Sex Differences in the Social Relationships of Wild Spider Monkeys (*Ateles geoffroyi yucatanesis*)

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Abstract

Spider monkeys are arboreal frugivorous primates that live in multi-male-multi-female societies characterised by a high degree of fission-fusion dynamics such that individuals from the same community are rarely all together. As data from wild communities of spider monkeys is sparse, I aimed to investigate sex differences in the distribution and usage of social behaviour in wild spider monkeys. Behavioural observations were collected from two well-habituated communities of spider monkeys, *Ateles geoffroyi yucatanesis*, located in Otoch Ma'ax Yetel Kooh reserve in the Yucatan Peninsula, Mexico, using focal animal continuous sampling and *ad libitum* sampling. All members of both communities were individually recognised producing individual level data that could be analysed statistically.

My results suggested that females dispersed upon reaching sexual maturity and although females preferentially embraced and arm-wrapped same-sex partners, affiliative behaviour among females was relatively rare. I found no evidence of a clear-cut female dominance hierarchy, although adult long-term resident females appeared to be dominant to adolescent or recent immigrant females. Female-female competition for food was not completely eliminated by fission-fusion social dynamics as female aggression and coalitionary arm-wrapping occurred more frequently in same-sex foraging subgroups and occurred more often than expected in a feeding context. As females did not attempt to mitigate this aggression using embraces, female-female social relationships were characterised as low quality. Female social relationships were significantly affected by the presence of young infants and females used embraces as a means of reassuring mothers of benign intent in order to gain access to infants.

Males appeared to remain in their natal group as no cases of male transfer were observed. All affiliative social behaviours were exchanged most frequently between males, suggesting that male social relationships are high quality. Male social relationships did not appear to be governed by a dominance hierarchy and I found no evidence of male aggression in the context of mating as all mating

occurred in secrecy. However, male social relationships were differentiated and male-male coalitionary attacks on community males were observed. Younger males preferentially embraced older males who received more embraces than they gave, and older males appeared to be dominant to younger males. Male social relationships were also affected by the presence of females as males embraced and arm-wrapped and more frequently in mixed-sex than same-sex subgroups. Male aggression, arm-wrapping and embraces also occurred more frequently following fusion. Increased aggression during periods of uncertainty such as fusion events suggests that male-male social relationships are insecure. However, that males appeared to use embraces to mitigate aggression further suggests that male social relationships are valuable.

Relationships between the sexes were more difficult to define. Embraces and arm-wrapping did not occur between the sexes and males preferentially directed aggression towards females, suggesting that male-female relationships were low quality. However, females preferentially groomed males rather than females and directed the majority of their grooming towards their mature sons. Furthermore, the vast majority of female-directed male aggression appeared to be a form of ritualised male sexual display directed towards cycling females. I therefore concluded that male-female relationships were not as low quality as had been previously reported but were notably different from the close bonds of spider monkey males.

My results also emphasise the importance of taking a more holistic approach to the study of animal behaviour. By investigating all types of adult relationships in spider monkeys and the factors that affect them such as competition for resources, male and female sexual strategies, and market effects, I was able to provide a detailed account of spider monkey social relationships that could be compared and contrasted with other species. Collectively my results indicated that spider monkey social relationships are similar to those of other primate species that adopt flexible grouping patterns, and take an intermediate value between the tolerant muriqui and more despotic chimpanzee. However, more data relating to spider monkey dominance relationships is required to determine if spider monkey social relationships are more closely related to muriquis or chimpanzees.

Chapter One

Introduction

Social interactions between two animals depend not only on the individual characteristics (age, sex, dominance rank, temperament) of the individuals involved, but also on the history of interactions between them, provided that they possess the ability for individual recognition, have sufficient memory to remember the outcome of previous interactions, and repeatedly meet each other (Hinde, 1976). Furthermore, earlier interactions influence later ones, such that any pair of individuals can establish a unique history of interactions (Hinde, 1979). The pattern of repeated interactions between two individuals can provide insight as to the social relationship between them and within a particular species, the general pattern of social relationships may be used to characterise the species' social system (Hinde, 1983). Among non-human primates the most complex social systems are found in gregarious species where group members rely on one another for predator protection and territory defence, but suffer the costs of increased competition for desirable resources such as food and mates. Consequently, social relationships within the group have both affiliative and agonistic components to varying degrees depending on the intensity of competition experienced and the need for cooperation.

Social behaviour is also affected by a number of external factors. Predation risk is thought to affect group cohesion and dispersal patterns, and competition for resources is thought to affect the general pattern of social interactions within the group. At the species level, a number of theoretical models have predicted distinct types of female social relationships from the species diet preferences, the distribution of food resources and corresponding competitive regimes (e.g. Isbell, 1991; Sterck, Watts & van Schaik, 1997; van Schaik, 1989; Wrangham, 1980). More recently, these models have been expanded to predict distinct types of male social relationships based on the distribution of fertile females and the corresponding competitive regime among males (van Hooff, 2000; van Hooff & van Schaik, 1992; 1994). Evidence also suggests that female grouping, dispersal and social relationships may be affected by male behaviour, in particular infanticide (van Schaik & Kappeler, 1997), and likewise, male competition for fertile females can be affected by female social relationships (Kappeler & van Schaik 2004; Setchell & Kappeler, 2003). Nevertheless, as each dyad within a group shares a unique history of interactions and not all individuals have to interact equally, huge variation in social relationships may be found within the same social system. In order to fully investigate primate social systems it is therefore also necessary to investigate how different individuals make decisions about how and with whom to interact and how the outcome of these decisions contribute to social relationships.

1.1. Relationship quality in non-human primates

The pioneering work of Hans Kummer described social relationships as social investments in which each dyad member aims to maximise gain through a series of interactions, while keeping personal costs to a minimum (Kummer, 1978). In order to weigh up potential costs and benefits of interactions, each individual must be aware of the various services they have to offer and thus their potential 'value' as an interaction partner. The three key factors contributing to an individual's value are: behavioural tendencies, which refer to the likelihood that the individual will behave in a way that benefits the partner, availability, which refers to the accessibility of the individual as a potential partner, and finally, the qualities the individual has on offer. Examples of desirable qualities include: willingness to mate, tolerance at feeding sites, and support during aggressive encounters in the form of coalitions or alliances (Cords, 1997; van Schaik & Aureli, 2000). An individual's 'score' on each of these factors will be dependent on their sex, social status, reproductive state, knowledge and skills. Consequently, no two individuals will have the same value causing each dyadic relationship to be unique (Kummer, 1978).

Social relationships are also influenced by the history of interactions between a dyad. As past interactions are likely to influence subsequent interactions, and each dyad shares a unique history of interaction, then it follows that each relationship must be unique in its present form (Hinde, 1979). The history of interactions between individuals may be used to make testable predictions about subsequent interactions, which is extremely important to researchers who are unable to observe relationships directly (Hinde, 1976). Relationship history has therefore been added to the concept of value described by Kummer (1978) to form two additional components of relationship quality: security, which refers to the perceived probability that the relationship will change based on the consistency of the partner's behavioural responses, and compatibility, which refers to the ease with which the individual can interact that is determined by the general tenor of their previous interactions (Cords, 1988; Cords & Aureli, 1993; 2000; Cords & Thurnheer, 1993).

1.1.1. Communicating relationship quality

Throughout their relationship history each partner's value is unlikely to remain constant due to changes in age, strength, social status and other factors. It is therefore important that each partner has the ability to reassess which services they have to offer and the relative importance of these services to their partner, which determine the subsequent exchange rate of services (van Schaik & Aureli, 2000). This communication of power and willingness to engage in an interaction may be exchanged before, during or after the interaction. When the interaction concerned involves particularly risky behaviour such as agonistic support, and the relationship is somewhat fickle such as male alliances, communication about the relationship is exchanged before the high risk interaction in the form of specialised signals (e.g. Colmenares, 1990; 1991; Noë, 1990; Smuts & Watanabe, 1990). These signals prior to aggressive interactions allow the individual to be assured of alliance partners' willingness to participate before making the decision to fight (van Schaik & Aureli, 2000). When the interaction is relatively low risk however, communication occurs during and after the interaction.

One of the key methods of communicating value during or after the interaction involves the exchange of social grooming (van Schaik & Aureli, 2000). Social grooming is relatively costly to the donor in the form of time (Seyfarth, 1980), but offers direct benefit to the recipient in the removal of ectoparasites (Hutchins & Barash 1976; Saunders, 1988: cited in Henzi & Barrett, 1999), tension reduction (Aureli, Preston & de Waal, 1999; Schino, Scucchi, Maestripieri & Turillazzi, 1998) and the release of β-endorphins (Keverne, Martensz & Tuite, 1989). Perceived relative value may be communicated by varying duration and frequency of grooming bouts offered and refusals to groom or time discrepancies in grooming bouts between the two partners (van Schaik & Aureli, 2000). Post-interaction communication of value occurs when grooming is exchanged for other commodities such as: increased tolerance of subordinate individuals by dominant animals in the form of lowered aggression (Fairbanks, 1980; Silk, 1982); increased access to resources such as food and water (de Waal, 1989; de Waal & Luttrell, 1989, Kapsalis & Berman, 1996b); or direct exchanges for food (de Waal, 1997) or infant handling (Henzi &

Barrett, 2002; Muroyama, 1994). Value is communicated by exchange rates for the various commodities that may be negotiated by refusals to engage in the interaction.

In addition to the fluctuations brought about by natural progressions in age and social rank, value may also be affected by external factors known as 'market effects' (Noë & Hammerstein, 1994; 1995; Noë, van Schaik & van Hooff, 1991). Within the biological market paradigm, an individual's value is not only dependent on what qualities or services they have to offer, but also the need for these commodities and the trader's ability to outbid the competition. For example, in the exchange of grooming for tolerance at feeding sites, two types of traders will occur: low-ranking individuals willing to trade grooming and high-ranking individuals willing to exchange tolerance. The relative frequencies of each trader class will affect the 'exchange rate' of grooming for tolerance. Exchanges will also be affected by the 'market value' of each commodity. For example, when asymmetries in power between dominants and subordinates are low or where resources are abundant, the need for tolerance from dominants will be reduced and thus their value is lower (Barrett, Henzi, Weingrill, Lycett & Hill, 1999; Henzi & Barrett, 1999; 2002).

1.1.2. Sources of relationship value in nature

Relationship value may come from a variety of sources in nature. Mere gregariousness provides value in the form of reduced predation rate caused by improved predator detection, prey dilution and cover, communal defence against predators, and reduced predator encounter rates due to prey clumping (Cheney & Wrangham, 1987; Cowlinshaw, 1994; Dunbar, 1988; Hill & Dunbar, 1998; Isbell, 1994; Janson, 1992). Some sources of value require only the exchange of low risk behaviours for mutual benefits such as alarm calling (Cheney & Seyfarth, 1990) or large groups working cooperatively to supplant smaller groups from high quality resource patches (Wrangham, 1980). In these circumstances associates tend to be animals with similar ecological interests. For example, females with infants often form distinct clusters as they share similar feeding and resting schedules (e.g. van Schaik & van Noordwijk, 1986).

Other forms of value require complex cooperative exchanges such as: grooming for infant access (Henzi & Barrett, 2002; Muroyama, 1994), cooperative hunting (e.g. Boesch & Boesch, 1989), selective tolerance around resources (e.g. Janson, 1985), services for mating privileges (e.g. Stanford, 1998), and agonistic support in the form of coalitions and alliances (e.g. de Waal, 1982; Seyfarth & Cheney, 1984). Coalitions and alliances should be formed where there is direct contest for limited resources and the coalition or alliance improves the fitness returns for both partners either directly or in the form of kin selection (de Waal & Harcourt, 1992). Alliances differ from coalitions because they are enduring cooperative relationships rather than a single interaction, and alliance partners share a complex history of coalition interactions which will add to the value of their relationship (de Waal & Harcourt, 1992; van Schaik & Aureli, 2000). Value may also come in the form of protective bonds. For example, females may place a high value on relationships with key males who will protect the female from harassment from undesirable or infanticidal males (Palombit, 1999; 2000; Smuts & Smuts, 1993; van Schaik, 1996; Watts, 1995).

1.2. Female-female relationship quality and socio-ecological models

Due to the energy demands of pregnancy and lactation, the primary source of competition among females is access to food resources because the net energy gain from food affects female reproductive success (Emlen & Oring 1977; Janson, 1988; van Schaik, 1983). Socio-ecological models assume that it is possible to predict the nature of female primate social relationships based on differences in the type and intensity of resource competition both within and between groups. The presence or absence of specific behavioural traits such as female philopatry, dominance hierarchies, and coalition formation has been linked to the distribution of food resources and consequent competitive regimes. Three main models of female primate relationships have been generated, all of which endorse the effect of food distribution on female behaviour but vary in their predicted outcomes of competitive regimes and on the importance of other factors such as predation and infanticide.

1.2.1. The ecological model

Wrangham (1980) produced the first ecological model of female primate behaviour, in which a framework was used to describe the conditions responsible for the evolution of two types of female societies. In this model, high quality and spatially clumped foods result in strong inter-group competition with females belonging to larger groups forming coalitions to usurp smaller groups from food patches. Due to the fitness implications of kin selection (Hamilton, 1964), coalitions partners are more likely to be direct kin causing a strong tendency for female philopatry. Where females are philopatric and feed on clumped resources, female relationships within the group can be characterised by linear, stable dominance hierarchies, maternal rank inheritance and rank related affiliative behaviour such as grooming. As a result, females belonging to larger groups or of high dominance rank should experience greater reproductive success due to increased success in contests for food. This type of society was termed 'female-bonded'. Conversely, where foods are uniformly distributed or too small to monopolise there should be little or no inter-group competition resulting in female dispersal and weak or absent dominance relationships within groups. This type of society was termed 'non-female-bonded'.

Wrangham's (1980) model remains the benchmark paper in this field but with subsequent research on a wider range of primate species it became apparent that a simple dichotomy between female-bonded and non-female-bonded societies was insufficient. Species with female philopatry but weak or unstable dominance relationships [e.g. blue monkeys (*Cercopithecus mitis*) and patas monkeys (*Erythrocebus patas*)] are a case in point (Cords, 1987). The model also assumes that the negative fitness consequences of inter-group competition are far greater than of intra-group competition yet a number of studies suggest otherwise (e.g. Janson, 1985). Furthermore, the predicted positive relationship between birth rates and group size was found in only a few species with female fitness maximised at intermediate group size in the majority of species (van Schaik, 1983). These conflicting results suggested that competition may occur in different forms which may vary independently within and between groups and that additional factors such as predation may also affect female social relationships.

1.2.2. The socio-ecological model

There is a wide range of evidence to suggest that group-living in diurnal primates serves to reduce predation risk (e.g. Cowlinshaw, 1998; Hill & Dunbar, 1998; Janson, 1992; 1998; Stanford, 1998). Expanding on Wrangham's (1980) model, van Schaik (1989) implicated predation risk as driving female gregariousness with the type and intensity of resource competition within and between groups shaping female primate relationships. This model was later expanded by Sterck *et al.* (1997) to include a wider range of species and the possible influence of infanticide risk. Two types of competition were described: scramble competition, where individuals lose access to resources because others have already found them and used them, and contest competition, which refers to asymmetry in how resources are partitioned caused by monopolisation of resources by dominant individuals (Nicholson, 1954; van Schaik, 1989).

Scramble competition predominates when resource patches are either of low nutritional value, are highly dispersed, or are very large relative to group size such that monopolisation of resources is either impossible or pointless. This type of competition is often associated with a folivorous diet. Contest competition occurs when patches are clumped, generally of high quality and are of an intermediate size such that certain individuals have the opportunity to exclude others from the resource. This type of competition is often associated with a frugivorous diet. As these types of competition can occur both within and between groups, there are four resultant categories: within-group scramble (WGS); within-group contest (WGC); between-group scramble (BGS); and between-group contest (BGC: Sterck *et al.*, 1997; van Schaik, 1989). However, as BGS merely reflects population density, (van Schaik, 1989), the socio-ecological model is only concerned with the remaining three.

High WGC alone leads to frequent, direct contests for food that lead to the evolution of decided dominance relationships based on consistent winners and losers in these contests (Sterck *et al.*, 1997; van Schaik, 1989; van Schaik & van Noordwijk, 1988). The outcome of contests and resulting dominance ranks are greatly influenced by coalitionary support during contests, which in accordance with kin selection theory, tends to be provided by immediate relatives of the combatant (Caldecott, 1986; Datta, 1992; Thierry, 2000). As with Wrangham's (1980) model, the need for coalitionary support in contests is linked to female philopatry as any female who attempts to disperse would lose the support of her allies. However, the increased predation risk associated with dispersal is also implicated in driving female philopatry (Sterck *et al.*, 1997; van Schaik, 1989). The resultant social structure contains stable, linear and nepotistic hierarchies, which determine the despotic appropriation of resources. This class has been termed: Resident-Nepotistic, (Sterck *et al.*, 1997) and corresponds to Wrangham's female-bonded society. Conversely, when WGC is weak and so WGS predominates, females have little to gain from forming coalitions and establishing dominance relations, as there is no direct contest for food. Without the need for coalitionary support, females are free to disperse from the natal group providing that predation risk is low. This class has therefore been termed Dispersed-Egalitarian (Sterck *et al.*, 1997) and corresponds with Wrangham's non-female-bonded society.

With weak WGC but strong BGC, females will benefit from residing in their natal groups as kin can work co-operatively in between-group contests and enjoy the safety provided by group life. As there is little contest competition for food within the group, no clear-cut dominance evolves. This class has been termed Resident-Egalitarian (Sterck *et al.*, 1997). Finally, where WGC is strong, but so is BGC, stable nepotistic dominance hierarchies will evolve, but dominance relationships should be more tolerant than the Resident-Nepotistic category. Greater tolerance exhibited by dominants serves to prevent subordinate defection to another group as this may enable the other group to displace the former group in between-group contests (van Schaik, 1989; Wrangham, 1980). Dominants therefore grant subordinates regular access to food as a means of ensuring subordinate residency, resulting in a more tolerant society and more egalitarian dominance relationships (van Schaik, 1989). This class has therefore been termed Resident-Nepotistic-Tolerant and may only arise if predation risk is sufficiently low that subordinate defection becomes possible (Sterck *et al.*, 1997).

1.2.3. A revised ecological model

A third ecological model was produced by Isbell (1991) and later expanded by Isbell and van Vuren (1996). Isbell used behavioural indicators from a range of species to elucidate the co-variation between scramble and contest competition. For example, species with linear dominance hierarchies indicative of WGC competition also had longer daily travel distances in larger groups, which is indicative of WCS. Similarly, species exhibiting agonism between groups indicative of BGC competition had larger home ranges in larger group suggesting additional BGS competition. In contrast to the other models, Isbell did not assume that group-living primates always incur a cost of feeding competition or that coalitionary support was responsible for female philopatry. The evolution of female philopatry was described as a two step process involving locational philopatry and social philopatry. Locational philopatry occurs when the costs of dispersal (e.g. loss of local knowledge, increased predation risk if dispersing alone, and the likelihood of receiving aggression from resident females when attempting to join a new group) outweigh the costs of remaining in the natal area (e.g. unfavourable sex ratio resulting in limited access to mates). The advantages of group foraging would then lead to the coalescing of females (social philopatry) who would be kin groups by default due to locational philopatry (Isbell, 1994; Isbell & van Vuren, 1996; Pusey & Packer, 1987).

When females are philopatric they may experience scramble and contest competition both within and between groups, or contest and scramble competition between groups with little or no feeding competition (scramble or contest) within groups. If food resources have a high nutritional value, are clumped and of intermediate size, then philopatric females will experience contest and scramble competition within and between groups. In these circumstances, stable dominance hierarchies will evolve causing rank-related social behaviour. Isbell (1991) referred to these characteristics as 'Syndrome 1', which relate to Wrangham's (1980) female-bonded and Sterck *et al.'s* (1997) Resident-Nepotistic categories but with no importance given to predation risk. When food resources are have a low nutritional value, are dispersed or occur in large patches, little or no feeding competition occurs within the group, but females may behave aggressively towards other groups in order to ensure exclusive access to the resources within their home range. These characteristics, referred to as 'Syndrome 2' relate to Sterck *et al.'s* Resident-Egalitarian society without the emphasis on predation risk. Finally, where food resources do not limit female reproductive success, females experience little or no competition within or between groups and therefore do not exhibit a dominance hierarchy or rank-related social behaviours. Females are free to disperse provided that reproductive success is increased by leaving the group. These characteristics are referred to as 'Syndrome 3' and corresponds to Wrangham's (1980) non-female-bonded and Sterck *et al.'s* (1997) Dispersed-Egalitarian categories.

1.2.4. Evidence for the socio-ecological models

Socio-ecological models predict specific social categories of female primate relationships and evidence of these relationships in nature is generally supportive. For example, Female-Bonded/Resident-Nepotistic/Syndrome 1 societies may be found in some macaques (genus *Macaca*), capuchins (genus *Cebus*), vervets (*Chlorocebus aethiops*) and the majority of baboon species (genus *Papio*). Females of these highly frugivorous species are philopatric and exhibit frequent direct competition for food (Cheney & Seyfarth, 1990; Janson, 1985; 1988; Lindberg, 1980; O'Brien, 1991; 1993; van Schaik & van Noordwijk, 1988), resulting in a positive correlation between net energy gain or reproductive success and dominance rank (Altmann, Hausfater & Altmann, 1988; Barton & Whiten, 1993; Saito, 1996). Kin correlated behaviour is frequent with females preferentially interacting with relatives (Chapais, 1983a; Cheney, 1978; Gouzoules & Gouzoules, 1987; Kapsalis & Berman, 1996a; Silk, 2002) and relying on kin for coalitionary support during contests (Bernstein & Ehart, 1986; Caldecott, 1986; Cheney, 1983; Datta, 1992; Silk, 1982). Dominance gradients are steep, producing marked asymmetries in power between dominant and subordinate individuals. Dominants are therefore more attractive as potential partners, resulting in rank-related social behaviour (Perry, 1996; Schino, 2001; Seyfarth, 1977; Silk, 1982).

The distinction between Resident-Nepotistic/Syndrome 1 and Resident-Egalitarian/Syndrome 2 has been supported by patas monkeys (Chism & Rowell, 1986; Isbell & Pruetz, 1998; Isbell, Pruetz, Lewis & Young, 1999), which show no evidence of formal dominance and little coalition formation despite female philopatry. Similarly, the Non-Female-Bonded/Dispersed-Egalitarian/Syndrome 3 class is found in species such as the mountain gorilla (*Gorilla gorilla beringei*), which are large bodied and thus experience low predation and which exhibit female dispersal, weak dominance hierarchies, no rank-related social behaviour, little female association and no coalition formation (Watts, 1994; 1996). However, it is only Sterck *et al.'s* (1997) model that includes the effects of infanticide and can explain female gorilla grouping around an alpha male to form a one-male–multi-female society.

According to van Schaik (1989) / Sterck *et al.'s* (1997) model, where infanticide risk is perceived to be low and species are large bodied with subsequent low predation, female groups may become less cohesive with large communities splitting to form smaller subgroups, particularly when foraging (van Schaik, 1989; Sterck *et al.*, 1997). Primate societies that allow for such flexible grouping have been termed 'fission-fusion' societies, and have been observed in chimpanzees (*Pan troglodytes*: Goodall, 1986), bonobos (*Pan paniscus*: Kano, 1992), spider monkeys (genus *Ateles*: Symington, 1990), and to a lesser degree woolly monkeys (genus *Lagothrix*: Di Fiore, 2003) and muriquis (*Brachyteles arachnoids*: Strier, 1989). Flexible grouping that responds to food supply enables females to minimise contest competition for food (Anderson, Nordheim, Boesch & Moermond, 2002; Chapman, Wrangham & Chapman, 1995; de Moraes, Carvalho & Strier, 1998; Mitani, Watts & Lwanga, 2002; Newton-Fisher, Reynolds & Plumtre, 2000; Strier, 1989; Symington, 1988a). Consequently, females are free to disperse, exhibit weak dominance hierarchies, no rank-related social behaviour, little female association and no coalition formation (Fedigan & Baxter, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Stewart & Harcourt, 1987; Strier, 1989; but see Witting & Boesch, 2003) and therefore correspond to the Non-Female-Bonded/Dispersed-Egalitarian/Syndrome 1 societies despite a frugivorous diet.

As predicted, by van Schaik (1989) / Sterck *et al.'s* (1997) model, female social relationships in some Resident-Nepotistic species are more tolerant than in others, as indicated by the *Macaca* genus. Here, variation is best described using a four-grade scale, rather than the distinction between Resident-Nepotistic and Resident-Nepotistic-Tolerant (Thierry, 2000). Dominance relationships vary from the highly despotic rhesus (*M. mulatta*) and Japanese macaques (*M. fuscata*) in the first grade to the more tolerant Sulawesi macaques (e.g. *M. nigra*) in the fourth grade (Thierry, 2000). Asymmetry in contests, dominance gradient, intensity of aggression and kin bias, decrease from the first to the fourth grade, whereas conciliatory tendency and the rate of affiliative behaviours such as social grooming, increase from the first to fourth grade (Aureli, Das & Veenema, 1997; Butovskaya, 1993; Chaffin, Friedman & de Waal, 1995; de Waal & Luttrell, 1989; Petit, Abegg & Thierry, 1996; Thierry, 2000; Thierry, Aureli, de Waal & Petit, 1997).

However, to date, no evidence has been found of especially high BGC in these more tolerant species suggesting that perhaps this variation in tolerance is the result of phylogenetic inertia rather than feeding competition (Thierry, Aiwaniuk & Pellis, 2000). Moreover, the Old World monkeys (*Cercopithecoidea*) show marked uniformity in their social organisation and cluster together as a highly derived group relative to all other primates, despite species radiation into different ecological niches (Di Foire & Rendall, 1994). Traits such as female philopatry, females grouping with same sex kin, strong female grooming relationships and well developed female dominance relations show high retention indices indicating that once these traits have evolved, they tend to persist in the descendent taxa (Di Foire & Rendall, 1994). The evolutionary history if a species must therefore also be taken into account when evaluating the effect of competitive regimes in shaping female primate social relationships.

Nevertheless, further evidence in support of the ecological models has been provided by direct species comparisons. Among two closely related, frugivorous squirrel monkey species, direct feeding competition both within and between groups was found to be extremely low in one species (red-backed squirrel monkey: *Saimiri oerstedi*) but high in the other (Bolivian squirrel monkey: *S. boliviensis*). *S. oerstedi* fed on small fruiting trees that could accommodate only three to four individuals, thus females exhibited female dispersal, weak dominance relationships and weak female association. Conversely, *S. boliviensis* fed on intermediate size fruiting tree and thus exhibited frequent female association, a female dominance hierarchy, female philopatry and female coalitions (Boinski, 1999; Boinski & Mitchell, 1994; Mitchell, Boinski & van Schaik, 1991). This study has since been extended to include a third species of squirrel monkey (common squirrel monkey: *Saimiri sciureus*) (Boinski *et al.*, 2002). *S. sciureus* exhibit a high rate of resource-based aggression and a stable linear dominance hierarchy but virtually no coalition formation and optional female dispersal that may take place before of after the first mating season. The authors claimed that small fruit patch size allowed one single female to successfully defend the patch without requiring coalitionary support from kin thus making female dispersal possible (Boinski *et al.*, 2002). However, as *S* *sciureus* are subject to moderate predation but still disperse when reproductive success is greater outside the natal group, this study is of greater support to the Isbell (1991) and Isbell and van Vuren (1996) models.

Socio-ecological models have also been used to explain variation in female social relationships among different groups of the same species. For example, despite their folivorous diet, certain groups of Hanuman langurs (*Presbytis entellus*) exhibit female philopatry and linear dominance hierarchies (Koenig, Beise, Chalise & Ganzhorn, 1998). Investigation of these groups has shown that the langurs concentrate their feeding on clumped, high quality leaves that are twice as nutritious as leaves eaten by other populations that occur at a low density. The existence of a female dominance hierarchy in this folivorous langur population could therefore be explained by high WGC resulting from the quality and distribution of food resources (Koenig *et al.*, 1998; Koenig, 2000).

Support for van Schaik (1989) / Sterck *et al.'s* (1997) model has been provided by variation in female social relationships in baboons as a consequence of variation in feeding competition (Barton, Byrne & Whiten, 1996). Olive baboons (*P. anubis*) exhibit clear-cut female dominance hierarchies, female coalitions, predominant female-female grooming and have been described as female bonded (Barton & Whiten, 1993). In contrast, chacma baboons (*P. ursinus*) show only weak female dominance relationships, no female coalitions and predominant male-female grooming (Byrne, Whiten & Henzi, 1990; Whiten, Byrne & Henzi, 1987). Variation in social behaviour was linked to competitive regime as olive baboons spent a larger percentage of time feeding on clumped foods than did chacma baboons (Barton *et al.,* 1996). High predation was also cited as a cause of female bonding in olive baboons as when predation pressure is low females can spread out, causing the level of WGC to be low even if the food is clumped (Barton *et al.*, 1996). Similarly, high predation pressure without WGC competition is more likely to lead to the social structure of the Hamadryas baboon (*P. hamadryas*), in which small units coalesce into larger aggregations but retain their distinctness (Dunbar, 1988).

However, more recent studies have provided support for specific aspects of Sterck *at al.'s* (1997) and Isbell (1991) / Isbell and van Vuren's (1996) models. For example, in a group of brown capuchins (*Cebus apella nigritus*) combined contest and scramble competition within groups, with only contest competition between groups, was found to affect female social relationships, indicating that scramble and contest competition vary independently (Izar, 2004). Female social relationships most closely resembled the Resident-Nepotistic-Tolerant category described by the Sterck *et al.* (1997) model as the Isbell (1991) model does not consider scramble and contest competition to vary independently and has no syndrome relating to the Resident-Nepotistic-Tolerant society. However, occasional female transfer from the natal group was also observed, which supports Isbell & van Vuren's (1996) explanation of female dispersal whereby dispersal occurs if reproductive success is perceived to increase when the female leaves her existing group. Furthermore, Izar's study group was cohesive despite low predation risk (Izar, 2004), providing support for the Isbell (1991) model which does not consider predation to be contributing factor in the evolution of female relationships. However, it is important to remember that the current predation risk in a given habitat is likely to be very different from the ancestral predation risk that lead to the evolution of the species' society. Indeed, Izar points out that her study site has suffered 500 years of human impact, and that as large predators are most threatened by anthropogenic disturbance (Izar, 2004; Mazzoli, Graipel & Dunstone, 2002) the number of large predators in the area was likely to have decreased significantly over the years. In these circumstances it is virtually impossible to assess the impact of predation on the evolution of female social relationships.

It has also proved difficult to quantify the proposed relationships between competitive regimes and female reproductive success. The vast majority of studies have been unable to take direct measures of net energy gain or reproductive success and were therefore unable to investigate their direct link to feeding competition (Isbell & Young, 2002; Koenig, 2002). Most studies of male social relationships have also been unable to collect the necessary genetic data required to fully investigate the link between competition and reproductive success (Kappeler & van Schaik, 2002; van Hooff, 2000). Moreover, the majority of recent research has aimed to model variation in female primate societies as a product of feeding competition (e.g. Wrangham, 1980; Isbell, 1991; Sterck *et al.*, 1997; van Schaik, 1989), but have not considered the relative contributions of phylogeny, mating systems, and male behaviour in shaping female primate relationships, which could explain irregularities in the predicted distribution of behaviour (Cords, 2002; Janson, 2000).

1.3. Infanticide and male policing

The importance of ecology in shaping female social relationships has recently been challenged by growing documentation that infanticide also contributes to female behaviour (Janson, 2000; van Schaik, 1996). Evidence from wild populations suggests that infanticide is an adaptive male reproductive tactic (Borries, Launhardt, Epplen & Winkler, 1999; Struhsaker & Leland, 1987; van

Schaik, 2000a, but see Bartlett, Sussman & Cheverud, 1993) as with no infant to feed, a mother will cease lactation and may be fertilised soon after. In support of this theory, genetic data have indicated that males never attack or kill their own offspring (Borries *et al.*, 1999; Soltis, Thomsen, Matsubayashi & Takenaka, 2000). Infanticide can be a major source of infant mortality in primates, accounting for 34 – 64% of all infant deaths in some species (Crockett & Sekulic, 1989; Hrdy, Janson & van Schaik, 1995; Watts, 1989). Females are particularly susceptible to infanticide where lactation is long relative to gestation (van Schaik, 2000b; 2000c; van Schaik, Pradhan & van Noordwijk, 2004) and when their social groups are subject to male takeovers or hostile encounters with extra group males (e.g. gorillas: Watts, 1989 and langur species: Steenbeek, 2000; Sterck, 1997). These conditions are found in a number of primate societies suggesting that infanticide is likely a serious threat to female primate reproductive success, which has lead to the evolution of female behavioural strategies aimed at offsetting infanticide risk. The low observed rates of infanticide in the majority of primate species therefore do not represent intrinsic risk as observations occur after these counterstrategies are in place (Hill & Dunbar, 1998; Janson, 1998).

One female strategy to reduce infanticide is to rely on the likely father of the offspring for protection (e.g. Borries *et al.*, 1999; Watts, 1996). As males are likely to vary in their fighting ability, groups of females should aggregate around key males, with group size limited by the number of females that each male may defend. These conditions correspond with many of the species categorised as Dispersed-Egalitarian by Sterck *et al.* (1997) in which females who are not subject to high predation, do not experience contest competition between groups and so have no other reason for forming cohesive groups, cluster around effective male protectors. As primate social behaviour is constrained by the amount of social time available in the daily activity budget (Dunbar, 1992), females do not have enough time to interact socially with all group members and therefore must limit their social exchanges to the partners they perceive to hold the most value. When infanticide risk is high, females need to ensure they receive protection from the father of their offspring. Females must therefore direct the vast majority of their affiliative social behaviour (e.g. grooming) to the male concerned, leaving notably less time available to interact with other group females, which is likely to effect the quality of their relationships with other females.

Infanticide risk has also been cited as one of the selective forces that shape female dispersal patterns. In a recent review of 37 primate species with female dispersal, rates of dispersal in nulliparous and parous females varied independently. Dispersal patterns of nulliparous females were best explained by inbreeding avoidance but group transfer decisions in parous females appeared to be heavily influenced by perceived infanticide risk (Sterck & Korstjens, 2000). Where inter-group encounters gave parous females the option of transferring to a new group, females without infants tended to emigrate, whereas females with infants tended to remain with the father of their offspring (Steenbeek, 1999; Sterck & Korstjens, 2000). Moreover, where inter-group encounters resulted in infanticide, females often chose to disperse with the infanticidal male presumably because their resident male had already proved to be an inadequate protector (Sterck, 1997; Stewart & Harcourt, 1987; Watts, 1989; 1990).

Female primates also appear to regulate group size and sex ratios in order to reduce infanticide risk. In the folivorous, dispersed-egalitarian species Thomas langurs (*Presbytis thomasi*), mean group size was found to be much lower than would be predicted by ecological pressures alone and was directly related to the number of males in the group (Steenbeek & van Schaik, 2001). Groups may be one-male-multi-female or multi-male-multi-female, but as females rely on protector males to defend their infants, groups with a higher number of adult males have been found to attract more females (e.g. langurs: Sterck & van Hooff, 2000; gorillas: Robbins, 1995). Conversely, groups with a high number of receptive females relative to adult males are more susceptible to attacks by infanticidal males (Steenbeek, 2000). In addition to voluntary female dispersal, group females may regulate group composition by evicting nulliparous females approaching reproductive age, thus reducing the risk of attack to resident parous females (e.g. red howler monkeys, *Alouatta seniculus*: Crockett & Janson, 2000).

Female primate relationships are also affected by other male behaviours such as herding or intervention in female aggressive interactions known as 'male policing'. Male herding behaviour in hamadryas baboons physically prevents interactions between familiar and often related females from neighbouring clans resulting in long periods of separation (Kummer, 1995; Swedell, 2002). Male herding behaviour therefore disrupts female social relationships causing a reduction in frequency of interaction. When related and familiar females do find themselves in the same unit, attempts at coalitionary aggression toward other unrelated females are quashed by the unit male (Colmenares, unpublished data, cited in Watts, Colmenares & Arnold, 2000). This male policing of female interactions also causes a decrease in value of the related females' relationship as if coalitions against other females (that may lead to improved access to desirable commodities) are prevented, the related females will have little to gain from the relationship.

Male policing of female interactions has been observed in a wide range of species. Males intervene in female contests at particularly high rates where females may transfer between groups such as mountain gorillas (Watts, 1991; 1997) and Thomas langurs (Steenbeek, 1996). Male protection during conflicts is likely to discourage females from transferring to another group and encourage new immigrant females to stay so male policing can be interpreted as an adaptive behaviour aimed at increasing male reproductive success (Sterck *et al.* 1997; Watts 1997; Watts *et al.*, 2000). However, not all male interventions are impartial as males will often intervene in fights by forming a coalition with one of the combatants, usually the weaker of the two (e.g. macaques: Ehardt & Bernstein, 1992). This form of male policing may affect female relationships by minimising rank-related differences in energy gain and subsequent reproductive success (Watts *et al.*, 2000).

1.4. Male-male relationship quality and intra-sexual selection

The majority of literature on primate males has concentrated on their relative numbers in groups (Kappeler, 2000); however more recent research has aimed to investigate male competition for resources and the evolution of male primate social relationships (Kappeler, 1999a; van Hooff, 2000; van Hooff & van Schaik, 1992; 1994). While both sexes compete for access to resources, the primary resource for which they compete is different. Due to anisogamy and the corresponding energetic demands of reproduction, the primary source of competition among female primates refers to feeding access. Male primates on the other hand, do not have the concerns of costly gametes, pregnancy or lactation to content with, such that in most primate species, male reproductive success is almost entirely dependent on successful fertilisations. Primate males should therefore compete for potential mating opportunities (Emlen & Oring, 1977; van Schaik, 1983; Wrangham, 1980) and as a result, male-male relationships should be generally more aggressive and less stable in nature than female-female relationships because it is not possible to share fertilisations in the same way as is possible with food (van Hooff & van Schaik, 1992, 1994; van Schaik & Aureli, 2000).

1.4.1. Correlates of male-male competitive regimes

As with feeding competition, male-male competition for access to females may be characterised by scramble competition, where individuals lose access to resources because others have already found them and used them, and contest competition, where individuals actively compete for resources resulting in asymmetrical partitioning (Nicholson, 1954; van Schaik, 1989). The predominant type of competition is dependent on the distribution of the resource in space and time and its subsequent monopolisability. If females are clumped in distribution then contest competition between males may prevail. If these groups of females are intermediate in size then they may be monopolised by one powerful adult male, resulting in a one-male–multi-female society, in which the resident male actively competes with extra-group males for access to receptive females. If female groups are large, contest competition may still prevail but one resident male is unlikely to be able to prevent other adult males from joining the group, resulting in a multi-male - multi-female society (Altmann, 1990; Crockett & Eisenberg, 1987; Dunbar, 1988; Mitani, Gros-Louis & Manson, 1996a; van Schaik & van Hooff, 1983). Here, male contest competition for females may occur both within and between groups with resident males forming coalitions against extra-group males (van Hooff & van Schaik, 1992; 1994).

Where males compete for access to fertile females via contest competition, decided dominance relationships are predicted to evolve based on consistent winners and losers in contests. More powerful, dominant males are therefore able to monopolise access to receptive females resulting in a corresponding skew in male reproductive success (Cowlishaw & Dunbar, 1991; van Hooff, 2000). As power and dominance directly affect reproductive success, there should be selective pressure for males to evolve physical characteristics aimed at improving fighting ability, such as large body size and enlarged canine teeth (Setchell & Kappeler, 2003). As females are not subject to such intense competition these physical characteristics should mainly occur in males, resulting in sexual dimorphism (Setchell & Kappeler, 2003).

When female groups are large and primarily arboreal or adopt flexible grouping patterns, males are less able to monitor the movements of group females making monopolisation of females extremely difficult. Consequently, groups tend to be multi-male - multi-female in which males compete for fertilisations via scramble competition (Mitani *et al.*, 1996a; van Hooff, 2000). It has also been proposed that if females become receptive at different times then males may actively compete for access to oestrous females, but if females are receptive for only a short period of time and synchronize their receptive periods, then monopolisation again becomes virtually impossible, and scramble competition prevails (Kappeler & van Schaik, 2004; van Hooff & van Schaik, 1994). As monopolisation of receptive females is not possible, the skew in male reproductive success may not necessarily occur and as mating success is not directly linked to fighting ability, sexual dimorphism should be less pronounced (van Hooff, 2000). Although direct contests for females rarely occur, this is not to say that competition for fertilisations is not intense. Males may adopt a number of post-copulatory strategies such as frequent mating and ejaculatory plugs in order to out-compete rivals in sperm competition (Birkhead & Kappeler, 2004; Dixson, 1998). Frequent mating requires a large sperm stock so species that adopt this strategy should also have larger testes relative to body size when compared to other primate species (Harcourt, Harvey, Larson, & Short, 1981; Kappeler, 1997; Møller, 1988). However, the expected negative correlation between relative testes size and sexual dimorphism of body mass and canine size has not been found (Cowlishaw & Dunbar, 1992; van Hooff & van Schaik, 1994).

1.4.2. Male-male social relationships

Evidence to suggest that males compete for access to fertile females in the form of contest competition has been produced from a range of studies, with particular reference to the multi-male cercopithecines (e.g. Smuts, 1987a; Wrangham, 1980) and capuchin monkeys (e.g. Janson, 1988; Perry, 1997a) in which male-male aggression was found to increase in the presence of oestrous females (e.g. Bercovitch, 1986; Janson, 1984). The predicted link between overt male-male competition for females and selection for sexual dimorphism of body mass and canine size has also been supported by recent research that used the operational sex ratio (OSR) within a group as an indirect measure of male-male competition. The OSR reflects monopolisability of females in terms of: adult male: adult female ratios, mating season duration, the duration of female oestrous cycles, the number of oestrous cycles females experience before conceiving, and inter-birth intervals. Using independent contrasts analyses that control for the confounding effects of phylogeny, the OSR was found to positively correlate with sexual dimorphism of body mass (Mitani *et al.*, 1996b). Similarly, independent contrast analyses have shown a positive correlation between intensity of male-male aggression and male canine size (Plavcan, van Schaik & Kappeler, 1995).

Subsequent analyses have revealed that OSR correlates with canine size for multi-male species, but not for one-male species (Plavcan, 2004) suggesting that male reproductive skew in one-male species is not solely dependent on individual fighting ability male group tenure and the presence or absence of male coalition partners when defending group females (Altmann, 2000; Watts, 2000).

In addition to the intensity of male-male competition for fertile females, variation in male body mass and canine size may also be influenced by female mate choice (Paul, 2002). For example, in species where females preferentially mate with local dominant males, female mate choice should effectively reinforce reproductive skew and exaggerate sexual dimorphism (e.g. orangutans, *Pongo pygmeaus*: Utami & van Hooff, 2004; van Schaik & van Hooff, 1996; mandrills, *Mandrillus sphinx*: Setchell & Dixson, 2001a, 2001b; Setchell, Lee, Wickings & Dixson, 2001: geladas, *Theropithecus gelada* and Hamadryas baboons: Barton, 2000; gorillas: Watts, 1996). Conversely, female promiscuity as a counter-strategy to male coercion (Smuts & Smuts, 1993; van Schaik, Hodges & Nunn, 2000; van Schaik, van Noordwijk & Nunn, 1999) should reduce male reproductive skew and so lessen sexual dimorphism. These predictions have now been confirmed by independent contrasts analyses (Plavcan, 2004).

As predicted, in species where males actively compete for access to fertile females, dominance hierarchies have evolved based on consistent winners and losers in contests (e.g. Goodall, 1986; Hill, 1987; Packer, 1979). The dominance hierarchy acts as a queuing system for males, whereby the most dominant males gain 'priority of access' to fertile females (Altmann *et al.*, 1988) and obtain a larger proportion of the opportunities for copulations (Hill, 1987; Kano, 1996; Reed, O'Brien & Kinnaird, 1997). Recent DNA studies on wild primates have confirmed this effect of male rank on reproductive success (e.g. Berard, Nürnberg, Epplen & Schmidtke, 1993; de Ruiter, Scheffrahn, Trommelen, Uitterlinden, Martin & van Hooff, 1992; Keane, Dittus & Melnick, 1997; Pope, 1990), but have indicated that superior reproductive success in dominant males is achieved by controlling access to females when they are most likely to be ovulating, rather than a high frequency of mating. For example, in a wild group of long-tailed macaques (*M. fascicularis*) the highest ranking male sired more offspring than expected given his share of the copulations (de Ruiter *et al.*, 1992).

In certain species, the expected relationship between male dominance rank and priority of access to fertile females has not been observed (e.g. savannah baboons: Bercovitch, 1986; 1987; Noë & Sluijter, 1990; Smuts, 1985). Variation across primate species in the relationship between male dominance rank and mating success may be partly explained by group size. When group size increases, males lose their ability to monopolise access to females due to changes in power differentials and an increase in challenges from other group males (Dunbar & Cowlishaw, 1992; Cowlishaw & Dunbar, 1991). At the population level, Bulger (1993) showed that although male rank and mating success were correlated in the majority of savannah baboon troops, both the magnitude and direction of the correlation varied considerably. As female baboons express clear mating preferences for particular males (Bercovitch, 1995; Seyfarth, 1978a, 1978b; Smuts, 1985), it has been suggested that this observed variation may be due to female choice; however, it would appear that in baboons, the effects of female strategies are small relative to the effects of male reproductive strategies (Bercovitch, 1995).

Where primate groups adopt flexible grouping patterns, monopolisation of fertile females is likely to be difficult due to problems monitoring the reproductive state of all community females. Thus males compete for fertile females via scramble competition, causing direct contests for access to females and male-male coalitions will to be rare (van Hooff, 2000). Male social relationships within the group are therefore predicted to be relatively tolerant and affiliative (van Hooff, 2000). Consequently, tolerant social relationships and large relative testes size are the predicted hallmarks of males that compete for females via scramble competition. Evidence in support of this prediction can be found in the *Atelidae*, which have large testes size relative to body size (Dixson, 1998), exhibit tolerant male social relationships and live in societies with flexible grouping patterns with female-biased dispersal (muriquis: Milton, 1985; Strier, 1992; 1994; Strier, Dib & Figueira, 2002; woolly monkeys: Di Fiore, 2003; Di Fiore & Fleischer, 2005; spider monkeys: Eisenberg, 1973; Fedigan & Baxter, 1984; Symington, 1990). Male muriquis and woolly monkeys are not governed by a dominance hierarchy and do not coerce or harass fertile females and do not attempt to interfere with one another's copulations, neither as individuals nor as male coalitions (Di Fiore & Fleischer, 2005; Strier, 1994; 1997; Strier, Carvalgho & Bejar, 2000; Strier *et al.*, 2002). Less is known about males social relationships in spider monkeys, but males associate regularly exchange affiliative behaviour (Fedigan & Baxter, 1984) and are not thought to interfere with one another's copulations although mating tends to occur in secrecy away from other group members (Campbell, 2006; Fedigan & Baxter, 1984; Klein, 1971; van Roosmalen & Klein, 1988).

Flexible grouping with female-biased dispersal (Nishida & Hiraiwa-Hasegawa, 1987) and large testes size relative to body size (Harcourt et al., 1981) are also found in the genus *Pan* (chimpanzees and bonobos). Among male chimpanzees and bonobos male social relationship are undoubtedly more tolerant within groups than between groups and share many characteristics with those of the *Atelidae*. However, agonistically maintained dominance hierarchies can be found in both chimpanzees and bonobos and male dominance rank appears to affect access to fertile females (Kano, 1996; Nishida & Hosaka, 1996). Male chimpanzees frequently interrupt the mating attempts of other males (Goodall, 1986) and often form coalitions to attack consorting males and gain control of their females (Watts, 1998). Nevertheless, coalitions of subordinate males can easily defeat a dominant male (de Waal, 1982) indicating that power asymmetries between dominant and subordinates are not as high as in despotic male relationships (e.g. macaques). Male–male competition appears to be less frequent and less intense in bonobos due to prolonged female receptivity and thus reduced potential for monopolisation (Furuichi, 1987; Furuichi & Hashimoto, 2002). However, dominant males still appear to achieve higher mating success (Hohmann & Fruth, 2002; Kano, 1996) although in some cases this may be due to their central positions in the group rather than the outcome of direct contests as is the case for chimpanzees (Furuichi, 1997; Furuichi & Ihobe, 1994; Kano, 1996).

1.4.3. Male coalitions and alliances

Although dominant males in despotic societies are generally able to monopolise females, this relationship between rank and mating success can break down when subordinate males engage in queue-jumping behaviour such as coalitionary aggression (Alberts, Watts & Altmann, 2003; Bulger, 1993). A coalition of two or more subordinate males can often out-compete a more dominant male for access to a fertile female without permanently reversing ranks. One coalition member may then initiate mate guarding with the female and later copulate with her. If the mating results in fertilisation, the subordinate male will gain higher reproductive success than would be predicted by his dominance rank (Bercovitch, 1988; Noë & Sluijter, 1990; Smuts, 1985). In savannah baboons, the most dominant males are the most recent immigrants such that lower ranking males with longer residency have had time to develop cooperative relationships and have more information about reproductive states of females (Weingrill, Lycett, Barrett, Hill & Henzi, 2003). The most frequent coalition participants are therefore middle to low-ranking males, and this queue-jumping effect greatly influences the overall relationship between male dominance rank and reproductive success (Bercovitch, 1988; Noë & Sluijter, 1990; Smuts, 1985).

Similar coalitionary mate guarding has also been reported in chimpanzees (Watts, 1998) and as with baboons, only one member of the coalition gains access to the female, suggesting that a complex system of trading for a variety of commodities is in operation (Noë, 1990; Noë, van Schaik & van Hooff, 1991;

Watts, 1998). Male coalitions and alliances have also been observed in other large multi-male primate groups such as Barbary (*M. sylvanus*: Kuester & Paul, 1992) and bonnet (*M. radiata*: Silk, 1992) macaques, although in these species, male coalitions serve to maintain or enhance dominance rank rather than obtain access to females via coalitionary mate guarding. In all species, coalition and alliance partners spend a large proportion of their time associating with one another and engaging in affiliative behaviour such as social grooming (e.g. Boesch & Boesch-Achermann, 2000; de Waal, 1982; Kuester & Paul, 1992; Newton-Fisher, 2002; Pope, 1990; Seyfarth, 1980; Silk, 1992; 1994). Coalition and alliance partners therefore tend to have strong social bonds and valuable cooperative relationships in which the balance of power between partners is reflected in the exchange rates of desirable services or commodities (de Waal & Harcourt, 1992; van Schaik & Aureli, 2000).

If coalition partners are related to one another, then both partners may receive inclusive fitness gains from successful coalitions (Hamilton, 1964). For example, male bonnet macaques and male red howler monkeys are more likely to support male conspecifics during contests if they are related to them (Pope, 1990; Silk, 1992) suggesting that kinship is a contributing factor to male bonding and the evolution of male cooperative relationships. Moreover, the majority of primate species that exhibit male-male tolerance or male bonding also show greater than average relatedness among males (hamadryas baboons: Kummer, 1995; muriquis: Strier, 1994; squirrel monkeys: Boinski, 1994; Mitchell, 1994; chimpanzees: Morin, Moore, Chakraborty, Jin, Goodall & Woodruff, 1994). However, in chimpanzees at Taï, relatedness levels among community males was not significantly higher than females (Vigilant, Hofreiter, Siedel & Boesch, 2001), despite female-biased dispersal. This surprising result was likely due to the regular occurrence of secondary female transfer.

Although a high degree of relatedness would predict affiliative and cooperative relationships, this is not always the case. Among chimpanzees, measures of association such as proximity and social grooming were not correlated with genetic relatedness (Goldberg & Wrangham, 1997; Mitani, Merriwether & Zhang, 2000) and no evidence for a role of kinship in the coalitions and alliances of savannah baboons has been reported (Noë, 1986; 1992), suggesting that males choose their coalition partners primarily for 'political' reasons rather than inclusive fitness benefits. The lack of inclusive fitness gains may also explain the opportunistic and apparently fickle nature of male coalitions (de Waal, 1982). The high rates of male association and affiliative behaviour in primate societies with male philopatry can also be explained in terms of familiarity rather than kin selection as repeated interactions enable group males to form cooperative relationships and strong bonds in the absence of kinship (de Waal, 1986; 1992). Moreover, if by working cooperatively to defend access to community females, males can increase their reproductive success, then male affiliative behaviour can be described as a case of mutualism.

