanding of animal behaviour but also have important implications for sociological and political studies.

Overall, the results of this study and the comparison with similar studies conducted on the Japanese macaques support the view that generalisation rarely provides good explanations of biological problems (Mayr, 1982). With the increasing amount of data available, it is becoming evident that statements such as "optimal group size" or "species-specific conciliatory tendency" are indeed meaningless. Animals show complex behavioural plasticity that helps them to cope with environmental fluctuations. Group size and composition, as well as many other ecological and behavioural characteristics, depends on many ecological factors (e.g. population density, food abundance and distribution, predation pressure). These factors interplay one another and their relative importance may vary in different parts of the geographical distribution of a species (Yamagiwa *et al.*, 2003). This is particularly true for generalist species that usually occupy different ecological niches and have a wide geographical distribution. For example, baboons (a species inhabiting many sub-Saharan areas of Africa) live in groups of different size and composition depending on the type of habitat they live in (Dunbar, 1988; Henzi and Barret, 2003). This is not to say that science does not possess any means to understand biological complexity. Indeed, the final goal of every biologist should be to discover the general rules governing nature. However, this search for biological explanations must recognise the variable importance and applicability of such general rules (Dunbar, 2002). These considerations apply to the two main theories proposed for the evolution of sociality in primates (see Chapter 1). These theories differ in the fact that one gives more importance to predation pressure while the other to food distribution in shaping social behaviour. The best biological explanation probably lies in the statement that the evolution of sociality was influenced mainly, but not only (see, for example, the importance of infanticide) by presence of predators and food distribution. However, their relative importance differs among species, populations or groups. These considerations should lead authors to suggest that, for example, food abundance is *one of the main factors* affecting the evolution of social behaviour rather than to statements such as food abundance is *the main factor* affecting the evolution of social behaviour. In this simple, but biologically meaningful difference lies the correct interpretation of biological complexity.

8.2 Possible Further Lines of Research.

A one-year long data collection often does not represent a sufficient period of time for detailed behavioural studies. In order to understand the complexity and relative importance of the ecological factors that affect social behaviour and conflict management long-term studies would be required. This study, however, has provided a general, and sometimes detailed account of the ecology and social behaviour of the Japanese macaque. As such, it may potentially represent a starting point for methodological improvements, further lines of research, and new ideas.

This study was more focused on social behaviour than on habitat characteristics and thus many ecological variables could not be measured due to the limited time available. Detailed phenological data should be collected to determine the spatial distribution of the different food sources, to measure the amplitude of seasonal variations of food abundance, and to assess the potential differences in terms of habitat productivity among the various parts of the study area. These data would clarify if the coastal forest of Yakushima Island is a rather stable habitat, if differences exist in the distribution of the main food sources eaten by the monkeys (i.e. fruit, seeds, and leaves) and how these food sources are available across the year. Based on these ecological characteristics, a wide range of data could be collected on the social behaviour of the Japanese macaques, possibly on groups of different size and composition (Johnson *et al*, 2002). These data would help understanding of whether the absence of any difference in grooming distribution and reconciliation among the seasons observed in this study (Chapter 4) is limited to small groups or is also found in larger groups. Moreover, they would allow analysis of how grooming inequality and reconciliation vary in relation to group size.

Data on ranging patterns and foraging behaviour in exclusive (i.e. inhabited by only one group) and overlapping areas would clarify the relative importance of inter-group scramble and contest competition in Yakushima macaques. In this respect it would also be necessary to gather information on the relationships between home-range size, group size and composition, and frequency and type of inter-group encounters. It is possible that large groups occupy more productive areas and, due to their size, they can easily displace the neighbouring groups (so they would have a higher ratio of encounters "won" per total encounters than small groups). Moreover, large groups may have a lower frequency of encounters than small groups as neighbouring/small groups may tend to avoid larger ones (see Chapter 5). If this is true, group size and fission would depend on habitat quality as well as on the type of interactions with the other groups. Groups increase their size depending on habitat productivity and inter- and intra-group food competition. We may hypothesise that group size increases without fission until the benefits of living in large groups (low level of inter-group food competition) outweigh the costs (increased intra-group food competition). This balance between benefits and costs, and the size at which groups tend to fission thus clearly depends not only on habitat quality but also on the size and composition of neighbouring groups. Without long-term data we cannot give a definitive answer on whether these speculations do apply to the Japanese macaque.

Finally, another aspect that would require additional data regards the type of interactions among resident males and their effects on male participation in inter-group encounters and/or on emigration. Data on grooming and reconciliation among males in groups with different socionomic sex ratio (SSR) would help to clarify if amicable social relationships are related to the number of males in a group and if such relationships follow the same pattern observed among females (i.e. grooming inequality is lower the lower in the number of females in a group). Such amicable relationships may also be favoured by a high risk of extra-group mating and/or male transfer. Resident males might maintain good relationships with one another in order to collaborate to avoid extra-group mating or male immigration into their group (although amicable relationships and collaboration do not necessarily have a cause-effect relationship; van Hooff, 2000). For high-ranking resident males such collaboration might result in an increased reproductive success while low-ranking males might be tolerated more, or for longer in the group. If this hypothesis is correct and if grooming distribution among males is related to number of males in a group, as it is among females, then a positive relationship between level of amicable interactions between group males and their aggressive participation in inter-group encounters should be found. Moreover, males in small groups and/or with a low SSR should be more cohesive and equally aggressive during inter-group encounters than large groups and/or groups with a high SSR (as the former should be more at risk of extra-group mating attempts and/or male immigration).

During the course of this study, low-ranking/sub-adult males often were the most responsive monkeys to react to vocalisations of foreign groups. Other studies have demonstrated that male emigration is affected by the type of interaction animals exchange with foreign groups (e.g. Cheney and Seyfarth, 1990b). These data suggest that monkeys are able to associate their behaviour to the long-term effects that this may have. In this respect it would be interesting to analyse the response of monkeys of different age and/or rank to vocalisations of foreign groups using play-back experiments. These experiments have already been used with other primate species (e.g. chimpanzees) and have given interesting results (Wilson *et al.*, 2001). Moreover, data on the type of male participation in inter-group encounters and on the effects of this response on emigration should also be collected. These data would shed light on the complex decision-making of the Japanese macaques and on their ability to plan and follow long-term strategies.

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