1.5. Male-female relationship quality and inter-sexual selection

Due to anisogamy and differential parental investment, male reproductive success may be maximised by mating with multiple females, whereas females should choose discriminately between the available males (Darwin, 1871; Trivers, 1972). Differences between male and female reproductive strategies can lead to a conflict of interest between the sexes as both sexes strive to maximise their reproductive success. In some cases, maximisation of reproductive success of one sex can be detrimental to the other sex, the most obvious examples of this being sexual coercion and infanticide. Inter-sexual selection has therefore resulted in the evolution of male and female sexual strategies and counterstrategies, which shape male-female relationships.

One such strategy is the formation of close bonds between females and the father of their dependent offspring. As post-copulatory bonds limit male access to additional fertile females and are antecedent to female mate choice, male mating effort should generally exceed paternal effort and affiliative interactions between the sexes should be restricted to during the oestrus phase (Palombit, 2000). This prediction is upheld for the majority of mammalian species (Clutton-Brock, 1989), but in a number of primate species males and females maintain stable affiliative relationships outside of the breeding context, which play a vital role in infant survival (e.g. baboons: Smuts, 1985; Japanese macaques: Takahata, 1982a, 1982b; rhesus macaques: Chapais, 1983b; Hill, 1990; chimpanzees: de Waal, 1982; ring-tailed, *Lemur catta* and red-fronted lemurs, *Eulemur fulvus rufus*: Kappeler, 1993; mountain gorillas: Watts, 1992; review: van Schaik & Kappeler, 1997).

1.5.1. Male and female reproductive strategies

Due to anisogamy and differences in parental investment, male and female reproductive strategies are often at odds with one another. The most extreme example of this is infanticide. Infanticide benefits males by inducing female oestrus in females that were previously lactating, but this has obvious devastating consequences for female reproductive success. This conflict of interest has led to the evolution of female counterstrategies aimed at manipulating male behaviour and either confirming or confusing paternity certainty using biological and behavioural adaptations (Kappeler & van Schaik, 2004; van Schaik *et al.*, 2000; van Schaik *et al.*, 2004).

Females may benefit from concealing the exact timing of ovulation because, if accompanied by promiscuous mating, can confuse paternity and subsequently provoke protective behaviour toward the infant from a number of males and reduce the probability that males will attack the infant (Paul, 2002; van Schaik *et al.*, 2000). Female promiscuity is not possible if dominant males can monopolise oestrus females, but in seasonal breeders closely synchronised female oestrous greatly reduces male monopolising powers (Eberle & Kappeler, 2002; Emlen & Oring, 1977; van Schaik *et al.*, 1999). Similarly, extending the female receptive period in non-seasonal breeders can produce overlap in oestrus that also limits the ability of one male to monopolise access to all fertile females (e.g. bonobos: Kano, 1996). However, 'advertising' oestrus with visual or olfactory cues can incite male-male competition ensuring that only the best quality males gain access to each female, providing her offspring with the best possible genes. Moreover, advertising ovulation, coupled with selective mating can increase paternity certainty, securing better protection for the resultant offspring from the dominant male (Palombit *et al.*, 1997; Paul, 2002).

Biasing paternity in favour of preferred male(s) and confusing paternity to reduce the risk of infanticide are clearly at odds with one another, presenting females with something of a dilemma (van Schaik *et al.*, 1999; 2000; 2004). Among the great apes and Old World monkeys, this dilemma may be alleviated by exaggerated sexual swellings that indicate the probability of ovulation. The long duration and gradual change in size of exaggerated sexual swellings enable females to bias male behaviour by altering the costs and benefits of mate guarding so that only the 'best' males tend to mate-guard at peak swelling (Nunn, 1999; Zinner, Nunn, van Schaik & Kappeler, 2004). As a result, paternity can be biased towards these dominant males who are then more likely to protect the offspring. However, as peak swelling is only a probabilistic indicator of ovulation, and continues after ovulation, dominant males are often unable to restrict access to females throughout the entire peak swelling phase, allowing subordinate males the chance to mate with female and occasionally sire offspring. It has been hypothesised that a subordinate male that mated with a female during peak swelling will be unlikely to kill the females' next born infant as it is possible that it may be his offspring (Nunn, 1999; Zinner *et al.*, 2004). This graded signal hypothesis of exaggerated sexual swellings (Nunn, 1999) has been supported in chimpanzees as there is an increase in swelling size at the timing of ovulation, but peak swelling continues for up to 4 days after ovulation (Deschner, Heistermann, Hodges & Boesch, 2004). However in other species, that also have female sexual swelling (e.g. long-tailed macaques) males were able to detect female ovulation with surprising accuracy (Englehardt *et al.*, 2004).

In addition to these biological adaptations, male behaviour may be manipulated by the actions of females. Female transfer decisions may reduce the likelihood of infanticide, particularly when secondary transfer is possible (e.g. Thomas langurs: Steenbeek, 2000). In some species, resident females may influence the success of male immigration attempts (e.g. Smuts, 1987b) or refuse to accept new males after group takeover (e.g. Dunbar, 1984). Females may also exert mate choice in the form of post-copulatory vocalisations at the time of ovulation to ensure mate-guarding by the most dominant male (Maestripieri & Roney, 2005). However, attempts to determine the degree to which female behaviour can influence male mating success have produced conflicting results. In some studies, female choice appears to be the deciding factor in male mating success (e.g. spider monkeys: van Roosmalen & Klein, 1988; captive Japanese macaques: Soltis, *et al.*, 1997b), whereas in other studies females counterstrategies to male coercion appear unsuccessful (e.g. savannah baboons: Bercovitch, 1995) and have little affect on male mating success (e.g. wild Japanese macaques: Soltis, Tomsen & Takenaka, 2001).

1.5.2. Male-female affiliative bonds

One particular group of primates that exhibit long-term bonds between male and females are the Callitrichidae (marmosets and tamarins). These small Neotropical species adopt a cooperative breeding strategy characterised by high rates of paternal care (Santos, French & Otta, 1997; Tardif, Carson & Gangaware, 1986) and delayed dispersal of adult offspring, which assist parents in rearing of subsequent offspring (French, 1997; Solomon & French, 1997). Callitrichid mating systems vary considerably, but in all cases, breeding adults maintain long-term social and sexual bonds (Baker, Dietz & Kleiman, 1993; Deitz & Baker, 1993; Digby, 1995; Garber, Ençarnación, Moya & Pruetz, 1993). Due to the rate at which females can reproduce and that females give birth to twins, paternal care and that of additional adults is believed to be essential for the survival of offspring in the wild (Goldizen, Mendelson & Terborgh, 1996). As a combined parental effort is a requirement of successful breeding, male-female relationships are extremely valuable to both sexes and are therefore maintained with high rates of affiliative behaviour (Schaffner & Caine, 2000).

Enduring social relationships between the sexes may also occur when females give birth to single young and 'classic' forms of paternal care such as carrying and thermoregulation are absent (Palombit, 1999). It is also possible for the quality of male-female relationships to vary independently of mating system (Kappeler & van Schaik, 2002; Palombit, 2000) suggesting that there are other adaptive benefits of male-female bonds. As infanticide risk appears to have a notable influence on male and female behaviour, it has been hypothesised that females form long-term bonds with males who will protect their offspring from infanticidal males (Hrdy, 1979; van Schaik & Dunbar, 1992).

Although a male's protection of an infant does not *a priori* imply a social bond with its mother, in non-human primates individuals show a tendency to preferentially aid those with whom they have interacted affiliatively in the recent past (Harcourt, 1992). Similarly, if a high probability of male paternity increases the likelihood of male defence of an infant, then prenatal association between the mother and protector may facilitate infant protection (Palombit, 2000). Females should therefore aim to maintain relationships with protector males both before and after the birth of infants resulting in close between the sexes. If close association with males is considered a female counterstrategy to infanticide, then it also follows that females should take greater responsibility for maintaining this relationship, thus initiating and giving more affiliative behaviour than they receive (Palombit, 2000).

Close bonds between resident males and lactating females exist in a number of species where infanticide accounts for a large proportion of infant deaths (e.g. mountain gorillas: Watts, 1989; chacma baboons: Palombit Cheney & Seyfarth, 2001; langurs: Steenbeek, 1996; Borries *et al.*, 1999; lemurs: Kappeler, 1993; van Schaik & Kappeler, 1997 for a review). In a number of species, likely sires tend to be in close proximity to their infants (Paul, Preuschoft & van Schaik, 2000) and actually defend infants against attacks by other males (Borries *et al.*, 1999; review: van Schaik, 2000a). Females are generally responsible for maintaining these relationships via social grooming (e.g. Stewart & Harcourt, 1987; Watts, 1990; 1996; Palombit, Seyfarth & Cheney, 1997) and among chacma baboons, females are known to actively compete for access to male 'friends' (Palombit *et al.*, 2001). In some species (e.g. gorillas: Robbins, 1995) these friendships are long-term, but in the majority of species male-female friendships only occur when the female is lactating with no manifestation of this relationship before birth of after the death of the infant (Smuts, 1985; 1987;

Palombit *et al.*, 1997). Playback experiments have confirmed this observation as males were significantly more likely to respond to the screams of a female 'friend' when she was lactating compared to after the death of her infant, suggesting that the friendship depended on the presence of young infants (Palombit *et al.*, 1997). Similar short-term male-female 'friendships' have also been observed in Japanese and rhesus macaques (Takahata, 1982, 1982b; Chapais, 1983b, 1983c).

Female preference for interacting with particular males results in huge variation in male-female relationship quality as females direct virtually all their affiliative behaviour to kin and their particular male 'friend' leaving little or no time for interaction with other males. A similar dichotomy in male-female primate interactions can be found between males and oestrus or anoestrus females. For example, in chimpanzees, social interactions between males and anoestrus females are rare (e.g. Pepper, Mitani & Watts, 1999), whereas short-term relationships between males and oestrus females are common place (Matsumoto-Oda, 1999), and these short-term bonds are equally maintained by both partners using complementary sexual and affiliative behaviour (Matsumoto-Oda, 2002).

1.5.3. Sexual Coercion

Across primate species, high-ranking males tend to monopolise the vast majority of mating (Cowlishaw & Dunbar, 1991). However, individual differences in temperament and behaviour mean that not all high-ranking males are desirable partners. When females do not wish to mate with a particular male, they may be subjected to sexual coercion, particularly in species with pronounced sexual dimorphism (Clutton-Brock & Parker, 1995; Smuts & Smuts, 1993). Sexual coercion generally refers to sexual harassment whereby males direct often severe aggression towards oestrus females in order to coerce them into mating. Infanticide may also be considered an extreme form of sexual coercion (Smuts & Smuts, 1993). Recent theory suggests that both male and female group-living primates will desire a certain degree of paternity confusion to lower the risk of attack from other males on their offspring. However, the degree of female promiscuity desired by males is considerably less than that desired by females, which leads to a conflict of interest between the sexes (van Schaik, Pradhan & van Noordwijk, 2004). Consequently, oestrus females not only receive sexual harassment from less desirable or low-ranking males but also from preferred or dominant males.

Coercion is costly to female reproductive success as it limits female choice of sexual partners, often thwarting female attempts to obtain the best genes for their offspring (Clutton-Brock, 1989). Female primates have therefore evolved a number of counterstrategies to sexual coercion such as synchronised oestrus or exaggerated sexual swellings that indicate the probability, but not certainty of ovulation (Nunn, 1999; van Schaik *et al.*, 2000; Zinner *et al.*, 2004). Similarly, male-female 'friendships' may also safeguard females from aggression from other adult or sub-adult males, which is the likely explanation for these friendships in East African baboons, among which infanticide is rare (Collins, Busse & Goodall, 1984). Male-female primate relationships are therefore complex, are both affiliative and agonistic in nature, and vary considerably in value.

1.10. Thesis Outline

The majority of primate literature is based on Old World monkeys and apes, with relatively little known about the arboreal, forest dwelling, New World species, or prosimians that are so difficult to observe (Kappeler, 1999b; Kappeler & van Schaik, 2002; Pereira & Kappeler, 1997). From the limited data that has been collected on New World species, it appears that patterns of dispersal and behaviour are very different from those observed in Old World species, and the relative importance of affiliative behaviour such as social grooming also appears to differ, (Dunbar, 1992) indicating that these species warrant further investigation. It is therefore important to study these New World and prosimian species in order to fully understand the evolution of the primate order. The study of the New World primates is also important to our understanding of evolution in general. Of particular importance are the arboreal, forest dwelling primates known as the *Atelinae*, which include spider monkeys, woolly monkeys and muriquis. All these species adopt flexible grouping patterns to varying degrees (Di Fiore, 2003; Strier, 1989; 1999; Symington, 1990), with spider monkeys showing a high degree of fission-fusion dynamics in their social system, such that community individuals are rarely all together (Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1990). This kind of social system has also been reported in the genera *Pan* (chimpanzees: Goodall, 1986; bonobos: Kano, 1992), the bottlenose dolphins (Connor, Smolker & Richards, 1992), spotted hyenas (East, Hofer & Wickler, 1993), and traditional human societies (Dunbar, 1998).

Under these circumstances, community members are not only required to keep track of third party relationships as is the case for species that live in cohesive groups, but must also gain information surrounding changes to their own social relationships and to third party relationships as a result of social interactions that occurred in different subgroups. Individuals must also learn to adjust their behaviour depending on the individuals present in their subgroup, which is particularly important when referring to dominance hierarchies. Consequently, there is a strong selection pressure for the evolution of intelligent and cognitively advance individuals who can thrive in such a complex environment. An understanding of the social interactions of species that live in societies characterised by a high degree of fission-fusion may therefore provide insight into human social and cognitive evolution.

Although the majority of species that live in societies characterised by a high fission-fusion dynamic have been studies in detail, data on the social interactions of spider monkeys is sparse, which is in part due to problems associated with locating and following community males (e.g. Chapman, 1990). Consequently, studies of wild spider monkeys have focussed on variation in subgroup competition and flexible grouping patterns as a strategy for reducing feeding competition (e.g. Chapman, 1990; Chapman *et al.*, 1995; Shimooka, 2003; Symington, 1988a) rather than the implications of flexible grouping on social interactions. To date a small number of studies have provided a limited insight into spider monkey social relationships. Fedigan & Baxter (1984) described the distribution of key social behaviours across age and sex classes, but were unable to make statistical comparisons because members of their study community could not be individually recognised. Symington has provided accounts of demography and activity budgets (1988b) and has compared sex differences in association patterns and the distribution of social grooming (1990). In each of these studies, affiliative social behaviour was exchanged most frequently between males, but there has been some disagreement as to whether females preferentially interact with same-sex or opposite-sex partners.

Prevalence for female-directed male aggression has been reported in three separate study communities (Campbell, 2003; Fedigan & Baxter; Symington, 1987 PhD thesis cited in Smuts & Smutts, 1993), but the function of this behaviour remains unclear. Spider monkey sexual behaviour has been investigated in a close community of spider monkeys on Barro Colorado Island in Panama (Campbell, 2006), and has indicated that mating tends to occur in secrecy and is generally initiated by females. Social interactions in the context of fusion events have been investigated both in the wild (Schaffner, Verpooten & Aureli, 2003) and in a captive setting (Schaffner & Aureli, 2005) and have indicated that aggression and species-specific social behaviour are exchanged at a higher rate following fusion. However, sex differences in this behaviour are yet to be investigated. Schaffner & Aureli (2005) also demonstrated that female spider monkeys use embraces as a means of gaining access to other females' infants and provided evidence to suggest that spider monkey social relationships are regulated by embraces rather than grooming, although further investigation is required to determine the function of the species specific embraces.

A further problem with current primate research is that male-male, female-female and male-female social relationships tend to be investigated in isolation despite the fact that these relationships are known to influence one another. As each dyadic social relationship has a unique history of interaction, considerable variation in relationship quality may be found within and between sexes. Relationship quality may also change over time due to fluctuations in market effects caused by environmental or social changes (Barrett & Henzi, 2002). In order to fully investigate primate social relationships in a particular species it is therefore necessary to take a holistic approach that incorporates many factors that influence the quality and nature of interactions (see Figure 1).

I aimed to investigate social interactions in wild spider monkeys (*Ateles geoffroyi yucatanesis*) in order to define the nature of spider monkey social relationships and to identify variation in relationship quality. In this current investigation, observations were conducted on two previously habituated communities of spider monkeys, and all individuals, including the males were encountered on a regular basis and were individually recognised. It was therefore possible to investigate social interactions at the individual level and conduct refined statistical analyses of observed differences in behaviour. The four data chapters in this thesis cover key issues between male-male, male-female and female-female social relationships and the various factors that affect their quality.

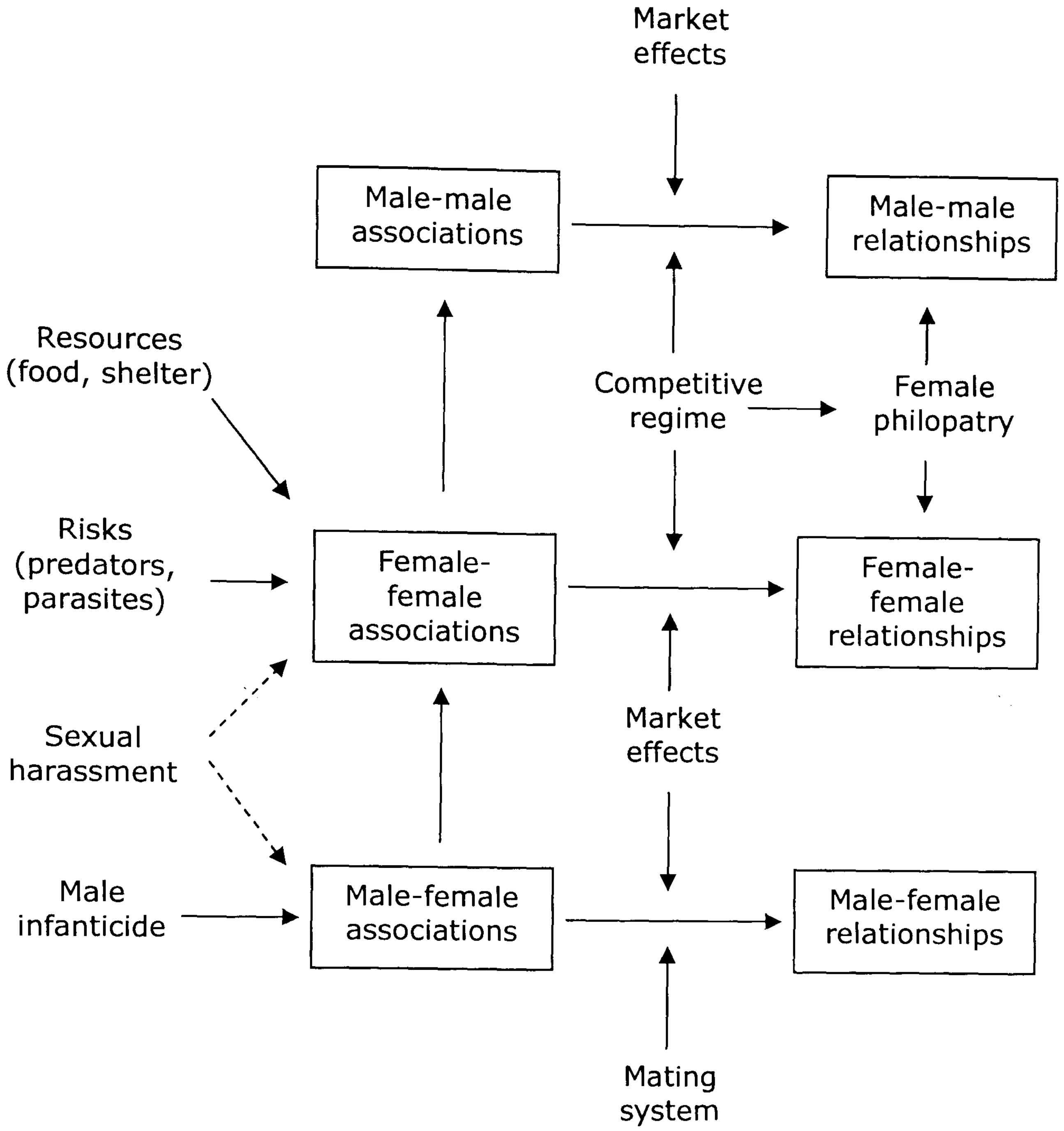

Figure 1: Factors affecting same-sex and mixed-sex relationships among adult non-human primates (redrawn from van Schaik & Aureli, 2000).

Among spider monkeys dispersal appears to be female-biased (Symington, 1987), thus it was hypothesised that relationship quality would be higher among community males when compared to female-female or male-female social relationships. Individuals that share a high-quality relationship are predicted to associate frequently and exhibit high rates of affiliative behaviour, whereas the reverse is true for low-quality relationships. Aggression may still occur in high quality relationship but individuals are predicted to employ specific behaviour to mitigate the negative effects of aggression with valuable conspecifics (Aureli & de Waal, 2000). Chapter three describes sex differences and the effects of age and kinship on the distribution of affiliative and aggressive behaviours with special attention to species-specific social behaviours.

Chapter four investigates the contextual use of social behaviour within same-sex relationships. Female primates are predicted to compete primarily for access to food, whereas males are predicted to compete for access to fertile females (Emlen & Oring, 1977). The occurrence of male-male and female-female agonistic and affiliative behaviour in the contexts of feeding and same-sex versus mixed-sex subgroups were therefore investigated. The context of fusion as a possible source of conflict was also investigated for males and females.

Relationship quality is heavily influenced by the relative value each individual assigns to their social partners. Value is generally assessed by the commodities and services each individual has to offer and their current exchange rate within a biological market place (Noë & Hammerstein, 1994). One such desirable commodity among female primates is infant access (Barret & Henzi, 2002). Chapter five investigates the effect of an infant 'market' on female spider monkey relationships and aims to determine whether social behaviour is exchanged for infant access using the biological markets paradigm.

Social relationships are known to be shaped by conflict and cooperation. As male and female reproductive strategies are often at odds with one another, male-female relationships may be subject to conflict in the form of sexual coercion that includes infanticide and sexual harassment (Smuts & Smuts, 1993). Previous studies of spider monkeys have described unusually high rates of female-directed male aggression (Fedigan & Baxter, 1984), although the probable function of this aggression remained unclear. This female-directed male aggression is described and evaluated in light of three possible explanations in Chapter six.

The findings of these four data chapters permit an overall discussion of spider monkey social relationships and factors that affect their quality in Chapter seven. The spider monkey social system is discussed in relation to other species with high fission-fusion dynamics in their social organisation, and in relation to other primates in general.

Chapter Two

Methodology

2.1. Study Site

Research was conducted at the *Otoch Ma'ax Yetel Kooh* protected area, next to the village of Punta Laguna, Yucatan Peninsula, Mexico (20°38' N, 87°38' W, 14m elevation: see Figure 2.1). The climate in this region of Mexico is tropical and seasonally dry with a mean annual temperature of 25°C and a mean annual rainfall of approximately 1500mm, 70% of which falls between May and October. The 53.67km^2 study site was declared as a protected area in June, 2002 by Mexican Federal authorities and contains patches of old and regenerating, tropical semi-evergreen forest and fields used for slash and burn agriculture (see Figure 2.2). Of the protected area, 7.7km^2 consist of medium forest with trees of up to 25m in height distributed in patches of varying size. A further 29km^2 consist of 30-50 year old successional forest, referred to as *kelenché* (Maya for "young tree or forest") in which tree height does not exceed 10m. A line transect census carried out in 1997-1998 (Ramos-Fernandez & Ayala-Orozco, 2003) revealed a very high density of spider monkeys in the old-growth forest (87 ind/km^2 ± 2.2) which is higher than any other population density of *Ateles geoffroyi* (Costa Rica: 6-9 ind/km^2 in Freese, 1976, and 25 ind/km^2 in Chapman, 1990, and 49 ind/km^2 in McDaniel, 1994: PhD thesis cited in Ramos-Fernandez, Vick, Aureli, Schaffner & Taub, 2003; Guatemala: 45 ind/km^2 in Coelho, Bramblett, Quick & Bramblett, 1976, and 26 ind/km^2 in Cant, 1978). The unusually high population density in old-growth forest at *Otoch Ma'ax Yetel Kooh* is likely to be due to the reduction in habitat area caused by agriculture (Ramos-Fernandez *et al.*, 2003). This explanation is supported by the McDaniel (1994) study that also showed high population density in a site consisting of fragments of old-growth forest within a matrix of regenerating forest and cattle ranches. One of the largest patches of old growth forest surrounds a 2km wide, large fresh water lagoon (see Figure 2.3). Two communities of spider monkeys (Eastern and Western) were known to utilise the large number of fruiting trees located in this patch of forest and have been habituated to human observers.

Yucatan Peninsular

Figure 2.1: Map of Mexico showing location of Yucatan Peninsula.

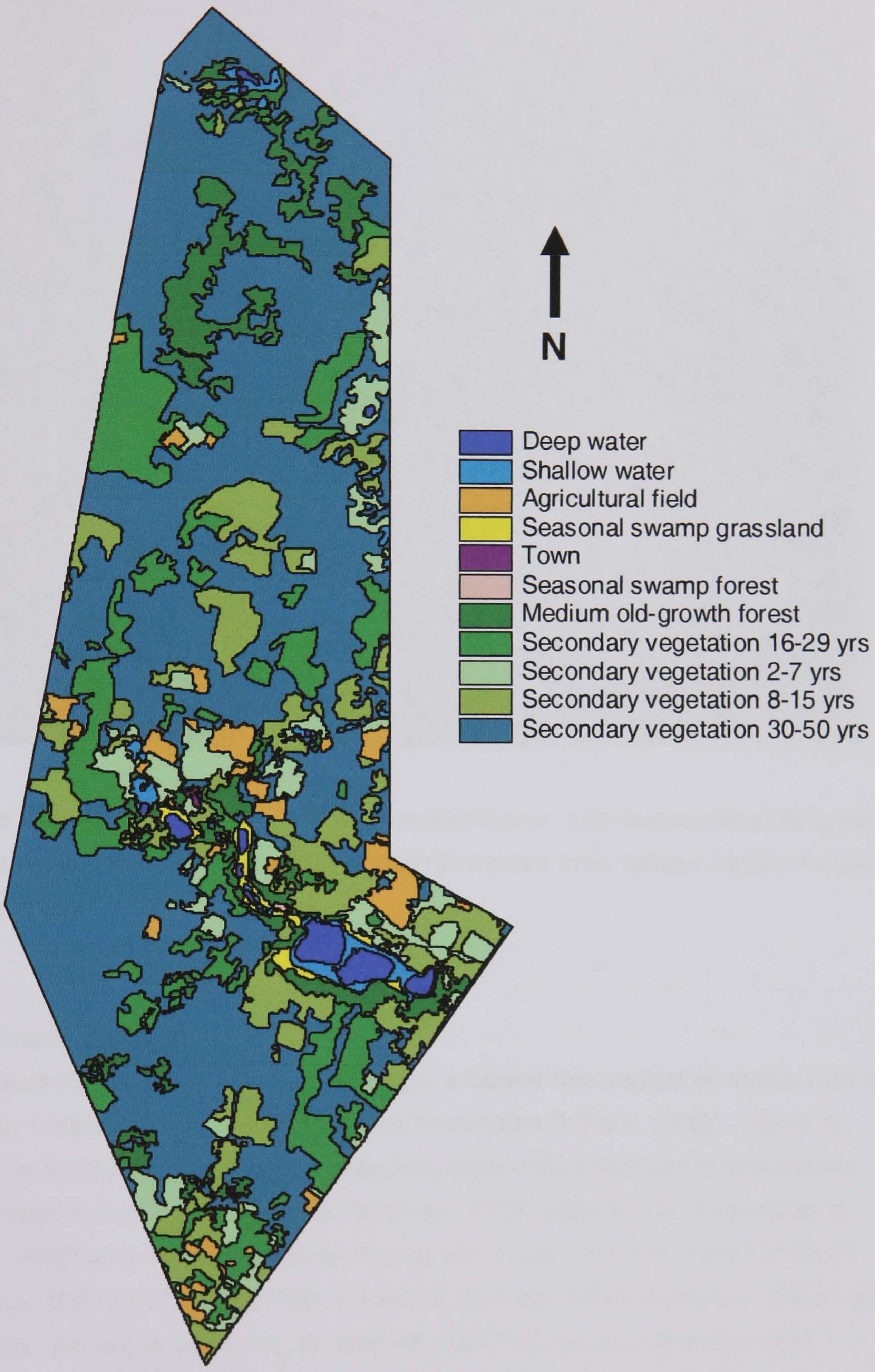

Figure 2.2: *Otoch Ma'ax Yetel Kooh* protected area in the state of Yucatan, Mexico (adapted from Ramos-Fernandez, Vick, Aureli, Schaffner & Taub, 2003).

Figure 2.3: Aerial photograph of fresh water lagoon and surrounding old growth forest within the *Otoch Ma'ax Yetel Kooh* protected area (photo credit: Ramos-Fernandez)

2.2. Study Species

Species of the genus *Ateles* are large, arboreal Neotropical primates with long slender limbs and prehensile tails (van Roosmalen & Klein, 1988). Based on differences in pelage, four *Ateles* species, each with a number of subspecies, have been recognised (Kellogg & Goldman, 1944: cited in van Roosmalen & Klein, 1988) and subsequently confirmed using mitochondrial DNA (Collins & Dubach, 2000) and nuclear DNA (Collins & Dubach, 2001) analyses. The largest of these species, *A. paniscus*, is covered with long, glossy black hair and occupies the north-eastern portion of the Amazon Basin (van Roosmalen & Klein, 1988). *A. belzebuth* has a number of different subspecies that range across the western and southern Amazon Basin incorporating Venezuela, Colombia, Ecuador and Brazil (Ferrari & Lopes, 1996). *A. hybridus*, formerly a subspecies of *A. belzebuth*, is located primarily along the Magdalena River valley in Colombia and in the mountainous areas of north western Venezuela (Norconck, Sussman & Phillips-Conroy, 1996). *A. geoffroyi*, which includes as subspecies the two former species *A. geoffroyi* and *A. fusciceps*, ranges across Central America from approximately 23°N in Tamaulipas, Mexico and 19°N in Jalisco, Mexico through to western Columbia and Ecuador (van Roosmalen & Klein, 1988). Spider monkeys are diurnal and arboreal and are primarily found in the upper levels of the forest, spending over 50% of their time in the upper canopy (van Roosmalen & Klein, 1988). Although spider monkeys prefer undisturbed, evergreen forest, when this type of habitat is limited in extent, communities appear able to survive in a range of forest types including disturbed regenerating forest (Sorensen & Fedigan, 2000). The primary mode of locomotion in *Ateles* is brachiation with intermittent leaping, climbing and quadrupedal walking and running (Cant, Youlatos & Rose, 2001; Youlatos, 2002). All *Ateles* species are primarily frugivorous and feed largely on a wide variety of mature fruits (van Roosmalen & Klein, 1988). Their diet is also supplemented with young leaves and seeds, floral buds, flowers, pseudobulbs, bark, decaying wood, honey and insects with the estimated importance of fruit in the diet ranging from 82.9 – 90% (van Roosmalen & Klein, 1988).

Spider monkeys live in societies with flexible grouping, in which subgroup size may be altered to fit the size and distribution of food patches (Symington, 1988a). Spider monkey societies are characterised by male philopatry and female dispersal, which occurs as females reach sexual maturity (Symington, 1987). Their life history is slow in comparison to other monkeys. Infant are carried by their mothers for the first 4 – 6 months after birth and are not fully weaned until the birth of the next infant at around 30 – 40 months (Milton, 1981; Symington, 1987). Individuals are sexually active from around 6 years of age but do not reach their fully adult size until around 8 years of age (van Roosmalen & Klein, 1988).

This current research was conducted on *A. geoffroyi yucatanesis* located in the Yucatan Peninsula of Mexico. This subspecies have short coarse hair that is generally brown in colouration although in many individuals the hair on the back has a red tint and the chest may vary from lighter brown to white colouration. Hands and feet are black and adults also have back colouration around the eyes. Some individuals may have white hairs around the face like a beard or moustache and some adult males have a patch of orange/yellow hair on their chest. Adult males are only slightly larger than females, but females are easily distinguished from males by their elongated clitoris.

2.3. Study Population

The two spider monkey communities that utilise the main old-growth forest fragment surrounding the fresh water lagoon have been studied continuously since January 1997. The two communities were not provisioned and all members of both communities were individually recognised. When the study began in 2003 there were initially 19 individuals in the Eastern community and 41 individuals in the Western community (see Table 2.1). In the Eastern community, three sub-adult females emigrated and one adult female immigrated within the first observation year and approximately half way through the second observation year, one of the adult males disappeared and has not been seen since. In the second observation year, two adult females immigrated into the Western community and four sub-adult females emigrated from the community during the same year. Over the course of the two observation years five infants were born into the Eastern community and 12 infants were born into the Western community. The mean inter-birth interval for these communities calculated from January 1997 to 2002 was 32 months (± 6 SD, range 24 to 46: Ramos-Fernandez, *et al.*, 2003), which is comparable to those found by Milton (1981) in *A. geoffroyi* at Barro Colorado Island, Panama (32 ± 3 SD, range 28 to 36), Chapman and Chapman (1990) in *A. geoffroyi* at Santa Rosa National Park, Costa Rica (36 and 37 months) and Symington (PhD thesis 1987; cited in Ramos-Fernandez *et al.*, 2003) in *A. belzebuth chamek* at Manú, Peru (34.5 ± 5.8 SD, range 25 to 42). Inter-birth intervals from 2002 to the most recent births were within the same range.

From January 1997 through to December 2000, the two communities were observed to forage on a total of 55 species, although 85% of their total foraging time was spent consuming fruits of the following species: *Ficus cotinifolia, Ficus ovalis, Manilkara zapota, Metopium bronwei, Protium copal,* genus *Malmea, Guazuma ulmifolia, Sideroxylon capiri, Spondias mombin* and the fruit and leaves of *Brosimum alicastrum* and *Enterolobium cyclocarpum* (Ramos-Fernandez *et al.*, 2003). Of these species, *M. bronwei* and *G. ulmifolia* were found in higher densities in the successional forest (*kelenché*) than in the old-growth forest (Ramos-Fernandez *et al.*, 2003). In the majority of observations from January 1997 to December 2000, both communities were located in the old-growth forest although subgroups have been observed to travel up to 5km into the successional forest to find food. The Eastern community's home range for this same time period, defined by the minimum polygon enclosing all locations where community members were observed was 0.95km^2, of which 0.29km^2 corresponds to old-growth forest and 0.66km^2 to *kelenché* (Ramos-

Fernandez & Ayala-Orozco, 2003). The Western community was observed in a total area of 1.66km^2, of which 0.29km^2 was old-growth forest and 1.37km^2 was *kelenché* (Ramos-Fernandez & Ayala-Orozco, 2003). However, these estimates of home range size are subject to error due to the difficulty of following subgroups in the *kelenché* (Ramos-Fernandez, personal communication). It is therefore possible that both groups utilised the *kelenché* to a greater extent than these estimates would suggest. It is also possible that subgroups travelled across areas of *kelenché* to arrive at additional patches of old-growth forest. Furthermore, as the *kelenché* regenerates it provides increasingly more fruit for the monkeys, which is likely to affect foraging patterns and home range size (Ramos-Fernandez *et al.*, 2003).

Table 2.1: Composition of the two study communities during 2003 and 2004.

Eastern Community

	2003			2004		
	Male	Female	Total	Male	Female	Total
Adult	4	7	11	4*	8	12
Sub-adult	0	3	3	0	0	0
Juvenile	0	0	0	1	2	3
Infant	3	2	5	5	2	7
Total	7	13	19	10	12	22

Western Community

	2003			2004		
	Male	Female	Total	Male	Female	Total
Adult	9	15	24	9	17	26
Sub-adult	0	4	4	0	4	4
Juvenile	0	2	2	2	6	8
Infant	3	8	11	7	11	18
Total	12	29	41	18	38	56

* One adult male disappeared on 13.07.04 and has not been seen since.

2.4. Data Collection

Observations were conducted during two separate field seasons at *Otoch Ma'ax Yetel Kooh* from 17.01.03 through to 26.09.03 and from 01.03.04 through to 31.10.04. From Monday to Friday each week, I observed one of the two spider monkey communities for a six-hour period with two of the local assistants. Due to the high fission-fusion dynamics in spider monkey societies, community members were rarely all together and were most often encountered in subgroups. A subgroup was defined as one or more individuals travelling together that were separated from other community members by at least 30m. Each six-hour observation was conducted from sunrise to midday or from midday until sunset with the remainder of the day and weekends used to transcribe data from the Dictaphone into various computer files. Observation times and the study community observed were alternated each day so that at the end of each month, each group had received approximately the same number of morning and afternoon observations.

Data were collected using, *ad libitum* samples and 20-minute focal animal samples with continuous recording of all behaviours listed in the behavioural ethogram (see Table 2.2). Two 20-minute focal samples were recorded each hour using a Sony M450 dictaphone and all individuals (excluding infants) in the subgroup were sampled before repeated samples of the same individuals were attempted. Throughout the focal sample, the start and finish time of all behaviours, subgroup composition, and changes in location were recorded. When social interactions were observed, the direction, context and outcome of behaviour plus all individuals involved were recorded. Special events involving aggression or species-specific affiliative behaviour (arm-wrapping, place-sniffing, grappling, embraces, kisses and pectoral sniffs) were also recorded *ad libitum*. All instances of group fission and fusion were recorded, noting the individuals leaving or joining the group and the exact time that the event occurred.

Table 2.2: Ethogram of spider monkey behaviour used for the study.

Behavioural Pattern	Description
INDIVIDUAL / SELF-DIRECTED BEHAVIOUR	
Place Sniff / Lick	Monkey touches nose or tongue to substrate previously occupied by other individual (indicate individual)
Feed	Monkey masticates food while food is in hand or mouth
Move	Monkey moves from substrate to substrate by walking, running or brachiation
Null	Monkey is temporarily out of view from the observer
Rest	Monkey is stationary on substrate, either sitting, lying or dangling
Scratch	Repeated scraping of fingers on individuals' own fur or body
Scent Mark	Monkeys rubs chest area against substrate or sits on substrate and moves in a pull / drag motion
Self Groom	Monkey manipulates own fur with hands or mouth, often removing lice or debris, which may or may not be ingested
Vigilant	Monkey is stationary with head raised, scanning the surroundings and looking into the distance
AGONISTIC SOCIAL BEHAVIOUR	
Bite	Teeth and mouth of individual clamp down on body of another
Chase	Rapid follow of a retreating individual
Displace	Monkey causes another individual to move from their original position by approaching or starting towards them
Lunge	Fast charge at another
Strike	Hand swung forward to hit another individual
Threat	Fixed gaze on another with mouth slightly opened and a little bit of teeth showing. May also involve extreme retraction of lips with full teeth exposure
AFFILIATIVE SOCIAL BEHAVIOUR	
Approach	Monkey moves within one metre of another individual
Arm Wrap	Two monkeys wrap their arms round the shoulders of the other, with both monkeys facing in the same direction. While arm-wrapping, the monkeys direct coalitionary aggression toward conspecifics, human observers or other animals.
Copulate	Female sits on male's lap. Male responds by wrapping his legs round the female's thighs. Intromission may last 10-30 minutes
Embrace	Monkey wraps one or both arms around another individual
Face Greet	Monkey gazes in direction of other and purses lips outward in a wide kiss-like gesture
Face Touch	Monkey places hand(s) or fingers gently on the face of another
Kiss	Monkey briefly places lips on the mouth or face of another

Behavioural Pattern	Description
Genital Inspection	Monkey sniffs, touches or places entire hand on the genitals of another
Grapple	Sustained contact with two individuals that may contain, but is not limited to elements of facial greeting, face touching, embracing, tail wrapping, pectoral sniffing and genital contact. Monkeys may also move apart, maintaining intense face to face visual contact and then move together, like a slow passionate dance
Groom	Monkey manipulates fur of another individual with hands and / or mouth
Infant-Handling	Monkey sniffs, nuzzles, kisses, touches or carries an infant. This does not include mother-infant interactions
Play	Sustained contact with two or more individuals that may contain, but is not limited to: chasing, mock biting, slapping and wrestling. Often occurs in conjunction with panting
Pectoral Sniff	Monkey places nose at the chest or arm region of another
Solicit Grooming	Monkey presents arm, back or other part of body to another individual

2.6. Data Analysis

Spider monkeys live in societies with high fission-fusion dynamics in which community members are rarely all together. As a result of this social system, daily observations were made on different subgroups of varying size and composition causing individual differences in the total amount of time in view. All individuals that were observed for less than three hours during focal samples were removed from the data set to prevent unrepresentative rates or percentages of behaviour. Each individual also had a unique total amount of time in view together with each of their community members. In order to calculate rates of individual behaviour and social exchanges it was therefore necessary to account for the differences in time in view. Hourly rates of individual or self directed behaviour (see Table 2.2) were calculated for each focal animal by dividing the total frequency of behaviour by the total amount of time that the particular individual was observed during focal samples. In order to determine rates of social behaviour (see Table 2.2) it was necessary to calculate the unique amount of time that the focal animal was observed in the same subgroup as each of their potential interaction partners. Due to the nature of focal animal sampling, a dyadic social interaction could only be observed if a sample was being conducting on one of the dyad members. Therefore the unique time in view for each dyad was calculated using the total amount of time that A was in view with B from A's focal samples summed with the total amount of time that B was in view with A from B's focal samples. Hourly rates of social behaviour for each dyad were then calculated by dividing the total frequency of behaviour by the unique observation time for that dyad. The hourly rate of a given behaviour for each individual was the sum of the rates across all its dyads.

Durations of grooming and proximity were presented as the percentage of unique observation time for the dyad each individual spent grooming or in proximity to the other dyad member. The percentage of time in view that each individual spent grooming or in proximity was averaged across all dyads. For any given analysis, individuals that had less than three 20-minute focal samples in view with all other individuals involved in the analysis were removed from the data set.

As embraces, kisses and pectoral sniffs generally occurred in rapid succession, the term 'embraces' was used to refer to any combination of these behaviours. Embraces could be unidirectional (directed from one individual towards another) or bidirectional (the initial embrace is reciprocated resulting in a mutual embrace). Where embraces were mutual, both partners were recorded as giving and receiving the embrace.

Before attempting statistical analyses, hourly rates of behaviour were normalised using the transformation: Square Root (x+0.5), where x is the rate of behaviour (Keppel & Wickens, 2004). Percentage data were normalised using the ARCSINE transformation (Howell, 2002).

Chapter Three

Sex Differences in Behaviour

3.1. Fission-fusion societies and the socio-ecological model

According to the socio-ecological model (van Schaik, 1989, Sterck *et al.*, 1997) female primates that feed primarily on fruit should experience strong within-group competition for food, as fruit, particularly ripe fruit, is a high quality resource that is distributed in discrete patches. Frequent direct contests for food should select for linear dominance relationships and female philopatry should be favoured because females rely on kin for coalitionary support in contests both within and between groups (Koenig, 2002; Sterck *et al.*, 1997; van Schaik, 1989; van Schaik & van Noordwijk, 1988; Wrangham, 1980). The resultant Resident-Nepotistic social structure should contain stable, linear and nepotistic hierarchies, which determine the despotic appropriation of resources (Sterck *et al.*, 1997). However, where grouping is flexible and may be adjusted in response to food supply, females are able to reduce contest competition for food (Anderson *et al.*, 2002; Chapman, 1990; Chapman *et al.*, 1995; de Moraes, Carvalho & Strier, 1998; Mitani *et al.*, 2002; Newton-Fisher *et al.*, 2000; Strier, 1989; Stevenson, Quiñones & Ahumada, 1999; Symington, 1988a). Consequently, females have little to gain from forming coalitions and establishing dominance relations, as there is little or no direct contest for food. Without the need for coalitionary support and low predation pressure, females are free to disperse from the natal group. As a result, female social relationships may be classed as Dispersed-Egalitarian (Sterck *et al.*, 1997) despite a frugivorous diet.

Primate societies that allow for such flexible grouping have been termed 'fission-fusion' societies. In these societies, individuals belong to large, distinct communities, which split to form temporary subgroups such that community individuals are rarely all together. Examples of this social system may be found in the genera *Pan* (chimpanzees: Goodall, 1986, and bonobos: Kano, 1992) and *Ateles* (spider monkeys: Fedigan & Baxter, 1984; Symington, 1990). In *Ateles* and *Pan*, subgroups may be isosexual or bisexual and may vary is size due to the constant fission and fusion of subgroups (Boesch & Boesch-Achermann, 2000; Chapman, 1990; Chapman *et al.*, 1995; Hohmann & Fruth, 2002; Hiraiwa-Hasegawa, Hasegawa & Nishida, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Mitani, Watts & Lwanga, 2002; Symington, 1990; White, 1988).

Fission-fusion social organisation is found to a lesser degree in other *Atelinae* species (woolly monkeys: Di Fiore, 2003; muriquis: Strier, 1989; 1999) and also in Hamadryas and gelada baboons (Kummer, 1971), although in these baboons species, the smallest subgroup size is the one-male unit rather than the individual. Thus, the dichotomy between 'fission-fusion' and cohesive societies has become somewhat blurred and the term 'fission-fusion is more representative of a spatial cohesion and social flexibility continuum (Aureli, Schaffner & Boesch, in prep). Consequently, *Ateles* and *Pan* that were originally described as 'fission-fusion societies', are more accurately described as living in social systems characterised by a 'high degree of fission-fusion' or a high 'fission-fusion dynamic' (Aureli, Schaffner & Boesch, in prep).

3.2. Dispersal and philopatry in the *Atelinae* and *Pan*

As predicted by the socio-ecological model, the majority of females living in fission-fusion societies disperse from their natal groups upon reaching sexual maturity (Goodall, 1986; Kano, 1992; Nishida & Hiraiwa-Hasegawa, 1987; Rosenberger & Strier, 1989; Stevenson, Quiñones & Ahumada, 1999; Symington, 1987). In chimpanzees, genetic data have confirmed that most, but not all, females disperse upon reaching sexual maturity (Morin *et al.*, 1994), whereas males appear to remain in their natal groups (Goldberg & Wrangham, 1997; Mitani, Merriwether & Zang, 2000). Those few females that remain in their natal group tend to be the daughters of high-ranking females (Hiraiwa-Hasegawa *et al.*, 1984). Studies of bonobos have reported female biased dispersal (Furuichi *et al.*, 1998; White, 1988), which has now been confirmed with genetic data (Gerloff, Hartung, Fruth, Hohmann & Tautz, 1999). In woolly monkeys recent genetic data has confirmed that in some, but not all groups studied, adult males were more closely related than adult females suggesting a tendency for female dispersal (Di Fiore & Fleischer, 2005). Other results have not been confirmed with genetic data. Strier (1991) reported five cases of emigration and eight cases of immigration by nulliparous muriqui females, but saw no cases of male transfer. Data from spider monkeys is less extensive, but at least five cases of emigration by nulliparous females have been observed, and after two of these cases, females were observed associating with a neighbouring community (Symington, 1987; 1998b; 1990).

3.3. Sex differences in behaviour

With the exception of bonobos (Kano, 1992), unrelated adult females living in societies with a high fission-fusion dynamic in the wild show little evidence of mutual attraction. Friendly or supportive behaviours such as social grooming are rarely observed between adult females (Di Fiore & Fleischer, 2005; Fedigan & Baxter, 1984; Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Strier, *et al.*, 1993; Printes & Strier, 1999; Symington, 1990) and linear dominance hierarchies among females have not been detected (Chapman, 1990; Di Fiore & Fleischer, 2005; Nishida & Hiraiwa-Hasegawa, 1987; Printes & Strier, 1999; Pusey, Williams & Goodall, 1997). However, in chimpanzees (Wrangham, Clark & Isabirye-Basuta, 1992), spider monkeys (Chapman, 1990) and muriquis (Printes & Strier, 1999), adolescent females (resident or recent immigrants) appear subordinate to adult resident females, indicated by patterns of aggression (spider monkeys) displacements (muriquis) and formal submission (chimpanzees). Chimpanzees at Taï, Ivory Coast appear to follow a different pattern, however, as the high proportion of monopolisable food in their diet (e.g. meat and large nuts requiring tools to crack) and larger subgroups due to leopard predation have resulted in a linear dominance hierarchy among females (Wittig & Boesch, 2003).

Among chimpanzees, females often travel alone with their offspring, only occasionally accompanied by nulliparous females who interact with their infants (Nishida & Hiraiwa-Hasegawa, 1987; Wrangham, *et al.*, 1992; Wrangham, 2000; but see Boesch & Boesch-Achermann, 2000). Similarly, female spider monkeys and muriquis spend the majority of their time foraging and feeding in 'individually dispersed' subgroups that communicate primarily by vocalisations (Fedigan & Baxter, 1984; Strier *et al.*, 1993). Although social interactions between females are rare, in chimpanzees (Wrangham *et al.*, 1992) and muriquis (Printes & Strier, 1999) adult resident females are more socially integrated than adolescent females, indicated by a higher number of nearest neighbours. Woolly monkeys groups tend to be more cohesive, yet female-female social relationships are similarly non-affiliative and the preferred proximity partners of females are males (Di Fiore & Fleischer, 2005; Stevenson, 1999). Thus, female-female social relationships are low quality and correspond to the Dispersed-Egalitarian category proposed by Sterck *et al.* (1997). Female bonobos are an exceptional case, as unrelated females use sexual behaviour (genital-genital rubbing) to form close affiliative bonds (Kano, 1992; Hohmann & Fruth, 2000; de Waal, 1995).

Unlike bonobos (Hohmann & Fruth, 2002; Kano, 1992) and chimpanzees at Taï, (Boesch & Boesch-Achermann, 2000), chimpanzees, muriquis and spider monkeys live in sex-segregated societies, with males and females spending the majority of their time in same-sex subgroups (e.g. Chapman, 1990; Nishida & Hiraiwa-Hasegawa, 1987; Symington, 1990; Stanford, 1998; Strier, 1990; 1997). However, despite their sex-segregated society, time spent in proximity when resting (Fedigan & Baxter, 1984; Goodall, 1986; Strier *et al.*, 2002) and patterns of association, (Pepper *et al.*, 1999; Newton-Fisher, 1999; Symington, 1990) are highest among male-male dyads, followed by male-female dyads and lastly female-female dyads. Social grooming interactions in spider monkeys and chimpanzees follow a similar pattern (Fedigan & Baxter, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Symington, 1990; Watts, 2000a), although the overall rate of grooming is much lower in spider monkeys (Symington, 1990). These data suggest that relationship quality is highest among males.

As the primary source of competition among males is access to fertile females, male-male aggression is directly related to the species' mating system. Although female chimpanzees and bonobos form fluid subgroups, there is evidence to suggest that dominant males are able to monopolise mating access. Male bonobos and chimpanzees actively compete with one another for access to oestrous females, often interfering with one another's copulations and forming coalitions to defend access to the female (Furuichi, 1997; Hohmann & Fruth, 2003; Klinkova *et al.*, 2005; Newton-Fisher, 2002; Nishida & Hosaka, 1996; Watts, 1998). Consequently, dominant males are presumed to achieve high mating success at the expense of low ranking males (e.g. Boesch & Boesch-Achermann, 2000; Furuichi, 1997; Nishida & Hiraiwa-Hasegawa, 1987; Kano, 1996), which has been confirmed in both chimpanzees and bonobos using DNA paternity data (Constable, Ashley, Goodall & Pusey, 2001; Gerloff *et al.*, 1999). This pattern of behaviour, combined with the presence of male-male coalitions (Nishida & Hosaka, 1996; Watts, 1998), frequent contests involving aggression (Goodall, 1986), and linear male dominance hierarchies detectable from the direction of pant-grunting and unidirectional aggression (de Waal, 1982; Newton-Fisher, 2002; Nishida & Hosaka, 1996; Watts, 2000b), suggests that males compete for fertilisations via contest competition. However, their large testes size relative to body size and tolerant male relationships when compared to the majority of primate species suggest that males also compete for fertilisations using scramble competition.

Social relationships among male muriquis are extremely tolerant (Strier, Carvalgho & Bejar, 2000). Males routinely mate with several females and do not attempt to interfere with one another's copulations, neither as individuals nor as male coalitions (Strier, 1997; Strier *et al.*, 2000). Male muriquis do not exhibit agonistically mediated dominance hierarchies (Strier, 1990; 1992) and their large testis size is consistent with the hypothesis that males compete for fertilisations using copious quantities of sperm rather than overt contests for access to females (Milton, 1985; Strier *et al.*, 2002). These data suggest that male muriqui social relationships correspond to the 'Resident-Egalitarian' female relationships described by Sterck *et al.* (1997). The *Atelinae* show low-level social grooming across all age-sex classes when compared to other gregarious non-human primate species, possibly because the absence of opposable thumbs in Atelines has reduced the efficacy of grooming (Strier, 1987; 1993; Symington, 1990). Atelines do however have a suite of unique friendly and supportive behaviours including embraces, kisses, pectoral sniffs and arm- or tail-wrapping and it is possible that these behaviours play a similar role to social grooming in regulating social relationship (Schaffner & Aureli, 2005). In muriquis, embraces are positively associated with time spent in proximity when resting and are exchanged at higher rates between males when compared to male-female or female-female dyads (Strier *et al.*, 2002). Male-male embraces were also more frequently exchanged between sub-adult - adult dyads (Strier *et al.*, 2002).

Behavioural data on male spider monkeys are scarce due to problems observing male subgroups in the wild (Fedigan & Baxter, 1984; Chapman, 1990). It is therefore unclear if male spider monkeys are governed by an agonistically mediated dominance hierarchy. Spider monkeys have large relative testis size and may use copulatory plugs (Dixson, 1998) so it is likely that they compete for fertilisations using sperm competition. Aggression between males is generally low (Fedigan & Baxter, 1984), but as mating tends to occur in secrecy away from other group members (Campbell, 2006; Klein, 1971; van Roosmalen & Klein, 1988; Chapter 6) it is unlikely that males are as tolerant of each other as male muriquis. As with muriquis, spider monkey embraces are exchanged most frequently between males, although it is unclear whether females preferentially embrace males or other females (Fedigan & Baxter, 1984).

Association, time spent in proximity and social grooming in bonobos and woolly monkeys follow a different pattern. Although male bonobos are generally the philopatric sex, the relationships between them are generally the weakest within the group (Hohmann & Fruth, 2002; Hohmann, Gerloff, Tautz & Fruth, 1999; Kano, 1992). There are two reasons for this unexpected finding. Firstly, unrelated female bonobos maintain strong affiliative bonds with the use of genital-genital rubbing (Hohmann & Fruth, 2000; de Waal, 1995), and secondly, male bonobos maintain strong bonds with their mothers throughout their adult lives (Hohmann *et al.*, 1999; Furuichi, 1997; Kano, 1992). Consequently, relationship quality in bonobos is highest among adult females, followed by male-female dyads and lastly, male-male dyads (Boesch, 2002; Hohmann & Fruth, 2002; Nishida & Hiraiwa-Hasegawa, 1987; Stanford, 1998). Due to the high rates of sexual behaviour exchanged during periods of uncertainty, and the strong bonds between mothers and their sons, aggression in bonobos is generally milder and less frequent than in chimpanzees (Kano, 1992). In woolly monkeys, affiliative interactions are most likely to occur between the sexes, (primarily from female to male) or, like muriquis, between sub-adult and adult males (from sub-adult to adult) (Di Fiore & Fleischer, 2005). Although adult males tend to avoid one another, male-male relationships in woolly monkeys are characterised by low-level aggression and tolerance in the context of mating (Di Fiore & Fleischer, 2005).

3.4. Relationships between the sexes

Unlike the majority of mammals, anthropoid primate societies are typically characterised by long term associations between the sexes (van Schaik, & Kappeler, 1997). However, such associations may not remain constant over time and are likely to be affected by female reproductive state. Among chimpanzees, association and affiliation between males and anoestrus females are generally infrequent, whereas males and oestrus females are more sociable (Matsumoto-Oda, 1999; 2002). Oestrus females spend more time grooming and in proximity to males that do anoestrus females and oestrus females appear to direct their attention towards high ranking males (Matsumoto-Oda, 2002). Male chimpanzees are also more likely to groom and share meat with oestrus females than anoestrus females (Matsumoto-Oda, 2002). Chimpanzees at Taï follow a different pattern as male-female affiliative associations persist throughout the female reproductive cycle (Boesch & Boesch-Achermann, 2000).

Across all known populations, male chimpanzees are dominant to females and are reported to direct, often severe aggression towards cycling females as a means of sexual coercion (Goodall, 1986; Wrangham, 2000; 2002), although female-directed male aggression appears to occur at a low rate at Taï (Boesch & Boesch-Achermann, 2000). Mating often occurs in full view of the rest of the group, although this tends to be restricted to copulations involving dominant males who are less likely to be disturbed by their male conspecifics (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987). At Taï and other field sites, males and oestrus females are also reported to form mating consortships where a male and female travel together, away from the rest of the group and maintain an exclusive mating relationship (Boesch-Achermann, 2000; Goodall, 1986; Wallis, 1997). These consortships are often aggressively maintained by the male (Goodall, 1986).

Spider monkeys also appear to form mating consortships as mating tends to occur in secrecy away from the rest of the group (van Roosmalen & Klein, 1988; Campbell, 2006; Chapter 6). Spider monkey consortships do not appear to be aggressively maintained (Campbell, 2006), but male spider monkeys preferentially direct aggression towards females (Fedigan & Baxter, 1984; Campbell, 2003). However, female-directed male aggression among spider monkeys appears to be highly ritualised (Fedigan & Baxter, 1984), thus it is possible that it may be a form of display rather than actual attempts to cause harm (Chapter 6). Nevertheless, male spider monkeys are dominant to females as indicated by patterns of unidirectional aggression (Fedigan & Baxter, 1984; Symington, 1988b). As female spider monkeys do not advertise oestrus with visual cues such as sexual swellings, it is unclear if male interactions with females are affected by female reproductive state, but in general, affiliative interactions between the sexes appear to be relatively rare (Fedigan & Baxter, 1984). Male-female interactions in muriquis are also relatively rare, but unlike spider monkeys and chimpanzees, female-directed male aggression has not been reported in this species (Strier, 1997; Strier *et al.*, 2000). Relationships between the sexes are extremely tolerant and males do not coerce or harass fertile females. Furthermore, mating occurs in full view of conspecifics, who do not attempt to interfere with the copulation (Strier, 1997; Strier *et al.*, 2000).

Among woolly monkeys, associations between all age-sex classes are reported to be low, but when affiliative interactions do occur, they tend to be between the sexes, primarily directed from female to male (Di Fiore & Fleischer, 2005). Dominance and aggressive interactions among woolly monkeys are not well documented, but recent data suggest that the frequency of aggression between mixed-sex dyads is at chance level, and males and females are equally likely to be recipients of aggression (Di Fiore & Fleischer, 2005). As with muriquis, mating among woolly monkeys occurs in full view of conspecifics and aggression in the context of mating appears to be limited to males chasing females in response to repeated (and apparently unwanted) solicitations, or female attempts to interrupt others' copulations (Di Fiore & Fleischer, 2005).

Bonobo society is characterised by tolerant relationships between the sexes and strong inter-sexual bonds (Hohmann *et al.*, 1999; Nishida & Hiraiwa-Hasegawa, 1987). Although affiliative interactions occur most frequently between females (Hohmann & Fruth, 2002), long-term associations occur predominately between males and females (Hohmann *et al.*, 1999). A large proportion of these long-term associations are between mothers and their adult sons, and mothers also assist their sons in dominance rank acquisition (de Waal, 1995; Furuichi, 1997). Dominance between males and females is unclear, although females tend to have priority of access to food (Furuichi, 1997). As a result of equal dominance, lengthy female oestrus indicated by sexual swellings and female willingness to copulate during non-reproductive periods, female bonobos are not subject to sexual coercion from males (Furuichi, 1997; Kano, 1992; Takahata, Ihobe & Idani, 1996).

3.5. Chapter aims and predictions

Detailed accounts of social relationships in spider monkeys are rare. Existing studies have been unable to quantitatively compare rates of behaviours within and between sexes due to problems with individual identification or lack of data on community males (e.g. Fedigan & Baxter, 1984; Symington, 1990). Furthermore, existing studies have not fully investigated the distribution of species-specific behaviour (e.g. embraces and arm-wrapping) and have indicated only that these behaviours are exchange more frequently between males, but not whether females preferentially interact with males or other females. This chapter therefore aimed to quantify a range of social behaviours exchanged within and between sexes at the individual level, thus making statistical comparisons possible. Particular attention was paid to species-specific friendly behaviour.

Due to female-dispersal (Symington, 1987) and male reliance on coalition partners to defend access to females from extra-community males (Strier, 1994) time spent in proximity and rates of affiliative behaviours were predicted to be highest among males. Males were therefore expected to preferentially interact with same-sex partners. As feeding competition is reduced by flexible grouping, and females are the dispersing sex, social relationships between female spider monkeys are likely to be low quality. It was therefore predicted that females would preferentially interact with opposite-sex partners. Agonistically maintained dominance hierarchies were not predicted for either males or females and both males and females were expected to show low-level aggression with same-sex partners because males likely compete for fertilisations via scramble competition (Dixson, 1998) and contest competition for food is reduced by the high fission-fusion dynamics the species social organisation (Symington, 1988a). Based on previous reports (Campbell, 2003; Fedigan & Baxter, 1984), males were also predicted to preferentially direct aggression towards females, causing males to be dominant to females. As data from woolly monkeys (Di Fiore & Fleischer, 2005) and muriquis (Strier *et al.*, 2002) suggest that male-male affiliative behaviour is more likely to occur between males of different ages, a similar effect was predicted to occur in spider monkeys. An effect of age on female social interactions was also predicted, based on the observation that adolescent females are subordinate to adult resident females in chimpanzees (Wrangham *et al.*, 1992) and muriquis (Printes & Strier, 1999). As kinship was known for all adult-sub-adult female dyads in both study communities, it was also possible to investigate the effect of kinship on relationships between adolescent and adult females.

Finally, this chapter investigated the effects of age and kinship on male-female social interactions, although the effects of kinship were limited to interactions between younger males and females due to unknown relatedness between older males and females. Previous studies of spider monkeys have not examined the effects of age and kinship on male-female relationships, thus it is difficult to make specific predictions about these interactions. However, it is possible that the predicted male propensity to direct aggression toward females may be affected by the age of both the male attacker and female victim. These aggressive interactions are also likely to be affected by the degree of relatedness between individuals.

3.6. Methodology

3.6.1. Subjects

Data were collected on all adult and sub-adult individuals in both the Eastern and Western communities at Punta Laguna. To obtain reliable estimates however, only individuals observed for more than three hours of focal sampling were included in the analysis. Results relating to the sex distribution of behaviour were produced using data from 4 adult males and 8 adult females from the Eastern community, and 7 adult males and 14 adult females from the Western community. When investigating the effect of age on social interactions, data from 3 sub-adult females from the Eastern community and 4 sub-adult females from the Western community were included in the analysis. The effect of age on female-female relationships was investigated by comparing adult females and sub-adult females that had not yet emigrated to a new community. To investigate the effect of age on male-male relationships, adult males from both communities were divided into two subsets: older and younger males. Older males were considered those individuals that were fully adult when individually identified in 1997 and were therefore at least 14 years old at the start of my data collection; younger males were considered those individuals that were juveniles or infants when first identified in 1997 and were approximately 6 to 10 years old in 2003. Older males also had a patch of orange-yellow chest hair that was highly visible against their brown hair. The Eastern community contained 1 older male and 3 younger males, whereas the Western community contained 3 older males and 4 younger males.

3.6.2. Data Collection

Data were collected using focal animal sampling with continuous recording on a dictaphone (see Chapter 2). Data were collected using a pre-defined ethogram of behaviour (Table 2.2, Chapter 2).

3.6.3. Data Analysis

Activity budgets were produced for each individual based on the percentage of observation time spent in various activities (feeding, moving, resting, self-directed, social and vigilant). Behaviours feeding, moving, resting and vigilant are defined in Table 2.2. The social category includes all agonistic and affiliative social behaviours listed in Table 2.2 and the self-directed category includes self-grooming and scratching, also defined in Table 2.2. Differences in percentage of time males and females allocated to each activity were investigated using a series of independent t-tests with Bonferoni's correction for multiple tests. Significance for these t-tests was therefore set to $p \leq 0.008$. Two-way mixed design ANOVAs were used to examine whether there were differences in social behaviour depending on subject's sex and the sex of the interaction partner (same-sex or opposite-sex). The same test was employed to investigate whether male-male and female-female social behaviour was affected by the age of the subject and the age of the interaction partners (same-age or different-age to the actor). The older male from the Eastern community was omitted from this analysis as he did not have the opportunity to interact with males of the same age. With the exception of arm-wrapping and proximity that were symmetrical behaviours without an obvious actor and recipient, differences in male-male and female-female behaviour in terms of the age of the subject and the direction of the behaviour (given or received) were also examined. As arm-wrapping behaviour was only ever observed in same-sex dyads, rates of male-male and female-female arm-wrapping were compared using an independent t-test. Comparisons for females were likely confounded by parent-offspring relationships between adult and sub-adult females, therefore behaviour by adult and sub-adult females directed to kin and non-kin were compared using further 2x2 mixed design ANOVAs. This analysis included only those females who had the opportunity to interact with kin. As each female only had one kin member in the group (parent or offspring) percentage of time in view spent in proximity to kin was the same value for adult and sub-adult females. Therefore, an independent t-test was employed to compare the mean percentage of time in view adult and sub-adult females spent in proximity to unrelated females.

The effect of age on male-female social interactions was also investigated. Approaches and time spent in proximity by older and younger males directed to adult and sub-adult females were compared using 2x2 mixed design ANOVAs. This test was also used to compare approaches and time spent in proximity by adult and sub-adult females with older and younger males. Grooming was not observed between males and sub-adult females, therefore grooming by older versus younger males towards adult females was compared using an independent t-test and grooming by adult females towards older versus younger males was compared using a paired t-test. As embraces and arm-wrapping between the sexes were rare, statistical analysis of these behaviours was not possible. This was also the case for female aggression directed to males. Males did not direct any aggression towards sub-adult females, thus the rates of female-directed male aggression by older and younger males were compared using an independent t-test. It was not possible to investigate the effect of kinship on older male social interactions as their mothers were not known, however the effect of kinship on younger male interactions with adult females was investigated in 4 of the 7 younger males (the mother of one male from the Eastern community was no longer in the community, presumed dead, and 2 males in the Western community did not meet the minimum criteria of three 20-minute focal samples in view with their mothers to give an accurate account of social interactions).

Where significant interactions were obtained from the ANOVAs, un-confounded comparisons of the means were made post-hoc using Cicchetti's modification of Tukey's HSD test (Schweigert, 1994), with Howell's correction for repeated measures (Howell, 2002) for analysis of the repeated factor.

3.7. Results

3.7.1. Sex differences in behaviour

The first sex differences in behaviour refer to the activity budgets of males and females (Figure 3.1). Females were found to spend a significantly greater percentage of observation time feeding than males [t (31) = 3.76, p = 0.001] and males spent more time socially interacting than did females [t (31) = 5.58, p < 0.001]. No other sex differences were found for the other activities [moving: t (31) = 0.32, p = 0.753; resting: t (31) = 0.34, p = 0.739; self-directed: t (31) = 1.76, p = 0.088; vigilant: t (31) = 1.80, p = 0.082]. As predicted, all affiliative interactions occurred most often between males (Table 3.1). Grooming interactions followed the predicted pattern of males preferentially grooming same-sex partners and females preferentially grooming opposite-sex partners, although this interaction between factors only approached significance (Table 3.1). This pattern was not reflected in other behaviours.

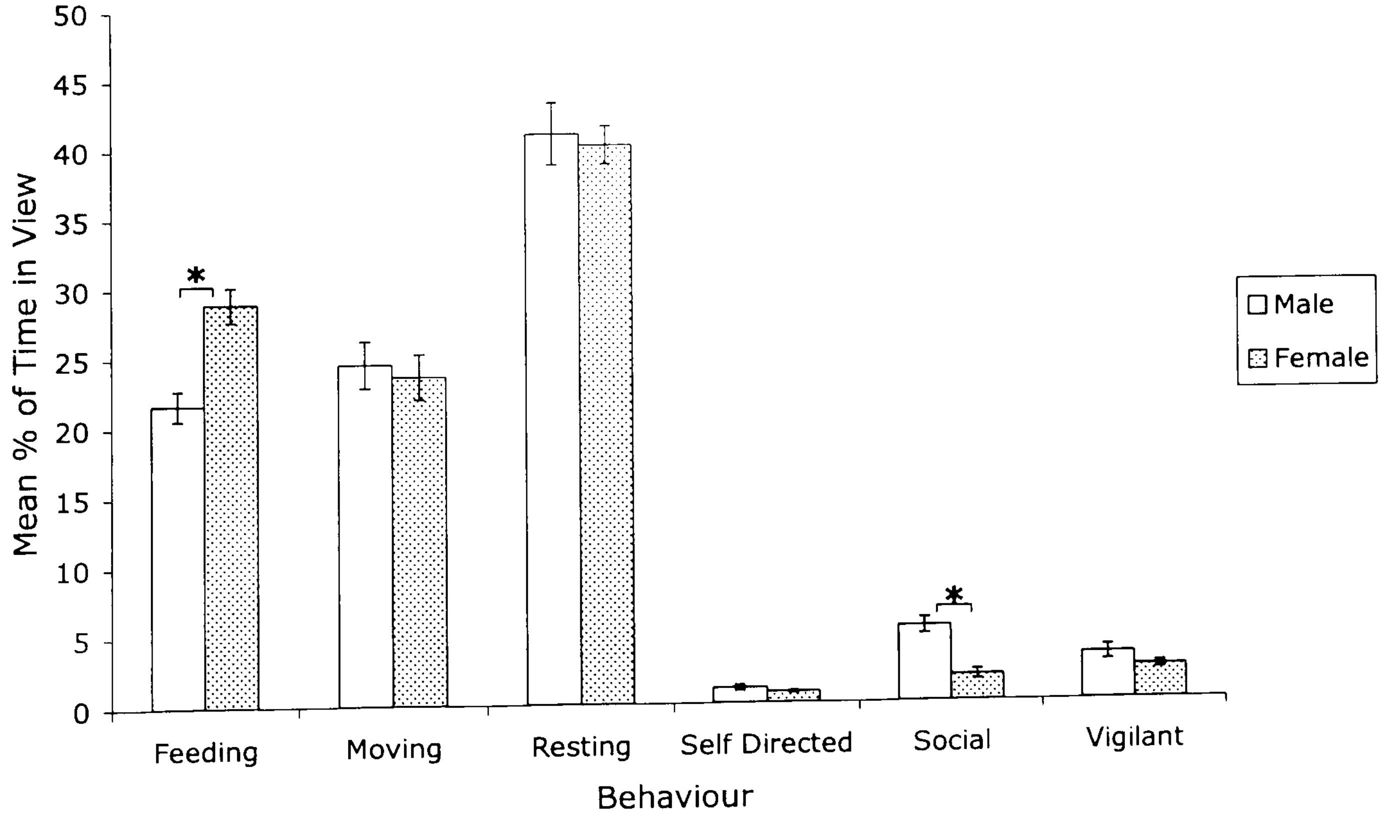

Figure 3.1: Mean (± S.E.M.) percentage of daily activity budget males and females allocated to various behaviours.

Table 3.1: Mean (± S.E.M.) values of behaviour males and females directed to same-sex and opposite-sex partners, compared using 2x2 mixed-design ANOVAs. * Arm-wrapping was only exchanged within sexes, thus means were compared using an independent t-test.

	Male Actor		**Female Actor**					
Behaviour	**Same-sex partner**	**Opposite-sex partner**	**Same-sex partner**	**Opposite-sex partner**	**Main Effect of Sex**	**Main Effect of Partner**	**Interaction**	***t*-test**
Approach	2.62 ± 0.43	1.36 ± 0.23	1.73 ± 0.36	0.52 ± 0.12	F (1, 31) = 9.81 $p = 0.004$	F (1, 31) = 16.06 $p < 0.001$	F (1, 31) = 0.03 $p = 0.866$	-
Embrace	1.17 ± 0.35	0.03 ± 0.02	0.59 ± 0.15	0.00 ± 0.00	F (1, 31) = 6.94 $p = 0.013$	F (1, 31) = 44.59 $p < 0.001$	F (1, 31) = 5.11 $p = 0.031$	-
Arm-wrap	0.61 ± 0.16	0.00 ± 0.00	0.12 ± 0.06	0.00 ± 0.00	-	-	-	t (31) = 4.27 $p < 0.0001$
Aggression	0.04 ± 0.02	0.80 ± 0.32	0.03 ± 0.02	0.01 ± 0.01	F (1, 31) = 21.61 $p < 0.001$	F (1, 31) = 16.03 $p < 0.001$	F (1, 31) = 19.69 $p < 0.001$	-
Grooming	0.52 ± 0.17	0.30 ± 0.16	0.01 ± 0.01	0.21 ± 0.10	F (1, 31) = 8.93 $p = 0.005$	F (1, 31) = 0.05 $p = 0.822$	F (1, 31) = 3.95 $p = 0.056$	-
Proximity	6.83 ± 0.80	2.98 ± 0.73	2.66 ± 0.41	2.57 ± 0.91	F (1, 31) = 6.76 $p = 0.014$	F (1, 31) = 7.94 $p = 0.008$	F (1, 31) = 8.77 $p = 0.006$	-

Males and females showed different preferences for proximity partners (Table 3.1). Post-hoc analysis confirmed that males spent more time in proximity to same-sex partners than opposite sex partners (*p* <0.05), and as females showed no preference between same-sex and opposite-sex partners, males spent more time in proximity to same-sex partners than did females (*p* <0.01). A different pattern was found for approaches, embraces and arm-wrapping, as males and females preferentially directed these behaviours to same-sex partners. Males and females approached opposite-sex partners but did so at significantly lower rates than same-sex partners (Table 3.1). A similar pattern was obtained for embraces, but as males sometimes embraced opposite-sex partners but females never did, a significant interaction between variables was found (Table 3.1). Post-hoc analysis of the interaction indicated that both males (*p* <0.01) and females (*p* <0.01) embraced same-sex partners more often than opposite-sex partners and that males embraced same-sex partners more often than did females (*p* <0.01). The preference for same-sex partners in arm-wrapping was sufficiently strong that this behaviour never occurred between the sexes. As with all other affiliative behaviours, arm-wrapping occurred at significantly higher rates between males (Table 3.1). Grappling was only ever observed between males and thus it was not necessary to confirm this sex difference statistically.

Aggression occurred most frequently between the sexes (from males to females), and males and females directed aggression differently, yielding a significant interaction between factors (Table 3.1). Post-hoc analysis confirmed that males directed aggression towards opposite-sex partners at a significantly higher rate than towards same-sex partners (*p* <0.01) and that males were aggressive towards opposite-sex partners more frequently than were females (*p* <0.01). Although there was no significant difference in female aggression between same-sex and opposite-sex partners, female-to-male aggression only occurred when females chased males who had been harassing their infants.

3.7.2. Male-male social interactions

Male-male aggression was so rare in the Western community that it was not possible to investigate dominance relationships. As the Eastern community only contained four adult males, it is difficult to draw conclusions about a dominance hierarchy. However, male-male aggression occurred more frequently in this community and appeared to follow a non-random pattern. The oldest male in the community (PA: aged >14 in 2003) never received aggression from any of the other three males. Conversely, the youngest adult male in the community (LI: aged 6 in 2003) was the main recipient of aggression and never directed aggression toward the other three males. The remaining two males were of a similar age (BE and DA: aged approximately 9 years in 2003) but their pattern of aggression was very different. BE received no aggression from the other males and appeared closely bonded with PA as indicated by high rates of affiliative behaviour, time spent in proximity and because PA was BE's most frequent subgroup companion. However, unlike PA, BE was only ever aggressive towards DA when in a coalition with PA. DA only ever directed aggression towards LI.

Interestingly, at the beginning of the second field season PA disappeared from the community for approximately three months. During PA's absence BE developed the orange/yellow patch of fur on his chest found in older males. BE and DA appeared to form close bonds and were frequently observed arm-wrapping, grooming and embracing. DA and BE also frequently formed coalitions against LI during this period. Upon PA's return, BE's behaviour toward DA became somewhat fickle. When PA was not present in the subgroup, BE behaved affiliatively toward DA but when PA was present, BE was observed to reject DA's advances in favour of PA. Similarly, PA was only aggressive toward DA when BE was present. Over the weeks that followed after PA's return, PA and BE formed a formidable coalition and were observed to attack DA on several occasions, three of which resulted in wounding. Approximately two and a half months later, DA disappeared from the community and never returned as of the writing of this chapter. The new colouration on BE's chest was still present at the end of the study.

Analysis of the effect of age on male-male social interactions produced the following results. There was a main effect of age on male-male arm-wrapping as older males arm-wrapped more frequently than younger males [older males: 1.02 ± 0.06, younger males: 0.84 ± 004; $F(1, 8) = 6.38$, $p = 0.035$]. Older and younger males gave and received embraces at different rates [$F(1, 9) = 11.49$, $p = 0.008$: Figure 3.2]. Post-hoc analysis indicated that older males received embraces at a significantly higher rate than did younger males ($p < 0.01$) and that older males received significantly more embraces than they gave ($p < 0.05$).

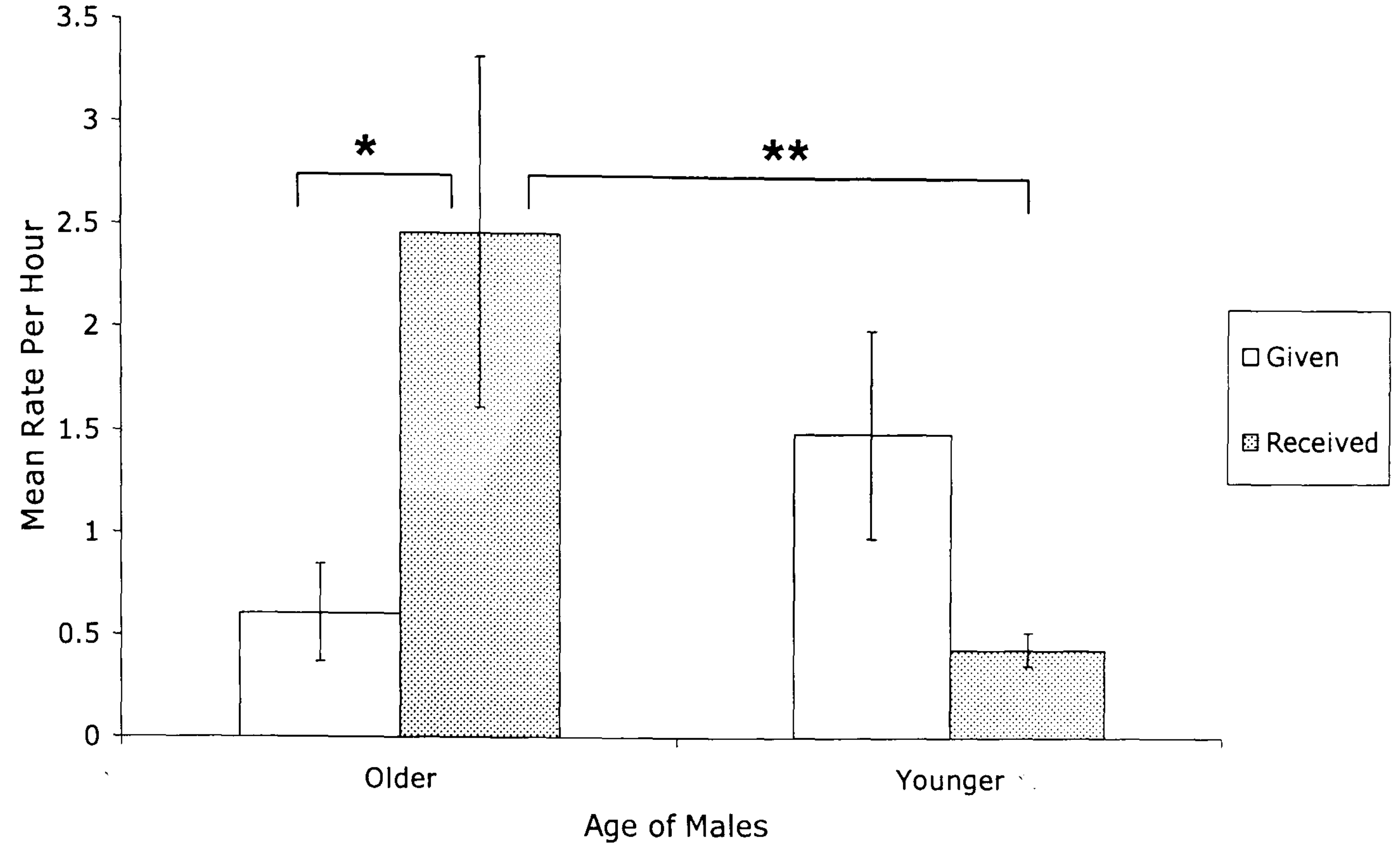

Figure 3.2: Mean (± S.E.M.) rates of embraces given and received by older and younger males

Figure 3.3: Mean (± S.E.M.) rates of embraces by older and younger males directed to same age and different age partners.

It was predicted that older males would embrace same age partners and that younger males would embrace different age partners. Although there was a trend toward an interaction, these differences were not significant [*F* (1, 8) = 3.49, *p* = 0.089: Figure 3.3]. Closer examination of the data indicated that embraces by younger males were confounded by PA's temporary disappearance from the Eastern community. During this time, two of the younger males (BE and DA) embraced at very high rates, whereas when PA was in the community, they directed their embraces toward PA rather than each other. Approaches, grooming and time spent in proximity were unaffected by male age (Table 3.2).

Male-male grappling was also affected by age, and was only ever observed between younger and older males. Three cases were observed in detail in the Western community. In all three cases, the younger male approached the older male and was responsible for maintaining contact if the older male moved away. In all cases grappling began with an embrace from the younger male to the older male accompanied with low pitch vocalisations. The two males then sat in a ventral-ventral position with their tails wrapped around one another. One male would then lean backwards pulling the other male on top of him, who would then sniff and lick the pectoral gland of the male beneath him. After a minute or so they would change positions. In two of the three observed cases, grappling culminated in mutual genital stimulation. Interestingly, in one of the three cases, grappling took place out of visual contact from the other adult males in the subgroup (one older male and three other younger males). When the other older male attempted to make visual contact, the grappling dyad leapt apart and began foraging in separate trees. One other case of grappling was observed in detail between and adult and juvenile male from the Eastern community. This case did not involve genital contact and was primarily directed from the juvenile toward the adult.

Table 3.2: Mean (± S.E.M.) values of behaviour given and received by older and younger males and by older and younger males to same age and different age partners, compared using 2x2 mixed-design ANOVAs.

	Older Male		**Younger Male**				
Behaviour	**Given**	**Received**	**Given**	**Received**	**Main Effect of Age**	**Main Effect of Direction**	**Interaction**
Approach	2.21 ± 0.60	4.15 ± 1.45	2.90 ± 0.60	1.75 ± 0.38	$F(1, 9) = 0.90$ $p = 0.367$	$F(1, 9) = 0.22$ $p = 0.648$	$F(1, 9) = 3.23$ $p = 0.064$
Groom	0.50 ± 0.25	0.56 ± 0.19	0.50 ± 0.25	0.57 ± 0.25	$F(1, 9) = 0.001$ $p = 0.986$	$F(1, 9) = 0.002$ $p = 0.966$	$F(1, 9) = 0.28$ $p = 0.610$
	Same-Age Partner	**Different-Age Partner**	**Same-Age Partner**	**Different-Age Partner**	**Main Effect of Age**	**Main Effect of Partner**	**Interaction**
Approach	0.54 ± 0.01	0.40 ± 0.05	0.45 ± 0.10	0.89 ± 0.23	$F(1, 8) = 1.24$ $p = 0.298$	$F(1, 8) = 0.34$ $p = 0.575$	$F(1, 8) = 1.58$ $p = 0.244$
Groom	0.43 ± 0.25	0.64 ± 0.42	0.48 ± 0.20	0.64 ± 0.28	$F(1, 8) = 0.01$ $p = 0.947$	$F(1, 8) = 1.81$ $p = 0.285$	$F(1, 8) = 0.05$ $p = 0.835$
Proximity	5.10 ± 2.19	6.45 ± 2.69	5.59 ± 0.91	8.17 ± 1.86	$F(1, 8) = 0.29$ $p = 0.604$	$F(1, 8) = 1.41$ $p = 0.269$	$F(1, 8) = 0.14$ $p = 0.719$

3.7.3. Female-female social interactions

In line with previous studies, all sub-adult females that were approaching sexual maturity disappeared from their respective natal communities (see Chapter 2). Prior to three of these disappearances, the sub-adult females were observed travelling and foraging alone on the outskirts of their community home range. Three cases of immigration by likely nulliparous females were also observed (see Chapter 2).

Female-female aggression occurred infrequently and rarely escalated beyond threat displays. Displays most often involved a coalition of females who arm-wrapped and threatened the target female. No evidence of an agonistically maintained hierarchy among adult females was found in either the Eastern or Western community. Contrary to prediction, adolescent natal females were not subordinate to adult females, although this conclusion was based on an absence of aggression or formal submission rather than equal dominance ranks between females. Nevertheless, adult resident females were observed to displace adolescent females at food resources on three separate occasions, but adolescent females never displaced adult females.

There was also a tendency for long-term resident females to threaten and chase new immigrant females, and immigrant females did not appear to become fully integrated into the community until they had given birth to their first offspring (see Chapter 5). As newly immigrant females were also wary of human observers, focal observations of these females were extremely limited such that the majority of these females could not be included in statistical analysis. It was therefore not possible to investigate differences in the social interactions of newly immigrant versus long-term resident females.

Time spent in proximity was unaffected by female age [main effect age: F (1, 26) = 3.4, p = 0.075; main effect partner F (1, 26) = 1.31, p = 0.263; interaction: F (1, 26) = 2.74, p= 0.110; adults: same age 2.47 ± 0.39, different age 2.82 ± 0.79; sub-adults: same age 5.62 ± 2.02, different age 2.77 ± 0.34]. Time spent in proximity to non-kin did not differ significantly between adult and sub-adult females [t (12) = 0.68 p= 0.508; adults: 1.88 ± 0.54, sub-adult: 2.52 ± 0.75). Grooming interactions were however, affected by both age and kinship. Both adult and sub-adult females gave roughly as much grooming as they received but sub-adult females spent more time engaged in grooming interactions (given and received) than adult females [F (1, 27) = 4.76, p = 0.039: Figure 3.4].

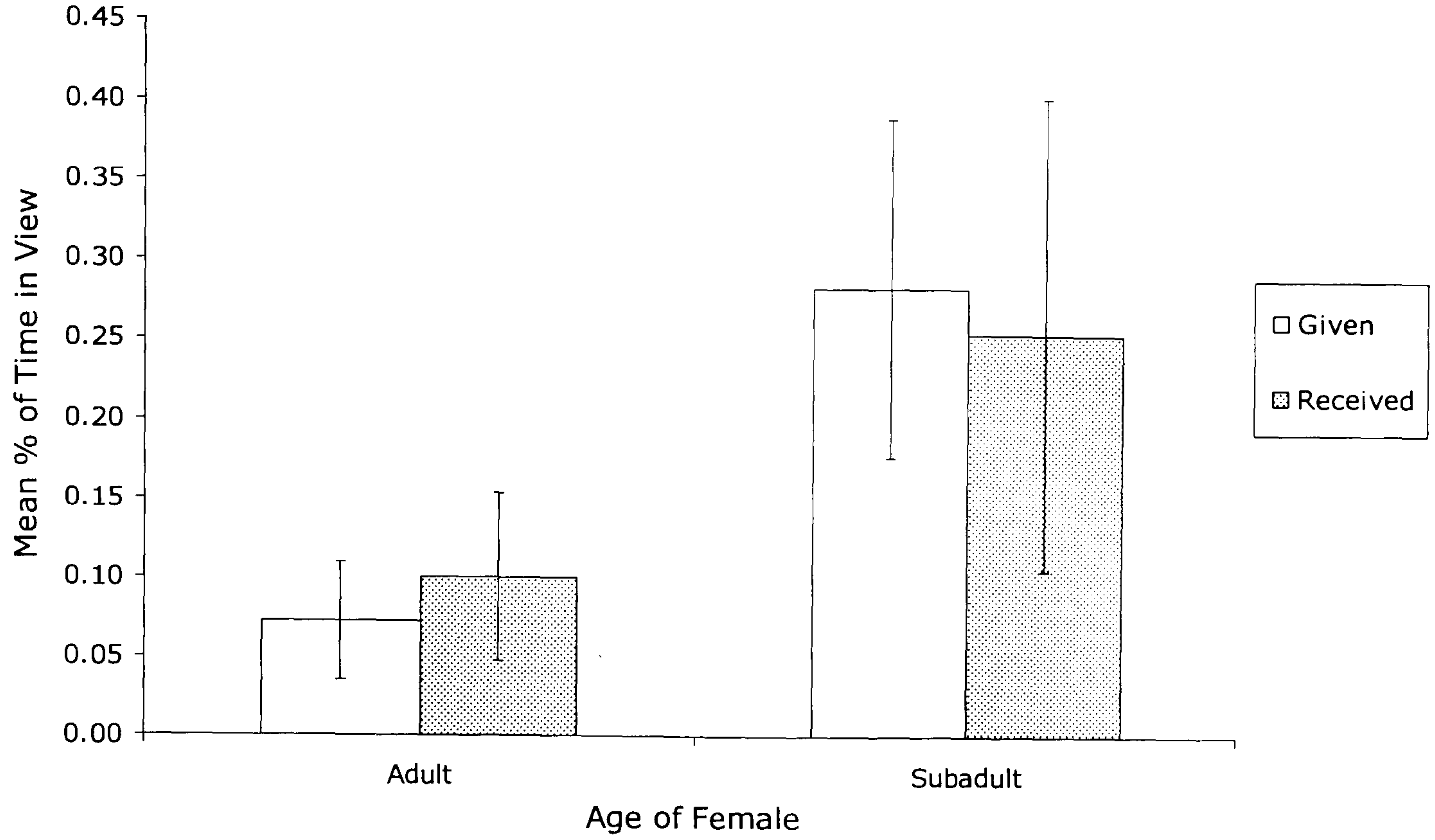

Figure 3.4: Mean (± S.E.M.) percentage of time in view adult and sub-adult females spent giving and receiving grooming.

Subsequent analysis indicated that both adult and sub-adult females preferentially groomed different age partners [*F* (1, 26) = 13.08, *p* = 0.001: Figure 3.5] and that sub-adult females spent more time grooming than adult females [*F* (1, 26) = 4.79, *p* = 0.038: Figure 3.5]. However, these results were likely confounded by kinship as both adult and sub-adult females, preferentially groomed kin [*F* (1, 12) = 13.41, *p* = 0.003: Figure 3.6]. Grooming between unrelated sub-adult females never occurred and grooming between unrelated adults occurred at an extremely low rate (Table 3.1).

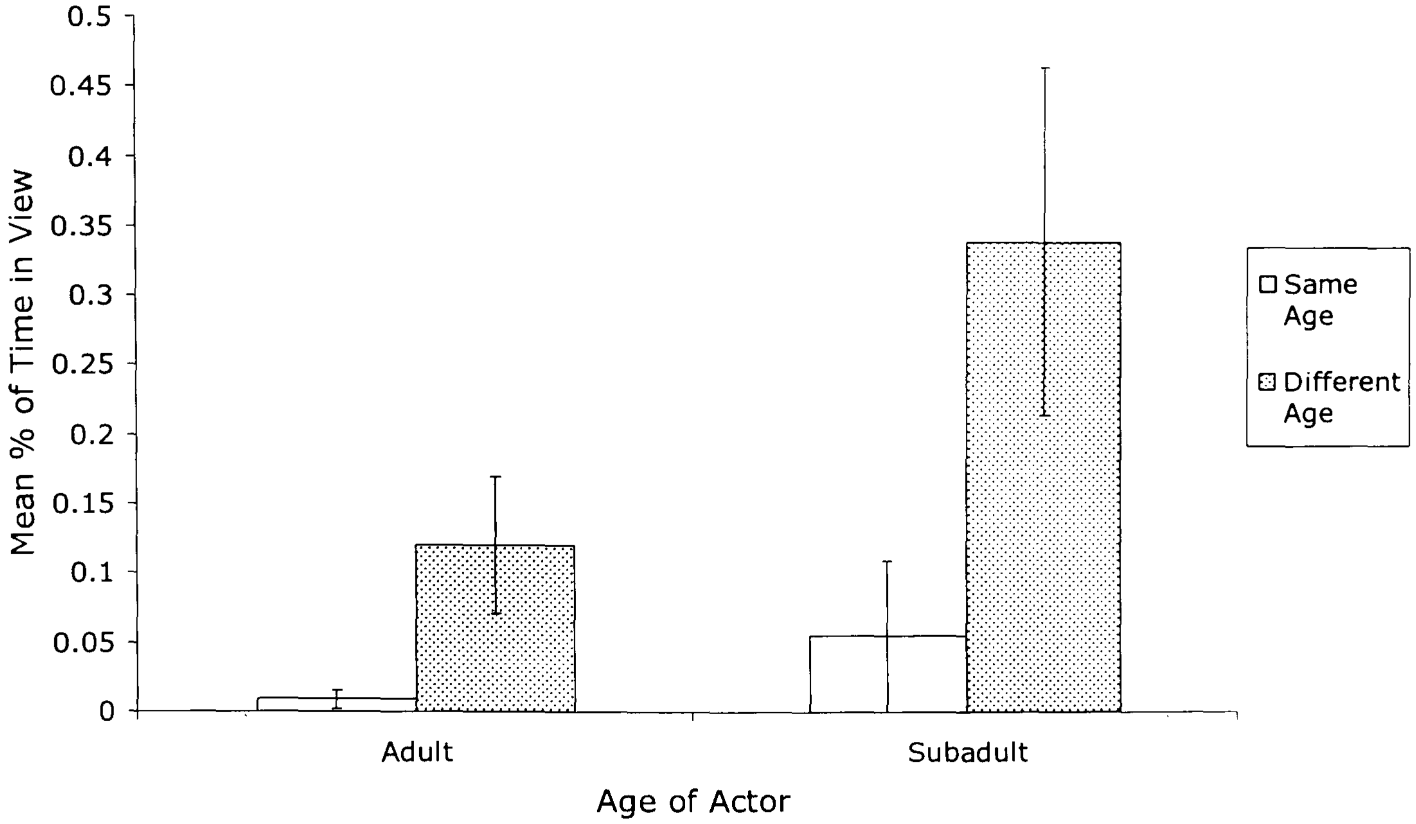

Figure 3.5: Mean (± S.E.M.) percentage of time in view adult and sub-adult females spent grooming same age and different age female partners

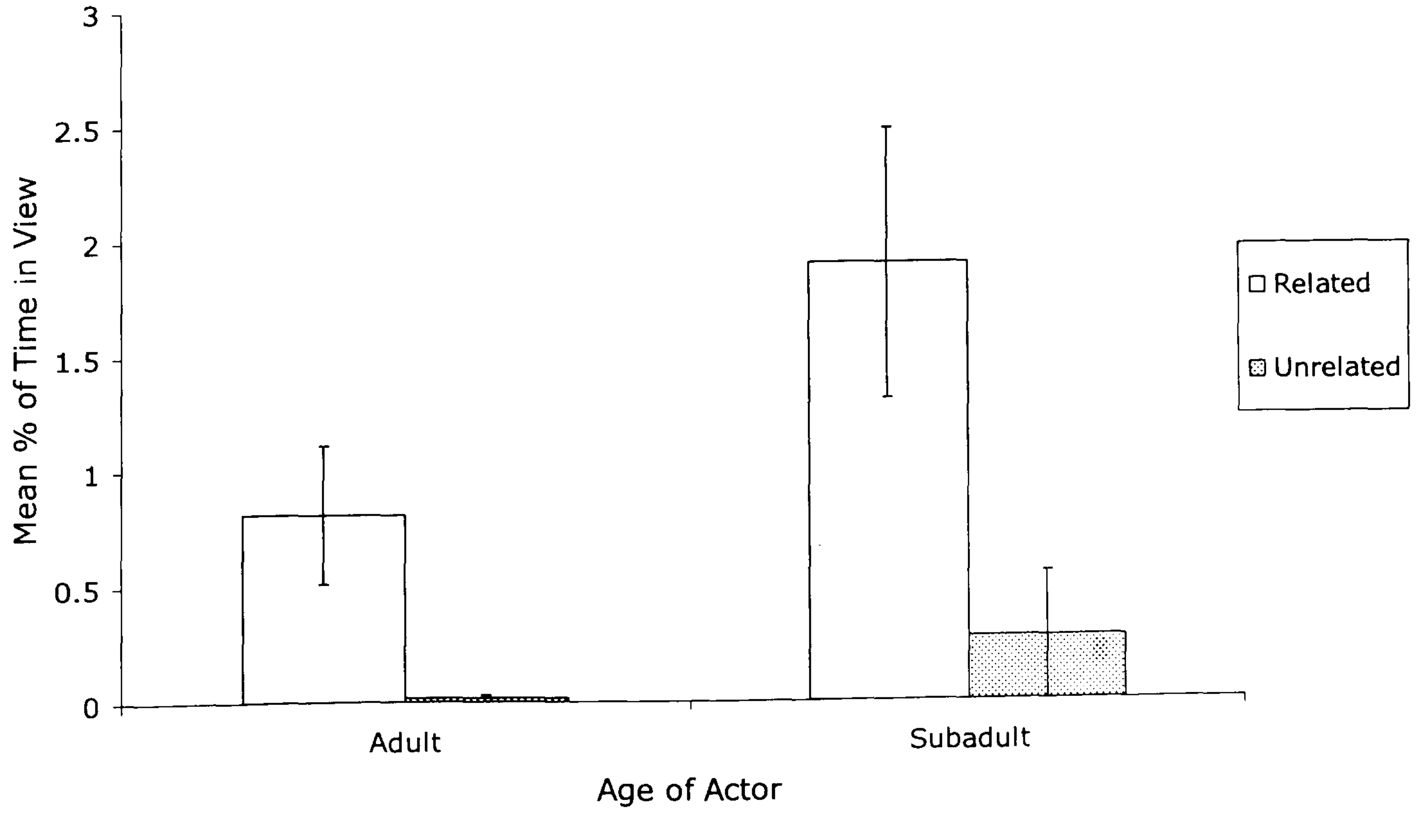

Figure 3.6: Mean (± S.E.M.) percentage of time in view adult and sub-adult females spent grooming related and unrelated female partners.

Approaches given and received were unaffected by female age [main effect age: *F* (1, 26) = 0.002, *p* = 0.961; main effect direction: *F* (1, 26) = 0.36, *p* = 0.552; interaction: *F* (1, 26) = 2.05, *p* = 0.164; adults: given 1.82 ± 0.30, received 2.14 ± 0.30; sub-adults: given 2.49 ± 0.98, received 1.49 ± 0.44]. However, subsequent analysis indicated that adult and sub-adult females showed different preferences when approaching other females [*F* (1, 26) = 12.73, *p* = 0.001: Figure 3.7]. Post-hoc analysis of the interaction indicated that adult females approached same-age partners more frequently than different-age partners (*p* <0.01) and that sub-adult females approached different-age partners more frequently than did adult females (*p* <0.01). Approaches were also affected by kinship as indicated by a significant preference for approaching unrelated females [*F* (1, 12) = 7.51, *p* < 0.018: Figure 3.8].

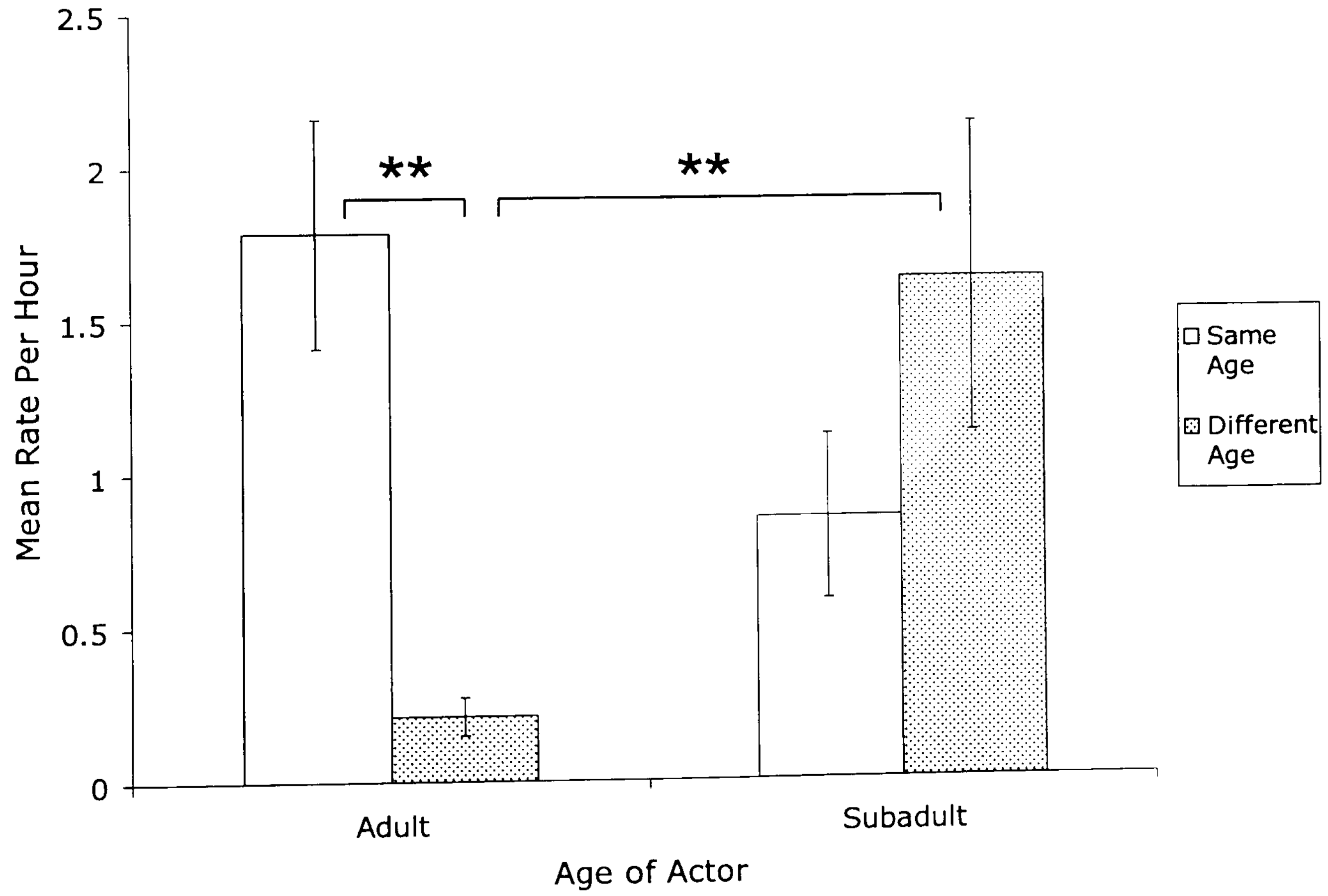

Figure 3.7: Mean (± S.E.M.) rates of approaches by adult and sub-adult females to same age and different age female partners.

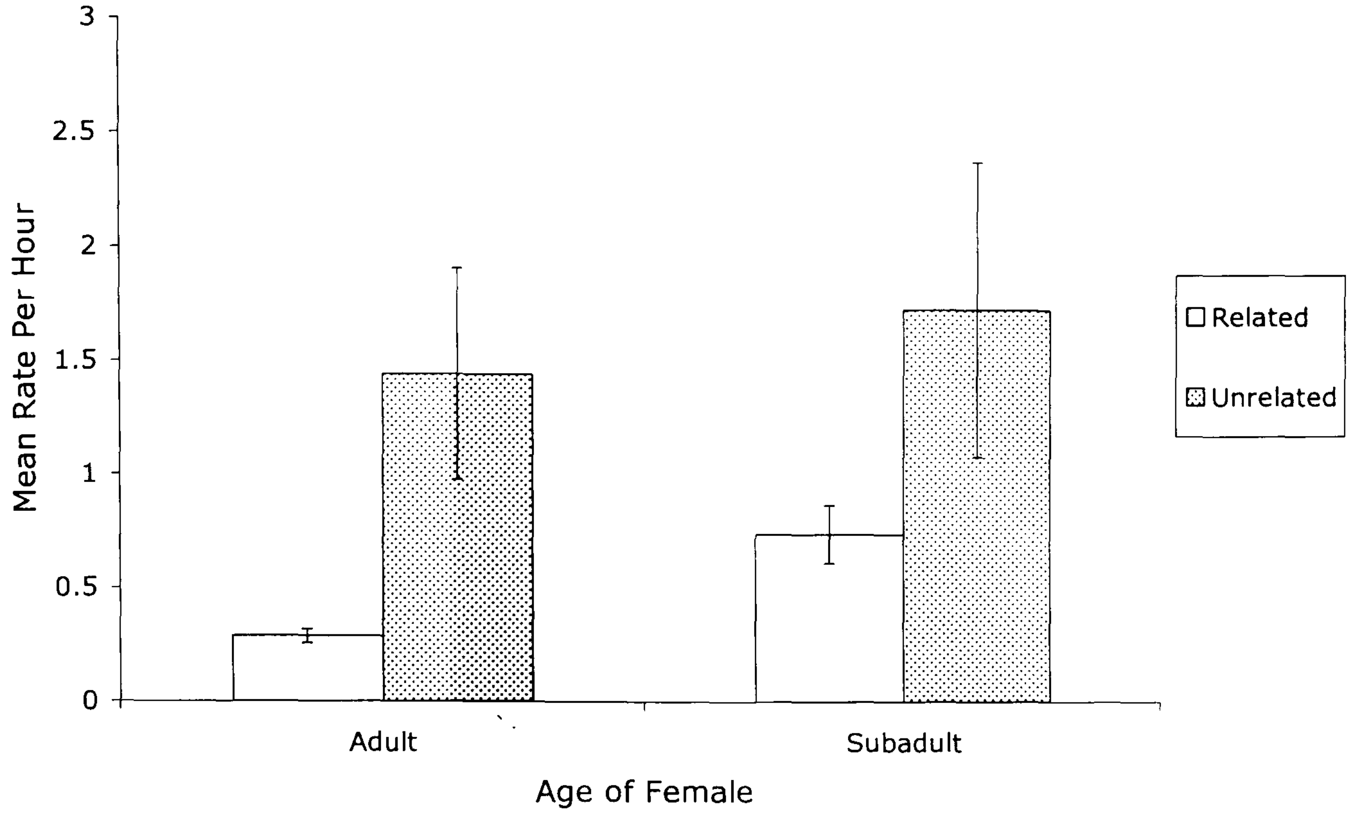

Figure 3.8: Mean (± S.E.M.) rates of approaches by adult and sub-adult females to kin and non-kin females.

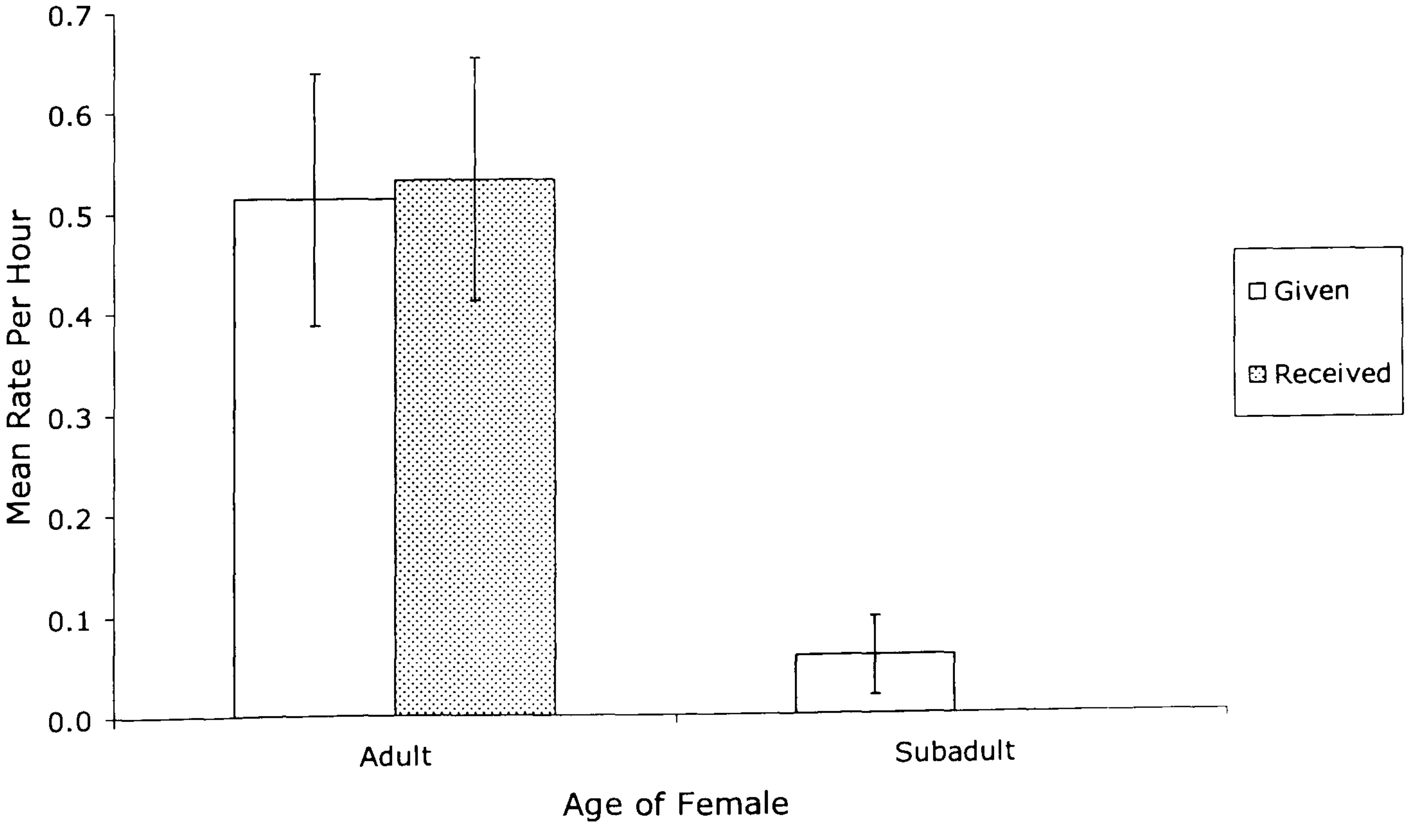

Figure 3.9: Mean (± S.E.M.) rate of embraces given and received by adult and sub-adult females.

Adult females gave and received embraces at similar rates, and although sub-adult females did not receive any embraces, there was no significant difference between their embraces given and received (Figure 3.9). However, embraces were exchanged at significantly higher rates between adult females compared to sub-adult females [*F* (1, 26) = 11.05, *p* = 0.003: Figure 3.9]. When analysed in more detail, results indicated that adult females only ever embraced same age partners (0.59 ± 0.02) whereas sub-adult females only embraced different age partners (0.10 ± 0.01). Embraces were also only exchanged between unrelated females (adults: 0.65 ± 0.29, sub-adults: 0.008 ± 0.005). Arm-wrapping only occurred between adult, unrelated females (0.11 ± 0.04). As these differences reflected an all or nothing preference it was not necessary to make statistical comparisons.

3.8. Male-female social interactions

As predicted, unidirectional aggression was strongly biased (Table 3.1), suggesting that males were dominant to females (but see Chapter 6). This aggression was however limited to adult females as no aggression was observed between males and sub-adult females. Older and younger males were equally likely to direct aggression towards adult females [*t* (9) = 1.09, *p* = 0.306; older males: 1.05 ± 0.14, younger males: 0.91 ± 0.06], and although the effect of kinship on aggression could not be investigated for older males, younger males were only aggressive towards unrelated adult females. Older and younger males preferentially approached adult females rather than sub-adult females [*F* (1, 8) = 29.81, *p* = 0.001: Figure 3.10], whereas adult and sub-adult female approaches were unaffected by male age [main effect of age: *F* (1, 26) = 0.58, *p* = 0.452; main effect of partner: *F* (1, 26) = 1.72, *p* = 0.201; interaction: *F* (1, 26) = 0.27, *p* = 0.606; female adults: older male 0.38 ± 0.12, younger male 0.13 ± 0.04; female sub-adults: older male 0.19 ± 0.09, younger male 0.10 ± 0.06]. Younger males and adult females approached their mothers/sons and unrelated members of the opposite sex at similar rates (Figure 3.11). However, younger males approached at a higher overall rate than did adult females [*F* (1, 6) = 10.32, *p* = 0.018: Figure 3.11].

Figure 3.10: Mean (± S.E.M.) rate of approaches by older and younger males to adult and sub-adult females

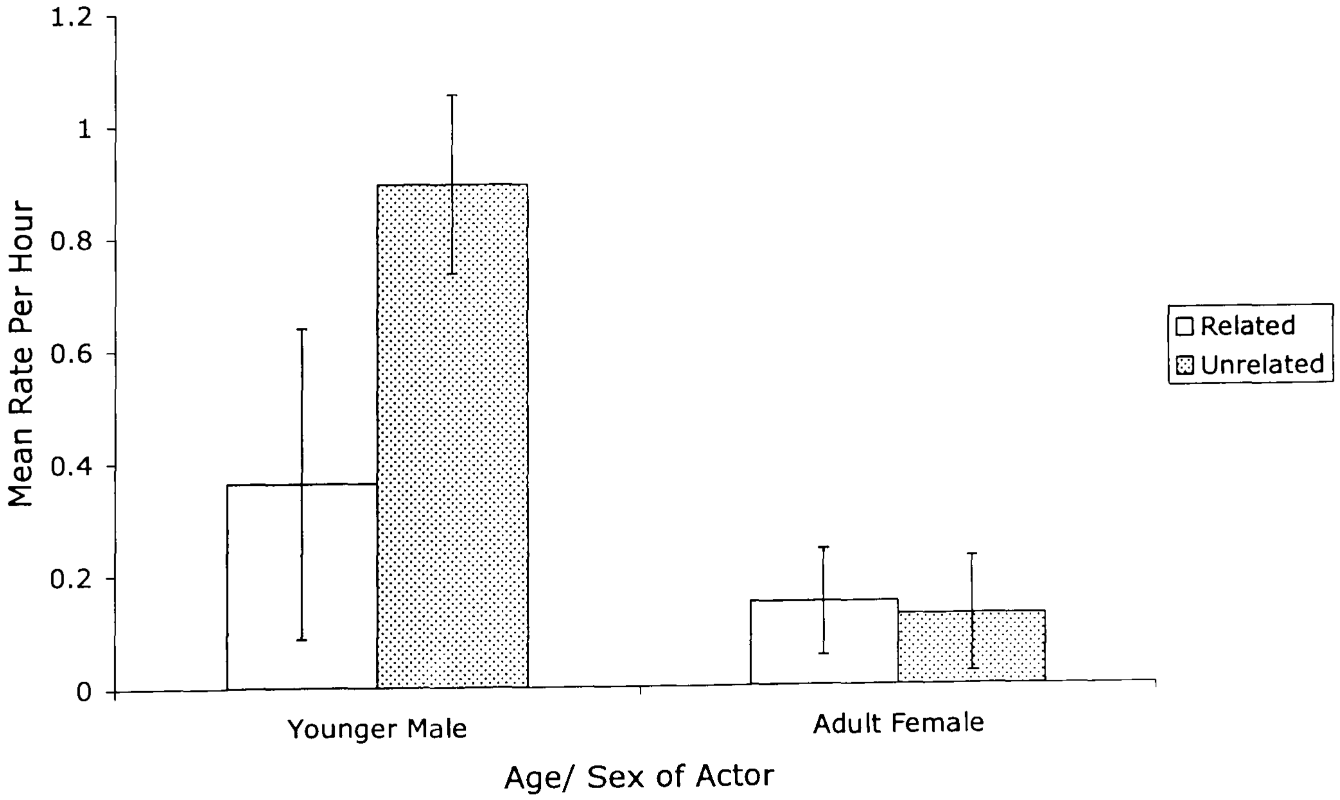

Figure 3.11: Mean (± S.E.M.) rate of approaches given by younger males to related and unrelated adult females and by adult females to related and unrelated younger males.

Younger males did not groom sub-adult females and there was only one case of grooming by an older male to a sub-adult female that lasted for just a few seconds. The degree of relatedness between these two individuals was not known. No significant difference was found in the mean percentages of observation time older and younger males spent grooming adult females [*t* (9) = 1.23, *p* = 0.25; older males: 0.38 ± 0.24, younger males: 0.14 ± 0.06]. Sub-adult females were never observed to groom older males and only one instance of grooming from a sub-adult female to an unrelated younger male was observed. There was also no significant difference in the percentage of time adult females spent grooming older and younger males [*t* (17) = -1.17, *p* = 0.26; older males: 0.17 ± 0.10, younger males: 0.23 ± 0.14]. Grooming interactions between younger males and adult females were affected by kinship as the only younger males groomed by adult females were their sons and the majority of younger males preferentially groomed their mothers. However, this difference only approached significance, possibly due to the small sample size [*F* (1, 6) = 4.00, *p* = 0.09: Figure 3.12].

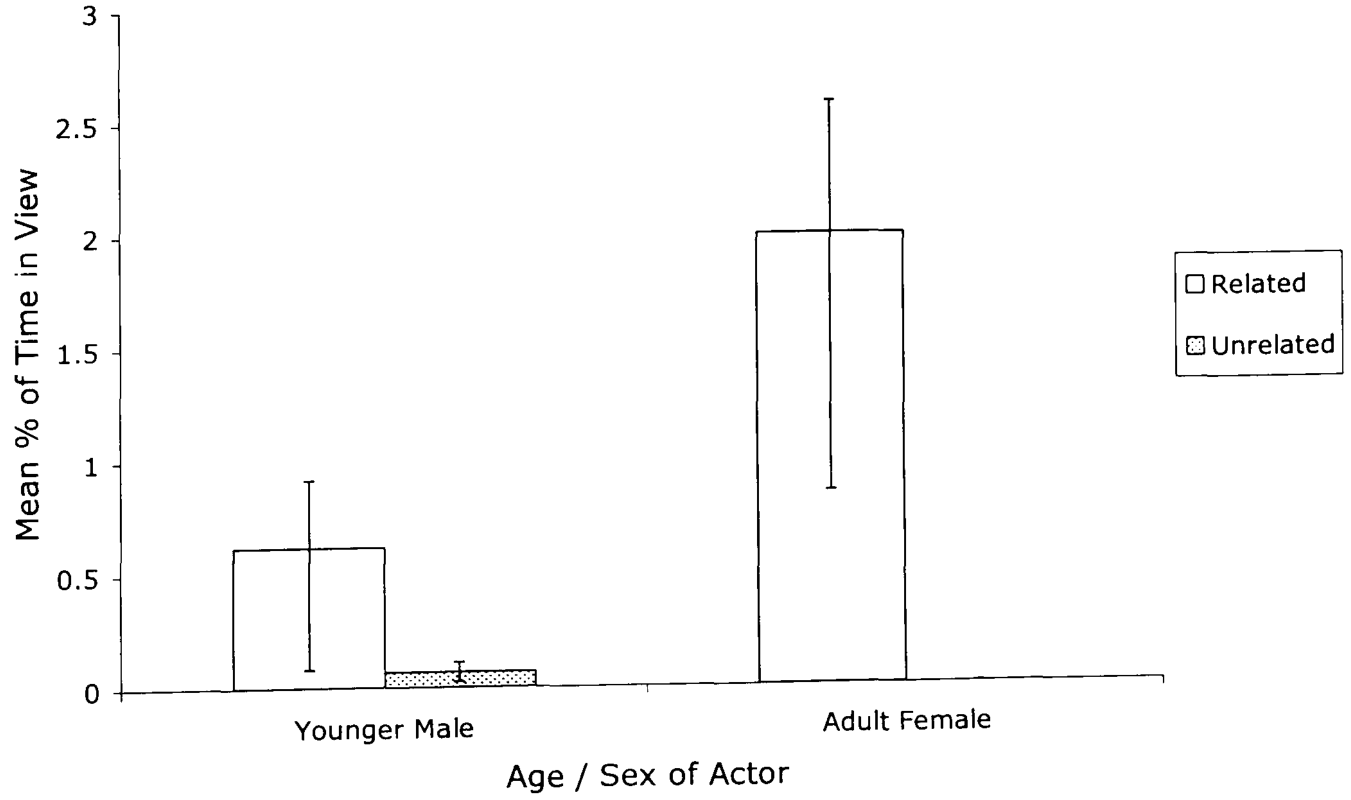

Figure 3.12: Mean (± S.E.M.) percentage of time younger males spent grooming related versus unrelated adult females and adult females spent grooming related versus unrelated younger males.

In terms of time spent in proximity, older and younger males showed no significant preference between adult and sub-adult females [main effect of male age: $F(1, 8) = 1.98$, $p = 0.19$; main effect of female age: $F(1, 8) = 3.64$, $p = 0.09$; interaction: $F(1, 8) = 0.11$, $p = 0.74$; older males: adult female 3.09 ± 1.09, sub-adult female 1.51 ± 1.39; younger males: adult female 2.30 ± 0.93, sub-adult female 0.05 ± 0.04]. Similarly, adult and sub-adult females showed no significant preference between older and younger males as proximity partners [main effect of female age: $F(1, 22) = 0.59$, $p = 0.45$; main effect of male age: $F(1, 22) = 2.21$, $p = 0.15$; interaction: $F(1, 22) = 0.02$, $p = 0.89$; adult females: older male 3.99 ± 1.84, younger male 1.66 ± 0.44; sub-adult females: older male 2.90 ± 1.95, younger male 0.05 ± 0.04]. There was no significant difference in the percentage of time younger males and adult females spent in proximity to unrelated opposite sex partners [$t(6) = -1.1$, $p = 0.32$].

As embraces and arm-wrapping events between the sexes were so rare (Table 3.1), it was not possible to determine whether these behaviours (between the sexes) were affected by the ages of the actor and recipient. However, in addition to the data presented in Table 3.1, it was possible to confirm that neither older nor younger males were observed to embrace or arm-wrap sub-adult females and sub-adult females never embraced or arm-wrapped males (older or younger).

3.8. Discussion

The primary aim of this chapter was to quantify the distribution of social behaviours within and between sexes, with particular reference to species-specific embraces and arm-wrapping. As predicted by patterns of dispersal, males preferentially interacted with same-sex partners as time spent in proximity and all affiliative behaviours were exchanged most often between males. Rates of aggression within the sexes were very low, and whereas female aggression to opposite-sex partners was also low, males were often aggressive towards unrelated opposite-sex partners (Chapter 6). Females were predicted to preferentially interact with opposite-sex partners, which appeared to be true only for grooming interactions, although differences in grooming partner preference between males and females only approached significance. Females showed no preference for being in proximity to either sex, but for all other behaviours, females directed behaviour toward same-sex partners at significantly higher rates than opposite sex partners.

The preference for same-sex partners was particularly strong for embraces and arm-wrapping. Only a few cases of male to female embraces were observed and females never embraced males. Arm-wrapping never occurred between the sexes.

High rates of affiliative behaviour exchanged between males correspond to findings from chimpanzees and muriquis, which may be attributed to the pattern of male philopatry reported for all three species (Morin *et al.*, 1994; Goldberg & Wrangham, 1997; Mitani *et al.*, 2000; Strier, 1991; Symington, 1987; 1998b; 1990, but see Vigilant *et al.*, 2001). Although a higher degree of relatedness among male spider monkeys is yet to be confirmed with genetic data, the combination of female dispersal from the natal group, no secondary female transfer, and male philopatry reported in Punta Laguna and other field sites (e.g. Chapman, 1990; Symington, 1987) strongly suggest that male spider monkeys from the same community are closely related. However, kinship is not necessarily a prerequisite for affiliation among males (Goldberg & Wrangham, 1997; Mitani, *et al.*, 2000; Strier *et al.*, 2002), particularly if males must rely on other community males to successfully defend their females from extra-community males. Over time, this history of cooperation between individuals is likely to have a positive effect on relationship quality.

Cooperative relationships between males have been reported in muriquis and chimpanzees. Males from these species are known to work cooperatively to attract females to their community (muriquis: Strier, 2000) or defend their females from extra-community males (chimpanzees: Goodall, 1986; Boesch & Boesch-Achermann, 2000). Coordinated male raiding parties in neighbouring territories, bearing a striking resemblance to those of chimpanzees have been observed in the spider monkeys at Punta Laguna (Aureli, Schaffner, Verpooten, Slater & Ramos-Fernandez, 2006), indicating a similar high degree of cooperation among community males. This high degree of cooperation and familiarity among philopatric males can explain the high rates of affiliative behaviour exchanged between male spider monkeys. Like chimpanzees, coalitionary inter-community aggression has also been observed in Punta Laguna between the Western community males and unknown sexually mature males (Aureli *et al.*, 2006), although affiliative inter-community encounters have also been observed between the Eastern and Western community males (Ramos-Fernandez, unpublished data).

Female preference for opposite-sex grooming partners was concordant with previous reports on spider monkeys (Fedigan & Baxter, 1984; Symington, 1990) and chimpanzees (Wrangham *et al.*, 1992; Watts, 2000a). Previous studies of spider monkeys have indicated that time spent in proximity when resting was highest among males, followed by male-female dyads and lastly female-female dyads (Fedigan & Baxter, 1984; Symington, 1990), but have not reported whether this pattern was the result of male or female preferences. My results have confirmed that whereas males spend more time in proximity to other males, females show no preference for proximity partners of either sex, and as males approached females more often than females approached males, it is likely that males are responsible for maintaining proximity. Previous studies of spider monkeys have not reported whether females preferentially embrace same-sex or opposite-sex partners, but my results have indicated that with the exception of grooming and proximity, females showed a strong preference for same-sex partners, and like for males, this preference was most pronounced for species-specific embraces and arm-wrapping. This differs somewhat from studies that suggest the female-female social relationships among spider monkeys are of the lowest quality (e.g. Fedigan & Baxter, 1984; Symington, 1990), emphasising the importance of investigating species-specific behaviours in addition to social grooming.

With the exception of bonobos (de Waal, 1995; Kano, 1992; 1996), females belonging to societies with a high fission-fusion dynamic generally exhibit tolerant but non-affiliative social interactions. In all these species, there is strong evidence to suggest that females are the dispersing sex (Di Fiore & Fleischer, 2005; Goodhall, 1986; Kano, 1992; Nishida & Hiraiwa-Hasegawa, 1987; Strier, 1991; Symington, 1987; 1998b; 1990), and the rarity of coalitions and almost non-existent social grooming between adult females suggest that female social relationships are best described by Sterck et *al.*'s (1997) Dispersed-Egalitarian. That females preferentially directed species-specific affiliative behaviour to same-sex partners, strongly suggests that these behaviours serve a different function to grooming and proximity and may not necessarily be indicators of relationship quality (see Chapters 4 and 5).

It is unlikely that exchanges of embraces and arm-wrapping between adult females were affected by kinship as my observations suggest that females disperse from their natal group upon reaching sexual maturity. Furthermore, interactions involving adult and sub-adult females indicated that species-specific behaviour was hardly ever exchanged between different-age female dyads. There are however, a number of other factors that may have contributed to these unexpected results in the Punta Laguna spider monkey population. Firstly, it is likely that embraces play a different role to social grooming and are linked to tolerance at feeding sites (Chapter 4). Secondly, there is compelling evidence to suggest that female-female social relationships are affected considerably by the presence of young infants and that embraces are the primary behaviour involved in these interactions (Chapter 5). Finally, it is possible that females are reluctant to approach, embrace or arm-wrap adult males due to fear of attack. The high rates of female-directed male aggression in spider monkeys would certainly suggest that females should be wary of community males (Chapter 6). Further findings on male-female interactions generally supports this last view as although females showed a preference for grooming males, they were in fact exclusively grooming their sons, who were never involved in attacks against them.

Male-male aggression at Punta Laguna was generally low, which is similar to findings from other populations (Fedigan & Baxter, 1984; Symington, 1990). Due to this low rate of aggression and the small sample size in one of the communities, it was not possible to examine the presence or absence of an agonistically maintained dominance hierarchy among community males at Punta Laguna. Similarly, as mating occurred in secrecy from other community members (a phenomenon also observed in other study communities e.g. Campbell, 2006), it was not possible to investigate male tolerance in the context of mating. However, the very fact that mating occurred in secrecy and that copulating pairs maintained a high level of vigilance and made no copulatory vocalisations, which was also reported by Campbell (2006), suggests that copulating pairs were fearful of harassment by conspecifics. Data from the four males in the Eastern community shared many similarities with reports of opportunistic relationships among male chimpanzees, in which coalition partners may change depending on the availability of partners (e.g. de Waal, 1982). Collectively, these data suggest that male-male spider monkey relationships show a closer resemblance to those of chimpanzees than muriquis.

As predicted, like in other *Atelinae* species, exchanges of affiliative behaviour between males were affected by age. Older males received embraces at significantly higher rate than did younger males, and younger males gave more embraces than they received. This effect was due to the younger males' preference for embracing older males. Although anecdotal, a similar effect was found for grappling behaviour, which only ever occurred between older and younger males and was always instigated and maintained by the younger male. Approaches, social grooming and proximity were unaffected by male age, suggesting that the formation and continuation of social bonds between older and younger males are made possible by embraces and grappling. Arm-wrapping behaviour followed a different pattern as older males arm-wrapped at higher rates than did younger males, but showed no preference for younger or older male partners. This difference is likely because arm-wrapping functions as a coalitionary behaviour in which two or more individuals, arm-wrap and then threaten a third party (conspecific, human observer or other animal) whereas embraces and grappling appear serve a signals of benign intent that reduce uncertainty surrounding social relationships (Chapter 4).

An effect of age on male-male social relationships has also been reported in muriquis and woolly monkeys. Among muriquis, younger males preferentially associated with older males and were responsible for maintaining these associations (Strier *et al.*, 2002). Although adult male woolly monkeys tend not to interact with one another, sub-adult males were reported to associate with adult males at greater than chance level and social grooming was highest between sub-adult male – adult male dyads (Di Fiore & Fleischer, 2005). As male muriquis and woolly monkeys are highly tolerant in the context of mating (Strier *et al.*, 2002; Di Fiore & Fleischer, 2005), exhibit low-level aggression and form no clear-cut dominance hierarchies, it is unclear what the younger males gain from these associations with older males.

In spider monkeys however, younger males are reported to receive aggression from older males, which can be severe. In the previous year to my data collection, a younger male was killed by older resident males in the Eastern community at Punta Laguna (Valero, Schaffner, Vick, Aureli & Ramos-Fernandez, 2006). Similar fatal attacks on younger community males have also been observed at another field site (Campbell, in press). Although relatively rare, these attacks and the risk of subsequent attacks will likely have a notable affect on social relationships between older and younger males. Younger male spider monkeys may therefore experience heightened uncertainty when approaching older males and may use embraces as a means of signalling benign intent and thus reducing the likelihood of receiving aggression.

As predicted by patterns of dispersal and fission-fusion social organisation, female spider monkeys at Punta Laguna showed no evidence of an agonistically maintained dominance hierarchy. Dominance relationships facilitate the despotic appropriation of monopolisable food resources and are usually found among females that feed primarily on fruit (van Schaik, 1983; 1989; Wrangham, 1990). In societies with a high fission-fusion dynamic however, grouping is flexible and may change to accommodate food supply and foraging patch size (Chapman *et al.*, 1995; Symington, 1988a), thus female social relationships are predicted to be more tolerant and less differentiated than other frugivorous species. The low rate of female-female aggression at Punta Laguna supports this view.

Reports from muriquis and chimpanzees have indicated that adolescent and recent immigrant females are subordinate to resident adult females as indicated by patterns of formal submission (Wrangham, Clark & Isabirye-Basuta, 1992) or displacements (Printes & Strier, 1999). As both aggression and displacements were rarely observed between resident adult females and resident adolescents at Punta Laguna, it was not possible to determine whether this was also true of female spider monkeys. However, there were a number of coalitionary attacks by resident females toward recently immigrated females, and newly immigrant females were generally found on the periphery of subgroups. Unfortunately, these females were also extremely wary of human observers, making it difficult to collect data on their social interactions.

As with male-male interactions, female-female social interactions were affected by age. Both adult and sub-adult females received approximately as much grooming as they gave, although overall, sub-adult females spent more time involved in grooming interactions than did adult females. Both adult and sub-adult females also showed a strong preference for grooming different-aged partners. However, all these results were confounded by kinship as both adults and sub-adults preferentially groomed their kin. That the proportion of time engaged in grooming was higher in sub-adults compared to adults is likely because all sub-adults had female kin available to groom, whereas a number of adult females did not. Therefore, due to the higher rates of grooming between kin, grooming involving sub-adults was disproportionately high relative to adults.

Time spent grooming between female kin was approximately three times higher than between unrelated females, suggesting that kinship is a prerequisite for the establishment of grooming relationships between female spider monkeys. This view is concordant with the findings of Ahumada (1992), who found high rates of grooming between adult females in a closed community of spider monkeys where many of the adult females were related. Kin-bias in grooming is typical of non-human primates (Gouzoules & Gouzoules, 1987; Silk, 2002), but the exceptionally low rate of grooming observed between adult females appears to be a characteristic of the Atelinae (Fedigan & Baxter, 1984; Strier, 1990). There is evidence to suggest that adult female spider monkeys regulate their social relationships using embraces rather than grooming (Schaffner & Aureli, 2005; Chapter 5), thus it remains unclear why there should be such a strong preference for grooming and a complete absence of embraces between adult females and their adolescent female kin.

Female-female embraces were also affected by age as adults exchanged embraces more frequently than did sub-adults. Adult females only ever embraced same age partners and sub-adult females only embraced different aged partners. The higher rates of embraces exchanged between adult females may be linked to the use of embraces to gain access to food sources (see Chapter 4) and young infants (see Chapter 5). That the adult females were able to displace sub-adult females (albeit rarely) from food sources and that sub-adult females had no infants, can explain why adult females were never observed embracing sub-adult females. Sub-adult females were observed being displaced by adult females at feeding sites on three separate occasions, indicating two important factors. Firstly, sub-adult female access to food was affected by the presence of adult females, and secondly, that these displacements did not occur very often. It is therefore possible that sub-adult females embrace adult females at feeding sites and were subsequently granted access to food (Chapter 4). As all sub-adult females had already emigrated from their natal groups when the birth peak occurred in the second field season in the study, sub-adults females did not have the opportunity to use embraces as a means of gaining infant access, which may explain why sub-adult females embraced other females at a lower rate than did adult females. Attraction to other's infants may also explain why adult females preferentially approached unrelated adult females.

Relationships between the sexes were also affected by age and kinship. Although there was a tendency for female-directed male aggression, no aggression was observed between older or younger males and sub-adult females. Although relatedness between older males and adult females was unknown, younger males directed aggression exclusively to unrelated females. These findings add weight to the view that female-directed male aggression in spider monkeys is related to sexual behaviour, perhaps in the form of sexual coercion (Fedigan & Baxter, 1984; Symington, 1987 cited in Smuts & Smuts, 1993; Chapter 6).

Similarly, grooming did not occur between adult males and sub-adult females. Females showed no preference for grooming either older or younger males;

however a closer inspection revealed that this result was confounded by kinship as the only younger males groomed by females were their sons. It was not possible to determine whether this was also the case between older males and females as relatedness was not known. However, as social interactions between the sexes were rare, and males showed a preference for directing aggression towards females, it is possible that females were extremely wary of adult males and were only willing to engage in potentially risky behaviour such as social grooming, with close kin, from whom they were unlikely to receive aggression.

Previous reports of spider monkeys have concluded that relationships quality is highest among males, followed by male-female relationships and is lowest in female-female social relationships (e.g. Fedigan & Baxter; Symington, 1990). As predicted by dispersal patterns my findings suggest that male-male relationships can generally be characterised as high-quality, but with some reservations as younger males clearly do not have the high-quality relationships that older males have with each other. The high rates of embraces and grappling from younger males to older males may function as a form of appeasement to achieve reassurance that reduces the likelihood of attack. With two recent reports of lethal aggression in spider monkeys by older males towards younger males (Campbell, in press, Valero *et al.*, 2006), behaviours aimed at reducing uncertainty are likely to be particularly important to young male spider monkeys. If this is true, then high rates of these behaviours may provide an indirect indication of valuable but insecure social relationships. The next step in understanding the function of embraces may be to investigate whether younger males who embrace older males more frequently, have a greater chance of survival within the community and are less likely to receive aggression.

My results indicated that relationships between the sexes were generally low-quality, with the possible exception of female relationship with their adult sons. This emphasises the importance of distinguishing between related and unrelated individuals when describing social relationships, which previous studies that cited male-female relationships as intermediate between male-male and female-female may not have considered. Female-female social relationship were also characterised as low-quality, which is in line with patterns of dispersal and previous reports of natural populations of spider monkeys (Fedigan & Baxter, 1984; Symington, 1990). However, rates of arm-wrapping and embracing exchanged between females were considerably higher than those between males and females, suggesting that female-

female social relationships may be of a higher quality than male-female (but see Chapter 5).

Collectively, these results describe a sex-segregated society in the Punta Laguna population, similar to that reported in other spider monkey populations (Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1990). However, unlike previous research, this current study has provided the first statistical analysis of the distribution of a full range of social behaviours within and between sexes. This study has also provided the first detailed insight into the social relationships of male spider monkeys in their natural habitat. Results have indicated that male-male spider monkey relationships bear many similarities to male-male relationships in chimpanzees, but with notably lower rates of aggression. It is likely therefore, that male-male social relationships in spider monkeys occupy an intermediate position between muriquis and chimpanzees species on the tolerant-despotic continuum. However, this conclusion is only tentative as knowledge of spider monkey dominance interactions and mating behaviour is so sparse.

Chapter Four

Context of Social Behaviour

4.1. Contested resources

Due to the energy demands of pregnancy and lactation, female reproductive success is dependent on the net energy gain from food. Consequently, the primary source of competition among females is access to food resources (Emlen & Oring 1977; Janson, 1988; van Schaik, 1983). Male primates on the other hand, do not have the concerns of pregnancy or lactation to contend with, such that in most primate species, male reproductive success is almost entirely dependent on successful fertilisations. Consequently, primate males compete primarily for potential mating opportunities (Emlen & Oring, 1977; van Schaik, 1983; Wrangham, 1980). As it is not possible to share fertilisations in the same way as is possible with food, male-male relationships are generally more antagonistic and less stable in nature than female-female relationships (van Hooff & van Schaik, 1992, 1994; van Schaik & Aureli, 2000).

Competition for resources exists in two distinct forms: scramble competition, in which any individual can alter the net energy gain of all others in the population, and contest competition, which refers to the appropriation of resources by dominant individuals (Koenig, 2002; Nicholson, 1954; van Schaik, 1989). Where scramble competition prevails, the decrease in reproductive success caused by competition is shared more or less equally by all individuals in the population (Koenig, 2002). In these circumstances, individuals have little to gain from forming coalitions and establishing dominance relations, as there is no direct contest for resources (Sterck *et al.*, 1997; van Schaik, 1989; Wrangham, 1980). Conversely, with predominant contest competition, decided dominance relationships evolve based on the consistent winners and losers of conflicts over resources (Sterck *et al.*, 1997; van Schaik, 1989; van Schaik & van Noordwijk, 1988). As dominant individuals monopolise access to resources, reproductive success is skewed in favour of dominants (Koenig, 2002).

4.2. Female-female competition in the *Atelinae* and *Pan*

Due to the high fission-fusion dynamics in chimpanzee, bonobo and spider monkey societies, males and females are not always in the same subgroups within the wider community, and each individual has the option of associating with subgroups of different sizes and compositions. Flexible grouping therefore enables individuals to preferentially associate with individuals that share their feeding requirements and daily activity budget. Consequently, pregnant or lactating females are often found in the same subgroups as they are unable to move at the same speed as other individuals and their energy needs are sufficiently high that they must spend a larger proportion of their day feeding (Symington, 1988b; Wrangham *et al.*, 1992). However, associating with other females can be costly in terms of feeding competition (c.f. van Schaik, 1989; Wrangham, 2000).

The *Atelinae* and *Pan* feed primarily on ripe fruit, thus contest competition for food is expected to predominate due to the clumped distribution of high quality food patches (van Schaik, 1989; Wrangham, 1980). However, flexible grouping that responds to food supply can enable females to minimise contest competition for food despite their dependence on ripe fruit (Chapman & Chapman, 2000). In chimpanzees and spider monkeys subgroup size is directly related to the density and distribution of fruiting trees suggesting that individuals reduce feeding competition by maintaining optimal group sizes (Anderson *et al.*, 2002; Chapman, 1990; Chapman *et al.*, 1995; Mitani *et al.*, 2002; Newton-Fisher *et al.*, 2000; Symington, 1988a). A similar although slightly weaker relationship can be found in bonobos and muriquis, who also reduce feeding competition by supplementing their diet with leaves (de Moraes *et al.*, 1998; White, 1998). Woolly monkeys are more cohesive than the other Atelines and therefore the relationship between food availability and subgroup size is weak (Stevenson *et al.*, 1999).

As female chimpanzees and spider monkeys do not normally supplement their diet with leaves and have higher energetic requirements than males, the relationship between female subgroup size and food availability is more pronounced (Chapman *et al.*, 1995; Shimooka, 2003). During periods of fruit scarcity female chimpanzees travel and forage in small parties or alone with their dependent offspring (Chapman *et al.*, 1995; Wrangham, Chapman, Clark-Arcadi & Isabirye-Basuta, 1996; Wrangham *et al.*, 1992), whereas male-male associations are more constant (Matsumoto-Oda, Hosaka, Huffman & Kawanaka, 1998). Similarly, associations between male spider monkeys at La Macarena, Colombia are reported to remain constant across seasons whereas females associate with each other less frequently during fruit-poor seasons (Shimooka, 2003). The relationship between subgroup size and food availability is less pronounced among female chimpanzees at Taï as females appear to maintain larger subgroups in response to leopard predation (Boesch & Boesch-Achermann, 2000).

That females may use flexible grouping to reduce feeding competition, has been cited as an explanation for the weak dominance hierarchies and rarity of coalitions exhibited by female chimpanzees and spider monkeys (Fedigan & Baxter, 1984; Nishida & Hiraiwa-Hasegawa, 1987; Sterck *et al.*, 1997). In line with this explanation, a formal linear dominance hierarchy has been detected among female chimpanzees at Taï (Wittig & Boesch, 2003) that experience predation by leopards and are therefore forced to spend more time in large subgroups (Boesch & Boesch-Achermann, 2000). However, flexible grouping is unlikely to completely eliminate feeding competition as female efforts to reduce subgroup size may be thwarted by male efforts to associate with females. Indeed, evidence from a number of field sites suggests that the presence of oestrus females plays a significant role in determining chimpanzee and bonobo subgroup size, as males are attracted to subgroups containing oestrus females regardless of the ecological costs of large groups (Anderson *et al.*, 2002; Boesch, 1996; Hohmann & Fruth, 2002; Matsumoto-Oda, 1999; Matsumoto-Oda *et al.*, 1998; Mitani *et al.*, 2002). The relationship between oestrus females and subgroup size has not yet been investigated in spider monkeys.

Consequently, female chimpanzees and spider monkeys are still likely to experience some, albeit reduced, contest competition for food. Although female-female aggressive interactions in chimpanzees are rare, up to 80% of all female-female aggression occurs in a feeding context (Goodall, 1986; Muller, 2002; Nishida, 1989). Female-female aggression in spider monkeys is also low (Fedigan & Baxter, 1984; Symington, 1988b; Chapter 3), but the proportion of this aggression that arises during feeding has not yet been reported. Among bonobos a greater reliance on leaves combined with flexible grouping appears to have successfully reduced contest competition for food, as both for species, aggression in the context of feeding is rare and has been replaced by non-aggressive displacements of younger or newly immigrant females by older, resident females (Furuichi, 1997; Printes & Strier, 1999). In contrast, aggression in woolly monkeys is highest among females and occurs most often in feeding trees and is likely due to the higher degree of group cohesion in this species (Di Fiore & Fleischer, 2003).

The relationship between female competition, dominance rank and reproductive success is not well understood in species with a high fission-fusion dynamic. For example, dominance relationships between female chimpanzees at Gombe are very weak and can only be described using broad rank categories, yet high-ranking females are reported to have significantly higher infant survival, faster maturing daughters and lower inter-birth intervals (Pusey *et al.*, 1997). Broad rank categories have also been detected among female spider monkeys where high-ranking females were found to have shorter inter-birth intervals than low-ranking females (29.0 versus 36.6 months: Symington, 1987). Similar age-based-ranking that determines access to food has been detected among female bonobos, muriquis and woolly monkeys, but the relationship between dominance rank and female reproductive success has not been investigated directly (Di Fiore & Fleischer, 2003; Furuichi, 1997; Kano, 1992; Printes & Strier, 1999).

4.3. Male-male competition in the *Atelinae* and *Pan*

As with feeding competition, male-male competition for access to females may be characterised as scramble or contest competition, depending on the distribution of fertile females and their corresponding monopolisability (van Hooff, 2000; van Hooff & van Schaik, 1992, 1994). Where female groups are large and primarily arboreal or adopt flexible grouping patterns, males are expected to compete for fertilisations via scramble competition due to difficulties in monitoring the movements of group females (Mitani *et al.*, 1996a; van Hooff, 2000). This prediction appears correct for woolly monkeys and muriqui males who routinely mate with several females and do not attempt to interfere with one another's copulations (Di Fiore & Fleischer, 2003; Strier, 1997; Strier *et al.*, 2000).

In contrast, male chimpanzees and bonobos actively compete with one another for access to oestrous females, interfere with one another's copulations and form coalitions to defend access to females (Hohmann & Fruth, 2003; Newton-Fisher, 2002; Nishida & Hosaka, 1996; Watts, 1998). Consequently, dominant males achieve high mating success at the expense of low ranking males (Constable, *et al.*, 2001; Gerloff *et al.*, 1999). In chimpanzees, the rate and intensity of male-male aggression is reported to increase when oestrus females are present in the subgroup (Muller, 2002) and data from numerous field sites has confirmed frequent male-male aggression in the context of mating (Boesch & Boesch-Achermann, 2000; Goodall, 1986; Muller, 2002; Nishida, 1990). In bonobos at Lomoko, 24% of male-male aggression was reported to occur in the context of mating and the rate of male-male aggression increased significantly when oestrus females were present in the group (Hohmann & Fruth, 2003). These data clearly indicate that a major source of conflict between males is access to fertile females.

Aggression between male spider monkeys is generally low (Fedigan & Baxter, 1984; Chapter 3), making it difficult to determine dominance relationships. The relationship between male dominance rank and reproductive success therefore remains unclear. Similarly, as females do not advertise oestrus with sexual swellings (Dixson, 1998; Klein, 1971), it is difficult to investigate male-male competition for fertilisations. However, the very fact that spider monkey mating occurs in secrecy away from other group members (Campbell, 2006; Klein, 1971; van Roosmalen & Klein, 1988; Chapter 6), suggests that males are not tolerant of one another in the context of mating.

One further context of male-male aggression reported in chimpanzees refers to the first five minutes following a fusion event, during which time individuals must assess their relationships with conspecifics. At Kanyawara and Gombe up to 38% of all male-male aggression occurred in the context of fusion (Goodall, 1986; Muller, 2002). Conversely, female-female aggression following fusion was either absent or rare (0% Kanyawara: Muller, 2002; 5% Gombe: Goodall, 1986). The relationship between fusion and aggression does not appear to have been investigated in bonobos or woolly monkeys and has not been investigated in muriquis due to the rarity of intra-group aggression (Strier *et al.*, 2000). However, in spider monkeys, aggression is reported to occur at higher rates in the first five minutes following fusion (Schaffner, Verpooten & Aureli, 2003), although sex differences in this behaviour are yet to be investigated.

4.4. Managing aggression

Aggression is a high-risk behaviour therefore individuals are expected to develop mechanisms for managing aggression. The most widely used mechanism in the animal kingdom is the formation of dominance relationships, and in turn hierarchies, in which dominant individuals enjoy preferential access to resources. Once a dominance relationship has been established the outcome of contests can be predicted based on the relative dominance rank of combatants and thus actual conflict can be prevented (Drews, 1993). Clear-cut dominance relationships have been reported in male chimpanzees and bonobos (de Waal, 1982; Newton-Fisher, 2002; Nishida & Hosaka, 1996; Watts, 2000b) and among female chimpanzees at Taï (Wittig & Boesch, 2003). Weaker dominance relationships hierarchies based on age and group tenure have been reported in female muriquis (Printes & Strier, 1999), bonobos (Furuichi, 1997), and female chimpanzees from other field sites (Pusey *et al.*, 1997; Wrangham *et al.*, 1992). Unlike chimpanzees and bonobos, spider monkeys have no formal submissive gestures, and as aggression across all age-sex classes is low, it is difficult to determine dominance relationships (Chapter 3). Attempts have been made to determine broad dominance ranks for females at other field sites, although aggressive interactions were only observed between a small proportion of females (Chapman, 1990; Symington, 1987: PhD thesis cited in Symington, 1988a).

There are two possible reasons why spider monkeys do not have clear-cut dominance relationships and exhibit low-level aggression. The first is that they compete via scramble competition (Sterck *et al.*, 1997; van Schaik, 1989) and the second is that they manage potential sources of conflict using alternative social behaviour such as greetings. Greetings in the form of embraces or socio-sexual behaviours have been reported in a number of species characterised by a high fission-fusion dynamic. In bonobos, genital-genital rubbing between females has been linked to tension reduction (Hohmann & Fruth, 2000), and in spotted hyenas (*Crocuta crocuta*), high-risk behaviour involving the exposure of genitalia is often exchanged after periods of separation (East *et al.*, 1993) and has been interpreted as a signal of appeasement, assessment and reassurance (Colmenares, Hofer & East, 2000). In chimpanzees, affiliative behaviour in the form of 'embraces' and 'kisses' are sometimes exchanged during fusion events (Goodall, 1986; Nishida, Kano, Goodall, McGrew & Nakumura, 1999), however, these reunions are generally characterised by aggressive displays followed by social grooming (Goodall, 1986).

Spider monkeys also exchange embraces which are positively associated with the reunion of individuals after a brief period of separation, however in contrast to chimpanzees, grooming in spider monkeys is not associated with fusion events (Schaffner & Aureli, 2005; Aureli & Schaffner, in prep.). Spider monkey embraces are also positively associated with bouts of infant handling, which are generally tension-loaded interactions (Schaffner & Aureli, 2005; Chapter 5). Furthermore, aggression following fusion is less likely to occur between individuals who just embraced each other (van Roosmalen and Klein, 1988; Aureli & Schaffner, in prep). Consequently, embraces have been interpreted as a signal of benign intent aimed at reducing tension (Schaffner & Aureli, 2005; Schaffner *et al.*, 2003). Embraces are also frequently observed in muriquis who exhibit low-level aggression across all age/sex classes (Strier, 1994). It is therefore possible that spider monkeys use embraces to manage aggression.

4.5. Chapter aims and predictions

Data on the social interactions of spider monkeys is sparse and although the contextual use of social behaviour has been studied in captive groups (Pastor-Nieto, 2001; Schaffner & Aureli, 2005), detailed accounts from wild communities have been less forthcoming. Data from wild populations are particularly important to investigate the effects of ecological factors such as feeding competition and a high fission-fusion dynamic. This chapter therefore aimed to investigate the context of male-male and female-female social behaviour with particular reference to competition for resources and the effects of flexible grouping on behaviour.

The first predictions tested referred to sex differences in grouping. As a result of feeding competition, females were predicted to spend more time solitary than males. As males are attracted to fertile females, males were predicted to spend more time in mixed-sex subgroups than females. As males compete for access to fertile females, male-male aggressive and coalitionary behaviour was predicted to occur more frequently in mixed-sex subgroups than in same-sex subgroups. Similarly, as embraces may serve to reduce uncertainty (Schaffner & Aureli, 2005), and the presence of females is a potential source of conflict, males were also predicted to approach one another and exchange embraces more frequently in mixed-sex subgroups than in same-sex subgroups. In line with previous reports of wild spider monkeys (Chapman, 1990; Symington, 1988a), females were predicted to spend more time feeding when in same-sex subgroups. Provided that this prediction was met, female-female aggression, coalitionary arm-wrapping, approaches and embraces were predicted to occur at a higher rate in same-sex subgroups. As available evidence suggests that spider monkeys do not regulate their social relationships using grooming (Schaffner & Aureli, 2005; Chapters 3 & 5), male-male and female-female grooming was predicted to be unaffected by subgroup type. As males and females may only interact when in mixed-sex subgroups, it was predicted that both sexes should spend less time in proximity to same-sex conspecifics when in mixed-sex subgroups.

As the primary source of conflict among females is access to food, it was also predicted that the percentage of female-female aggression, arm-wrapping and embraces occurring in the context of feeding would be greater than expected based on the percentage of time in view females spent feeding. Male-male aggression, arm-wrapping and embraces were not predicted to be affected by feeding. Another potential source of conflict for both sexes is the high degree of uncertainty surrounding social relationships in the first few minutes following a fusion event. However, as male-male social relationships are likely to be less secure than female-female relationships due to the risk of severe aggression, this uncertainty following fusion was predicted to be higher among males. Therefore the percentage of male-male aggression, arm-wrapping and embraces occurring in the context of fusion was predicted to be higher than expected based on the percentage of time in view males spent in fusion events.

4.6. Methodology

4.6.1. Subjects

Data were collected on all adults in both the Eastern and Western communities at Punta Laguna. To obtain reliable estimates, only individuals observed for more than three hours of focal sampling were included in the analysis. Results were therefore produced using data from 4 adult males and 8 adult females from the Eastern community, and 7 adult males and 14 adult females from the Western community.

4.6.2. Data Collection

Data were collected using focal animal sampling with continuous recording on a dictaphone (see Chapter 2). Focal data were collected using a pre-defined ethogram of behaviour (Table 2.2, Chapter 2) and all instances of group fission and fusion that occurred during the focal were recorded, noting the individuals leaving or joining the subgroup and the exact time that the event occurred (see Chapter 2). Due to the presence of local assistants it was also possible to record aggression, embraces, arm-wrapping and group fission and fusion that occurred outside of focal data collection. Non-focal data were collected *ad libitum* (see Chapter 2), and like for the focal samples, the timing of the event, the individuals involved, the outcome of the event and the general context of behaviour (feeding, moving or resting) in the group prior to the event were recorded. Two distinct data sets were then created: the focal sample data set, which contained data on all behaviour observed during focal samples, and a special events data set containing all the embraces, arm-wrapping, aggression and fission-fusion events observed during focal samples together with all cases of these behaviours recorded *ad libitum*.

4.6.3. Data Analysis

The percentage of observation time spent solitary, in same-sex subgroups and in mixed-sex subgroups was calculated for each individual and summarised to produce a mean value for males and females in each of the different subgroup types. The percentages of time males and females spent in each subgroup type were compared using independent t-tests with Bonferroni's correction for multiple tests. Significance for these tests was therefore set to ≤0.015. As these results indicated that males and females allocated their time differently, individual rates of social behaviour while each individual was in same-sex and in mixed-sex subgroups were calculated separately using the methodology described in Chapter 2. Mean rates and percentages of time spent in isosexual behaviour by males and females while in same-sex and mixed-sex subgroups were then compared using 2x2 mixed design ANOVAs. Where significant interactions were obtained from the ANOVAs, un-confounded comparisons of the means were made post-hoc using Cicchetti's modification of Tukey's HSD test (Schweigert, 1994), with Howell's correction for repeated measures (Howell, 2002) for analysis of the repeated factor.

Expected and observed percentages of isosexual embraces, arm-wrapping and aggression occurring in specific contexts were then compared using the special events data set due to the low rates of isosexual behaviour, especially aggression, in the focal data set. The context of behaviour was defined as feeding if the individuals involved in the social interaction had been feeding prior to the interaction. Where each member of a dyadic social interaction was engaged in different activities prior to the interaction, the behaviour of the majority of the subgroup was also considered. For example, if one member of the dyad had been feeding, the other resting, and the majority of the group had been feeding then the context was recorded as feeding. Fusion context was defined as the first five minutes following a fusion event. Expected values were calculated for each individual using the percentage of time in view from focal samples that the individual spent in feeding or fusion context, respectively. Individual observed values were calculated as the percentage of total isosexual aggression, arm-wrapping or embraces from the special events data set that were performed by the individual in the given context. Mean expected and observed values were compared using paired t-tests.

Finally, the percentage of time each sex spent feeding in same-sex versus mixed-sex subgroups was compared using paired t-tests. These data were produced at the individual level from the focal sample data set.

4.7. Results

Due to the high degree of fission-fusion dynamics in spider monkey societies, males and females may differ in the time they spend alone, in same-sex or in mixed-sex subgroups. Females were found to spend significantly more time solitary than males [*t* (31) = 3.34, *p* = 0.002: Figure 4.1] and significantly more time in same-sex subgroups than males [*t* (31) = 3.20, *p* = 0.003: Figure 4.1]. Conversely, males were observed to spend a greater percentage of their time in mixed-sex subgroups [*t* (31) = 6.88, *p* < 0.001: Figure 4.1].

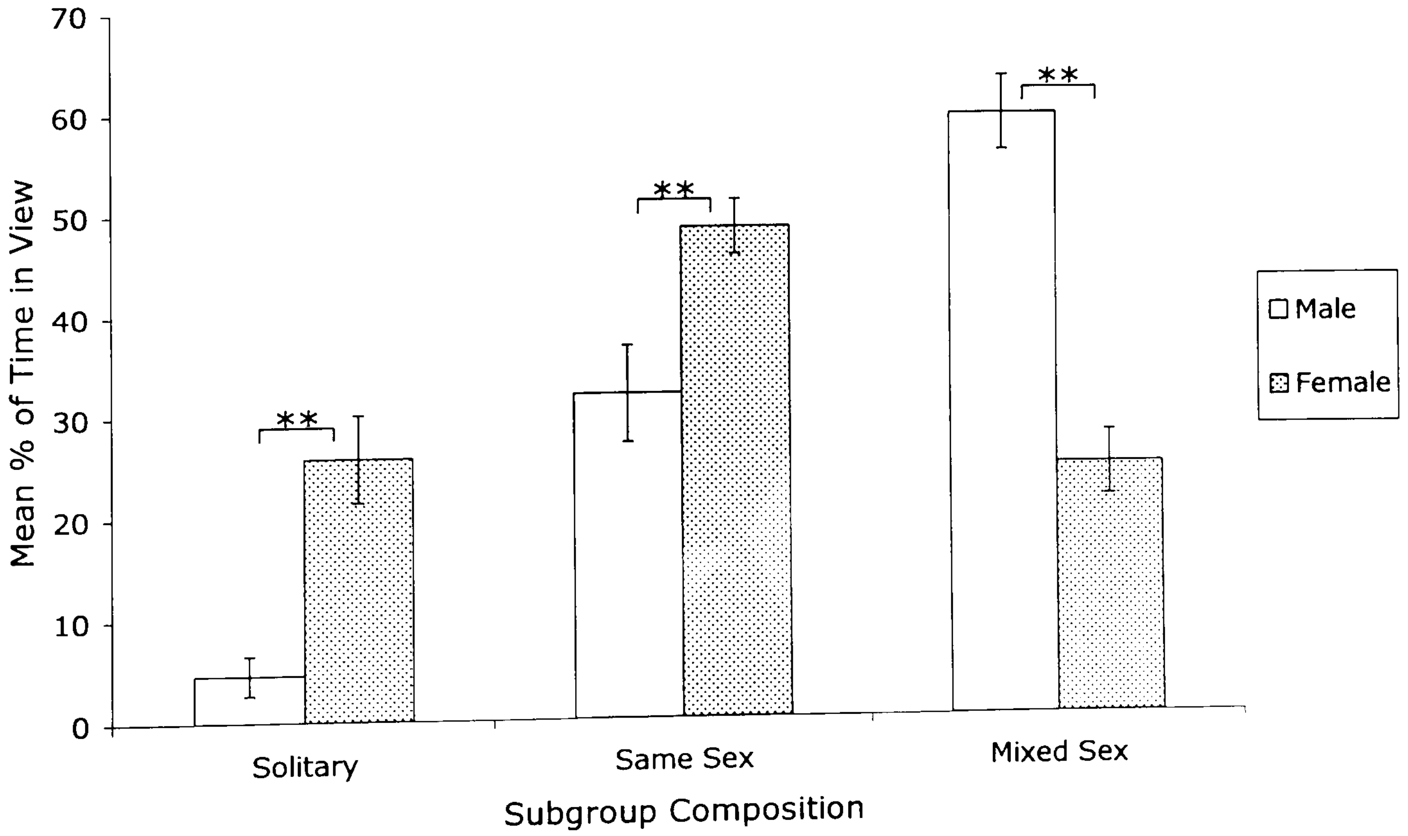

Figure 4.1: Mean percentage (± S.E.M.) of observation time in which males and females were found solitary, in same-sex subgroups, and in mixed-sex subgroups.

As predicted, male and female isosexual approaches and embraces were affected by subgroup type (Table 4.1). Post-hoc analysis of the interaction between actor sex and subgroup type indicated that males and females approached and embraced at similar rates when in same-sex subgroups, but in mixed-sex subgroups, males approached and embraced each other more often than did females (approaches: $p < 0.01$, embraces: $p < 0.05$). Furthermore, males approached and embraced each other at a significantly higher rate when in mixed-sex subgroups than same-sex subgroups ($p < 0.05$), whereas females approached and embraced each other more frequently in same-sex subgroups than mixed-sex subgroups ($p < 0.05$).

A similar pattern was found for isosexual arm-wrapping (Table 4.1). Post-hoc analysis of the interaction between sex and subgroup indicated that male and female arm-wrapping occurred at similar rates when in same-sex subgroups, but males arm-wrapped more frequently than did females when in mixed-sex subgroups ($p < 0.01$). Males arm-wrapped at a significantly higher rate when in mixed-sex compared to same-sex subgroups ($p < 0.01$), but contrary to my prediction, there was no significant difference in the rate of female arm-wrapping when in same-sex versus mixed-sex subgroups, resulting in a main effect of subgroup type on arm-wrapping. Contrary to my prediction, isosexual aggression was not significantly affected by subgroup type as the interaction between actor sex and subgroup type only approached significance (Table 4.1). This unexpected result was most likely due to the extremely low rates of isosexual aggression obtained from the focal data set.

Male and female isosexual grooming were not significantly affected by subgroup type (Table 4.1). However, the relatively high percentage of time allocated to male-male grooming in same sex subgroups resulted in a main effect of subgroup type on grooming interactions. As predicted males spent less time in proximity to same-sex conspecifics when in mixed-sex subgroups, but time spent in proximity by females did not change with subgroup type. However, the difference in male proximity was sufficiently large to produce a main effect of subgroup type on time spent in proximity (Table 4.1). A main effect of sex was found for all behaviours except aggression (Table 4.1) as males consistently interacted more frequently than did females (see Chapter 2).

Table 4.1: Mean (± S.E.M.) values of male and female isosexual social behaviour while in same-sex and mixed-sex subgroups, compared using 2x2 mixed design ANOVAs.

	Male – Male		**Female – Female**				
Behaviour	**Same-sex Subgroup**	**Mixed-sex Subgroup**	**Same-sex Subgroup**	**Mixed-sex Subgroup**	**Main Effect of Sex**	**Main Effect of Subgroup**	**Interaction**
Approach	1.67 ± 0.29	2.28 ± 0.63	1.57 ± 0.32	0.51 ± 0.12	F (1, 29) = 8.63 p = 0.006	F (1, 29) = 1.33 p = 0.317	F (1, 29) = 4.79 p =0.037
Embrace	0.41 ± 0.09	1.36 ± 0.32	0.60 ± 0.19	0.11 ± 0.06	F (1, 29) = 10.48 p = 0.003	F (1, 29) = 1.04 p = 0.316	F (1, 29) = 15.89 p < 0.001
Arm-wrap	0.25 ± 0.11	1.17 ± 0.41	0.12 ± 0.06	0.01 ± 0.01	F (1, 29) = 19.73 p < 0.001	F (1, 29) = 8.29 p = 0.007	F (1, 29) = 16.59 p < 0.001
Aggression	0.04 ± 0.03	0.04 ± 0.02	0.10 ± 0.04	0.01 ± 0.01	F (1, 8) = 0.09 p = 0.773	F (1, 29) = 2.79 p = 0.106	F (1, 29) = 3.19 p = 0.079
Grooming	0.59 ± 0.20	0.37 ± 0.11	0.03 ± 0.02	0.00 ± 0.00	F (1, 29) = 23.83 p < 0.001	F (1, 29) = 3.94 p = 0.057	F (1, 29) = 2.20 p = 0.149
Proximity	6.83 ± 0.80	2.98 ± 0.73	2.66 ± 0.41	2.57 ± 0.91	F (1, 29) = 65.63 p < 0.001	F (1, 29) = 8.43 p = 0.007	F (1, 29) = 3.01 p = 0.098

The primary source of competition among females refers to access to food resources. Therefore, significantly higher rates of female-female aggression and arm-wrapping were predicted to occur in same-sex subgroups providing that females spent more time feeding when in same-sex subgroups. Indeed, this was the case: females spent significantly more time feeding in same-sex subgroups than mixed-sex subgroups [*t* (20) = 2.56, *p* = 0.019: Figure 4.2], although this difference was less than 10%. Males also appeared to spend more time feeding when in same-sex versus mixed-sex subgroups [Figure 4.2], but statistical analysis indicated that this difference was not significant, [*t* (9) = 1.61, *p* = 0.143].

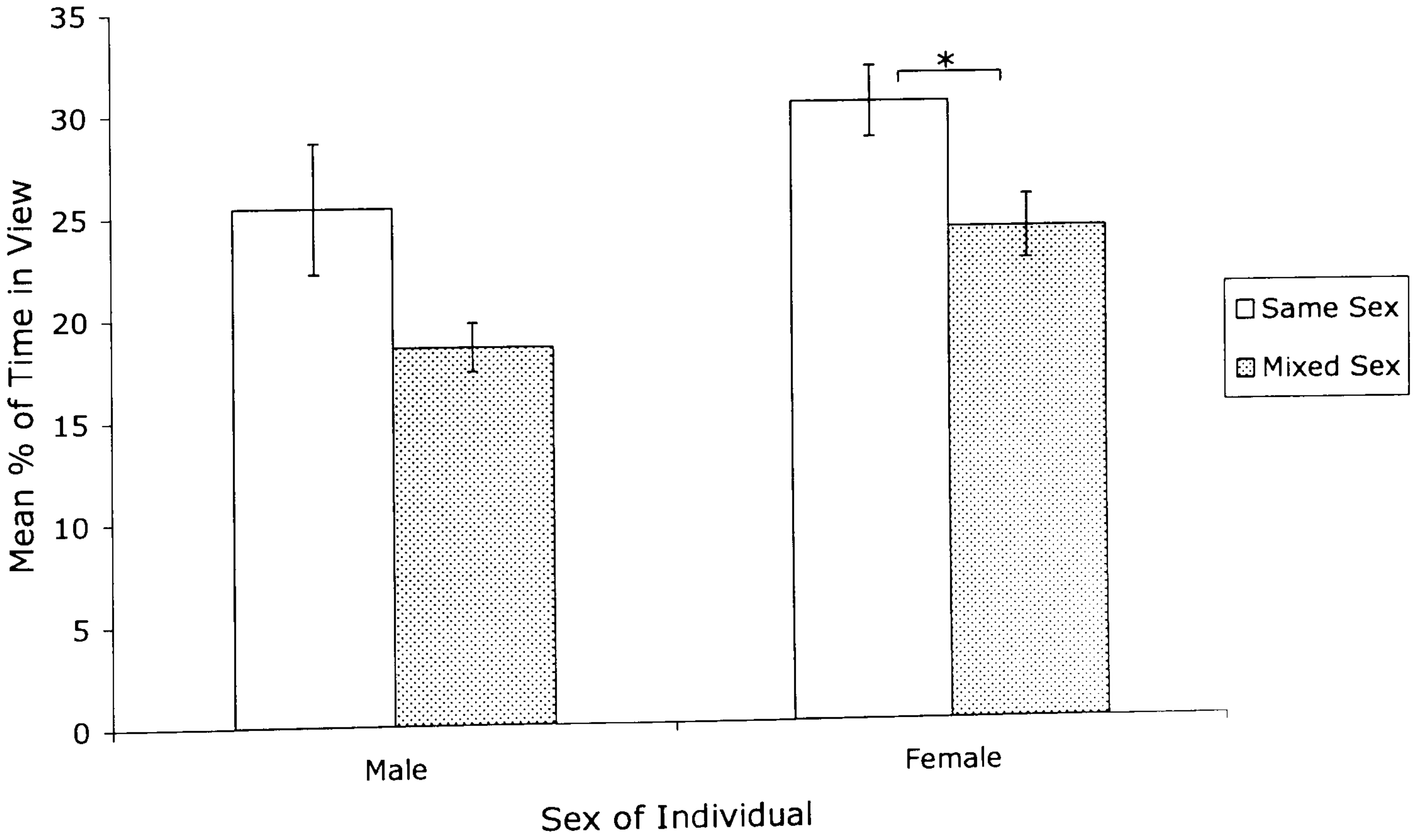

Figure 4.2: Mean (± S.E.M.) percentage of time in view males and females spent feeding in same-sex and mixed-sex subgroups.

To further investigate the relationship between feeding competition and social behaviour, observed and expected rates of aggression, arm-wrapping and embraces occurring in a feeding context were compared. The observed percentage of female-female aggression occurring in a feeding context was significantly higher than expected [*t* (7) = 5.56, *p* = 0.001: Figure 4.3]. The mean percentage of female-female coalitionary arm-wrapping occurring in a feeding context was also significantly higher than expected [*t* (10) = 6.19, *p* = 0.001: Figure 4.3]. However, female-female embraces were not linked to feeding competition as there was no significant difference between the observed and expected percentage of female-female embraces occurring in a feeding context [*t* (15) = 0.21, *p* = 0.837: Figure 4.3]. Conversely, male social behaviour was not found to be related to feeding. There were no significant differences between the observed and expected percentages of male-male aggression [expected: 20.70 ±1.68, observed: 12.86 ±9.69; *t* (4) = 0.73, *p* = 0.504], arm-wrapping [expected: 21.65 ±1.07, observed: 24.06 ±4.48; *t* (10) = 0.56, *p* = 0.589] or embraces [expected: 21.65 ±1.07, observed: 19.91 ±5.42; *t* (10) = 0.24, *p* = 0.818] occurring in a feeding context.

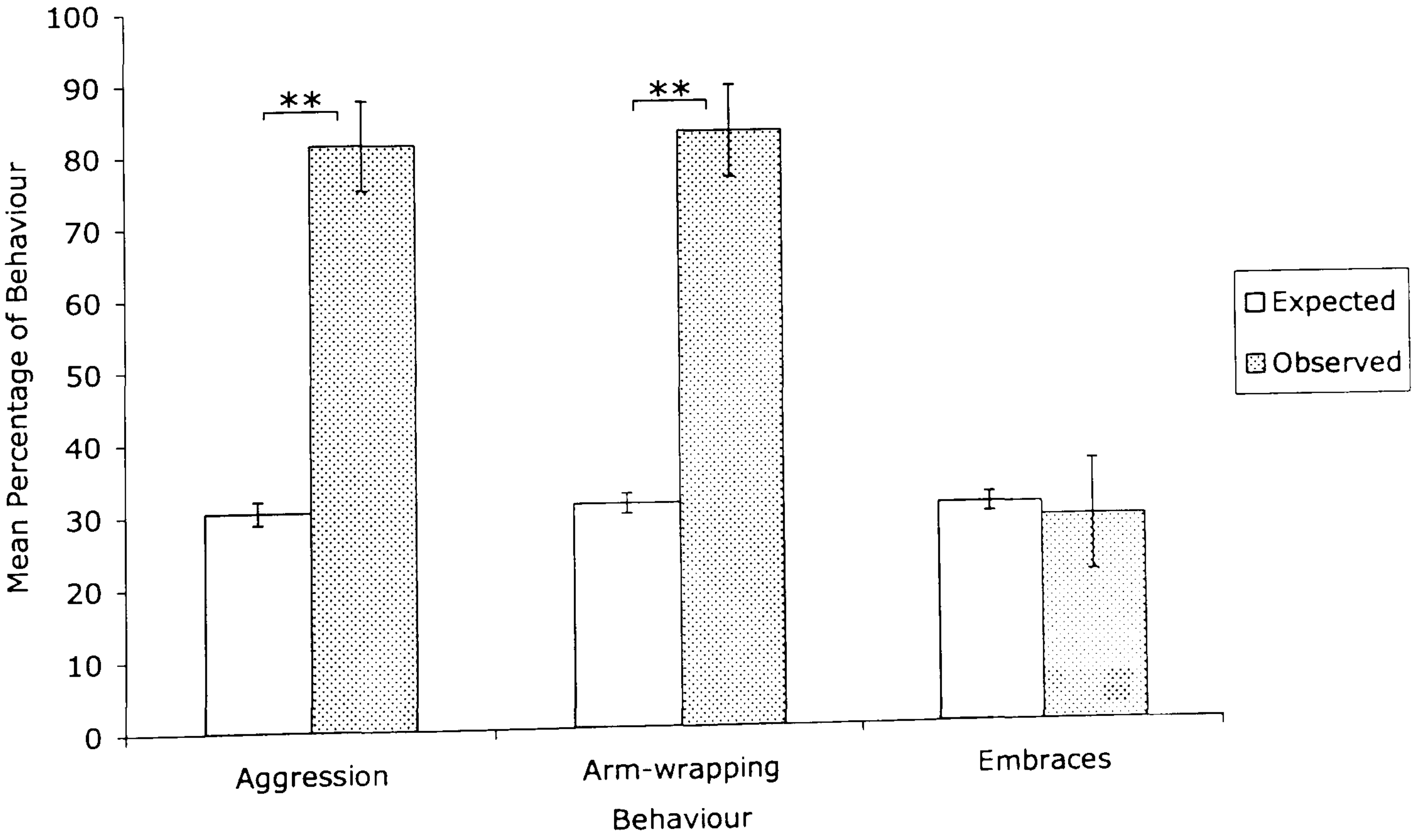

Figure 4.3: Mean (± S.E.M.) expected and observed percentage of female isosexual behaviour occurring in a feeding context.

As fusion events have been cited as a source of uncertainty, particularly among males, a large percentage of aggression, arm-wrapping and embraces were predicted to occur in the first five minutes following fusion. As predicted, the observed percentages of male-male aggression [*t* (4) = 3.76, *p* = 0.020: Figure 4.4], arm-wrapping [*t* (10) = 5.67, *p* < 0.001: Figure 4.4], and embraces [*t* (9) = 8.35, *p* < 0.001: Figure 4.4] occurring during fusion were significantly higher than expected. Female-female aggression and embraces were also higher than expected during fusion, although these differences were only approaching significance [expected aggression: 4.71 ±0.61, observed aggression: 21.31 ±8.39; *t* (7) = 1.83, *p* = 0.092; expected embraces: 5.32 ±0.46, observed aggression: 12.37 ±3.83; *t* (7) = 1.95, *p* = 0.088]. There were no significant differences between the expected and observed percentages of female-female arm-wrapping [expected: 4.98 ±0.47, observed: 10.56 ±4.67; *t* (11) = 1.15, *p* = 0.274].

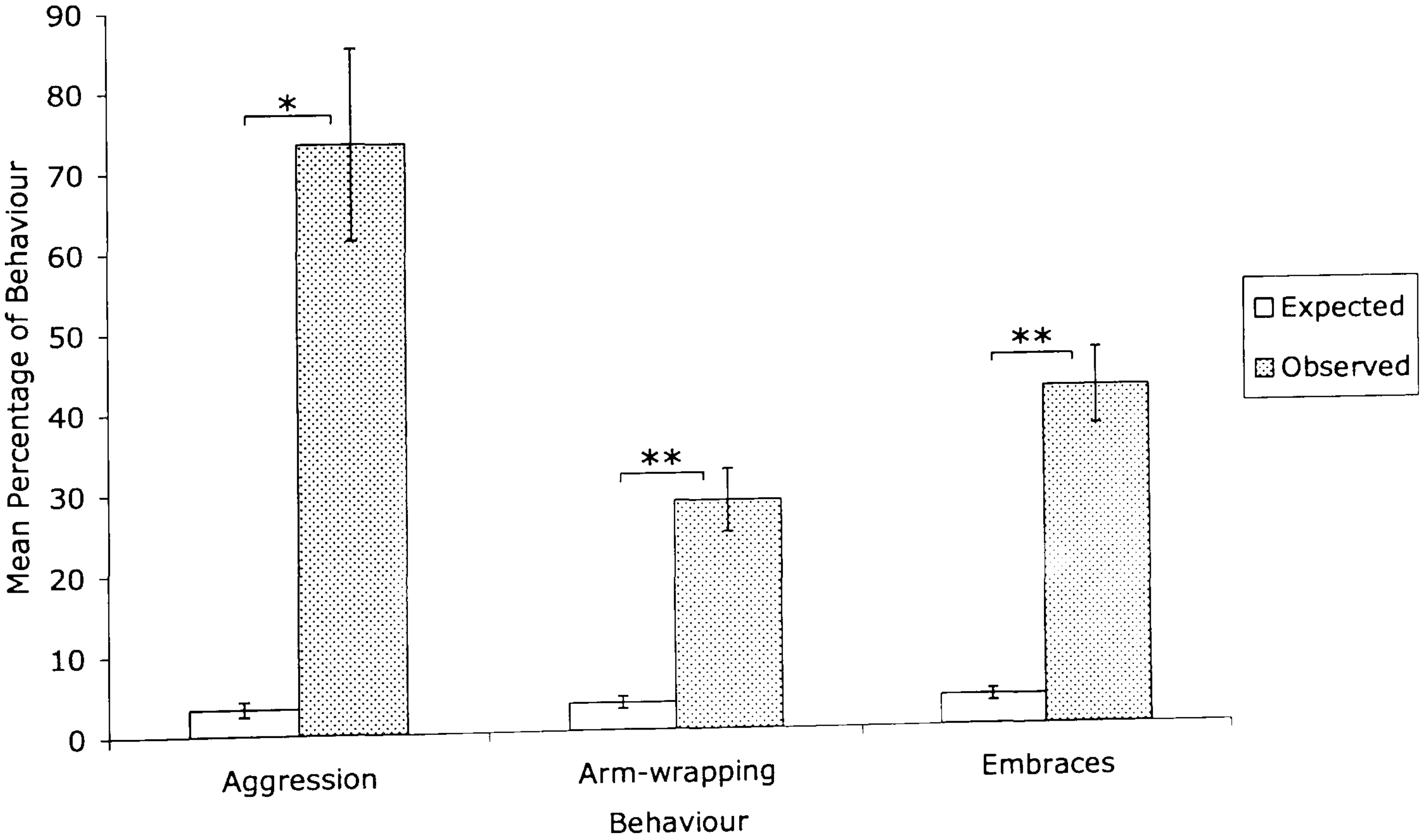

Figure 4.4: Mean (± S.E.M.) expected and observed percentage of isosexual aggression by males occurring during fusion.

4.8. Discussion

I investigated the context of spider monkey social behaviour with particular reference to contested resources and the high fission-fusion dynamic in this species' social organisation. One of the key aspects of flexible grouping is that community members are able to vary the amount of time they spend in solitary, in same-sex or mixed-sex subgroups. In line with previous studies, female spider monkeys at Punta Laguna spent on average, significantly more time alone than did males, which is likely to be a strategy to reduce feeding competition. Female-female competition for food is expected to be greater than that of males as the energetic requirements of pregnancy and lactation mean that female reproductive success is directly related to food intake (Emlen & Oring 1977; Janson, 1988; van Schaik, 1983). Like chimpanzees, spider monkeys are highly frugivorous and deplete the fruit trees in which they feed (Chapman, 1988). Therefore by foraging alone or in small subgroups during time of fruit scarcity, females can minimise contest competition for food without altering the degree of frugivory in their diet (Chapman, 1990; Chapman *et al.*, 1995; Symington, 1988a).

As predicted, males spent significantly more time in mixed-sex subgroups than did females, which may be attributed to male attraction to fertile females. Among chimpanzees and bonobos males are attracted to subgroups containing oestrus females and have a tendency to join them regardless of the number of high-ranking males already in the group, or the ecological costs of large groups (Anderson *et al.*, 2002; Boesch, 1996; Hohmann & Fruth, 2002; Matsumoto-Oda, 1999; Matsumoto-Oda *et al.*, 1998; Mitani *et al.*, 2002). This may also be the case for spider monkeys as, like chimpanzees and bonobos (Boesch & Boesch-Achermann, 2000; Nishida, Takasaki & Takahata, 1990; Kano, 1992), female spider monkeys have long inter-birth intervals compared to other non-human primates (Chapman & Chapman, 1989; Ramos-Fernandez *et al.*, 2003; Symington, 1987: PhD thesis cited in Ramos-Fernandez *et al.*, 2003), making them an extremely limited and scarce resource, and therefore the primary focus of male attention. Female spider monkeys do not advertise oestrus visually making it more difficult for males to assess the number of oestrus females in a subgroup, but it is possible that male spider monkeys are able to detect female oestrus using olfactory cues (Campbell, 2003; Chapter 6).

My results also indicate that females spent nearly 50% of their time in same-sex subgroups, which was significantly more than males. This finding is in line with data from Santa Rosa, Costa Rica in which same-sex subgroups containing more than one female and dependent offspring accounted for nearly 48% of all observations (Chapman, 1990). The energy requirements of lactating females are generally higher than those of other age/sex classes, therefore females with offspring will need to spend a high proportion of their time feeding and resting. Females may therefore associate together as they can coordinate their behaviour more readily with one another than with other conspecifics, and because these associations allow for the socialisation of their dependent offspring (Chapman & Chapman, 2000). However, such associations would only be beneficial in times of fruit abundance due to the associated costs of large subgroups.

That males spent significantly less time in same-sexed subgroups than females is likely the result of sampling bias rather than male behaviour. When in same-sexed subgroups, male spider monkeys range further and travel faster than subgroups with females and offspring (Chapman, 1990) making it extremely difficult for researchers to follow them. This was also the case at Punta Laguna as all-male subgroups often travelled very fast toward the boundaries of their home range, located in regenerating forest with poor visibility and few trails. Under these circumstances it was extremely difficult to follow the males and data collection was abandoned. The reported male preference for mixed-sex subgroups is therefore likely to be higher than the reality as I could not always collect data when males were in same-sex subgroups.

Flexible grouping was also found to have a significant effect on male and female isosexual social behaviour. Males arm-wrapped at a significantly higher rate when in mixed-sex compared to same-sex subgroups, but contrary to prediction, there was no significant difference in the rate of female-female arm-wrapping when in same-sex versus mixed-sex subgroups. These results may be explained by qualitative differences between male-male and female-female arm-wrapping. When arm-wrapping, spider monkeys often direct aggression towards a third party. For males this third party is most often a human observer or a random object, whereas for females, the third party is nearly always a female conspecific. It is therefore possible that male-male arm-wrapping serves to reaffirm and strengthening social bonds by uniting against a common enemy, which may be particularly needed when male social bonds are tested by the presence of females. Strengthening social bonds by uniting against a common enemy may also be true of female-female arm-wrapping, but for females this common enemy is a female conspecifc who may retaliate. Female-female arm-wrapping is therefore a more risky behaviour which is only likely to be used in aggressive situations. Although females spent more time feeding when in same-sex subgroups the difference was only slight and thus feeding competition, which is the primary source of conflict for females (Emlen & Oring, 1977; van Schaik, 1983), would not necessarily have been greater in same-sex subgroups. This may also explain why the rate of female-female aggression was not significantly greater in same-sex subgroups compared to mixed-sex subgroups.

Female-female aggression in the context of feeding was investigated directly using the special events data set, which contained all observed cases of aggression. Using this data, the percentage of female-female aggression that occurred in a feeding context was significantly higher than expected whereas male-male aggression was not. This pattern was repeated for coalitionary arm-wrapping, confirming that female spider monkeys primarily compete for access to food, whereas males do not. This finding is in line with theoretical predictions (Emlen & Oring 1977; van Schaik, 1983) and observations of female social interactions in other species characterised by high fission-fusion dynamics (Di Fiore & Fleischer, 2003; Furuichi, 1997; Printes & Strier, 1999; Wrangham *et al.*, 1992; 2000).

Approaches and embraces were also affected by subgroup type. Males approached and embraced one another at significantly higher rates when in mixed-sex subgroups compared to same-sex subgroups, whereas females approached and embraced one another at significantly higher rates when in same-sex subgroups. Embraces appear to signal benign intent and provide reassurance of continued cooperation (Schaffner & Aureli, 2005; Schaffner, *et al.*, 2003), thus individuals that share valuable relationships are expected to exchange embraces at high rates when in tension-loaded situations to mitigate the negative effects of aggression. The primary source of competition among males is access to fertile females (Emlen & Oring, 1977; van Schaik, 1983), thus it is likely that males experienced increased uncertainty surrounding their social relationships when in mixed-sex subgroups, and used embraces to reduce the likelihood of aggression. The primary source of competition among females is feeding competition, but as the percentage of time spent feeding in same-sex compared to mixed-sex subgroups was only slightly higher, it seems unlikely that the high rate of embraces in same-sex subgroups was a response to feeding competition. The high rates of female-female embraces occurring in same-sex subgroups was therefore most likely due to the presence of another tension-loaded situation such as infant handling (see Chapter 5).

In support of this view, there was no significant difference between the observed and expected percentage of female-female embraces that occurred in a feeding context. As embraces are considered a signal of benign intent and continued cooperation during tense situations, it appears paradoxical that females did not exchange embraces when feeding. However, the overall rate of female-female aggression in Punta Laguna was very low (0.03 bouts hr^{-1}) and females were never observed to bite or wound female conspecifics, thus it is possible that the potential for isosexual aggression was not a major problem for females and did not warrant the use of embraces. Furthermore, female-female relationships in spider monkeys are generally of low-quality (Fedigan & Baxter, 1984; Symington, 1990; Chapter 3), thus the potential risk of damage to isosexual relationships caused by aggression may not be a major concern for females. As predicted, male-male embraces were not affected by the presence food.

The special events data were also used to investigate the context of fusion on male and female behaviour. The first five minutes following a fusion event have been cited as a period of uncertainty as during this time individuals must rapidly assess their relationships with conspecifics that they have not been in contact with for some time. In both chimpanzees and spider monkeys, aggression is reported to occur at a high rate during this period (Aureli & Schaffner, in prep; Goodall, 1986; Muller, 2002; Schaffner *et al.*, 2003), however in chimpanzees, only male-male aggression is increased in the context of fusion (Goodall, 1986; Muller, 2002). A similar pattern was reflected in my results as the percentage of aggression that occurred in the context of fusion was significantly higher than expected for males but was only approaching significance for females. The percentage of male-male arm-wrapping that occurred in the context of fusion was also significantly higher than expected, but female-female arm-wrapping was unaffected by fusion. Embraces are also reported to occur at higher rates following fusion in chimpanzees and spider monkeys (Goodall, 1986; Nishida *et al.*, 1999; Schaffner & Aureli, 2005, in press), although sex differences in this behaviour have not been reported. As with aggression, the observed percentage of embraces that occurred in the context of fusion at Punta Laguna was significantly higher for males but only approached significance for females.

These differences between male and female behaviour in the context of fusion can be related to sex differences in the frequency and intensity of aggression, and the value and security of social relationships (c.f. Cords & Aureli, 2000). As previously mentioned, female-female aggression in spider monkeys is infrequent and mild, and female social relationships are of low quality (Chapter 3). Thus, when compared to male spider monkeys, females have less to fear from same-sex conspecifics during fusion events, and as their relationships are not particularly valuable, uncertainty surrounding their social relationships is not necessarily a major source of concern. However, as the increase in aggression and embraces during fusion was approaching significance, this is an area that warrants further research.

Male-male aggression, although far from frequent, can be intense and injurious (Chapter 3), and has been observed to be fatal (Valero *et al.*, 2006; Campbell in press). Therefore uncertainty surrounding male social relationships is likely to be high. Male social relationships are also valuable, as males rely on male conspecifics to defend community females from extra-community males (Aureli *et al.*, 2006), such that the potential costs of damaging their relationship with aggression are predicted to be high. Indeed, arm-wrapping and aggression between males occur more frequently than expected at fusion. Therefore, in order to reduce the likelihood of aggression and reassure valuable male conspecifics of continued cooperation, males must rapidly signal their benign intent to male conspecifics by using embraces at fusion. In support of this explanation, data from spider monkeys indicate that individuals that embraced following fusion were less likely to be aggressive towards one another (Aureli & Schaffner, in prep). Embraces appear therefore to be related to tension reduction and conflict management at fusion.

In conclusion male and female spider monkeys compete for different resources: females compete for access to food, whereas males compete for access to fertile females. Female-female social interactions occurred more frequently in same-sex subgroups compared to mixed-sex subgroups, which may have been due to an increase in time spent feeding. Male-male social interactions occurred more frequently in mixed-sex subgroups, which is likely due to increased uncertainty surrounding their relationships caused by the presence of females. Male-male social interactions also occurred at higher than expected rates following fusion, which is likely because male-male relationships are generally of higher quality, but are less secure than female-female relationships. There was however one finding that was somewhat puzzling and therefore warranted further investigation, namely that female-female embraces were not related to feeding, but occurred at significantly higher rates when in same-sex subgroups. It is therefore possible that females use embraces to signal benign intent in another tension-loaded context that occurs more frequently in same-sex subgroups (Chapter 5).

Chapter 5

The Effect of Infants on Female Social Relationships

5.1. The 'infant effect'

The costs and benefits of dyadic social interactions are dependent on the relative 'value' each individual allocates to potential partners (Kummer, 1978), which determines the exchange rate for desirable commodities and services (van Schaik & Aureli, 2000). One factor that appears to affect relationship value in female primates is the presence of young infants. Female primates are intensely interested in other females' infants and are highly motivated to interact with them. Among Old World monkeys for example, females with young infants spend more time in close proximity to other female conspecifics, receive less aggression and receive more affiliative behaviour than females without infants (e.g. Hinde & Powell-Proctor, 1977; Maestripieri, 1994a; Martel, Nevison, Rayment & Simpson, 1994; Muroyama, 1994; Seyfarth, 1980). Mothers receive more affiliative behaviour than they give and social interactions are generally maintained by the female partners, rather than the mothers (Hinde & Powell-Proctor, 1977; Maestripieri, 1994a; Muroyama, 1994). Mothers receive significantly more affiliative behaviour when in physical contact to their infants (Hinde & Powell-Proctor, 1977), suggesting that these social encounters are driven by female attraction to the infant rather than the mother. Preliminary evidence also suggests that female attraction to infants is hormonally modulated by reproductive state (Maestripieri & Wallen, 1995). Furthermore, affiliative behaviour received by the mother is negatively correlated with infant age, as when the infant becomes older it spends less time in physical contact to its mother and other females are able to interact with the infant directly rather than using the mother as a means of gaining access to her infant (Hinde & Powell-Proctor, 1977; Maestripieri, 1994a).

In some species (e.g. capped langurs: *Presbytis pileata*) female attraction to infants extends to alloparental care, which benefits the handler by providing experience of mothering, and the mother by providing more time to rest and forage for food (Stanford, 1992). These kinds of interactions can be described as positive infant handling (Maestripieri, 1994b; Paul & Kuester, 1996; Schino, Speranza, Ventura & Troisi, 2003). In the majority of species however, attraction to infants does not result in direct care and is restricted to just a few seconds of contact. Group females often crowd around new mothers and attempt to greet, sniff, nuzzle and inspect newborn infants while they are in contact with their mothers (e.g. Altmann, 1980; Maestripieri, 1994a, 1994b; O'Brien & Robinson, 1991; Paul & Kuester, 1996; Silk, 1999). Such brief interactions with infants are unlikely to be particularly beneficial to either the mother or handler, but can be explained as a by-product of selection for appropriate maternal care because females who are intensely attracted to infants will likely make good mothers (Paul & Kuester, 1996; Silk, 1999). Such interactions are best described as neutral infant handling as they do not provide any obvious costs or benefits to the mother or infant (Maestripieri, 1994b; Paul & Kuester, 1996; Schino, *et al.*, 2003).

Infant-handler interactions may also involve excessively rough pulling of the infant away from the mother, interruptions to suckling, and in some species, the actual kidnapping of infants (rhesus macaques: Maestripieri, 1993a; white-faced capuchins: Manson, 1999; bonnet macaques: Silk, 1980; 1999; Barbary macaques: Paul & Kuester, 1996; capped langurs: Stanford, 1992). These infant-handler interactions can be described as negative infant handling (Maestripieri, 1994b; Paul & Kuester, 1996; Schino, *et al.*, 2003). Potentially damaging infant handling can be quite common in female primates, especially if the mother and handler are unrelated (e.g. Maestripieri, 1994a; 1994b; Schino et *al.*, 2003). Among New World monkeys, negative infant-handling was rarely observed among closely related female capuchins (Manson, 1999), but among unrelated female spider monkeys, injurious interactions with infants have been observed in a number of cases (Chapman, Fedigan, Fedigan & Chapman, 1989).

Although attraction to infants makes infant handling a desirable service, it does not provide any direct benefit for the mother and may have negative fitness consequences for the infant. Even neutral infant handling carries a potential risk as nearly all instances of negative infant handling stem from neutral interactions (Schino *et al.*, 2003) and it is not possible for the mother to determine the outcome of each handling bout *a priori*. Consequently, infant handling is likely to be an anxiety-eliciting situation for mothers (e.g. rhesus macaques: Maestripieri, 1993b), thus mothers are expected to be reluctant to grant access to their infants (Maestripieri, 1994a). Females wishing to handle infants must therefore reassure the mother that no harm will come to her infant. Potential handlers may achieve this by signalling their benign intent or by offering a service of their own to be exchanged with the mother for access to her infant. One such service is social grooming.

5.2. Social grooming as a service

As social grooming concentrates on the parts of the body that the recipient cannot reach (Barton, 1985), it provides a service that cannot be attained alone. Grooming appears to have fitness benefits directly through the removal of ectoparasites (Hutchins & Barash 1976; Saunders 1988: PhD thesis cited in Henzi & Barrett, 1999) and indirectly through increased sociality (Silk, Alberts & Altmann, 2003). Grooming also triggers the release of β-endorphins, resulting in a highly pleasurable experience for recipient (Keverne *et al.*, 1989) and has been linked to reduced risk of aggression (Fairbanks, 1980; Silk, 1982), and tension reduction (Aureli *et al.*, 1999; Schino *et al.*, 1998). Social grooming is therefore a desirable service. Social grooming is however a time-consuming behaviour (Seyfarth, 1980), and as daily activity budgets are heavily constrained by time (Dunbar, 1992); individuals should be reluctant to offer this service without some kind of reward in exchange. Owing to the various benefits to the recipient, it seems reasonable to consider social grooming as a payoff currency in its own right and so bouts of social grooming may be traded directly (Henzi & Barrett, 1999). Consequently, grooming bouts may be exchanged on a cooperative and reciprocal basis to ensure that all individuals reap the benefits of social grooming. These bouts should therefore be approximately time-matched (e.g. Barrett & Henzi, 2001; Muroyama, 1991).

If social grooming is a valuable service, then it should also be possible to trade grooming for some 'value equivalent' resulting in two different trader classes: 'reciprocal traders', who exchanged grooming with one another, and 'interchange traders' who exchange grooming for other commodities (Hemelrijk & Ek, 1991). As these trader classes are relative and not absolute, each individual has the potential to be both types of trader depending on their value in relation to their social partner. For example, a nulliparous female may choose to be a reciprocal trader when interacting with another non-mother but when interacting with a mother, she may choose to be an interchange trader offering grooming in exchange for infant access (Barrett & Henzi, 2001, 2006; Henzi & Barrett, 2002).

Within the 'Biological Markets' paradigm, decisions regarding exchange partners will be influenced by 'exchange rate' of commodities, determined by the need for the commodity and the trader's ability to outbid the competition (Noë & Hammerstein, 1994, 1995). Evidence to support these predictions has been provided by two studies of female chacma baboons (Barrett *et al.*, 1999; Henzi & Barrett, 2002), the latter of which has since been extended to include additional data (Barrett & Henzi, 2006). In the first study, social grooming interactions reflected the market value of tolerance at feeding sites. When feeding competition was low, grooming bouts were time-matched irrespective of rank distance, but when feeding competition increased, high-ranking females received more grooming than they gave possibly because they could exchange grooming for tolerance at feeding sites (Barrett *et al.*, 1999). In the second study, grooming bouts between mothers and non-mothers, initiated by potential handlers, were often accompanied by infant handling (Henzi & Barrett, 2002). Such grooming bouts were significantly less likely to be reciprocated by the mother than grooming bouts that did not involve infant-handling, suggesting interchange of grooming for infant-handling. Availability of infants created a market effect as the 'price' paid for infant handling (i.e. amount of grooming time invested by the potential handler) was inversely related to the number of infants present in the group (Barrett & Henzi, 2006; Henzi & Barrett, 2002).

Other studies have also emphasised the importance of social grooming as a commodity in Old World monkeys (Cooper & Bernstein, 2000; Hemelrijk, 1994; Manson, Navarrete, Silk & Perry, 2004; Payne, Lawes & Henzi, 2003) and apes (Hannah-Stewart, 2004), but the relative importance of social grooming to New World monkeys has received far less attention (Schino, 2001). Social grooming interactions among the female-bonded capuchins follow a similar pattern to the Old World monkeys both in the wild (Perry, 1996) and captivity (di Bitetti, 1997; Parr, Matheson, Bernstein & de Waal, 1997) and as with Old World monkeys, time-matching of grooming bouts is affected by dominance rank (Manson *et al.*, 2004). In addition to capuchins, grooming as a means of maintaining social bonds has been cited for wild woolly monkeys (Di Fiore & Fleischer, 2005; Stevenson, 1998), marmosets (Evans & Poole, 1984; Schaffner, Shepherd, Santos & French, 1995) and for closely related females in a captive group of spider monkeys, where grooming was associated with co-feeding (Pastor-Nieto, 2001). However, studies of other captive groups of spider monkeys have reported very low rates of social grooming, (e.g. Klein & Klein, 1971; Schaffner & Aureli, 2005) and even lower rates have been reported from the wild, especially among females (Ahumada, 1992; Fedigan & Baxter, 1984; Symington, 1990; Chapter 3). Grooming is also virtually absent in the closely related muriqui

(Strier, 1992; 1994) suggesting that both spider monkeys and muriquis rely on other behaviours to regulate and maintain their social relationships.

5.4. Spider monkey embraces

Female spider monkeys rarely groom and appear to regulate their social relationships using embraces, kisses and pectoral sniffs (Fedigan & Baxter, 1984; Klein & Klein, 1971; Schaffner & Aureli, 2005; Chapters 3 and 4). Embraces have also been observed in muriquis (Strier *et al.*, 1993), and chimpanzees (Goodall, 1986), which, like spider monkeys, have a high fission-fusion dynamic in their societies. In both chimpanzees and spider monkeys, embraces are exchanged during periods of uncertainty such as fusion events (Goodall, 1986; Nishida *et al.*, 1999; Schaffner & Aureli, 2005), and have been interpreted as a signal of benign intent (Schaffner & Aureli, 2005; Schaffner *et al.*, 2003; Chapter 4).

Embraces may also enable spider monkeys to gain access to desirable commodities. In a group of captive spider monkeys, rates of embraces were positively correlated with rates of co-feeding (Pastor-Nieto, 2001) and in another captive group, females received significantly more embraces in the first six months after the birth of their infant (a period during which the infant is almost always on, or in close proximity to the mother) compared to before the birth (Schaffner & Aureli, 2005). Similarly, in a wild group of spider monkeys, females with infants received more embraces than females without infants (Fedigan & Baxter, 1984). Among Old World monkeys and apes, individuals are more likely to be granted access to commodities such as food and infants on receipt of social grooming. As spider monkeys rarely groom, it is possible that individuals gain access to commodities by exchanging embraces.

5.5. Chapter aim and predictions

Evidence from captive spider monkeys suggests that embraces may be exchanged for access to desirable commodities such as food and young infants. As social grooming is rarely exchanged in this species, and the primary source of affiliative interaction is embraces, it may be possible that embraces are considered a service. 'Reciprocal traders' of embraces may therefore exchange embraces directly (Chapter 3) but in the presence of a commodity with a high market value individuals may opt to become 'interchange traders'. This chapter therefore aims to investigate the effect of infants on female social interactions with particular reference to the exchange of embraces for infant handling within a biological market place. This aim will be achieved by testing a number of predictions adapted from Henzi and Barrett (2002).

If female spider monkeys direct affiliative behaviour towards mothers as a means of gaining access to their infants then the following predictions can be made. Firstly, females should receive significantly more affiliative behaviour when they have young infants compared to all other times. Secondly, as spider monkeys appear to use embraces to regulate their social relationships then it follows that embraces, but not grooming, should be the primary affiliative behaviour directed towards the mother. If embraces act as a commodity exchanged for infant handling then a further two predictions must be supported, namely: when embraces are exchanged for infant handling then these interactions should be initiated by the potential handler rather than the mother, and females will be less likely to reciprocate embraces when they have young infants compared to all other times.

Although infant handling as a commodity is likely to retain its high market value to females who have infants of their own (Maestripieri & Wallen, 1995), access to other females' infants may no longer be dependent on embraces and may be achieved by trading infant-handling directly. It is therefore reasonable to predict that females with young infants are more likely to receive embraces from non-mothers rather than other mothers, and mothers may trade infant handling reciprocally without the need for embraces. If embraces are exchanged for infant handling within a biological market place then these interactions will be subject to fluctuations in the exchange rate of commodities. It can therefore be predicted that the number of bouts of infant handling received per embrace given will decrease with fewer other infants available in the group.

5.6. Methodology

5.6.1. Subjects

Sixteen focal females gave birth to infants during the study, which in the majority of cases (73.3%) were born during a birth peak between November and February. Of these 16 females, one female was excluded from the analyses due to insufficient observations after the birth of her infant. Of the remaining 15 females, four were likely primiparous and were estimated to be seven to nine years of age. The other 11 females were multiparous and at least 13 years of age as they were fully adult at the beginning of the long-term project in 1997. No indication of a dominance hierarchy among females was detected in either community (Chapter 3). For each of the 15 females data were divided into two separate periods: when the female had an infant <6 months old, and all other times. These two periods were chosen because when infant spider monkeys are less than six months of age they spent virtually all their time on, or in extremely close proximity to their mother (Symington, 1987) and access to the infant is entirely dependent on social tolerance from the mother. For the purpose of analyses, females were considered to be 'mothers' when they had infants <6 months old, and 'non-mothers' at all other times.

5.6.2. Data Collection

Data for the 15 females was collected using focal animal sampling with continuous recording using the behaviours listed in Chapter 2. Following Silk (1999), infant handling was defined as greeting, sniffing, nuzzling and inspecting newborn infants while they were in contact with their mothers. In spider monkeys these bouts of infant handling only last a few seconds, thus infant handling was measured as an all-or-nothing event. Cases of embraces, pectoral sniff and infant handling were also collected *ad libitum*. For the purpose of analyses, mutual embraces (i.e. where two monkeys embraced simultaneously) were classed as reciprocated embraces. The individual that approached was classed as the initiator of the embrace and the recipient of the approach was classed as the recipient of the embrace.

5.6.3. Data analysis

Two-way repeated measures ANOVAs were used to examine whether there were differences in approaches, embraces or grooming levels depending on subjects' maternal status (mother or non-mother) and direction of behaviour (given or received). Where significant interactions were obtained from the ANOVAs, un-confounded comparisons of the means were made post-hoc using Cicchetti's modification of Tukey's HSD test (Schweigert, 1994) with Howell's correction for repeated measures (Howell, 2002). The mean percentage of approaches followed by embraces, and the mean rates of embraces received by mothers from other mothers and non-mothers were compared using repeated measures t-tests. Reciprocity of embraces received by females when classed as mothers and non-mothers was also compared using a repeated measures t-test, although as some females did not exchange any embraces when they were non-mothers, reciprocity could only be compared for 7 of the 15 focal females. A sign test was used to determine whether the mothers or potential handlers initiated embraces followed by infant handling.

The exchange rate of embraces for infant handling was calculated in terms of the number of bouts of infant handling procured per embrace given to the mother using data from *ad libitum* and focal samples. It was not possible to investigate the effect of infant availability on the embrace-for-infant-handling exchange rate at the individual level because very few subjects were mothers for all possible categories of infant availability (1, 2, 3 or 4 infants present in the community), but most were mothers in more than one category, thus preventing independent or repeated measures analysis. Therefore, we performed the analysis at the dyadic level, for which the sample size was sufficient to include only the exchanges of embraces for infant handling from one category of infant availability per dyad. Where dyads exchanged embraces and infant handling in more than one category of infant availability, one category of data was chosen at random and included in the analysis. This method enabled a one-way independent measures ANOVA to be performed followed by Tukey's HSD tests. Similar analyses were performed for the distribution of infant age (means of infant age for the various embrace-for-infant-handling interactions of the same dyad within the same category of infant availability). All statistical analyses were two-tailed.

5.7. Results

A significant interaction between female reproductive state and direction of approaches indicated that females gave and received approaches differently when they were mothers compared to when they were non-mothers [F (1, 28) = 29.96, $p < 0.001$: Figure 5.1]. Post-hoc analysis indicated that subjects received significantly more approaches as mothers than as non-mothers ($P < 0.01$), but approached others less often as mothers than as non-mothers ($P < 0.01$). In addition, mothers were approached more often than they approached others ($P < 0.01$), whereas when those same subjects were non-mothers they approached others more frequently than they were approached ($P < 0.05$). These results confirm that adult female spider monkeys are attracted to young infants such that mothers are approached more often than non-mothers. This pattern was not however replicated in the percentage of time females spent grooming, which appeared to be unaffected by the presence of infants (mothers: 0.02 ± 0.01 given, 0.20 ± 0.18 received; non-mothers: 0.14 ± 0.12 given, 0.00 ± 0.00 received). No significant differences in grooming interactions between mothers and non-mothers were found either as a main effect of direction of behaviour [F (1, 28) = 0.06, p = 0.817], maternal status [F (1, 28) = 0.18, $p = 0.679$] or as and interaction between the two variables [F (1, 28) = 2.22, $p = 0.147$].

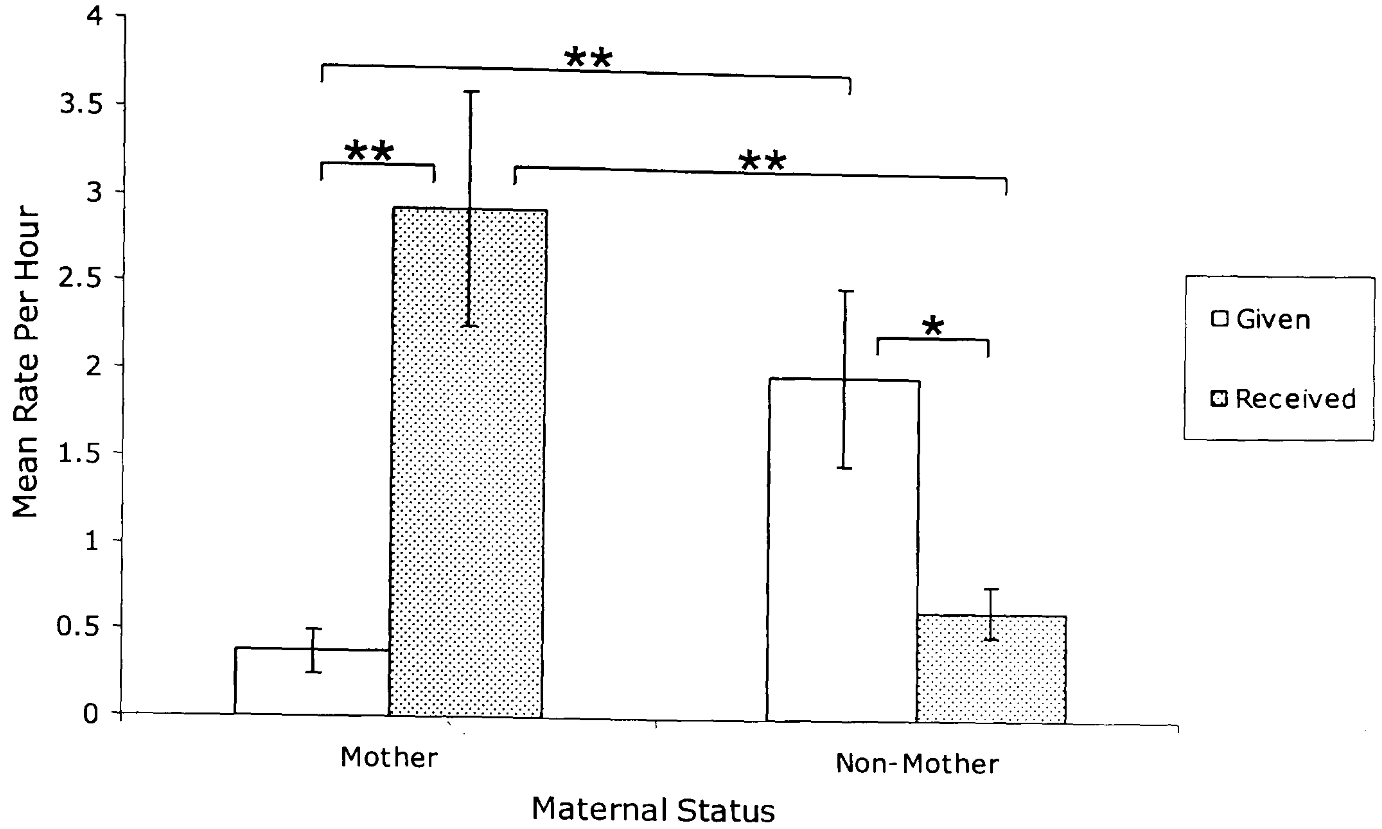

Figure 5.1: Mean (± SEM) hourly rates of approaches given and received by females when they were mothers compared to when they were non-mothers.

In contrast to the grooming results, rates of embraces were influenced by the presence of infants, indicated by a significant interaction between embraces given and received by mothers and non-mothers [F (1, 28) = 14.47, p = 0.001: Figure 5.2]. Post-hoc analysis indicated that mothers received significantly more embraces than non-mothers (p <0.01) and received significantly more embraces than they gave (p <0.01). These results further confirm that female spider monkeys are attracted to young infants, and in line with prediction, embraces appear to be the primary affiliative behaviour directed towards mothers as a means of gaining access to her infant. Furthermore, the increased rate of embraces received when females had infants was not simply driven by the increase in approaches received because the percentage of approaches immediately followed by embraces was significantly higher when females were mothers compared to non mothers [t (14) = 2.31, p = 0.036: Figure 5.3].

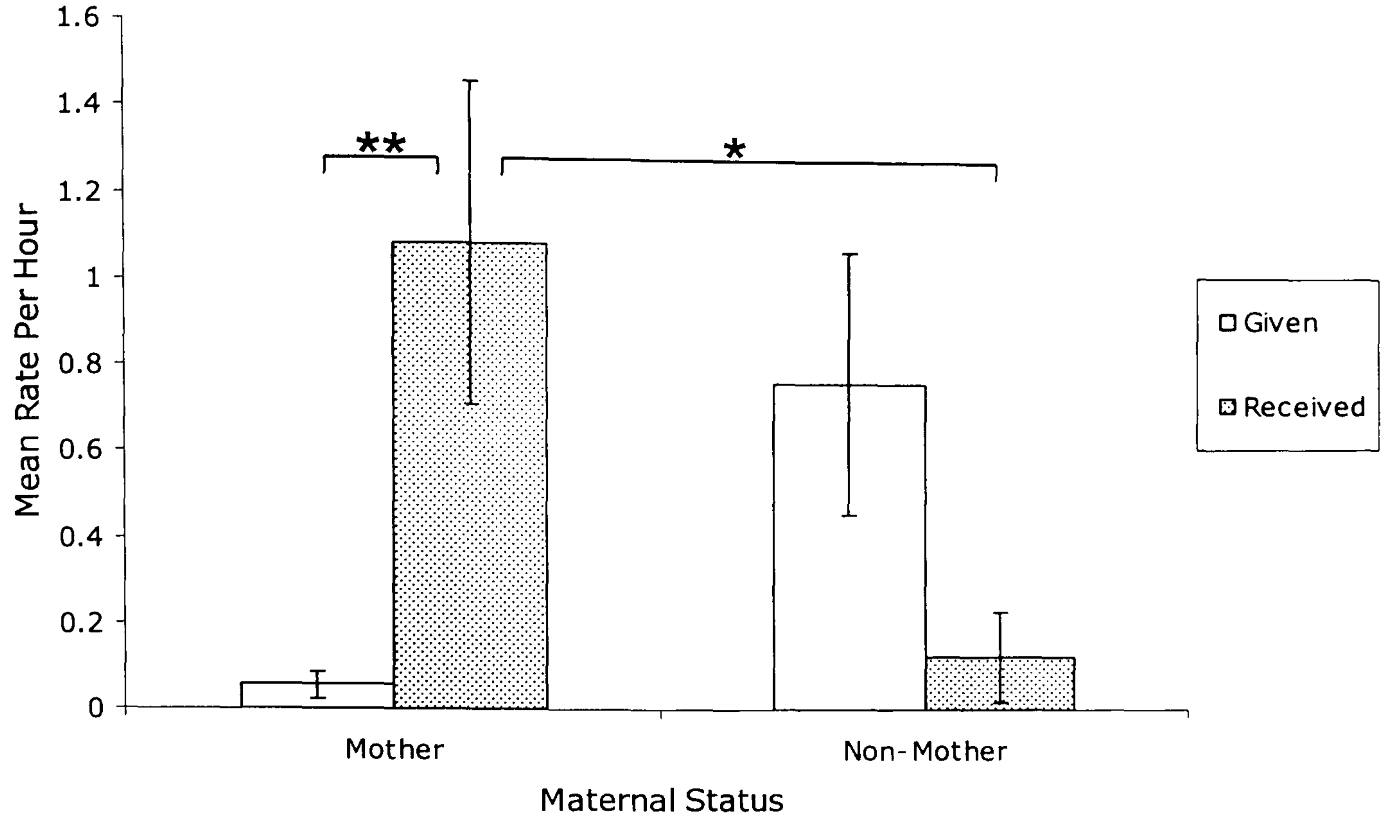

Figure 5.2: Mean (± SEM) hourly rates of embraces given and received by females when they were mothers compared to when they were non-mothers.

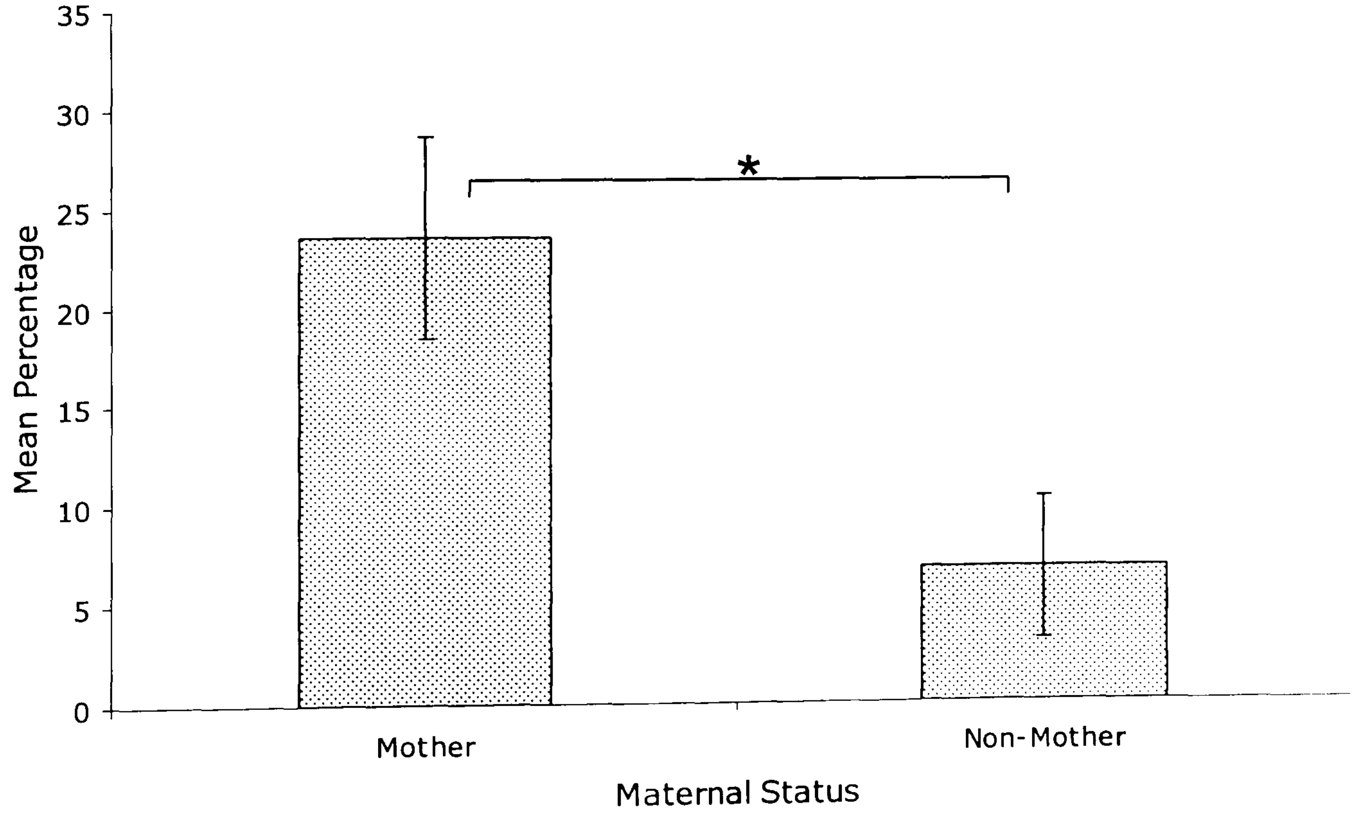

Figure 5.3: Mean (± SEM) percentage of approaches followed by embraces received by females when they were mothers compared to when they were non-mothers.

Given that grooming distributions were not affected by the presence of infants, the following analyses focused only on embraces. All embraces followed by infant-handling were initiated by the potential handler rather than the mother [sign test: N = 15, x = 0, *p* <0.001], and the percentage of embraces reciprocated by the recipient was significantly lower when the recipients were mothers compared to when they were non-mothers [0.05% compared to 34.57%: *t* (7) = -7.291, *p* <0.001]. Females who did not have infants of their own were more likely than mothers to use embraces as a means of gaining access to infants. Mothers received embraces at a significantly higher rate from non-mothers than from other mothers [*t* (14) = 3.07, *p* = 0.008: Figure 5.4]. Three instances of direct exchanges of infant handling were observed. In all cases the two mothers sat in close proximity and simultaneously handled each other's infant. Embraces were not exchanged during these interactions and bouts of infant handling lasted longer than the typical few seconds when embraces were exchanged for infant handling. In all three cases, the mothers had infants of a similar age, <2 months difference in age.

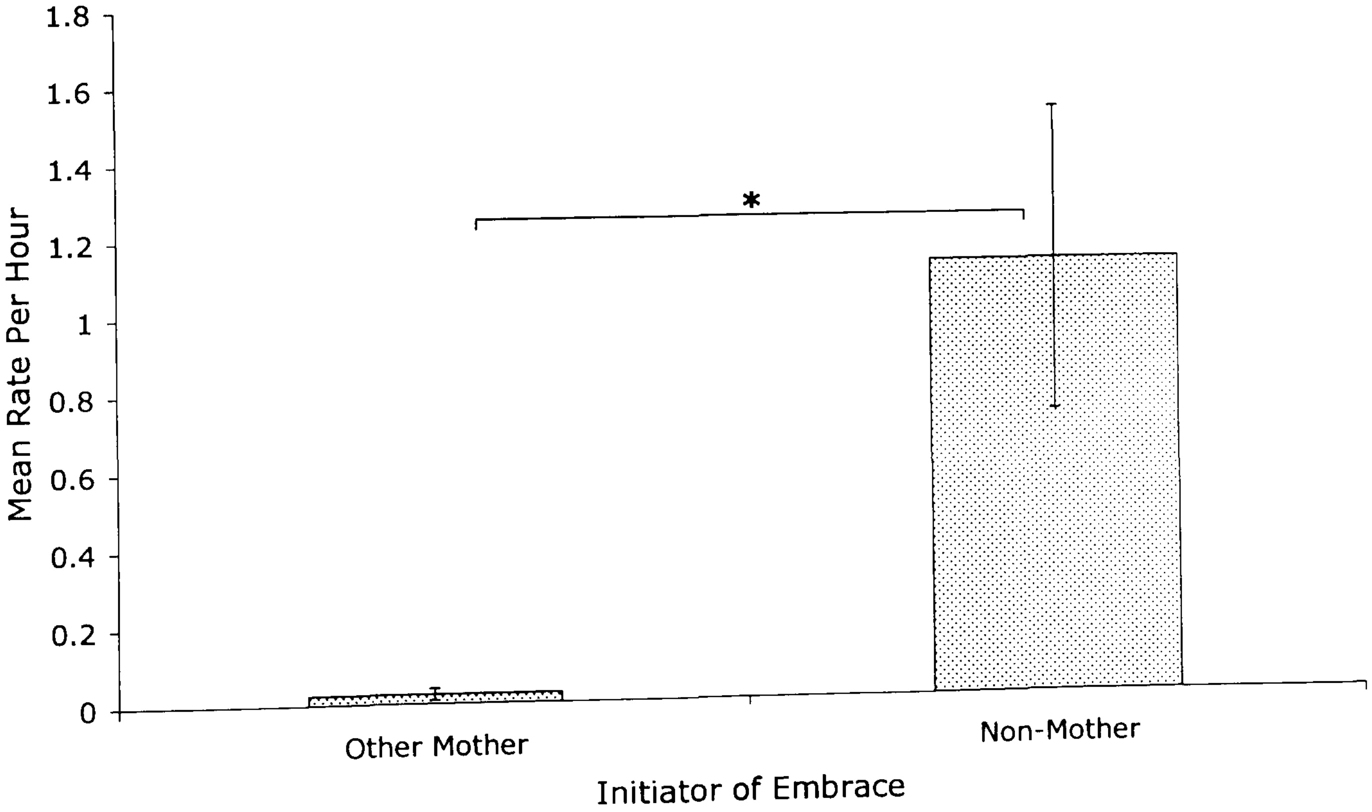

Figure 5.4: Mean (± SEM) rate per hour of embraces received by mothers from other mothers and non-mothers.

Although not recorded systematically, *ad libitum* observations suggested that maternal response to infant handling was determined by embraces, as in the few cases where non-mothers, attempted to handle infants without first embracing the mother, the mother turned away from the handler creating a physical barrier between her infant and the potential handler. Mothers responded to persistent unwanted attempts to handle infants by moving away from the handler, taking their infants with them. No cases of aggressive attempts to handle infants, or aggressive responses to infant handling by the mother were observed.

The final prediction tested referred to the fluctuations in the embrace-for-infant-handling exchange rate caused by variable infant availability. As predicted, there was a significant effect of infant availability on the exchange rate of embraces for infant handling. The number of bouts of infant handling received per embrace was significantly lower when there were fewer other infants available in the community [F (3, 23) = 4.31, p = 0.015: Figure 5.5]. Tukey's HSD post-hoc analysis confirmed a significant difference in exchange rate between 0 and 3 other available infants only (p = 0.017) and a difference between 0 and 2 available infants that was approaching significance (p = 0.066). This result was not confounded by a higher level of attractiveness when only one infant was available, as the rates of approaches received by mothers did not map on the expected pattern based on the exchange of embraces for infant handling [1 infant: 0.46 ± 0.12; 2 infants: 1.45 ± 0.19; 3 infants: 0.49 ± 0.11; 4 infants: 0.75 ± 0.20; F (3, 23) = 0.719, p = 0.513].

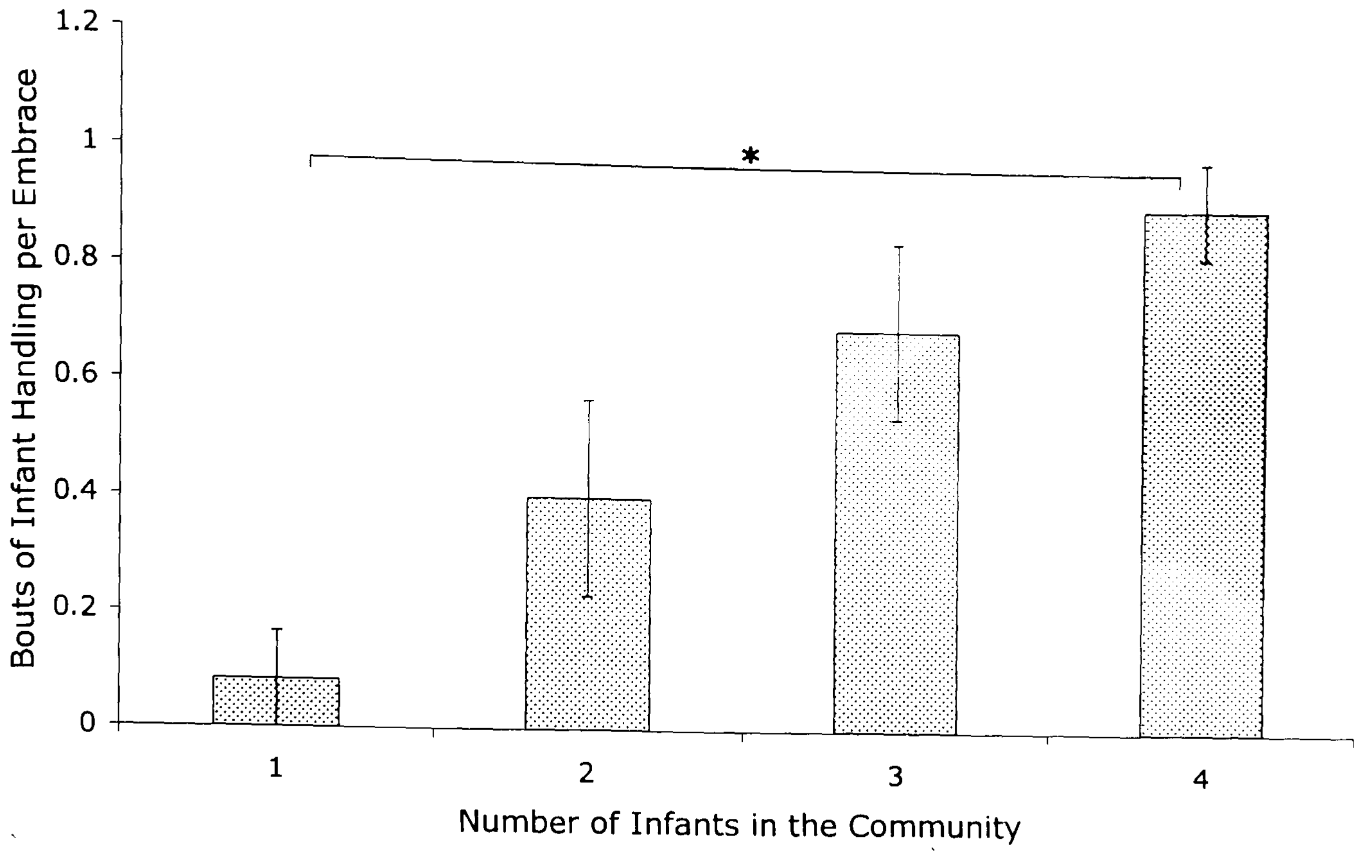

Figure 5.5: Variation in mean (± SEM) bouts of infant handling received per embrace given depending on availability of infants present in the group.

5.8. Discussion

Based on previous studies of the effect of infants on female social relationships, it was predicted that female spider monkeys would receive more affiliative behaviour when they were mothers compared to when they were non-mothers. It was also predicted that, as spider monkeys groom so infrequently, embraces, but not grooming interactions, would be affected by the presence of infants. Both of these predictions were supported as females received significantly more approaches and embraces when they were mothers compared to when they were non-mothers, whereas the rate of grooming received was unaffected. The increased rates of embraces and approaches received were not due to increased sociality on the part of the mother, as females approached and embraced female conspecifics at significantly lower rates when they were mothers compared to when they were non-mothers and always received more than they gave. Moreover, the increased rate of embraces received by mothers was not driven by the increased rate of approaches, suggesting that embraces were used to gain access to infants and were not just a by-product of female interest in others' infants.

Collectively, these findings indicate that female spider monkeys are attracted to others' infants and are highly motivated to interact with them. My results also indicate the presence of infants had a significant affect on female-female social relationships as 83% of all female-female embraces were exchanged in the presence of young infants, and the mean rate of embraces received by mothers was similar to the overall rate of male-male embraces described in Chapter 3 (mothers: 1.09 ± 0.37, males: 1.17 ± 0.35). However, it is important to remember that this increased attractiveness to other females is only temporary and when averaged over a longer time scale, female-female social relationships in spider monkeys are generally described as low quality (Fedigan & Baxter, 1984; Chapter 3). Thus, females with young infants become more valuable because while the infant remains in close proximity to its mother, access is dependent on tolerance from the mother (e.g. Hinde & Powell-Proctor, 1977; Maestripieri, 1994a). Consequently, females embrace mothers in exchange for infant handling. In support of this view, exchanges of embraces and infant handling were always initiated by the handler rather than the mother, and mothers were significantly less likely to reciprocate embraces than non-mothers.

Similar results have been reported in a captive group of spider monkeys where females received increased rates of embraces, but not grooming, when they had young infants (Schaffner & Aureli, 2005). This relationship between embraces and the presence of young infants has also been reported in two other studies. In the first study, a female received more embraces and pectoral sniffs following the birth of her infant, but when the infant died the level of embraces and pectoral sniff returned to pre-birth levels (Eisenberg & Kuehn, 1966) and in the second study of wild spider monkeys (Fedigan & Baxter, 1984), females with infants received higher rates of embraces. As data from captive spider monkeys (Schaffner & Aureli, 2005) and data from the wild (Schaffner, *et al.*, 2003) suggest that spider monkeys regulate their social relationships with embraces rather than grooming, then it is possible that embraces may be exchanged within a biological market place.

To investigate exchanges of embraces for infant handling within the biological markets paradigm (Noë & Hammerstein, 1994; 1995), two different trader classes were identified: 'reciprocal traders' and 'interchange traders'. It was predicted that because non-mothers have no infants of their own with whom to interact, they would act as interchange traders with mothers, offering embraces in exchange for infant handling. Conversely, mothers already have infants of their own and are expected to be less motivated to offer embraces for access to other's infants. If mothers do wish to interact with other's infants however, then they have the option of trading infant-handling reciprocally and do not have to offer embraces. Both these predictions were supported as female spider monkeys with young infants were significantly more likely to receive embraces from non-mothers than from other mothers and in three separate occasions, mothers were observed to exchange infant-handling reciprocally without offering embraces. Although the sample size of reciprocal infant handling was small, a different dyad was involved in each case suggesting that this was not just due to the temperament and behaviour of one particular mother. To confirm that exchanges of embraces for infant handling occurred within a biological market place, it was also necessary to investigate fluctuations in the exchange rate of commodities. As predicted, the number of bouts of infant handling received per embrace given was dependent on the number of other infants available in the group. When fewer infants were present, one embrace procured significantly fewer bouts of infant handling.

These exchanges of embraces for infant handling are remarkably similar to the exchanges of grooming for infant handling described for chacma baboons (Barrett & Henzi, 2006; Henzi and Barrett, 2002). When either spider monkey embraces or grooming in chacma baboons were exchanged for infant access, exchanges were initiated by the handler, were less likely to be reciprocated by the mother, were more likely to occur between different trader classes, and were significantly affected by infant availability. My findings therefore appear to provide substantial support for biological markets theory, confirming that embraces, in addition to grooming, may be exchanged for infant-handling within a biological market place. Due to the size of the Punta Laguna infant handling data set it was also possible to perform more robust analysis at the individual level and make direct comparisons between rates of behaviour given and received by each female when they were a mother compared to all other times. Furthermore, I showed that the effect of infant availability on the embrace-for-infant-handling exchange rate was not confounded by infant age.

As both grooming and embraces may be exchanged for infant access it is possible that these behaviours are similar in function. However, whereas it has been demonstrated that grooming offers a number of benefits to the recipient such as the removal of ectoparasites (Hutchins & Barash 1976; Saunders, 1988: PhD thesis cited in Henzi & Barrett, 1999) and the release of β-endorphins (Keverne, *et al.*, 1989), the effect of embraces on the recipient has yet to be investigated. Thus, it is unclear whether embraces can be viewed as a service that provides direct benefits. The increased rates of embraces received by mothers may therefore warrant another explanation. Embraces have been interpreted as signals of benign intent because when embraces are exchanged during tension loaded situations, the usual associated aggression is less likely to occur (Aureli & Schaffner, in prep; Schaffner & Aureli, 2005; Schaffner *et al.*, 2003).

Signals of benign intent may take a number of forms including vocalisations (Gouzoules & Gouzoules, 2002; Silk *et al.*, 2000). For example, female baboons and macaques that direct soft grunt vocalisations towards mothers before attempting to interact with their infants are less likely to receive aggression from the mothers (Silk, Cheney & Seyfarth, 1996; Silk, Rendall, Cheney & Seyfarth, 2003). However, signals with an associated cost to the sender provide more reliable signals because it would not be profitable for poorly motivated individuals to produce them (Zahavi, 1975; Zahavi & Zahavi, 1997). Embraces are costly to the actor due to the potential risk of injury, as embraces expose particularly vulnerable parts of the body to the partner and observed injuries in wild and captive groups of spider monkeys are consistent with exposure of these same body parts (Schaffner & Aureli, 2005; personal observation).

Infant handling is likely to be a source of uncertainty and tension for the mother due to the potentially fatal risks of negative handling of her infant, which is particularly prevalent among unrelated females (Maestripieri, 1994b; Schino *et al.*, 2003). As female spider monkeys emigrate upon reaching sexual maturity, adult females are unlikely to be related to their female conspecifics, and the risk of negative infant handling is likely to be high. Uncertainty surrounding the intentions of potential handlers may be exacerbated in spider monkeys due to the high degree of fission-fusion dynamics in their societies (Schaffner & Aureli, 2005). Changes to subgroup memberships prevent females from keeping track of all third party relationships so they are less able to predict the behaviour of a potential handler based on the handler's interactions with other mothers. Furthermore, female attacks on infants have been observed in a wild population of spider monkeys (Chapman *et al.*, 1989). The perceived risk of negative infant handling in the Punta Laguna study communities was therefore likely to be high, which may explain why costly signals of benign intent were necessary to gain access to infants.

In a tension loaded interaction such as infant handling, embraces may therefore serve as honest, reliable signals of benign intent, with sufficient power to convince a mother to grant access to her infant (Schaffner & Aureli, 2005). However, when fewer infants are present, all potential handlers will direct attention to the few remaining mothers. Potential handlers may also become frustrated at their reduced ability to gain access to infants, leading to attempts at kidnapping or negative infant handling (Maestripieri, 1993a). The increase in attention and potential increase in negative handling may cause more tension for the mothers. This increased tension will likely make females more reluctant to grant access to their infants (Henzi & Barrett, 2002). As a result, more embraces will be required to gain access to an infant when infant availability is low. The increase in tension when infant availability is low can explain the observed variation in the embrace-for-infant handling exchange rate, as when mothers are more anxious, more embraces will be required to reassure mothers before access to their infants is granted.

In conclusion, this study confirms that female spider monkeys relationships are significantly affected by the presence of young infants and that embraces, rather than grooming, are the primary behaviour used to gain access to infants. In support of biological markets theory, the embrace-for-infant-handling exchange rate was significantly affected by infant availability, suggesting that embraces provide a service that may be exchanged for access to commodities such as infants. However, as the effect of embraces on the recipient has not yet been investigated, I cannot rule out alternative explanations for fluctuations in the embrace-for-infant-handling exchange rate. Spider monkey embraces appear to serve as signals of benign intent and when fewer infants are available, mothers may require more reassurance before granting access to their infants. Consequently, the observed increase in the number of embraces required to gain access to infants when infant availability was low may not reflect a true 'market effect' because unlike grooming, embraces are not a service that may be traded for desirable commodities

Chapter 6

Female-Directed Male Aggression

6.1. Sex roles and sexual selection theory

In *The Descent of Man and Selection in Relation to Sex* (1871), Darwin produced the theory of sexual selection to explain the evolution of exaggerated and ornamental yet apparently useless traits, which were difficult to explain by natural selection. Sexual selection is based on "the advantage which certain individuals have over others of the same sex and species solely in respect of reproduction" (Darwin 1871, p. 216). The theory described two types of sexual struggle that could lead to this reproductive advantage: intra-sexual, in which individuals of the same sex, generally males, actively compete against their rivals to gain access to fertile partners, and inter-sexual selection, in which the same individuals attempt to excite or charm members of the opposite sex, usually the females, who then choose the most agreeable partners (Darwin, 1871). According to sexual selection theory, elaborate traits such as the male peacock's tail could evolve simply because they were rendered attractive to the female.

The different sex roles of competitive males and choosey females were further refined by Trivers' (1972) parental investment theory. Building on experiments by Bateman (1948: cited in Trivers, 1972), Trivers argued that when one sex invests more in their young than the other does, members of the more investing sex will become a limiting resource for members of the less investing sex. Relative parental investment also dictates the criteria for mate choice, as when parental investment of one sex strongly exceeds that of the other, the former sex is expected to be more discriminating in their choice of mate, in an attempt to obtain 'good genes' and services for the few offspring they will produce (Trivers, 1972). Among mammals therefore, the combined factors of anisogamy (Clutton-Brock, 1989), the energetic demands of pregnancy and lactation (Emlen & Oring, 1977), and female biased parental investment (Trivers, 1972) are predicted to produce competitive, indiscriminate males and choosey females.

However, recent research has indicated that neither competition over access to mates nor mate choice are restricted to one sex and both competition and mate choice can take on many forms (Kappeler & van Schaik, 2004; Paul, 2002). For example, competition for mates may involve scramble rather than contest competition in which males attempt to locate and fertilise females before their rivals do, or engage in post-copulatory sperm competition (e.g. muriquis: Strier *et al.*, 2002). Mate choice may be either direct, whereby females actively choose a preferred male, or indirect in the form of mating calls, sexual swellings or pheromones that instigate male competition by advertising female reproductive state (Kappeler & van Schaik, 2004; Paul, 2002; Wong & Candolin, 2005). Furthermore, the traditional view of passive and choosey females has been brought into question by observations of female primates that actively solicit copulations and mate promiscuously (e.g. Smuts, 1987a; van Noordwijk & van Schaik, 2000). It has also become apparent that male and female sexual strategies are often in direct conflict with one another (van Schaik *et al.*, 2004) causing female choice to be thwarted by male sexual coercion in the form of sexually selected infanticide (Hrdy, 1979) or sexual harassment (Smuts & Smuts, 1993).

6.2. Mating conflict and sexual coercion

Sexual coercion is defined as the use of force or the threat of force to increase the probability that a member of the opposite sex will engage in fertile matings at some cost to the recipient (Smuts & Smuts, 1993). Coercion is costly to female reproductive success as it limits female choice of sexual partners, often thwarting female attempts to obtain the best genes for their offspring (Clutton-Brock, 1989). Infanticide has also been cited as a product of sexual selection, as by killing infants that they did not sire, males can terminate female postpartum amenorrhoea and attempt to mate with the female in the near future (Hrdy 1979; van Schaik, 2000a). Infanticide may therefore be considered an extreme form of sexual coercion (Smuts & Smuts, 1993; van Schaik *et al.*, 2004).

The loss of an infant is clearly disastrous for female reproductive success and thus females are expected to evolve a number of counter strategies to infanticide. One option is to rely on the likely father of the offspring for protection (e.g. Borries *et al.*, 1999; Palombit *et al.*, 1997; Watts, 1996). A second female strategy, particularly relevant to multi-male societies, is to mate promiscuously as a means of confusing paternity (van Noordwijk & van Schaik, 2000; van Schaik *et al.*, 1999, 2000). Despite their attraction to certain (generally dominant) males, females are expected to direct some of their mating effort to other males in order to dilute paternity certainty and so reduce the risk of infanticide (van Schaik *et al.*, 2004). Preferred males will also benefit from a certain degree of female promiscuity to reduce the risk of infanticidal attacks on their offspring from other males. However, the degree of female promiscuity required by males to maximise their reproductive success is significantly lower than that preferred by females (van Schaik *et al.*, 2004). In the majority of cases therefore, preferred males should attempt to prevent females from mating with other males, resulting in a conflict of interest between the female and preferred male (van Schaik *et al.*, 2004). An additional conflict of interest will occur between the fertile female and less desirable (usually low-ranking) males who attempt to obtain a greater proportion of female matings than that preferred by the female for paternity confusion (van Schaik *et al.*, 2004). Consequently, oestrus females receive sexual harassment from both preferred and less desirable males (van Schaik *et al.*, 2004).

Sexual coercion of fertile females is relatively widespread across primates (Dixson, 1998), and quantitative data from several species confirm that females receive significantly more aggression when they are in oestrus compared to all other times (baboons: Bercovitch, 1995; Smuts, 1985; macaques: Soltis, Mitsunaga, Shimizu, Yahagihara & Nozaki, 1997; mountain gorillas: Nadler, 1989; chimpanzees: Goodall, 1986; Matsumoto-Oda & Oda, 1998; Wrangham, 2000; 2002). In several species males are reported to use aggression to initiate or maintain consortships with uncooperative females (e.g. chimpanzees: Goodall, 1986; rhesus macaques: Caldecott, 1986; Japanese macaques: Soltis *et al.*, 1997a; olive baboons: Smuts, 1985) and forced copulations have been observed in orangutans (Galdikas, 1985; Mitani, 1985) and chimpanzees (Goodall, 1986; Nishida, 1990).

Females are particularly vulnerable to sexual harassment where there is a high degree of sexual dimorphism in body size and weaponry, or when they do not have access to kin allies (Nadler, 1989; Smuts & Smuts, 1993; Strier, 1990). Where females remain in their natal groups, female coalitionary attacks are a frequent response to male harassment of females (e.g. pig-tailed macaques: Oi, 1990; rhesus macaques: Bernstein & Ehardt, 1986; Japanese macaques: Soltis *et al.*, 1997b; olive baboons, Smuts, 1987b) and in white-faced capuchins (Perry, 1997b), patas monkeys (Loy, 1989) and vervets (Andelman, 1985: PhD thesis cited in Smuts & Smuts, 1993) several females may attack a male who solicits sex from an unwilling female. Conversely, female-directed male aggression is particularly frequent in species where females disperse upon reaching sexual maturity, and so do not have female allies (e.g. chimpanzees, Goodall, 1986; orangutans: Milton, 1985; spider monkeys: Symington, 1987). It is also possible that female vulnerability in these three species is exacerbated by the high degree of fission-fusion dynamics in their societies, as females often forage alone making them vulnerable to attack. Interestingly, high rates of male sexual harassment of fertile females have been reported in bottlenose dolphins (Connor *et al.*, 1992; Scott, Mann, Watson-Capps, Sargeant & Connor, 2005), which also have a high fission-fusion dynamic in their societies (Connor *et al.*, 1992). Spotted hyenas also have a high degree of fission-fusion dynamics in their societies and despite female dominance over males, males occasionally direct aggression towards females during the stages of the female reproductive cycle where they are most likely to conceive litters, suggesting that this aggression is sexually motivated (Szykman *et al.*, 2003).

However, not all aggression directed to cycling females may be classified as sexual coercion. For example, in several primates, ritualized courtship displays incorporate agonistic behaviour directed to the fertile female (e.g. ritualised chasing in long-tailed macaques: van Noordwijk, 1985; stalking in rhesus macaques: Manson, 1991: PhD thesis cited in Smuts & Smuts, 1993; hair erection and bipedal swagger in chimpanzees: Goodall, 1986; and charging in gorillas: Nadler, 1989; but see Sicotte, 2002). The functional significance of this ritualized aggression during courtship is not well understood although it is possible that aggressive displays serve to demonstrate a male's health and vigour, thereby facilitating female mate choice (Smuts & Smuts, 1993). Aggressive displays may also serve to maintain dominance relationships (e.g. chimpanzees: Nishida, 2003), but in this case, aggression should be directed to anoestrus as well as oestrus females (Strier, 1994).

6.3. Sexual behaviour and female-directed male aggression in spider monkeys

Spider monkeys live in societies with flexible grouping patterns (Fedigan & Baxter, 1984; Symington, 1990) where monopolisation of fertile females is likely to be difficult due to problems monitoring reproductive state of dispersed females. Male spider monkeys are reported to have high-quality social relationships with other males (Fedigan & Baxter, 1984; Chapter 3), large relative testes size (Eisenberg, 1973), and use copulatory plugs (Dixson, 1998) suggesting that males compete for fertilisations via scramble competition. In the closely related muriqui, the absence of a male dominance hierarchy (Strier, 1994) and tolerant male-male relationships are also consistent with predominant scramble competition (Strier *et al.*, 2002). However, whereas muriqui sexual behaviour follows the relaxed pattern predicted by predominant scramble competition (Strier, 1997; Strier *et al.*, 2000), spider monkey matings tend to occur in secrecy away from other group members, in the presence of only the mating females' immature offspring (Campbell, 2006; Klein, 1971; van Roosmalen & Klein, 1988), suggesting that consorting pairs fear harassment from conspecifics.

This view is further supported by detailed observations of 18 spider monkey copulations by Campbell (2006). Seventeen of the 18 copulations took place out of visual contact with the remainder of the subgroup and in all cases the mating pair frequently scanned their surrounding environment suggesting that they were checking for approaching conspecifics. Moreover, neither the consorting pair nor the accompanying offspring made vocalisations of any kind until the mating pair had separated and were also observed to terminate copulation upon hearing approaching conspecifics (Campbell, 2006). Copulating spider monkeys may be particularly vulnerable to harassment from conspecifics as pairs are unable to separate for up to two minutes following ejaculation in what appears to be a form of copulatory lock (Campbell, 2006), which may contribute to the need to mate in secrecy.

The sexual behaviour of consorting spider monkeys does not appear to involve aggression between the sexes (Fedigan & Baxter, 1984; Klein, 1971) and female spider monkeys are reported to initiate mating by approaching the male and presenting their genitalia (Campbell, 2006; Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988). However, prior to consortship, females are reported to initially avoid males, who persist in approaching them (Fedigan & Baxter, 1984). Male spider monkeys are also known to direct a significant proportion of aggression towards females (Campbell, 2003; Fedigan & Baxter, 1984; Symington, 1987: PhD thesis cited in Smuts & Smuts, 1993). Typically these attacks consist of one or more males chasing their female victim, often for several minutes, while she screams, flees and often ends up cowering close to the ground (Fedigan & Baxter, 1984). These attacks have not been observed to precede copulation, although Symington (1987: PhD thesis cited in Smuts & Smuts, 1993) reported that attacks were only directed to cycling females. However, recent analysis of hormonal data found that only one of three females received more attacks when cycling with no peak in attacks during the peri-ovulatory period of the ovarian cycle (Campbell, 2003).

The function of these prolonged female-directed attacks in spider monkeys is not yet known. Smuts and Smuts (1993) interpreted these attacks as a form of sexual coercion, but attempts to support this hypothesis have proved inconclusive (Campbell, 2003). Some authors have suggested that the behaviours exhibited during these attacks seem so stereotyped that the aggression may constitute some form of ritualised courtship display rather than an actual attempt at physical harm (Fedigan & Baxter, 1984). As size dimorphism in spider monkeys is minimal to non-existent (van Roosmalen & Klein, 1988), it is possible that these attacks serve to intimidate equally-sized females in order to maintain male dominance (Strier, 1994). However, female-directed male aggression in spider monkeys is often accompanied by investigative behaviour such as place-sniffing (Campbell, 2003). Place-sniffing is one of a range of behaviours, including genital inspection and urine drinking, which occur at higher rates prior to copulation and are believed to provide males with an indication of female reproductive state (Klein, 1971; Pastor-Nieto, 2000; van Roosmalen & Klein, 1988). The temporal association with place-sniffing suggests therefore that female-directed aggression in spider monkeys is sexually motivated.

6.4. Chapter aims and predictions

Despite a number of detailed descriptions of female-directed male aggression in spider monkeys, the functional significance of this behaviour remains unclear. Attacks have been interpreted as a form of sexual coercion (Smuts & Smuts, 1993) or as a male strategy to intimidate equally sized females (Campbell, 2003; Strier, 1994). However, due to the ritualised nature of these attacks and their temporal association with place-sniffing behaviour it is also possible that these attacks function as a form of sexual display that assist female mate choice by demonstrating male health and vigour (Fedigan & Baxter, 1984). This chapter aims to investigate female-directed male aggression in the Punta Laguna population of spider monkeys in light of the 'sexual coercion', 'maintaining dominance over equally-sized females' and 'sexual display' hypotheses.

Each of the above mentioned hypotheses generate a number of testable predictions. If female-directed male aggression is a form of sexual coercion then these attacks are likely to be intense and should be limited to oestrus females. Attacks may also be associated with investigative behaviours such as place sniffing and should result in actual or attempted copulations immediately after the aggression. Conversely, if female-directed male aggression is a strategy used by males to dominate equally-sized females then aggression may not necessarily be intense and should be directed to all females, regardless of reproductive state. Here, attacks are unlikely to involve any kind of investigative or sexual behaviour. Finally, if female-directed male aggression is a form of male sexual display to influence female mate choice, aggression should not be intense and should be restricted to cycling females. Attacks should be associated with investigative behaviour and after some, but not necessarily all attacks, females should appear attracted to one of their male attackers. This attraction may then result in a consortship and subsequent copulation, although there may be some time delay between the aggression and subsequent mating.

6.5. Methodology

6.5.1. Subjects

All 23 adult females of the Punta Laguna communities could potentially receive aggression from group males, but to differentiate between the three hypotheses it was necessary to observe each female throughout their reproductive cycle. The gestation period for spider monkeys is approximately 7 to 7.5 months (Eisenberg, 1973; Symington, 1987) and data from two wild populations suggest lactation anoestrus to last for 23 months (Milton, 1981) and 26 months (Symington, 1987: PhD thesis cited in van Roosmalen & Klein, 1988). Mean inter-birth interval for the Punta Laguna population from 1997 to 2002 was within the same range reported in other wild populations at 32 months (Ramos-Fernandez *et al.*, 2003), which rises to 36 months when data from 2003 and 2004 are added. Based on this information, focal samples from each female were divided into three separate periods: cycling (from 11 to less than 7 months before the birth of her infant), pregnant (from 7 months to the day before the birth of her infant), and lactating (from 0 to less than 18 months after the birth of her infant). These conservative estimates of the cycling and lactating periods were used to eliminate data that could not be allocated to one of the three categories with reasonable certainty (e.g. 21 months after the birth of an infant during which the majority of females would be lactating but some females with a shorter inter-birth interval would be cycling). All observations that did not fall into these three categories were discarded. To be included in the analysis, females had to be observed for at least 1 hour in mixed-sex subgroups for each of the three reproductive periods. Seven females met the minimum criteria. To investigate the male preference for directed aggression towards opposite-sex partners, with and without the inclusion of prolonged chases, data were obtained from 11 adult males (4 from the Eastern community and 7 from the Western community).

6.5.2. Data Collection

As female-directed male aggression was a relatively rare behaviour, all observed occurrences were recorded using a Sony M450 dictaphone. Due to the extremely vocal nature of these aggressive interactions it is highly unlikely that any cases were missed by the observers. Male aggressive behaviours directed to adult females (threat, chase, lunge, strike and bite: defined in Table 2.2) were recorded, as were all cases of male-to-female place-sniffing (see Table 2.2). Following an aggressive interaction, any occurrences of affiliative or sexual behaviour between the male attacker and his female victim that occurred within 10 minutes of the aggression were recorded. All fission and fusion events following the aggression were also recorded for up to one hour following the aggression, noting the time of the event and the individuals leaving or arriving.

6.5.3. Data Analysis

Hourly rates of female-directed male aggression and place-sniffing were calculated for each of the seven females for each of the three reproductive periods. Individual rates for each reproductive period were calculated from the total frequency of aggression or place-sniffing received and the total time that the female was in view in mixed-sex subgroups. The total time in view in mixed-sex subgroups for each period was taken from the focal sample data set (subgroup composition was recorded during all focal samples). However, the frequencies of aggression and place-sniffing were calculated from all occurrences collected within and outside focal samples in order to increase the sample size of these rare events. For each hour that the monkeys were in view, only two 20-minute focal samples were collected. Consequently, the rates calculated for this analysis are approximately one third inflated. This method was considered acceptable for the purpose of these analyses, as rates were equally inflated for each of the reproductive periods and the purpose of the analysis was to compare rates between the three periods. The same method was employed to produce Figure 6.7, but in this case hourly rates of behaviour were calculated for each month before and after the birth of the infant.

The intensity of female-directed male aggression was classified into three categories: threat, prolonged non-contact chase, and physical aggression. A threat consisted of a facial and/or vocal threat, possibly accompanied with a short lunge. A prolonged chase consisted of one or more males chasing one female, but every time the males could make contact with the female, the males were seen to pull back and allow the females to get away before they continued the chase. These chases were extremely loud with growling vocalisations from the males and intense screaming from the female victim. Physical aggression consisted of a number of aggressive behaviours, including prolonged chases, but in these cases the males made contact with the female, often wrestling her to the ground and inflicting bite wounds. Each aggressive episode was classified using the highest intensity of aggression observed. Each episode of female-directed male aggression was classed as one bout of behaviour, irrespective of how many males were involved in the attack.

Mean rates of prolonged chases, physical aggression and place-sniffing behaviour received by females from males were compared for each reproductive period using repeated measures one-way ANOVAs with the Huynh-Feldt correction for sphericity (Keppel & Wickens, 2004). Significant differences were determined using Tukey's HSD post-hoc analysis with Howell's correction for repeated measures (Howell, 2002). The same method was used to compare the mean percentage of prolonged chases accompanied by place-sniffing by the male attacker (or at least one of the male attackers if a male coalition occurred) for each reproductive period.

To differentiate between the three hypotheses being tested, the outcome of each case of female-directed male physical aggression and female-directed male prolonged chases that occurred up to and including one hour after the aggression was allocated to one of the following categories: attacker(s) and victim remain in the subgroup, victim fissions, at least one attacker fissions, victim fissions with at least one attacker, and copulation between at least one of the attackers and the female victim. In the 'attacker(s) and victim remain in the subgroup' category both the male attacker(s) and female victim were observed to remain in their current subgroup for up to one hour of the aggressive interaction. Following the aggression, the attacker(s) and victim could be engaged in any behaviour from the ethogram presented in Chapter 2, with the exception of copulation. Other individuals that were not involved in the aggressive interaction may have fissioned during this time. The category 'victim fissions' referred to the victim leaving the subgroup after receiving male aggression, which she did alone or in the company of other individuals, excluding her male attacker(s). Similarly, 'attacker fissions' refers to at least one of the male attackers leaving the subgroup either alone or with other individuals but leaving the female victim behind. The category 'victim fissions with attacker' refers to the male attacker and female victim simultaneously leaving the subgroup together without any other individuals except dependent offspring. 'Copulation' referred to actual or attempted copulation by the male attacker(s) with the female victim within 10 minutes of the aggressive interaction. All cases in which the subgroup was not observed for at least one hour following the aggressive interaction were excluded from this final analysis.

Finally, if data were found to support the sexual display hypothesis then it is likely that the male preference for directing aggression toward females reported in Chapter 3 was somewhat misleading. To clarify the matter, mean rates of male aggression (including threats) directed to same-sex and opposite-sex partners, with and without the inclusion of male-female prolonged chases were compared using repeated measures t-tests. Unlike the previous analysis, these data were analysed from the perspective of the 11 adult male aggressors rather than the female recipients. All statistical analyses were two-tailed.

6.6. Results

All female-directed male aggression was directed by one or more males toward a single female. The vast majority of female-directed male attacks were prolonged chases (82%, N = 24; Figure 6.1). Of these prolonged chases, 38% (N = 9) were directed from two or more males towards a single female, with the remaining 62% (N = 16) performed by a lone male toward a single female. Seventy nine percent (N = 19) of all prolonged chases occurred when there was at least two males present in the subgroup, including male aggressors and bystanders. Physical aggression occurred in 16% of cases (N = 6; Figure 6.1), and 66% (N = 4) of this physical aggression involved 2 or more males attacking a single female, where there were at least two males present in the subgroup (aggressors and bystanders). Threats were a rare occurrence, accounting for less than 2% (N = 1) of female-directed male aggression, and all threats were directed from one male toward a single female. As threats were extremely rare, they were omitted from subsequent analysis.

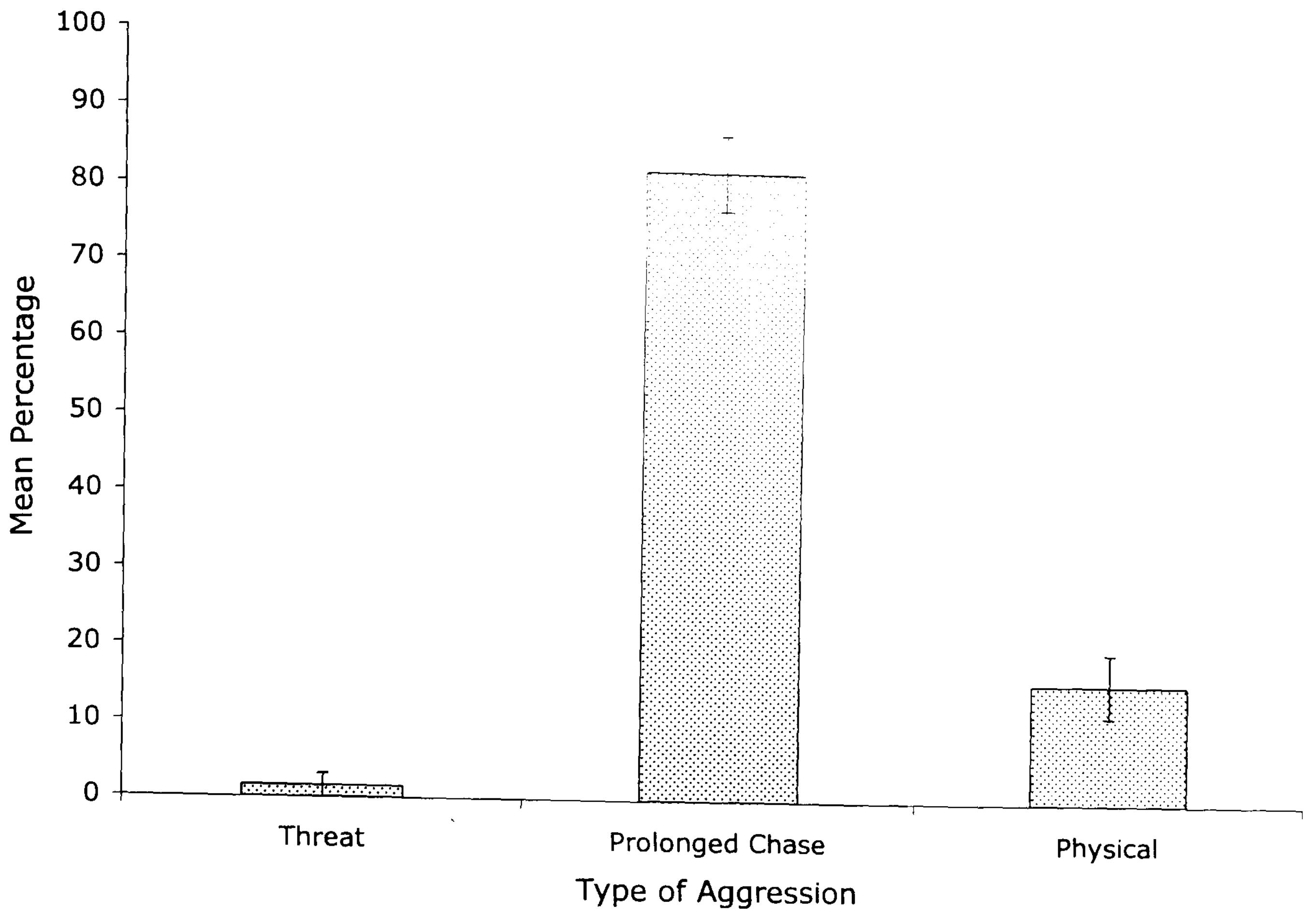

Figure 6.1: Mean (± SEM) percentage of female-directed male aggression that were threats, prolonged chases or physical aggression.

Contrary to the prediction of the sexual coercion hypothesis, the mean hourly rate of physical female-directed male aggression was unaffected by female reproductive state [cycling: 0.003 ± 0.003, pregnant: 0.006 ± 0.004, lactating: 0.013 ± 0.008; *F* (2, 12) = 0.996, *p* = 0.398]. Prolonged chases were however affected by female reproductive state [*F* (2, 12) = 11.52, *p* = 0.002: Figure 6.2], providing support for the sexual display hypothesis. Post-hoc analysis indicated that females received significantly higher rates of prolonged chases when they were cycling compared to when they were pregnant (*p* <0.01) and lactating (*p* <0.01), but there was no significant difference in rates of prolonged chases between pregnancy and lactation. As with previous studies, rates of female-directed male place-sniffing were heavily influenced by female reproductive state [*F* (2, 12) = 49.05, *p* <0.001: Figure 6.3], confirming that place-sniffing is a sexually motivated behaviour. Substrates previously occupied by females were place-sniffed by males at significantly higher rates when the females in question were cycling compared to when they were pregnant (*p* = <0.01) and lactating (*p* <0.01), but there was no difference in the rate of place-sniffing between pregnancy and lactation.

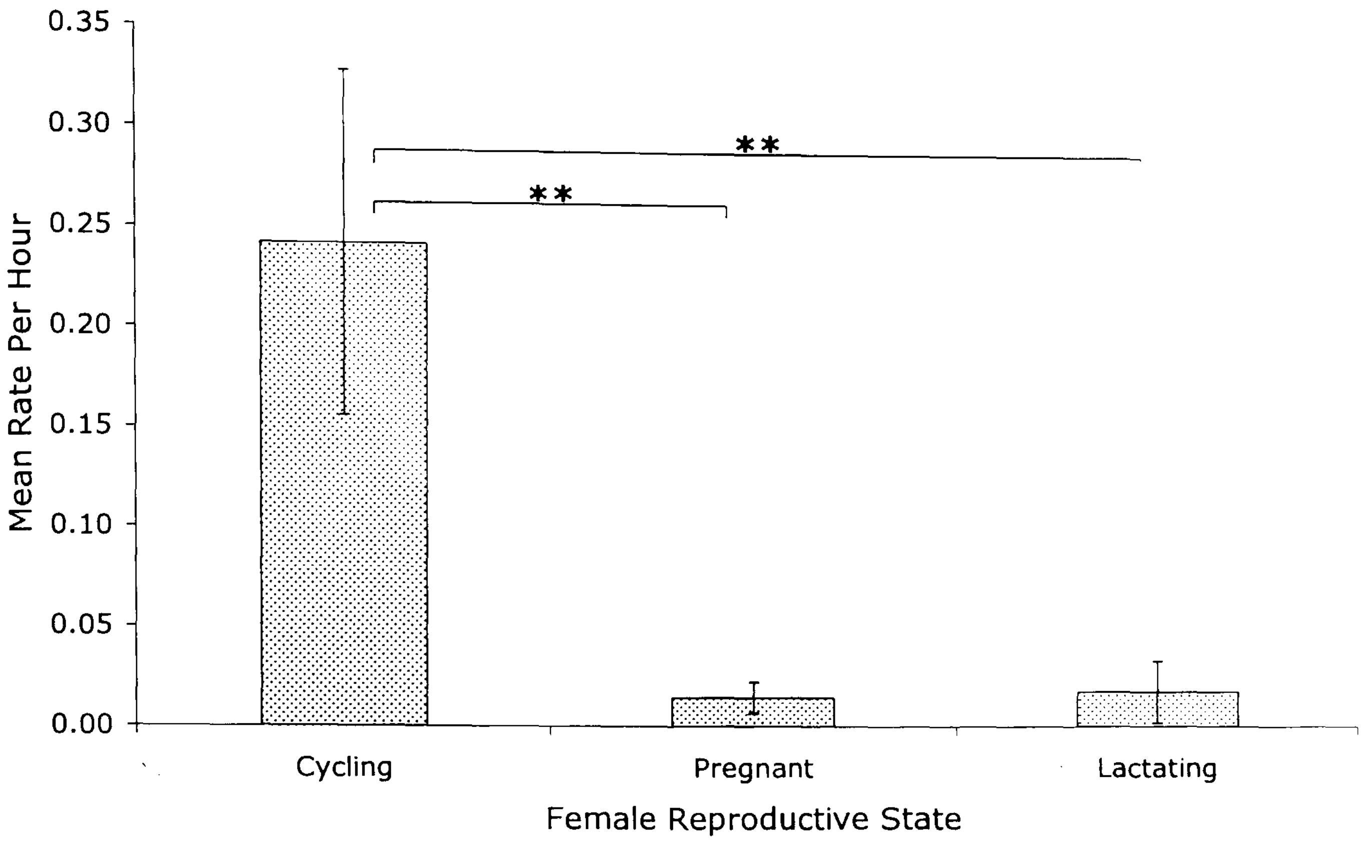

Figure 6.2: Mean (± SEM) hourly rates of female-directed male prolonged chases when female recipients were in various reproductive states.

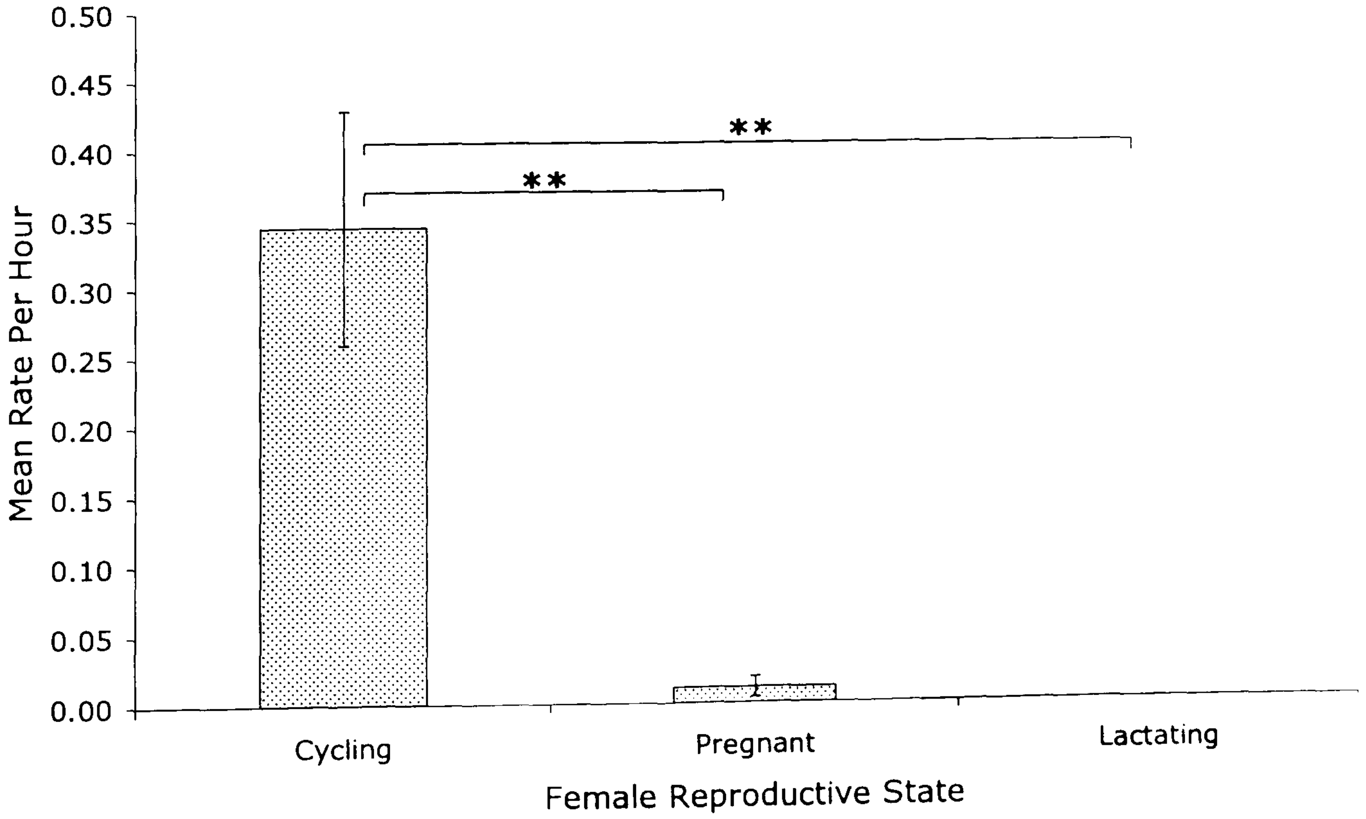

Figure 6.3: Mean (± SEM) hourly rates of female-directed male place-sniffing behaviour when female recipients were in various reproductive states.

Mean percentages of prolonged chases accompanied by place-sniffing were also affected by female reproductive cycle [*F* (2, 12) = 23.26, $p < 0.001$: Figure 6.4]. Post-hoc analysis indicated that the percentage of female-directed male prolonged chases accompanied by female-directed male place-sniffing was significantly higher when female recipients were cycling compared to when they were pregnant ($p < 0.01$) and lactating ($p < 0.01$), with no difference in percentages during pregnancy and lactation. During prolonged chases with accompanying place-sniffing, male attackers were observed to place-sniff the substrate previously occupied by their female victims either immediately before and/or after the chase. Place-sniffing occurred prior to the chase in the majority of cases (86%), with the exception of prolonged chases following a fusion event, where the male attackers began chasing a female victim upon encountering her subgroup.

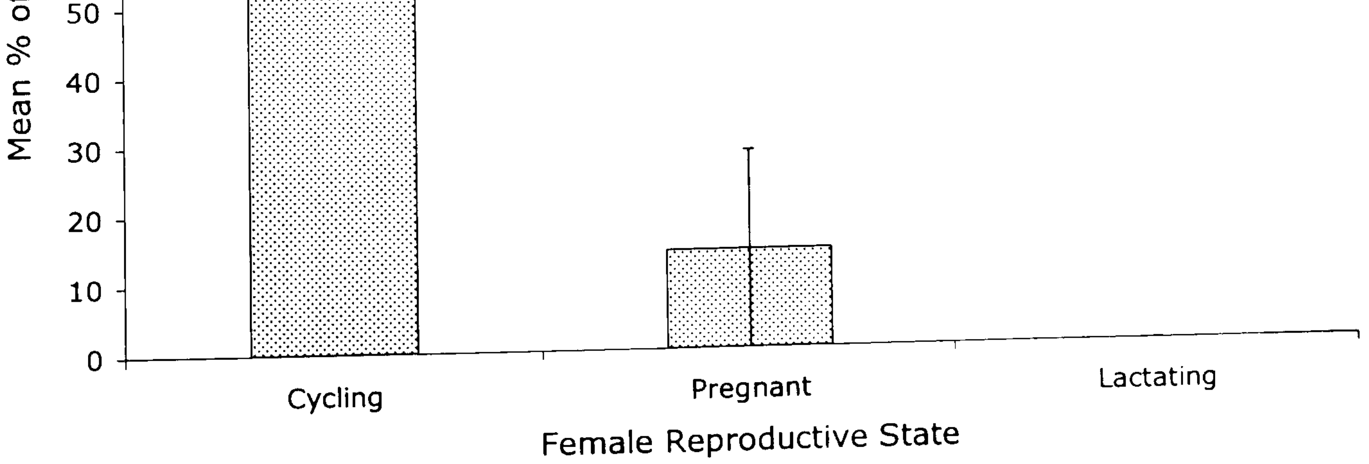

Figure 6.4: Mean (± SEM) percentage of female-directed male prolonged chases accompanied by place-sniffing behaviour when female recipients were in various reproductive states. In all cases, place-sniffing was performed by the male aggressor(s) and directed toward a substrate previously occupied by the female victim either immediately before and/or after the chase.

Detailed analysis of the relationship between female reproductive state and rates of prolonged chases and place-sniffing received is presented in Figure 6.5. Rates of both place-sniffing and prolonged chases peaked at 8-9 months before the birth of the infant, which was when the females were likely to be receptive. Between 7 and 8 months before birth, the mean rate of place-sniffing was still high but the mean rate of prolonged chases decreased considerably. As the gestation period for spider monkeys is 7-7.5 months (Eisenberg, 1973; Symington, 1987a), many, but not all females would have been pregnant during this period. However, place-sniffing as a means of detecting female oestrus may not be completely reliable as a small number of chases with place-sniffing occurred between 6 and 7 months before birth when the females were most definitely pregnant.

Where known, the outcome of physical aggression (88%, N = 7) and prolonged chases (84%, N = 21) were investigated. No actual or attempted copulations were observed following physical aggression or prolonged chases (Figure 6.6). Following physical aggression, the victim either left the subgroup (fissioned) leaving her male attacker(s) behind in (73%) or remained in the

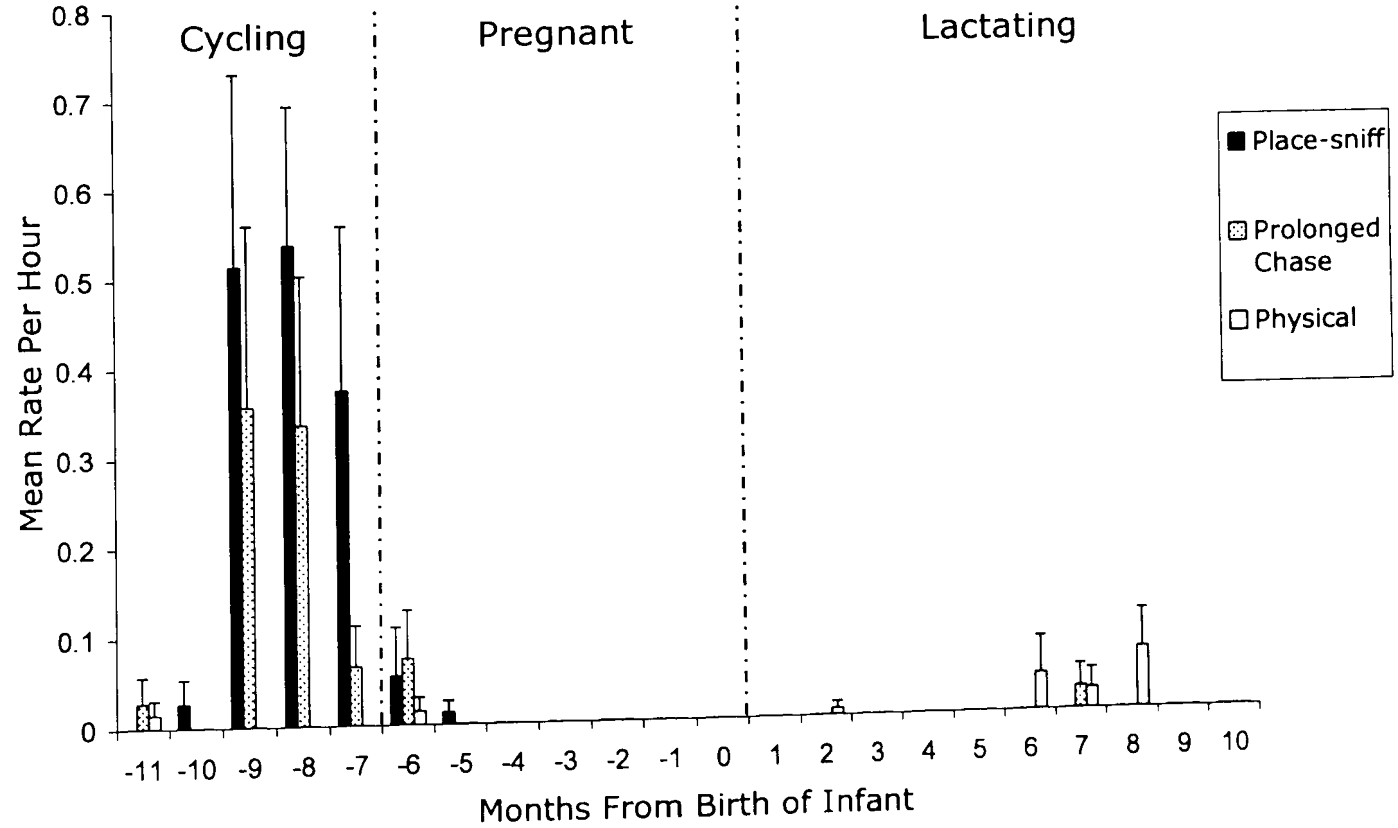

Figure 6.5: Mean (± SEM) hourly rates of female-directed aggression (chases and intense) and place-sniffing behaviour for each month before and after the female recipient had given birth to an infant.

subgroup with her attackers (27%). A different pattern was found for prolonged chases. In 48% of cases the male attacker and female victim remained in the same subgroup and the female victim fissioned from the subgroup in only 4% of cases. In 16% of prolonged chases, male attackers fissioned, and after 32% of prolonged chases females were observed to leave the subgroup with one of their male attackers (Figure 6.6). These fissions of the female with her attacker were not immediate and usually occurred within half and hour to an hour after the chase. The female victim was not coerced into leaving the subgroup with the chosen male attacker, and in over 93% of the cases where females fissioned with their male attacker, female victims were observed to approach the male and present their hind quarters prior to fission. Where females were chased by a coalition of males (n=14), the male they fissioned with appeared to have chased the female for longer than her other male attackers (5 of 8 cases of attacker-victim fission). After leaving their current subgroup, the male attacker and female victim moved silently through the forest. Consequently, we were unable to follow these pairs for longer than a few minutes.

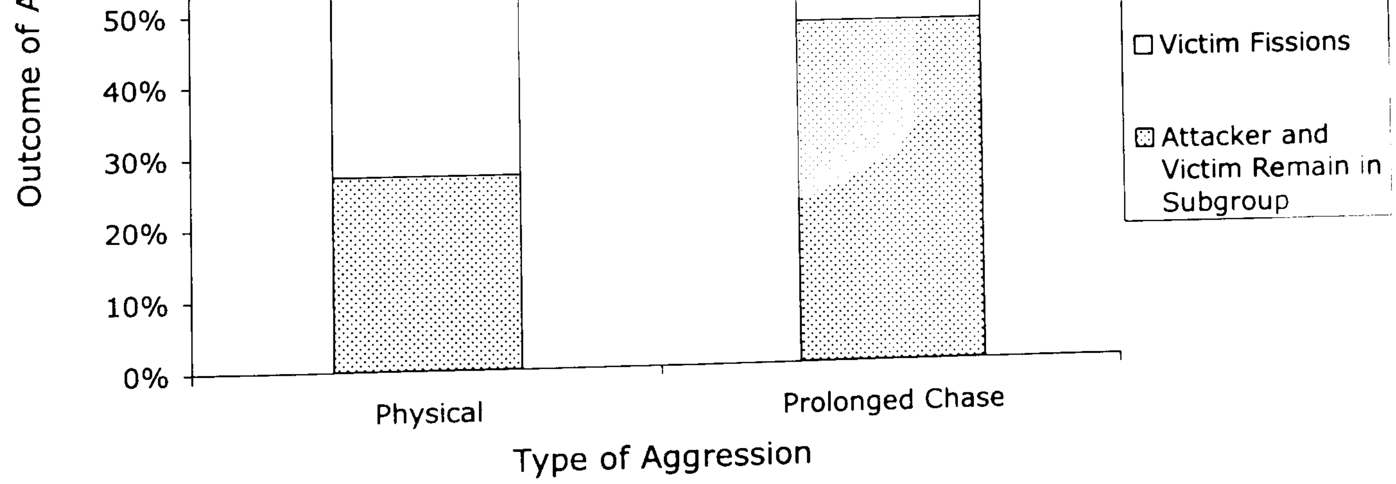

Figure 6.6: Outcomes of female-directed male physical aggression and female-directed male prolonged chases up to and including one hour after the aggressive interaction.

As data suggest that the majority of female-directed male aggression received by the 7 focal females were prolonged chases, it is likely that the male preference for directing aggression towards females reported in Chapter 3 was unrepresentative. When examining all cases of female-directed male aggression (threats, prolonged chases and physical aggression) from the perspective of the male attackers, males directed significantly higher rates towards females than towards other males [*t* (10) = 3.620, *p* = 0.005: Figure 6.7]. However, when all cases of prolonged chases directed to cycling females were removed from the data set, there was no significant difference in the mean rate of male aggression directed to male and female victims [*t* (10) = 1.808, *p* = 0.101: Figure 6.7]. Thus the male preference for directing aggression to opposite-sex partners reported in Chapter 3 was somewhat misleading.

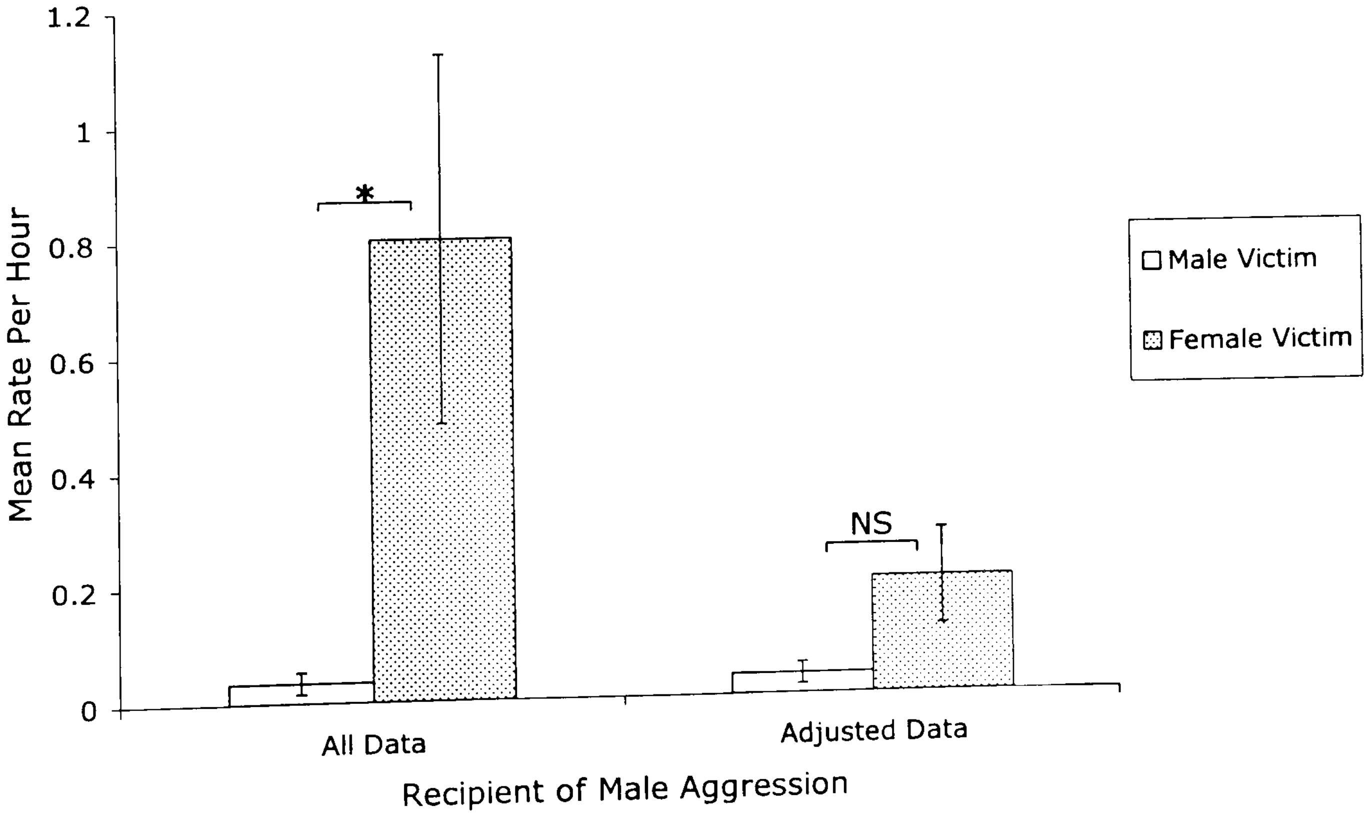

Figure 6.7: Mean (± SEM) hourly rate of male aggression directed to male and female adult individuals for all aggression data and adjusted data with prolonged chases of cycling females removed.

6.6. Discussion

Female-directed male aggression in spider monkeys was investigated in light of three mutually exclusive hypotheses: sexual coercion (Smuts & Smuts, 1993), maintaining dominance over equally-sized females (Strier, 1994), and male sexual display to aid female mate choice (Fedigan & Baxter, 1984). Contrary to the sexual coercion hypothesis, less than 20% of female-directed aggression was physical, and mean rates of physical aggression received by females were not influenced by their reproductive state and did not result in attempted or actual copulations. As males directed physical aggression towards all females regardless of their reproductive state, physical aggression, albeit relatively rare, may enable males to maintain dominance over equally-sized females, providing some support for the maintaining dominance hypothesis (Strier, 1994). Prolonged chases were generally accompanied by investigative place-sniffing behaviour and were directed almost exclusively towards cycling females, indicating that these chases were sexually motivated. Consequently, the maintaining male dominance hypothesis (Strier, 1994) could also be ruled out as an explanation of prolonged chases as if prolonged chases were used to maintain dominance over equally-sized females, male spider monkeys would need to chase all females rather than restricting prolonged chases to cycling females.

In support of the sexual display hypothesis, over 80% of female-directed male aggression was prolonged chases, which were generally accompanied by investigative place-sniffing behaviour and were directed almost exclusively towards cycling females. Contrary to previous reports of female-directed male aggression in spider monkeys (Campbell, 2003), during prolonged chases it was unclear if males were working cooperatively in a coalitionary attack or were all independently chasing the same female. However, prolonged chases appeared to lack the same level of coordination observed during physical aggression, and males noticeably pulled back whenever they were close to the female they were pursuing, suggesting that prolonged chases were a ritualised form of aggression (Fedigan & Baxter, 1984).

As predicted by the sexual display hypothesis, after some, but not all prolonged chases, females directed sexual behaviour to one of their male attackers. Prolonged chases often involved more than one male pursuing a single female. However, during each chase, one particular male was more persistent in chasing the female, and anecdotal observations suggested that it was this persistent male that received the female's attention after the attack. Following exchanges of affiliative and sexual behaviour, female victims were often observed to voluntarily leave their present subgroup with their male attacker.

Although it was not possible to confirm if these pairs had formed a consortship or mated, their silent travel away from their conspecifics gave the impression that these pairs did not want to be followed. As spider monkeys are reported to mate in secrecy (Campbell, 2006; Klein, 1971; van Roosmalen & Klein, 1988), it seems reasonable to suggest that these pairs had left their subgroup in order to mate. Furthermore, my observations of copulations in the Punta Laguna communities and reports from the community at Barro Colorado Island (Campbell, 2006) indicate that prior to copulation, the consorting pair silently fission from their subgroup and travel together towards a secluded area out of visual contact from conspecifics.

Both in the wild and captivity, high rates of place-sniffing have been observed prior to copulation (Klein, 1971; Pastor-Nieto, 2000; van Roosmalen & Klein, 1988) in addition to their association with prolonged chases (Campbell, 2003). Mean rates of place-sniffing and prolonged chasing at Punta Laguna peaked during the approximate timing of female cycling (7 – 9 months prior to birth). Peak rates of place-sniffing and prolonged chases were found in the month in which ovulation occurred and were not restricted to a small number of days, suggesting that rates of place-sniffing and prolonged chases did not peak at ovulation. A peak in prolonged chases at ovulation was not expected for two main reasons. Firstly, if prolonged chases are a form of ritualised male sexual display, then each male may need to display to the female several times before she will concede to copulation. Secondly, females may not wish to advertise the exact timing of ovulation due to the increased risk of infanticide associated with paternity certainty (Nunn, 1999; van Schaik *et al.*, 2000; Zinner *et al.*, 2004). Due to their long period of lactation relative to gestation, spider monkeys are particularly vulnerable to infanticide (van Schaik, 2000b; 2000c) and females are expected, therefore, to employ a number of strategies aimed a paternity confusion.

Female spider monkeys do not advertise receptivity with physiological changes to their genitalia such as sexual swellings (Dixson, 1998; Klein, 1971). It has been suggested however that the unusually large clitoris of female spider monkeys may deposit urine droplets on the surface of resting locations (Milton, 1985; Klein, 1971) and as female spider monkey urine is known to contain traces of reproductive hormones (Pastor-Nieto, 2000), females may advertise oestrus using olfactory cues. Male place-sniffing behaviour therefore appears designed to detect female reproductive state. The olfactory cues derived from male place-sniffing may act as a female strategy aimed at paternity confusion, provided that they indicate a high probability, but not certainty, that the female is ovulating. Certainly, place-sniffing as a means of detecting female ovulation was not completely accurate and continued at a reduced rate into the early stages of pregnancy. This view partly agrees with the hormonal data from Barro Colorado Island, where a female who received higher rates of aggression when cycling did not experience a peak in male aggression during the peri-ovulatory phase of the reproductive cycle (Campbell, 2003). However, the other two females tested did not receive significantly higher rates of aggression when cycling. These inconsistent results were likely confounded by the small sample size and also because Campbell did not make the distinction between prolonged chases and physical aggression in her analysis, indicating that the relationship between female reproductive state, place sniffing, and female-directed male aggression warrants further research using hormonal data.

If ritualised chases are a form of sexual display, triggered by olfactory cues from place-sniffing then it is likely that these chases provide females with an indication of male quality. According to the sex roles outlined by sexual selection theory, males should attempt to out-compete their rivals for access to fertile females, and because successful competitors are likely to have 'good genes', females are predicted to select the winners of these contests as mates (Darwin, 1871). In the majority of primate species living in multi-male groups, male-male competition gives rise to an agonistically maintained dominance hierarchy, thus females can be reasonably sure that dominant males are in possession of the best genes for their offspring. I was unable to detect a clear-cut dominance hierarchy among the male spider monkeys at Punta Laguna (Chapter 3), thus it is possible that females advertise oestrus using olfactory cues as a means of inciting male competition in order to facilitate female mate choice (Paul, 2002; Wong & Candolin, 2005). It has also be proposed that a female may avoid an approaching male and be chased by him in order to determine his health and vigour or to incite competition among surrounding males as a means of identifying the 'best' male present (Smuts & Smuts, 1993).

Observations of wild spider monkeys are consistent with this theory as female spider monkeys generally avoid males initially, who then persist in approaching them (Fedigan & Baxter, 1984). Similarly, although females are generally chased by more than one male, males do not appear to work cooperatively during prolonged chases as they do during physical aggression. My observations are consistent with the idea that the males chasing the females are in fact competing against one another in an attempt to advertise their strength and vigour to the female. However, these chases are qualitatively different from the ritualised mating displays found in other primates (e.g. long-tailed macaques: van Noordwijk, 1985) as female spider monkeys appear to be genuinely distressed by the aggression, despite the fact that they rarely fissioned from the group to evade their attacker and were often attracted to their attacker following the chase. Cycling females were also observed to avoid potential chases by leaving the subgroup upon detection of approaching males.

It is also possible that female-directed male aggression is a form of sexual display designed to display strength and vigour to other community males as a means of male-male competition. If this explanation were correct, all cases of prolonged chases would have to occur in mixed-sex subgroups containing more than one male. Although 79% of prolonged chases occurred in these circumstances, the remaining cases occurred when no other males were present in the subgroup to witness the display. It therefore seems unlikely that the sole purpose of these prolonged chases is for males to demonstrate their strength to their male competitors. However, prolonged chases as a form of male-male competition and as a display to aid female mate choice are not necessarily mutually exclusive. The circumstances in which these prolonged chases occur warrants further research, particularly because both the number of male aggressors and the total number of males present in the subgroup during the case can vary.

As spider monkey females are apparently reluctant to participate in these prolonged chases then this aggression could still be classified as sexual coercion, if by chasing females and displaying their strength males are able to coerce females into mating at a later date (Smuts, & Smuts, 1993). Among chimpanzees, males frequently direct severe aggression towards cycling females whose swellings have not yet reach full tumescence. Goodall (1986) proposed that these attacks serve to intimidate females and increase the chances that the female will submit to the male's advances in the future. If this is true then the apparent willingness of females to participate in consortships may reflect female submission as a consequence of previous aggression (Goodall, 1986; Smuts & Smuts, 1993). Similarly, female sexual behaviour directed towards male aggressors may therefore function as a means of reducing aggression rather than reflecting the females' attraction to her attacker (Smuts & Smuts, 1993). However, unlike chimpanzees, the vast majority of female-directed male aggression in spider monkeys is non-contact prolonged chases, which are unlikely to be effective as a form of intimidation.

Unfortunately, the relationship between male aggression, female submission, and subsequent conceptive matings is extremely difficult to test. In Japanese macaques, this relationship was investigated by comparing across heterosexual dyads the relationship between male aggression towards the female and the rate of fertile matings within the dyad (Soltis *et al.*, 1997a). Although a significant positive correlation was found between male aggression and fertile matings, results were confounded by female preference for particular males. Results were also likely affected by individual differences in the need to use force to gain access to females (Smuts & Smuts, 1993). In any case, such observations are unlikely to be possible in wild spider monkeys as this species mates in secrecy (Campbell, 2006; Klein, 1971; van Roosmalen & Klein, 1988), and due to high degree of fission-fusion dynamics in spider monkey societies, many cases of aggression and copulations are likely to be missed by the observer.

However, even without this information, I suggest that male aggression towards cycling females in spider monkeys is unlikely to result in female submission due to its lack of severity. In the reported cases of coercion in chimpanzees for example, aggression was described as severe and injurious (Goodall, 1986). A similar level of severity to that found in chimpanzees has been reported other species (e.g. Japanese macaques: Soltis *et al.*, 1997a; orangutans: Galdikas, 1985; hamadryas baboons: Kummer, 1995). Physical aggression in spider monkey was not associated with female reproductive state. Furthermore, during spider monkey prolonged chases, males were seen to pull back and allow the female to get away before they continued the chase, rather than physically attacking her. This pattern of behaviour is more representative of a sexual display than sexual coercion. In order to test this hypothesis further, quantitative data regarding the outcome of prolonged chases is required with particular reference to potential consortships between the female and her male aggressor.

In conclusion, the majority of female-directed male aggression in spider monkeys refers to a distinct form of male sexual display directed to cycling females as a means of demonstrating strength and vigour, which may enable females to choose the 'best' male for mating and may also enable males to communicate their fighting ability to their male competitors. Reports of female-directed prolonged chases from other field sites are also in line with my definition of ritualised displays (e.g. Campbell, 2003; Fedigan & Baxter, 1984; Symington, 1987: PhD thesis cited in Smuts & Smuts, 1993). Once these ritualised displays have been accounted for, males directed no more aggression to females than they did to other males. Among the remaining cases of female-directed male aggression, the physical attacks were directed to all females irrespective of reproductive state and may reflect a male strategy aimed a maintaining dominance over equally-sized females.

Chapter 7

Discussion

My study aimed to investigate the social interactions among wild spider monkeys in order to define the nature of spider monkey social relationships and to identify variation in relationship quality. Many studies of primate social relationships have concentrated on the relationships of one particular sex or have investigated the effects of a limited number of factors on social behaviour. In order to further investigate relationship quality in spider monkeys I have taken a more holistic approach and have referred to a wide range of factors that are likely to contribute to the evolution of social relationships. As with the majority of studies, female social relationships were investigated in light of food preferences and the corresponding competitive regime, but I also paid specific attention to the temporary influence of market effects on female social relationships. Male social relationships were evaluated in terms of competition for access to females and the species mating system, and male-female relationships were investigated with reference to the species mating system and male reproductive strategies such as infanticide and sexual coercion. In this discussion chapter, results from the four data chapters are used to quantify the quality of female-female, male-male and male-female social relationships in the spider monkeys at Punta Laguna. My findings are then related to other primate species that live in societies characterised by a high degree of fission-fusion dynamics.

7.1. Relationship quality among female spider monkeys

Spider monkeys live in societies characterised by a high degree of fission-fusion dynamics. According to the socio-ecological model, flexible grouping that allows subgroups size to be adjusted in response to food supply enables females to reduce contest competition for food, resulting in Dispersed-Egalitarian female social relationships despite a frugivorous diet (Sterck *et al.*, 1997). As the need for coalition partners is reduced, females are free to disperse from their natal group (predation permitting), and are likely to have low-quality social relationships. In line with previous studies (Fedigan & Baxter, 1984; Symington, 1987; 1990), my results support these predictions. During my study, all sub-adult females that were approaching sexual maturity disappeared from their natal community and three cases of immigration by likely nulliparous females were observed, confirming that dispersal in spider monkeys is female-biased. Females spent approximately 25% of their time alone, and showed no evidence of an agonistically maintained dominance hierarchy, which supports the view that female spider monkeys use flexible grouping to reduce contest competition for food (Chapman, 1990; Chapman *et al.*, 1995; Symington, 1988a). Nevertheless, flexible grouping did not completely eliminate contest competition for food as the percentage of female-female aggression and coalitionary arm-wrapping that occurred in a feeding context was significantly higher than expected. Furthermore, adult females appeared to be dominant to sub-adult females as indicated by displacements while feeding.

That I was unable to detect a dominance hierarchy among adult females conflicts with the findings of Chapman (1990) and Symington (1987; 1988a) who reported agonistically maintained dominance hierarchies among adult female spider monkeys. Neither Symington nor Chapman have reported how they calculated the dominance hierarchies at their field sites and have only referred to dominance relationships between females as an explanation of other findings, rather reporting dominance interactions directly. Chapman (1990) did however report that his dominance calculations were incomplete due to low rates of female-female aggression and a complete absence of aggression between many of the community females. Rates of female-female aggression were also low at Punta Laguna, and for that reason I did not have sufficient data to produce an accurate account of female dominance interactions. What little data I had, did not reveal any pattern of dominance between long-term resident females, but did indicate that long-term resident females were dominant to recent immigrant females, a phenomenon also reported by Chapman (1990) and Symington (1987; 1988a). Data referring to dominance interactions between female spider monkeys are therefore inconclusive, suggesting that this topic warrants further research.

Females were less sociable than males. Social grooming between unrelated adult females was virtually non-existent as females directed their grooming towards their immature offspring or towards male conspecifics. There is evidence to suggest that adult spider monkeys regulate their social relationships using embraces rather than grooming (Schaffner & Aureli, 2005), but females also exchanged embraces at low rates and did not appear to mediate aggression using embraces, as the rates of female embraces exchanged in a feeding context was not higher than expected. Coalitionary behaviour between females was not commonplace, with the exception of coalitionary aggression by long-term resident females directed towards recent female immigrants. Collectively, my data suggest that female social relationships in spider monkeys at Punta Laguna are best described as low-quality. These findings concur with reports of female social relationships in other spider monkey communities that also described female social relationships as low quality (e.g. Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1987; 1990). In line with these aforementioned studies, my results also conflict with the findings of Ahumada (1992) who reported high rates of social grooming between adult female spider monkeys at Barro Colorado Island, which were heavily confounded by a high degree of relatedness between adult females due to the island habitat and consequent prevention of female dispersal. Similar high rate of grooming among female spider monkeys have also been reported in a captive group of related females (Pastor-Nieto, 2001). However, in contrast to previous studies of spider monkeys, my findings were derived from a full repertoire of social interactions with specific reference to species-specific behaviour, collected from two communities of individually recognised spider monkeys, and have been analysed using robust statistical techniques; a combination of factors that has not previously been possible. My findings provide a more detailed insight into the social relationships of female spider monkeys than previous studies.

My study also provided systematic evidence of a significant effect of the presence of young infants on female social interactions. Females received significantly more approaches and embraces when they were mothers compared to all other times, and when young infants were present, the rate of female-female embraces was similar to that between males. Female primates are highly motivated to interact with others' infants, thus females with young infants become more valuable to their female group members because while the infant remains in close proximity to its mother, access is dependent on tolerance from the mother (Maestripieri, 1994a). Consequently, females embrace mothers as a means of gaining access to their infants, creating a 'market effect'. My findings therefore emphasise the importance of long-term studies of primate social behaviour as market effects can cause temporary, but significant changes to relationship quality, and if data is only collected for a short period it may produce an extremely biased view of social interactions.

7.2. Relationship quality among male spider monkeys

In line with previous reports (Chapman, 1990; Symington, 1987) males did not leave their natal group upon reaching sexual maturity and no cases of male immigration were observed, confirming that male spider monkeys are philopatric. Inclusive fitness benefits and familiarity among males may therefore explain why male spider monkeys at Punta Laguna preferentially interacted with same-sex partners, and exchanged affiliative behaviour at higher rates than did females. The occurrence of male-male aggressive interactions was generally low, and I did not detect a clear-cut dominance hierarchy among males. These data combined with high rates of affiliative behaviour exchanged between males and their large testis relative to body size suggests that males compete for access to fertile females via scramble competition. However, male-male interactions were affected by the presence of females as male coalitionary arm-wrapping and embraces occurred at high rates when males were in mixed-sex subgroups. Furthermore, as with previous reports (e.g. Campbell, 2006; van Roosmalen & Klein, 1988), mating always occurred in secrecy away from other community members and copulating pairs maintained a high level of vigilance and made no copulatory vocalisations, suggesting that they were attempting to avoid harassment from conspecifics.

Relationships between older and younger adult males were highly differentiated as older males were often aggressive towards younger males but younger males never directed aggression towards older males. Fatal attacks on younger community males by older resident males have been observed at Punta Laguna (Valero, *et al.*, 2006) and Barro Colorado Island (Campbell, in press), thus younger adult males are likely to feel insecure about their relationships with older males. In line with this view, older males also received embraces at significantly higher rate than did younger males and as younger male preferentially embraces older males, whereas older males preferentially embraced other older males, younger males gave more embraces than they received. Moreover, grappling was only ever observed between older and younger adult males and was always initiated by the younger male. As spider monkey embraces and grappling appear to function as signals of benign intent (Schaffner & Aureli, 2005; Schaffner *et al.*, 2003) and are used to mediate aggression (Schaffner & Aureli, in prep), it is not surprising that younger males preferentially directed embraces towards older males.

Male social interactions were also affected by fusion events as the percentage of male-male aggression, coalitionary arm-wrapping and embraces that occurred in the first five minutes following fusion was significantly higher than expected.

Following a fusion event, individuals must rapidly assess their relationships with members of the other subgroup, which is particularly important when social relationships are valuable but insecure. Male spider monkeys rely on other community males to defend community females from extra-community males (Aureli *et al.*, 2006), suggesting that male social relationships are valuable, which is confirmed by the high rates of affiliative behaviour exchanged between males in general and following fusion. Similarly, high rates of embraces exchanged between males suggest that social relationship are insecure which is likely because male-male aggression in spider monkeys can be intense, injurious and lethal (Valero *et al.*, 2006; Campbell in press). Thus, social relationships between male spider monkeys are best described as high-quality in terms of value but low-quality in terms of security.

It is difficult to compare my data with previous studies as other researchers have reported difficulties in habituating and collecting data on male spider monkeys as they are very difficult to follow due to the speed with which they travel, particularly when they are in same-sex subgroups (Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1988b). Consequently previous studies have been limited to investigating patterns of association (time spent together in the same subgroup) between males rather than providing details of social interactions. I also experienced problems following all-male groups, but due to the high level of habituation and extensive trail system at Punta Laguna I was able to follow males for sufficient time to collect reliable data. My data therefore provide the first real insight into the social relationships of male spider monkeys.

7.3. Relationship quality between male and female spider monkeys

Previous studies of wild spider monkeys have reported sex-segregated societies and low-quality relationships between the sexes (Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1990). In my study, males and females preferentially exchanged embraces with same-sex partners and coalitionary arm-wrapping never occurred between the sexes. Males also preferred to spent time in proximity to other males but females showed no preference for either sex. As males approached females more often than females approached males, it is likely that males were responsible for maintaining proximity. Social grooming, although rare, occurred relatively frequently between the sexes suggesting that males and females are more closely bonded than first thought. However, further examination of the data indicated that grooming between the sexes was almost exclusively between adult females and their sexually mature sons. The effect of kinship on male-female social grooming interactions in spider monkeys has not been investigated in previous studies, which have also reported relatively high rates of grooming between adult males and females (Ahumada, 1992; Chapman, 1990; Fedigan & Baxter, 1984; Symington, 1990). It is therefore possible that these results were also confounded by grooming between adult females and their mature sons.

Aggression between the sexes was also affected by kinship as males were never aggressive towards their mothers, but directed often severe aggression toward unrelated adult females. Females may therefore be reluctant to approach or engage in risky affiliative behaviour such as embraces or arm-wrapping with unrelated adult males due to fear of attack, thus males may have difficulty interacting with females due to female avoidance. Consequently, social relationships between unrelated adult male and female spider monkeys are best characterised as low quality. Conversely, females will have relatively little to fear from their own sons with whom they share cooperative and affiliative relationships, thus social relationships between related adult males and females are best described as high quality. When analysed together, these data give rise to an intermediate value for male-female grooming between male-male and female-female grooming. My study is the first to make this distinction between related and unrelated male and female spider monkeys.

Previous reports on spider monkeys have also reported high rates of female-directed male aggression (Campbell, 2003; Fedigan & Baxter, 1984; Symington, 1987: PhD thesis cited in Smuts & Smuts, 1993), which have been interpreted as sexual coercion (Smuts & Smuts, 1993) or a male strategy to dominate equally-sized females (Strier, 1994). However in my study, over 80% of female-directed male aggression could be characterised as ritualised chases directed cycling females as a form of sexual display. These ritualised chases were accompanied by male place-sniffing of substrates previously occupied by the female being chased suggesting that the chases were sexually motivated and were not simply male attempts to dominate females. Furthermore, females were often attracted to their male attackers, directed sexual behaviour towards them and then later fissioned together from the subgroup, possibly to form a mating consortship. As the chases were non-contact and females appear to be attracted to their attacker, the chases were interpreted as a form of sexual display (Fedigan & Baxter, 1984) rather than sexual coercion. The quality of social relationships between unrelated males and female spider monkeys may therefore not be as low as previously documented as a large proportion of the reported high rates of female-directed male aggression were likely ritualised chases rather than genuine attacks.

7.4. Comparisons with other species

High rates of affiliative behaviour exchanged between male spider monkeys correspond to findings from chimpanzees, bonobos and muriquis, which may be attributed to the pattern of male philopatry reported in these species (Morin *et al.*, 1994; Gerloff *et al.*, 1999; Goldberg & Wrangham, 1997; Mitani *et al.*, 2000; Strier, 1991; Symington, 1987; 1998b; 1990). Males from these species are also thought to work cooperatively to attract females to their community and defend their females from extra-community males (Aureli *et al.*, 2006; Boesch & Boesch-Achermann, 2000; Goodall, 1986; Kano, 1992; Strier, 2000), which is also likely to influence social exchanges between males. The low rate of aggression exchanged between community males at Punta Laguna and the absence of a clear-cut dominance hierarchy is similar to interactions between male muriquis (Strier *et al.,* 2002). Both muriquis and spider monkeys are arboreal and adopt flexible grouping patterns and in these circumstances males are expected to compete for fertilisations via scramble competition due to the difficulty in monitoring the reproductive state of dispersed females that limits monopolisation of cycling females (Mitani *et al.*, 1996a; van Hooff, 2000).

However, aggressive interactions and the somewhat fickle relationships between the four males in the Eastern community at Punta Laguna shared many similarities with the interactions of male chimpanzees and bonobos that exhibit opportunistic male coalitions. Male chimpanzees and bonobos exhibit clear-cut dominance hierarchies and overt contest competition for access to fertile females (Furuichi, 1997; Hohmann & Fruth, 2003; Newton-Fisher, 2002; Goodall, 1986; Nishida & Hosaka, 1996; Watts, 1998) suggesting that males compete for fertilisations via contest competition. My data indicate that social relationships between older and younger males are differentiated, and like muriquis and woolly monkeys, younger male spider monkeys preferentially interact with older males. However, I was not able to find evidence of a clear-cut dominance hierarchy among males. Aggression in the context of mating has not been observed in spider monkeys, but spider monkeys mate in secrecy suggesting that males are not tolerant toward each others' mating in the same way that male muriquis and woolly monkeys are. Social relationships between male spider monkeys therefore appear to take an intermediate position between the tolerance of muriquis and woolly monkeys and the more despotic relationships of male chimpanzees and bonobos.

With the exception of bonobos (de Waal, 1995; Kano, 1992; 1996), females belonging to societies with a high fission-fusion dynamic generally exhibit tolerant but non-affiliative social interactions. In all these species, there is strong evidence to suggest that females are the dispersing sex (Di Fiore & Fleischer, 2005; Nishida & Hiraiwa-Hasegawa, 1987; Goodhall, 1986; Kano, 1992; Strier, 1991; Symington, 1987; 1998b; 1990), and the rarity of coalitions and grooming between adult females suggest that female social relationships are best described as Dispersed-Egalitarian (Sterck *et al.,* 1997). My results and previous reports of social relationships in female spider monkeys (e.g. Fedigan & Baxter, 1984; Symington, 1990) generally concur with these reports of other species. Relationships among female spider monkeys are notably different from those of female woolly monkeys as female spider monkeys do not harass female conspecifics in the context of mating. Spider monkey female social relationships are therefore more similar to those of muriquis and chimpanzees.

As with muriquis (Printes & Strier, 1999) and chimpanzees (Wrangham, Clark & Isabirye-Basuta, 1992), I found that adolescent and recent immigrant female spider monkeys are subordinate to resident adult females as indicated by patterns of aggression and displacements. However, spider monkeys differ from muriquis and chimpanzees in terms of subgrouping. Muriquis regularly supplement their diet with leaves which reduces contest competition for food and thus muriquis are more cohesive than spider monkeys. Chimpanzees and spider monkeys are more frugivorous, but among chimpanzees adult females spend a large proportion of their time alone, whereas female spider monkeys are most often found in same-sex subgroups containing more than one adult female with dependent offspring (Chapman *et al.*, 1995). This difference in female grouping patterns between chimpanzees and spider monkeys is most likely due to differences in female-directed male aggression. Female chimpanzees tend to remain solitary even when food abundance could accommodate larger subgroups. Wrangham (2000; 2002) has suggested that as large groups of females attract males and as male chimpanzees are often aggressive towards females, female chimpanzees may remain solitary as a means of reducing male coercion. My results on spider monkeys have indicated that the vast majority of female-directed aggression among spider monkeys is actually a ritualised form of male sexual display. Consequently, female spider monkeys are unlikely to be as fearful of males as female chimpanzees and are therefore able to form larger subgroups. Chimpanzees at Taï are different again as females are most often observed in large mixed-sex subgroups, which appears to be a strategy to reduce leopard predation (Boesch & Boesch, 2000).

In terms of relationships between the sexes spider monkey relationships are similar to those of chimpanzees and woolly monkeys where males are dominant to females (Boesch & Boesch-Achermann, 2000; Di Fiore & Fleischer, 2005;

Goodall, 1986). However, unlike woolly monkeys, the strongest social bonds in spider monkeys are between males rather than between the sexes. As with bonobos, spider monkey mothers remain closely bonded with their adult sons, but in spider monkeys, females do not actively support their sons in dominance interactions. Male-female relationships in chimpanzees and spider monkeys were previously thought to be similar due to reports of sexual coercion of cycling females by adult males (Smuts & Smuts, 1993; Wrangham, 2000; 2002); however, my result indicate that the majority of female-directed male aggression in spider monkeys is actually a form of ritualised sexual display. Male-female relationships in spider monkeys are therefore more tolerant to those of chimpanzees, but less tolerant than those of muriquis that do not exhibit any aggression between the sexes (Strier *et al*., 2002).

The striking similarities between the social behaviour of spider monkeys and chimpanzees indicates provides further evidence that complex social systems characterised by high fission-fusion dynamics are an evolutionary adaptation to a particular set of environmental conditions. Both chimpanzees and spider monkeys are large bodied, frugivorous primates with high energy requirements causing feeding competition within groups to be extremely high. Flexible grouping appears to be a successful adaptation to this problem as by altering subgroup size in relations to food patch size, feeding competition may be greatly reduced (Chapman & Chapman, 2000). Similarly, *homo sapiens* are large bodied primates with high energy requirements, thus the high fission-fusion dynamics in traditional human societies are likely to have evolved for the same reasons, particularly as humans moved from a forest to savannah habitat where food is less abundant.

The complexity of social systems with high fission-fusion dynamics is also likely to have lead to high selection pressure for intelligent individuals with the cognitive plasticity required to adapt to changes in the social environment caused by flexible grouping. Thus, cognitive evolution within the primate order does not necessarily progress in a linear pattern from prosimians to monkeys, apes, and then humans because those species that adopt flexible grouping patterns are likely to be more cognitively advanced than closely related species that live in cohesive groups. In support of this view, brain mass in relation to body mass, and prefrontal cortex mass relative to total brain mass are larger in the genus *Ateles* (spider monkeys) in comparison to other monkeys. This pattern is also found in other animals such as dolphins, which live in societies characterised by high fission-fusion dynamics and exhibit extremely advanced cognition. According to the social brain hypothesis (Barton & Dunbar, 1996;

Dunbar, 1998), the cognitive evolution is directly related to social group size with species living in larger groups requiring larger brains keep track of the own social relationships and those of third parties. Thus, it also likely that cognitively evolution is intrinsically linked to the degree of cohesiveness of social groups because keeping track of third party relationships is more difficult in groups characterised by high fission-fusion dynamics. The cognitively abilities of species living in societies with flexible grouping patterns therefore warrants further research.

7.5. Directions for future research

My study has indicated that male social relationships are generally high quality, but with some provisos as interactions between older and younger adult males appeared to be tension-loaded as indicated by high rates of embraces. This tension was likely due to the younger males' perceived risk of attack, as older males have been observed to direct severe aggression toward younger males, which in some cases, have proved fatal (Campbell, in press; Valero *et al.*, 2006). Further investigation into male social relationships in spider monkeys could therefore concentrate on the progression of juvenile males into adulthood and whether male attacks on younger adult and juvenile males are an extreme form of male-male competition. If these attacks were linked to competition for females then it is likely that the frequency of these attacks would be linked to the sex ratio within the group. DNA paternity analysis could also determine whether male attackers were specifically targeting unrelated younger males as a means of increasing their own direct and inclusive fitness, by eliminating competition from unrelated males. DNA analysis could also be used to confirm the suspected female-biased dispersal and male philopatry and further clarify the importance of kinship in affiliative social interactions among spider monkeys.

Although my study has focused on the use of species-specific social behaviours, there are still many unanswered questions regarding the function of these behaviours. I found that embraces were associated with tension-loaded situations such as infant handling and fusion events. Embraces have been interpreted as signals of benign intent to reduce aggression (Schaffner & Aureli, 2005; Aureli & Schaffner, in prep), which implies that embraces are linked to tension reduction. Social grooming has also been linked to tension reduction in various non-human primate species as studies have investigated the effect of grooming on the heart rate and anxiety-related behaviour of non-human primates (Aureli, *et al.*, 1999; Schino *et al.*, 1998). It would therefore be extremely beneficial to our understanding of the function of spider monkey embraces if similar studies could be conducted on spider monkeys.

Finally, my thesis has provided an explanation for female-directed male aggression in spider monkeys that warrants further research. Non-contact prolonged chases were interpreted as a form of ritualised male sexual display as they were directed almost exclusively to cycling females, and the female victim often directed sexual behaviour towards her male attacker. Female victims were also observed to leave their present subgroup with their male attacker. Future research could therefore concentrate on following these pairs to see if they form a mating consortship. Campbell (2003) conducted hormonal analysis of female spider monkey faecal samples taken when females were cycling, pregnant and lactating, but due to the small sample size and the inclusion of physical aggression in the analysis, her results were inconclusive. Further research could therefore repeat this methodology using a larger sample of females and relating the findings to only female-directed male prolonged chases. Male-place sniffing as an indicator of female reproductive state could also be investigated further by performing hormonal analysis on the secretions deposited by cycling females on substrates.

7.6. Conclusion

My study has provided a detailed quantitative assessment of social relationships in wild spider monkeys that has incorporated the influence of ecological factors, mating systems, sexual harassment, infanticide, and market effects. In taking a more holistic approach, I have been able to analyse and evaluate the relative importance of these different factors in shaping social relationships. I found that the strongest social bonds among spider monkeys were between males as indicated by low rates of aggression and high rates of affiliative behaviour. However, male-male social relationships appear to be insecure, particularly between older males and younger males, as indicated by high rates of embraces (a signal of benign intent that reduces the likelihood of aggression). Males also exchanged embraces at high rates in tense situations such as following a fusion event or in the presence of females. Males were not observed to actively compete for access to fertile females, but male-male social interactions were significantly affected by the presence of females suggesting that male competition occurs at an intermediate level between despotic chimpanzees and tolerant muriquis.

Female-female social relationships were generally found to be low-quality, but were significantly affected by the presence of young infants, where females used embraces as a means of gaining access to others' infants. Flexible grouping as a means of reducing feeding competition was not completely effective as female aggression and coalitionary arm-wrapping were associated with feeding. However, female coalitions were rare and as females dispersed upon reaching sexual maturity, female-female social relationships correspond to the Dispersed-Egalitarian category outlined by Sterck *et al.* (1997). Relationships between the sexes were also found to be low quality, with the exception of relationships between mothers and their adult sons. I also examined female-directed male aggression that had previously been interpreted as sexual coercion and found that it was best described as a ritualised male sexual display.

References

Ahumada, J. A. (1992). Grooming behaviour of the spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *International Journal of Primatology, 13*, 33-49.

Alberts, S. C., Watts, H. & Altmann, J. (2003). Queuing and queue jumping: long-term patterns of dominance rank and mating success in male savannah baboons. *Animal Behaviour, 65*, 821-840.

Altmann, J. (2000). Models of outcome and process: Predicting the number of males in primate groups. In: P. M. Kappeler (Ed.), *Primate males: causes and consequences of variation in group composition* (pp 236-247). Cambridge: Cambridge University Press.

Altmann, J. (1990). Primate males go where the females are. *Animal Behaviour, 39*, 193-195.

Altmann, J. (1980). *Baboon mothers and infants*. Cambridge MA: Harvard University Press.

Altmann, J., Hausfater, G. & Altmann, S. (1988). Determinants of reproductive success in savannah baboons (*Papio cynocephalus*). In: T. H. Clutton-Brock (Ed.), *Reproductive success* (pp 403-418). Chicago: Chicago University Press.

Altmann, S. A. (1974). Observational study of behaviour: Sampling methods. *Behaviour, 49*, 227-265.

Anderson, D. P., Nordheim, E. V., Boesch, C. & Moermond, T. C. (2002). Factors influencing fission-fusion grouping in the chimpanzees in the Taï National Park, Côte d'Ivoire. In: C. P. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 90-101). Cambridge: Cambridge University Press.

Aureli, F., Das, M. & Veenema, H. C. (1997). Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis, M. fuscata* and *M. sylvanus*). *Journal of Comparative Psychology, 111*, 91-99.

Aureli, F., Cords, M., & van Schaik, C. P. (2002). Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour, 64*, 325-343.

Aureli, F., Preston, S. D. & de Waal, F. B. M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques: a pilot study. *Journal of Comparative Psychology, 113*, 59-65.

Aureli, F., Schaffner, C. M., Verpooten, J., Slater, K. & Ramos-Fernandez, G. (2006). Raiding parties of male spider monkeys: Insights into human warfare? *American Journal of Physical Anthropology, DOI: 10.1002/AJPA.20451*,

Baker, A. J., Dietz, J. M. & Kleiman, D. G. (1993). Behavioural evidence for monopolisation of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour, 46*, 1091-1103.

Barrett, L. & Henzi, S. P. (2006). Monkeys, markets and minds. In: P. M. Kappeler & C. P. van Schaik (Eds.), *Cooperation in Primates and Humans* (pp. 209-232). Berlin: Springer.

Barrett, L. & Henzi, S. P. (2002). Constraints on relationship formation among female primates. *Behaviour, 139*, 263-289.

Barrett, L. & Henzi, S. P. (2001). The utility of grooming to baboon troops. In: R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein (Eds.), *Economics in nature* (pp 119-145). Cambridge: Cambridge University Press.

Barrett, L. Henzi, S. P. Weingrill, T., Lycett, J. E. & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London Series B, 266*, 665-670.

Bartlett, T. Q., Sussman, R. W. & Cheverud, J. M. (1993). Infant killing in primates: A review of observed cases with specific reference to the sexual selection hypothesis. *American Anthropologist, 95*, 958-990.

Barton, R. A. (2000). Socioecology of baboons: The interaction of male and female strategies. In: P. M. Kappeler (Ed.), *Primate Males: causes and consequences of variation in group composition* (pp 97-107). Cambridge: Cambridge University Press.

Barton, R. A. (1985). Grooming site preferences in primates and their functional implications. *International Journal of Primatology, 6*, 519-532.

Barton, R. A., Byrne, R.W. & Whiten, A. (1996). Ecology, feeding competition and social structures in baboons. *Behavioural Ecology and Sociobiology 38*, 321-329.

Barton, R. A. & Dunbar, R. I. M. (1996). Evolution of the social brain. In: A Whiten & R. W. Byrne (Eds.) *Machiavellian Intelligence* (240-261). Cambridge: Cambridge University Press.

Barton, R. A. & Whiten, A. (1993). Feeding competition among olive baboons (*Papio anubis*). *Animal Behaviour, 46*, 777-789.

Berard, J. D., Nürnberg, P., Epplem, J. T. & Schmidtke, J. (1993). Male rank, reproductive behaviour, and reproductive success in free-ranging rhesus macaques. *Primates, 34*, 481-489.

Bercovitch, F. B. (1995). Female cooperation, consortship maintenance, and male mating success in savannah baboons. *Animal Behaviour, 50*, 137-149.

Bercovitch, F. B. (1988). Coalitions, cooperation and reproductive tactics among adult male baboons. *Animal Behaviour, 36*, 1198-1209.

Bercovitch, F. B. (1986). Male rank and reproductive activity in savannah baboons. *International Journal of Primatology, 7*, 533-550.

Bernstein, I. S. & Ehardt, C. L. (1986). The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Animal Behaviour, 34*, 739-747.

Birkhead, T. M. & Kappeler, P. M. (2004). Post-copulatory sexual selection in birds and primates. In: P. M. Kappeler & C. P. van Schaik (Eds.). *Sexual selection in primates: new and comparative perspectives* (pp 151-171). Cambridge: Cambridge University Press.

Boesch, C. (2002). Behavioural diversity in Pan. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 1-14). Cambridge: Cambridge University Press.

Boesch, C. (1996). Social grouping in Taï chimpanzees. In: W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), Great ape societies (pp 101-113). Cambridge: Cambridge University Press.

Boesch, C. & Boesch, H. (1989). Hunting behaviour of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology, 78*, 547-573.

Boesch, C. & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford: Oxford University Press.

Boinski, S. (1999). The social organization of squirrel monkeys: Implications for ecological models of social evolution. *Evolutionary Anthropology, 8*, 101-112.

Boinski, S. (1994). Affiliation patterns among male Costa Rican squirrel monkeys. *Behaviour, 130*, 191-209.

Boinski, S. & Mitchell, C. L. (1994). Male residence and association patterns in Costa Rican squirrel monkeys (*Saimiri oerstedi*). *American Journal of Primatology, 34*, 157-169.

Boinski, S, Sughrue, K., Selvaggi, L., Quatrone, R., Henry, M. & Cropp, S. (2002). An expanded test of the ecological model of primate social evolution:

Competitive regimes and female bonding in three species of squirrel monkeys (*Saimiri, oerstedi, S. boliviensis* and *S. sciureus*). *Behaviour, 139*, 227-261.

Borries, C. Launhardt, K., Epplen, C., Epplen, J. T. & Winkler, P. (1999). DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys. *Proceedings of the Royal Society of London, B, 266*, 901-904.

Bulger, J. B. (1993). Dominance rank and access to oestrous females in savannah baboons. *Behaviour, 127*, 67-103.

Butovskaya, M. L. (1993). Kinship and dominance styles in groups of three species of macaques (*M. arctoides, M. mulatta, M. fascicularis*). *Folia Primatologica*, 60, 210-224.

Byrne, R. W., Whiten, A. & Henzi, S. P. (1990). Social relationships of mountain baboons: Leadership and affiliation in a non-female-bonded monkey. *American Journal of Primatology, 20*, 313-329.

Caldecott, J. O. (1986). Mating patterns, societies, and ecogeography of macaques. *Animal Behaviour, 34*, 208-220.

Campbell, C. J. (in press). Lethal intragroup aggression in adult male spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology*.

Campbell, C. J. (2006). Copulation in free-ranging black-handed spider monkeys. *American Journal of Primatology, 68*, 1-5.

Campbell, C. J. (2003). Female-directed aggression in free-ranging *Ateles geoffroyi*. *International Journal of Primatology, 24*, 223- 237.

Cant, J. G. H. (1978). Population survey of the spider monkeys, *Ateles geoffroyi*, at Tikal, Guatemala. *Primates, 19*, 525-535.

Cant, Youlatos & Rose (2001). Locomotor behaviour of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: General patterns and nonsuspensory modes. *Journal of Human Evolution, 41*, 141-166.

Chaffin, C. L., Friedlen, K. & De Waal, F. B. M. (1995). Dominance style of the Japanese macaques compared with rhesus and stumptail macaques. *American Journal of Primatology, 35*, 103-116.

Chan, L. K. W. (1996). Phylogenetic interpretations of primate socioecology with special reference to social and ecological diversity in *Macaca*. In E. Martins (Ed.), *Phylogenies and the comparative method in animal behaviour* (pp 324-360). Oxford, Oxford University Press.

Chapais, B. (1983a). Dominance, relatedness and the structure of female relationships in rhesus monkeys. In: R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp 209-219). Oxford: Blackwell.

Chapais, B. (1983b). Structure of the birth season relationship among adult male and female rhesus monkeys. In: R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp 200-208). Oxford: Blackwell.

Chapais, B. (1983c). Adaptive aspects of social relationships among rhesus monkeys. In: R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp 286-289). Oxford: Blackwell.

Chapman, C. A. (1990). Association patterns of spider monkeys: The influence of ecology and sex on social organisation. *Behavioural Ecology and Sociobiology, 26*, 249-257.

Chapman, C. A. (1988). Patch use and depletion by the spider and howler monkeys of Santa Rosa National Park, Costa Rica. *Behaviour, 150*, 99-116.

Chapman, C. A. & Chapman, C. (2000). Determinants of group size in primates: The importance of travel costs. In: S. Boinski & P. A. Garber (Eds.), *On the move: How and why animal travel in groups* (pp 24-42). Chicago: University of Chicago Press.

Chapman, C. A. & Chapman, C. (1990). Reproductive biology of captive and free-ranging spider monkeys. *Zoo Biology, 9*, 1-9.

Chapman, C. A., Fedigan, L. M., Fedigan, L. & Chapman, C. (1989). Post-weaning resource competition and sex ratios in spider monkeys. *Oikos, 54,* 315-319.

Chapman, C. A., Wrangham, R. W., and Chapman, L. J. (1995). Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. *Behavioural Ecology and Sociobiology, 36,* 59-70.

Cheney, D. L. (1983). Extra familial alliances among vervet monkeys. In: R. A. Hinde (Ed.). *Primate social relationships: An integrated approach* (pp 278-286). Sunderland, MA: Sinauer Associates.

Cheney, D. L. (1978). Interactions of immature male and female baboons with adult females. *Animal Behaviour, 26,* 389-408.

Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species.* Chicago: University of Chicago Press.

Cheney, D. L. & Wrangham, R.W. (1987). Predation. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 227-239). Chicago: The University of Chicago Press.

Chism, J. B. & Rowell, T. E. (1986). Mating and residence patterns in male patas monkeys. *Ethology, 72,* 31-39.

Clutton-Brock, T. H. (1989). Mammalian mating strategies. *Proceedings of the Royal Society of London Series B, Biological Sciences, 236,* 339-372.

Clutton-Brock, T. H. & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour, 49,* 1345-1365.

Coelho Jr., A. M., Bramblett, C. A., Quick, L. B. & Bramblett, S. S. (1976). Resource availability and population density of primates: A socio bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates, 17,* 63-80.

Collins, D. A., Busse, C. D. & Goodall, J. (1984). Infanticide in two populations of savannah baboons. In: G Hausfater & S. B. Hrdy (Eds.) *Infanticide:*

Comparative and evolutionary perspectives (pp 193-215). New York, Hawthorne.

Collins & Dubach, (2001). Nuclear DNA variation in spider monkeys (*Ateles*). *Molecular Phylogenetics and Evolution, 19*, 67-75.

Collins & Dubach, (2000). Phylogenetic relationships among spider monkeys (*Ateles*) based on mitochondrial DNA variation. *International Journal of Primatology, 21*, 381-420.

Colmenares, F. (1991). Greeting behaviour between male baboons: Oestrous females, rivalry and negotiation. *Animal Behaviour, 41*, 49-60.

Colmenares, F. (1990). Greeting behaviour in male baboons, 1: Communication, reciprocity and symmetry. *Behaviour, 113*, 81-116.

Colmenares, F., Hofer, H. & East, M. L. (2000). Greeting ceremonies in baboons and hyenas. In: F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp 94). London: University of California Press.

Conner, R. C., Smolker, R. A. & Richards, A. F. (1992). Dolphin coalitions and alliances. In: A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 415-443). Oxford: Oxford University Press.

Constable, J. L., Ashley, M. V., Goodall, J., & Pusey, A. E. (2001). Non-invasive paternity assignment in Gombe chimpanzees. *Molecular Ecology, 10*, 1279-1300.

Cooper, M. A. & Bernstein, I. S. (2000).Social grooming in Assames macaques (*Macaca assamensis*). *American Journal of Primatology, 50*: 77-85.

Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus mitis*). *Behaviour, 139*, 291-314.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In: A. Whiten & R. W. Byrne (Eds.). *Machiavellian intelligence II: evaluations and extensions* (pp 24-49). Cambridge: Cambridge University Press.

Cords, M. (1988). Resolution of aggressive conflicts by immature long-tailed macaques (*Macaca fascicularis*). *Animal Behaviour, 36*, 1124-1135.

Cords, M, (1987). Forest guenons and patas monkeys: Male-male competition in one-male groups. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 98-111). Chicago: University of Chicago Press.

Cords, M. & Aureli, F. (2000). Reconciliation and relationship qualities. In: F. Aureli & F. B. M. de Waal (Eds.). *Natural conflict resolution* (177-198). London: University of California Press.

Cords, M. & Aureli, F. (1993). Patterns of reconciliation among juvenile long-tailed macaques. In: M.E. Pereira & L. M. Fairbanks (Eds.). *Juvenile primates: Life history, development and behavior* (pp 271-284). Oxford: Oxford University Press.

Cords, M. & Thurnheer, S. (1993). Reconciliation with valuable partners by long-tailed macaques. *Ethology, 93*, 315-325.

Cowlishaw, G. (1998). The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour, 135*, 431-452.

Cowlishaw, G. (1994). Vulnerability to predation in baboon populations. *Behaviour, 132*, 75-86.

Cowlishaw, G. & Dunbar, R. I. M. (1991). Dominance rank and mating success in male primates. *Animal Behaviour, 41*, 1045-1056.

Crockett, C. M. & Eisenberg, J. F. (1987). Howlers: Variation in group size and demography. In: B.B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.). *Primate societies* (pp 54-68). Chicago: University of Chicago Press.

Crockett, C. M. & Janson, C. H. (2000). Infanticide in red howlers: Female group size, male membership and a possible link to folivory. In: C. P. van Schaik & C. H. Janson (Eds.). *Infanticide by males and its implications* (pp 75-98).

Crockett, C. M. & Sekulic, R. (1984). Infanticide in red howler monkeys (*Alouatta seniculus*). In: G. Hausfater & S. B. Hrdy (Eds.), *Infanticide: Comparative and evolutionary perspectives* (pp 173-191). New York: Aldine de Gruyter.

Darwin, C. (1871). *The descent of man, and selection in relation to sex.* London: John Murray. Reprinted in 1998.

Datta, S. B. (1992). Effects of availability of allies on female dominance structure. In A. H. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 61-82). Oxford: Oxford University Press.

Deitz, J. M. & Baker, A. J. (1993). Polygyny and female reproductive success in golden lion tamarins (*Leontopithecus rosalia*). *Animal Behaviour, 46*, 1067-1078.

de Moraes, P. L., de Carvalho, O. & Strier, K. B. (1998). Population variation in match size and party size in muriquis (*Brachyteles arachnoides*). *International Journal of Primatology, 19*, 325-337.

de Ruiter, J.R., Scheffrahn, W., Trommelen, G. J. J. M., Uitterlinden, A. G., Martin, R. D. & van Hooff, J. A. R. A. M. (1992). Male social rank and reproductive success in wild long-tailed macaques: Paternity exclusions by blood protein analysis and DNA finger-printing. In: R. D. Martin, A. F. Dixson & E. J. Wickings (Eds.), *Paternity in primates: Genetic tests and theories* (pp 175-191). Basel: S. Karger.

Deschner, T., Heistermann, M., Hodges, L. K. & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behaviour in wild West African chimpanzees. *Hormones and Behavior, 46*, 204-215.

de Waal, F. B. M. (1997). The chimpanzee's service economy: Food for grooming. *Evolution and Human Behavior, 18*, 375-386.

de Waal, F. B. M. (1989). Food sharing and reciprocal obligations among chimpanzees. *Journal of Human Evolution, 18*, 433-459.

de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *Quarterly Review of Biology, 61*, 459-479.

de Waal, F. B. M. (1982). *Chimpanzee politics*. New York: Harper and Row.

de Waal, F. B. M. & Harcourt, A. (1992). Coalitions and alliances: A history of ethological research. In: A. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 1-19). Oxford: Oxford University Press.

de Waal, F. B. M. & Luttrell, L. M. (1989). Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stumptail monkeys. *American Journal of Primatology, 19*, 83-109.

Di Fiore, A. (2003). Ranging behaviour and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. *American Journal of Primatology, 59*, 47-66.

Di Fiore, A. & Fleischer, R. C. (2005). Social behaviour, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *International Journal of Primatology, 26*, 1137-1173.

Di Fiore, A. & Rodman, P. S. (2001). Time allocation of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in neotropical *terra firma* forest. *International Journal of Primatology, 22*, 449-480.

Di Fiore, A. & Rendall, D. (1994). Evolution of social organisation: A reappraisal for primates by using phylogenetic methods. *Proceedings of the Naturalist Academy of Science USA, 91*, 9941-9945.

Digby, L. J. (1995). Social organisation in a wild population of *Callithrix jacchus*: II. Intra-group social behaviour. *Primates, 36*, 361-375.

Dixson, A. F. (1998). *Primate sexuality*. Oxford: Oxford University Press.

Drews, C. (1993*). The concept and definition of dominance in animal behaviour. Behaviour, 125*, 285-313.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology, 6*, 178-190.

Dunbar, R. I. M. (1992). Time: A hidden constraint on the behavioural ecology of baboons. *Behavioural Ecology and Sociobiology, 31*, 35-49.

Dunbar, R. I. M. (1988). *Primate Social Systems*. London: Crook Helm.

Dunbar, R. I. M. (1984). *Reproductive decisions: An economic analysis of gelada baboon social strategies*. Princeton, NJ: Princeton University Press.

Dunbar, R. I. M. & Cowlishaw, G. (1992). Mating success in male primates: Dominance rank, sperm competition and alternative strategies. *Animal Behaviour, 44*, 1171-1173.

East, M. L., Hofer, H. & Wickler, W. (1993). The erect 'penis' is a flag of submission in a female-dominated society: Greetings in Serengeti spotted hyenas. *Behavioural Ecology and Sociobiology*, 33, 355-370.

Eberle, M. & Kappeler, P. M. (2002). Mouse lemurs in space and time: a test of the socioecological model. *Behavioural Ecology and Sociobiology, 51*, 131-139.

Ehardt, C. L. & Bernstein, I. S. (1992). Intervention behaviour by adult male macaques: Structural and functional aspects. In: A. H. Harcourt, F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 83-111). Cambridge: Cambridge University Press.

Eisenberg, J. F. (1973). Reproduction in two species of spider monkeys, *Ateles fusciceps* and *Ateles geoffroyi*. *Journal of Mammalia, 54*, 955-957.

Eisenberg, J. F. & Kuehn, R. E. (1966). The behaviour of *Ateles geoffroyi* and related species. *Smithson Miscellaneous Collection, 151*, 1-63.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science, 197*, 215-223.

Englehardt, A., Pfeifer, J. B., Heistermann, M., Niemitz, C., van Hooff, J. A. R. A. M. & Hodges, J. K. (2004). Assessment of female reproductive status by long-tailed macaques, *Macaca fascicularis*, under natural conditions. *Animal Behaviour*, *67*, 915-924.

Evans, S. & Poole, T. B. (1984). Long-term changes and maintenance of the pair bond in common marmosets, *Callithrix jacchus jacchus*. *Folia Primatologica*, *42*, 33-41.

Fairbanks, L. A. (1980). Relationships among adult females in captive vervet monkeys: Testing a model of rank-related attractiveness. *Animal Behaviour*, *28*, 853-859.

Fedigan, L. M. & Baxter, M. J. (1984). Sex differences and social organisation in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, *25*, 279-284.

Ferrari, S. F. & Lopes, M. A. (1996). Primate populations in Eastern Amazonia. In: M. A. Norconk, A. L. Rosenberger & P. A. Garber (Eds.) *Adaptive radiations of neotropical primates* (pp 53-55). New York: Plenum.

Freese, C. (1976). Censusing *Alouatta* piliata, *Ateles geoffroyi* and *Cebus capucinus* in the Costa Rican dry forest. In R. W. Thorington Jr. & P. G. Heltne (Eds.) *Neotropical primates: Field studies and conservation* (pp 4-9). Washington, DC: National Academy of Sciences.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology*, *18*, 855-875.

Furuichi, T. (1987). Sexual swelling, receptivity and grouping of wild pygmy chimpanzees at Wamba, Zaïre. *Primates*, *20*, 309-318.

Furuichi, T. & Hashimoto, C. (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 156-167). Cambridge: Cambridge University Press.

Furuichi, T. & Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour, 130*, 211-228.

Galdikas, B. M. F. (1985). Subadult male orang-utan sociality and reproductive behaviour at Tanjung Putting. *American Journal of Primatology, 8*, 87-99.

Garber, P. A., Ençarnación, F., Moya, L. & Pruetz, J. D. (1993). Demographic and reproductive patterns in moustached tamarin monkeys (*Saguinus mystax*): Implications for reconstructing platyrrhine mating systems. *American Journal of Primatology, 29*, 235-254.

Gerloff, U. Hartung, B., Fruth, B. Hohmann, G. & Tautz, D. (1999). Intracommunity relationships, dispersal pattern and paternity success in a wild living community of bonobos (*Pan paniscus*) determined from DNA analysis of faecal samples. *Proceedings of the Royal Society of London Series B: Biological Sciences, 266*, 1189-1195.

Goldberg, T.L. & Wrangham, R. W. (1997). Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. *Animal Behaviour, 54*, 559-570.

Goldizen, A. W., Mendelson, J. & Terborgh, J. (1996). Saddle-back tamarins (*Saguinus fuscicollis*) reproductive strategies: Evidence from a thirteen-year study of a marked population. *American Journal of Primatology, 38*, 57-84.

Goodall, J. (1986). *The chimpanzees of gombe*. Cambridge, MA: Harvard University Press.

Gouzoules, H. & Gouzoules, S. (2002). Primate communication: By nature honest, or by experience wise? *International Journal of Primatology, 23*, 821-848.

Gouzoules, S. & Gouzoules, H. (1987). Kinship. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp 209-305). Chicago: Chicago University Press.

Hamilton, W. D. (1964). The genetic evolution of social behaviour I, II. *Journal of Theoretical Biology, 7*, 1-52.

Hannah-Stewart, L. J. (2004). Relationship management in captive chimpanzees (*Pan troglodytes*) and baboons (*Papio cynocephalus*). PhD thesis, University of Liverpool.

Harcourt, A. H. (1992). Coalitions and alliances: Are primates more complex than non-primates? In: A. H. Harcourt & F. B. M. De Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 445-471). Oxford: Oxford University Press.

Harcourt, A. H., Harvey, P. H., Larson, S. G. & Short, R. V. (1981). Testis weight, body weight and breeding system in primates. *Nature, 293*, 55-57.

Hemelrijk, C. (1999). An individual orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society of London Series B: Biological Sciences, 266*, 361-369.

Hemelrijk, C. & Ek, A. (1991). Reciprocity and interchange of grooming and 'support' in captive chimpanzees, *Animal Behaviour, 41*, 923-35.

Henzi, S. P. & Barrett, L. (2002). Infants as a commodity in a baboon market. *Animal Behaviour, 63*, 915-921.

Henzi, S. P. & Barrett, L. (1999). The value of grooming to female primates. *Primates, 40*, 47-59.

Hill, D. A. (1990). Social relationships between adult male and female rhesus macaques II: Non-sexual affiliative behaviour. *Primates, 31*, 33-50.

Hill, D. A. (1987). Social relationships between adult male and female rhesus macaques: 1. Sexual consortships. *Primates, 28*, 439-456.

Hill, R. A. & Dunbar, R. I. M. (1998). An evaluation of the roles of predation rate and predation risk as selective pressures on primate grouping behaviour. *Behaviour, 135*, 411-430.

Hinde, R. A. 1983. A conceptual framework In: R. A. Hinde (Ed.) *Primate social relationships. An integrated approach*, (pp. 1-7). Oxford: Blackwell Scientific Publications.

Hinde, R. A. (1979). *Towards understanding relationships*. London: Academic Press.

Hinde, R. A. (1976). Interactions, relationships, and social structure. *Man*, *11*, 1-17.

Hinde, R. A. & Powell Proctor, L. (1977). Changes in the relationships of captive rhesus monkeys on giving birth. *Behaviour*, *61*, 304-321.

Hiraiwa-Hasegawa, M., Hasegawa, T. & Nishida, T. (1984). Demographic study of a large-sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: a preliminary report. *Primates*, *25*, 401-13.

Hohmann, G. & Fruth, B. (2003). Intra- and inter-sexual aggression in the context of mating. *Behaviour*, *140*, 1389-1413.

Hohmann, G. & Fruth, B. (2002). Dynamics in social organization of bonobos (*Pan pansicus*). In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *behavioural diversity in chimpanzees and bonobos* (pp 138-150). Cambridge: Cambridge University Press.

Hohmann, G., Gerloff, U., Tautz, D. & Fruth, B. (1999). Social bonds and genetic ties: Kinship, associations and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*, *136*, 1219-1235.

Howell, D. C. (2002). *statistical methods for psychology*. Belmont, CA: Duxbury Press.

Hrdy, S. B. (1979). Infanticide among animal: A review, classification, and examination of the implications for reproductive strategies of females. *Ethology and Sociobiology*, *1*, 13-40.

Hrdy, S. B., Janson, C. H. & van Schaik, C. P. (1995). Infanticide: Let's now throw the baby out with the bath water. *Evolutionary Anthropology, 3*, 151-4.

Hutchins, M. & Barash, D. P. (1976). Grooming in primates: Implications for its utilitarian functions. *Primates, 17*, 145-150.

Ihobe, H. (1992). Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaïre. *Primates, 33*, 163-179.

Isbell, L. A. (1994). Predation on primates: Ecological patterns and evolutionary consequences. *Evolutionary Anthropology, 3*, 61-71.

Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behaviour among primates. *Behavioural Ecology, 2*, 143-155.

Isbell, L. A. & Pruetz, J. D. (1998). Differences between vervets (*Cercopithecus aethiops*) and patas monkeys (*Erythrocebus patas*) in agonistic interactions between adult females. *International Journal of Primatology, 19*, 837-855.

Isbell, L. A., Pruetz, J. D., Lewis, M. & Young, T. P. (1999). Rank differences in ecological behaviour: A comparative study of patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*) . *International Journal of Primatology, 20*, 257-272.

Isbell, L. A. & Young, T. P. (2002). Ecological models of females social relationships in primates: Similarities, disparities and some directions for future research. *Behaviour, 139*, 177-202.

Isbell, L. A. & van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequence for group-living primates. *Behaviour, 133*, 1-36.

Izar, P. (2004). Female social relationships of *Cebus apella nigritus* in a Southeastern Atlantic forest: An analysis through ecological models of primate social evolution. *Behaviour, 141*, 71-99.

Janson, C. H. (2000). Primate socio-ecology: The end of a golden age? *Evolutionary Anthropology, 9*, 73-86.

Janson, C. H. (1998). Testing the predation hypothesis for vertebrate sociality: Prospects and pitfalls. *Behaviour, 135*, 389-410.

Janson, C. H. (1992). Evolutionary ecology of primate social structure. In: E. A. Smith & B. Winterhalder (Eds.), *Evolutionary ecology and human behavior* (pp 95-130). New York: Aldine de Gruyter.

Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*): quantitative effects of group size and tree productivity. *Behaviour, 105*, 53-76.

Janson, C. H. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella). Behavioural Ecology and Socio-biology, 18*, 125-138.

Janson, C. H. (1984). Female choice and mating system of the brown capuchin monkey, *Cebus apella* (Primates: Cebidae). *Zeitschrift für Tierpsychologie, 65*, 177-200.

Kano, T. (1996). Male rank order and copulation rate in a unit-group of bonobos at Wamba, Zaïre. In: W. C. McGrew, L. F. Marchant & T. Nishida, *Great ape societies* (pp 135-145). Cambridge: Cambridge University Press.

Kano, T. (1992). *The Last Ape: Pygmy chimpanzee behaviour and ecology.* Stanford, CA: Stanford University Press.

Kappeler, P. M. (2000). Primate males: history and theory. In P. M. Kappeler (Ed.), *Primate males* (pp 3-9). Cambridge: Cambridge University Press.

Kappeler, P. M. (1999a). Primate socio-ecology: New insights from males. *Naturwissenschaften, 85*, 18-29.

Kappeler, P. M. (1999b). Lemur social structure and convergence in primate socioecology. In: P. Lee (Ed.), *Comparative primate socioecology.* Cambridge: Cambridge University Press.

Kappeler, P. M. (1997). Intrasexual selection and testes size in strepsirrhine primates. *Behavioural Ecology, 8,* 10-19.

Kappeler, P. M. (1993). Variation in social structure: The effects of sex and kinship on social interactions in three lemur species. *Ethology, 93,* 125-145.

Kappeler, P. M. & Heymann, E. W. (1996). Nonconvergence in the evolution of primate life history and socio-ecology. *Biological Journal of the Linnean Society* 59, 297-326.

Kappeler, P. M. & van Schaik, C. P. (2004). Sexual selection in primates: review and selective preview. In: P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp 3-23). Cambridge: Cambridge University Press.

Kappeler, P. M. & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology, 23,* 707- 740.

Kappeler, P. M. & van Schaik, C. P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology, 92,* 51-69.

Kapsalis, E. & Berman, C. M. (1996a). Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I: Criteria for kinship. *Behaviour, 133,* 1209-1234.

Kapsalis, E. & Berman, C. M. (1996b). Models of affiliative relationships among free ranging rhesus macaques (*Macaca mulatta*) II: Testing predictions for three hypothesised organizing principles. *Behaviour, 133,* 1235-1263.

Keane, B., Dittus, W. P. J. & Melnick, D. J. (1997). Paternity assessment in wild groups of toque macaques, *Macaca sinca*, at Polonnaruwa, Sri Lanka, using molecular markers. *Molecular Ecology, 6,* 267-282.

Keppel, G. & Wickens, T. D. (2004). *Design and analysis: A researchers handbook fourth edition.* New Jersey: Pearson Education Ltd.

Kervene, E. B., Martensz, N. & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming interactions. *Psychoneuroendochrinology, 14,* 155-161.

Klein, L. L. (1971). Observations on copulation and seasonal reproduction of two species of spider monkeys, *Ateles belzebuth* and *A. geoffroyi. Folia Primatologica, 15,* 233-248.

Klein, L. L. & Klein, D. (1971). Aspects of social behaviour in a colony of spider monkeys (*Ateles geoffroyi*) at san Francisco Zoo. *International Zoo Yearbook, 22,* 175-181.

Klinkova. E., Hodges, J. K., Fuhrmann, K., de Jong, T. & Heishtermann, M. (2005). Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *International Journal of Primatology, 26,* 357-384.

Koenig, A. (2002). Competition for resources and its behavioural consequences among female primates. *International Journal of Primatology, 23,* 759-783.

Koenig, A. (2000). Competitive regimes in forest dwelling Hanuman langurs (*Seminopithecus entellus*). *Behavioural Ecology and Sociobiology, 48,* 93-109.

Koenig, A., Beise, J., Chalise, M.K. & Ganzhorn, J.U. (1998). When females should contest for food: Testing hypotheses about resource density, distribution size and quality with Hanuman langurs (*Presbytis entellus*). *Behavioural Ecology and Sociobiology, 42,* 225-237.

Kuester, J. & Paul, A. (1992). Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour, 120,* 192-217.

Kummer, H. (1995). *In quest of the sacred baboon.* Princeton NJ: Princeton University Press.

Kummer, H. (1978). On the value of social relationships to nonhuman primates: A heuristic scheme. *Social Science Information, 17,* 687-705.

Kummer, H. (1971). *Primate societies: Group techniques of ecological adaptation*. Chicago: Aldine Publishing Company.

Lindburg, D.G. (1980). *The macaques: Studies in ecology, behaviour and evolution*. New York: Van Nostrand Reinhold.

Maestripieri, D. (1994a). Social structure, infant handling and mothering styles in group-living Old World monkeys. *International Journal of Primatology, 15*, 531-553.

Maestripieri, D. (1994b). Influence of infants on females social relationships in monkeys. *Folia Primatologica*, *63*, 192-202.

Maestripieri, D. (1993a). Infant kidnapping among group-living rhesus macaques: Why don't mothers rescue their infants? *Primates*, *34*, 211-216.

Maestripieri, D. (1993b). Maternal anxiety in rhesus macaques 1. Measurement of anxiety and identification of anxiety-eliciting situations. *Ethology*, *95*, 19-31.

Maestripieri, D. & Roney, J. R. (2005). Primate copulation calls and postcopulatory female choice. *Behavioral Ecology*, *16*, 106-113.

Maestripieri, D. & Wallen, (1995). Interest in infants varies with reproductive condition in group-living female pigtail macaques (*Macaca nemestrina*). *Physiology & Behavior*, *57*, 353-358.

Manson, J. P. (1999). Infant handling in wild *Cebus capucinus*: testing bonds between females? *Animal Behaviour*, *57*, 911-921.

Manson, J. P., Navarette, C. D., Silk, J. B. & Perry, S. (2004). Time-matched grooming in female primates? New analyses from two species. *Animal Behaviour*, *67*, 493-500.

Martel, F. L., Nevison, C. M., Rayment, F. D. G. & Simpson, M. J. A. (1994). The social grooming of captive female rhesus monkeys: Effects of the births of their infants. *International Journal of Primatology*, *15*, 555-572.

Matsumara, S. (1999). The evolution of egalitarian and despotic social systems among macaques. *Primates, 40*, 23-31.

Matsumara, S. & Kobayashi, T. (1998). A game model for dominance relations among group-living animals. *Behavioural Ecology and Sociobiology, 42*, 77-84.

Matsumoto-Oda, A. (2002). Social relationships between cycling females and adult male Mahale chimpanzees. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 168-180). Cambridge: Cambridge University Press.

Matsumoto-Oda, A. (1999). Mahale chimpanzees: grouping patterns and cycling females. *American Journal of Primatology, 47*, 197-207.

Matsumoto-Oda, A. & Oda, R. (1998). Changes in the activity budget of cycling female chimpanzees. *American Journal of Primatology, 46*, 157-166.

Matsumoto-Oda, A., Hosaka, K., Huffman, M. A. & Kawanaka, K. (1999). Factors affecting party size of the chimpanzees of the Mahale Mountains. *International Journal of Primatology, 19*, 999-1011.

Mazzolli, M., Graipel, M. E. & Dunstone, N. (2002). Mountain lion depredation in southeastern Brazil. *Biological Conservation, 105*, 43-51.

Milton, K. (1985). Mating patterns of woolly spider monkeys (*Brachyteles arachnoids*): Implications for female choice. *Behavioural Ecology and Sociobiology, 17*, 53-59.

Milton, K. (1981). Estimates of reproductive parameters for free-ranging Ateles geoffroyi. *Primates, 22*, 574-579.

Mitani, J. C. (1985). Mating behaviour of male orangutans in the Kutai reserve. *Animal Behaviour, 33*, 392-402.

Mitani, J. C., Gros-Louis, J. & Manson, J. H. (1996a). Number of males in primate groups: Comparative tests of competing hypotheses. *American Journal of Primatology*, *38*, 315-332.

Mitani, J. C., Gros-Louis, J. & Richards, A. F. (1996b). Sexual dimorphism, the operational sex ratio, and the intensity of male competition in polygynous primates. *American Naturalist*, *147*, 966-980.

Mitani, J. C., Merriwether, D. A. & Zang, C. (2000). Male affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour*, *59*, 885-893.

Mitani, J. C., Watts, D. P. & Lwanga, J. S. (2002). Ecological and social correlates of chimpanzee party size and composition. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.) *Behavioural diversity in chimpanzees and bonobos* (pp 102-111). Cambridge: Cambridge University Press.

Mitchell, C. L., Boinski, S. & van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behavioural Ecology and Sociobiology* *28*, 55-60.

Møller, A. P. (1988). Ejaculate quality, testes size and sperm competition in primates. *Journal of Human Evolution*, *17*, 478-488.

Morales, J. C. & Melnick, D. J. (1998). Phylogenetic relationships of the macaques (Cercopithecidae: *Macaca*), as revealed by high resolution restriction site mapping of mitochondrial ribosomal genes. *Journal of Human Evolution*, *34*, 1-23.

Morin, P. A., Moore, J. J., Chakraborty, R., Jin, L., Goodall, J. & Woodruff, D. S. (1994). Kin selection, social structure, gene flow and the evolution of chimpanzees. *Science*, *265*, 1193-1201.

Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 112-123). Cambridge: Cambridge University Press.

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys (*Erythrocebus patas*). *Behaviour, 128,* 103-119.

Muroyama, Y. (1991). Mutual reciprocity and grooming in Japanese macaques (*Macaca fuscata*) *Behaviour, 119,* 162-170.

Nadler, (1989). Sexual intimidation in wild mountain gorillas. *International Journal of Primatology, 10,* 81-92.

Newton-Fisher, N. E. (2002). Relationships of male chimpanzees in the Budongo forest, Uganda. In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 124-137). Cambridge: Cambridge University Press.

Newton-Fisher, N. E. (1999). Association by male chimpanzees: A social tactic? *Behaviour, 136,* 705-730.

Newton-Fisher, N. E., Reynolds, V. & Plumtre, A. J. (2000). Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. *International Journal of Primatology, 21,* 613-628.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian Journal of Zoology, 2,* 9-65.

Nishida, T. (2003). Harassment of mature female chimpanzees by young males in the Mahale Mountains. *International Journal of Primatology, 26,* 503- 514.

Nishida, T. (1990). A quarter century of research in the Mahale Mountains: An overview. In: T. Nishida (Ed.), *The chimpanzees of the Mahale Mountains: Sexual and life history strategies* (pp 3-35). Tokyo: Tokyo University Press.

Nishida, T. (1989). Social interactions between resident and immigrant female chimpanzees. In: P. G. Heltne & L. Marquardt (Eds.), *Understanding chimpanzees* (pp 68-89). Cambridge MA: The Chicago Academy of Science.

Nishida, T. & Hiraiwa-Hasegawa, M. (1987). Chimpanzees and Bonobos: cooperative relationships among males. In: B. B. Smuts, D. L. Cheney, R. M.

Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 165-180). Chicago: The University of Chicago Press.

Nishida, T. & Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In W. C. McGrew, L. F. Marchant & T. Nishida (Eds.), *Great ape societies* (115-134). Cambridge: Cambridge University Press.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C. & Nakumara, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science, 107*, 141-188.

Nishida, T. Takasaki, H. & Takahata, Y. (1990). Demography and reproductive profiles. In: T. Nishida (Ed.), *The chimpanzees of the Mahale Mountains: Sexual and life history strategies* (pp 63-97). Tokyo: Tokyo University Press.

Noë, R. (1992). Alliance formation among male baboons: shopping for profitable partners. In: A. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 285-321). Oxford: Oxford University Press.

Noë, R. (1990). A veto game played by baboons: A challenge to the use of prisoner's dilemma as a paradigm for reciprocity and cooperation. *Animal Behaviour, 39*, 78-90.

Noë, R. (1986). Lasting alliances among male savannah baboons. In: J. C. Else & P. C. Lee (Eds.), *Primate ontogeny, cognition and social behaviour* (pp 381-92). Cambridge: Cambridge University Press.

Noë, R. & Hammerstein, P. (1995). Biological markets. *Trends in Ecology and Evolution, 10*, 336-339.

Noë, R. & Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioural Ecology and Sociobiology, 35*, 1-11.

Noë, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. (1991). The market effect: An explanation for pay-off asymmetries among collaborating animals. *Ethology, 87*, 97-118.

Noë, R. & Sluijter, A. A. (1990). Reproductive tactics of male savannah baboons. *Behaviour, 113*, 117-170.

Norconk, M. A., Sussman, R. W. & Philips-Conroy, J. P. (1996). Primates of Guyana Shield forests. In: M. A. Norconk, A. L. Rosenberger & P. A. Garber (Eds.), *Adaptive radiations of neotropical primates* (pp 69-83). New York: Plenum.

Nunn, C. L. (1999). The evolution of exaggerated sexual swellings in primates and the graded signal hypothesis. *Animal Behaviour, 58*, 229-246.

O'Brien, T. G. (1993). Allogrooming behaviour among adult wedge-capped capuchin monkeys. *Animal Behaviour, 46*, 499-510.

O'Brien, T. G. (1991). Female-male social interactions in wedge-capped capuchin monkeys and costs of group living. *Animal Behaviour, 41*, 555-567.

O'Brien, T. G. & Robinson, J. G. (1991). Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank, and relatedness. *Behaviour, 119*, 30-50.

Oi, T. (1990). Patterns of dominance and affiliation in wild pig-tailed macaques (*Macaca nemestrina nemestrina*) in West Sumatra. *International Journal of Primatology, 11*, 339-356.

Packer, C. (1979). Male dominance and reproductive activity in *Papio anubis*. *Animal Behaviour, 27*, 37-45.

Palombit, R. A. (2000). Infanticide and the evolution of male-female bonds in animals. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 239-268). Cambridge: Cambridge University Press.

Palombit, R. A. (1999). Infanticide and the evolution of pair bonds in nonhuman primates. *Evolutionary Anthropology, 7*, 117-129.

Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. (2001). Female-female competition for male 'friends' in wild chacma baboons, *Papio cynocephalus ursinus*. *Animal Behaviour*, *61*, 1159-1171.

Palombit, R. A., Cheney, D. L. & Seyfarth, R. M. (1997). The adaptive value of 'friendships' to female chacma baboons: Experimental and observational evidence. *Animal Behaviour*, *54*, 599-614.

Pastor-Nieto, R. (2000). Female reproductive advertisement and social factors affecting the sexual behaviour of captive spider monkeys, *Laboratory Primate Newsletter*, *39*, 5-9.

Pastor-Nieto, R. (2001). Grooming, kinship and co-feeding in a captive group of spider monkeys (*Ateles geoffroyi*). *Zoo Biology*, *20*, 293-303.

Paul, A. (2002). Sexual selection and mate choice. International Journal of Primatology, *23*, 877-904.

Paul, A. & Kuester, J. (1996). Infant handling by female Barbary macaques (*Macaca sylvanus*) at Affenberg Salem: testing functional and evolutionary hypotheses. *Behavioral Ecology and Sociobiology*, *39*, 133-145.

Paul, A., Preuschoft, S. & van Schaik, C. P. (2000). The other side of the coin: Infanticide and the evolution of male-infant interactions in Old World primates. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 269-292). Cambridge: Cambridge University Press.

Payne, H. F. P., Lawes, M. J. & Henzi, S. P. (2003). Competition and the exchange of grooming among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, *140*, 453-471.

Pepper, J. W., Mitani, J. C. & Watts, D. P. (1999). General gregariousness and specific social preferences among wild chimpanzees. *International Journal of Primatology*, *15*, 167-183.

Pereira, M. E. & Kappeler, P. M. (1997). Divergent systems of agonistic relationships in lemurid primates. *Behaviour*, *134*, 225-274.

Perry, S. (1997a). Male-male social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour, 134*, 477-510.

Perry, S. (1997b). Male-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *Behaviour, 134*, 477-510.

Perry, S. (1996). Female-female social relationships in wild white-faced capuchins (*Cebus capucinus*). *American Journal of Primatology, 40*, 167-182.

Petit, O, Abegg, C. & Thierry, B. (1997). A comparative study of aggression and conciliation in three cercopithecine monkeys (*Macaca fuscata, Macaca nigra, Papio papio*). *Behaviour, 134*, 415-432.

Plavcan, J. M. (2004). Measure of sexual selection and sexual dimorphism. In: P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp 230-252). Cambridge: Cambridge University Press.

Plavcan, J. M., van Schaik, C. P. & Kappeler, P. M. (1995). Competition, coalitions and canine size in primates. *Journal of Human Evolution, 28*, 245-276.

Pope, T. R. (1990). The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. *Behavioural Ecology and Sociobiology, 27*, 439-446.

Printes, R. C. & Strier, K. B. (1999). Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoids*). *International Journal of Primatology, 20*, 941-960.

Purvis, A. (1995). A composite estimate of primate phylogeny. *Philosophical Transcripts of the Royal Society of London, 384*, 405-421.

Pusey, A. F. & Packer, C. (1987). Dispersal and philopatry. In: B.B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 250-266). Chicago: Chicago University Press.

Pusey, A. F. Williams, J. & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science, 277*, 828-831.

Ramos-Fernandez, G. & Ayala-Orozco, B. (2003). Population size and habitat use of spider monkeys at Punta Laguna, Mexico. In: L. K. Marsh (Ed.), *Primates in fragments: Ecology and conservation* (pp 191-209). New York: Kluwer Academic/Plenum Press.

Ramos-Fernandez, G., Vick, L. G., Aureli, F., Schaffner, C. M. & Taub, D. M. (2003). Behavioral ecology and conservation status of spider monkeys in the Otoch Ma'ax Yetel Kooh protected area. *Neotropical Primates, 11*, 155-158.

Reed, C., O'Brien, T. G. & Kinnaird, M. F. (1997). Male social behaviour and dominance hierarchy in the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology, 18*, 247-260.

Robbins, M. M. (1995). A demographic analysis of male life history and social structure of mountain gorillas. *Behaviour, 132*, 21-47.

Rosenberger & Strier, (1989). Adaptive radiation of the Ateline primates. *Journal of Human Evolution, 18*, 717-750.

Saito, C. (1996). Dominance and feeding success in Japanese macaques (*Macaca fuscata*): Effects of food patch size and inter-patch distance. *Animal Behaviour, 51*, 967-980.

Santos, C. V., French, J. A. & Otta, E. (1997). Infant carrying behaviour in callitrichid primates: *Callithrix* and *Leontopithecus*. *Folia Primatologica, 18*, 889-908.

Schaffner, C. M. & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology, 26*, 1093-1105.

Schaffner, C. M. & Caine, N. G. (2000). The peacefulness of cooperatively breeding primates. In: F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp 155-169). California: University of California Press.

Schaffner, C. M., Shepherd, R. E., Santos, C. V. & French, J. A. (1995). Development of heterosexual relationships in Wied's black tufted-ear marmosets (*Callithrix kuhli*). *American Journal of Primatology, 36*, 185-200.

Schaffner, C. M., Verpooten, J., & Aureli, F. (2003). The behavioural consequences of fusion in a wild group of spider monkeys. *American Journal of Primatology, 60, Supp 1*, 140-141.

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*, 265-271.

Schino, G., Schucchi, S., Maestripieri, D., and Turillazzi, P. G. (1988). Allogrooming as a tension-reduction mechanism: a behavioural approach. *American Journal of Primatology, 16*, 43-50.

Schino, G., Speranza, L., Ventura, R. & Troisi, A. (2003). Infant handling and maternal response in Japanese macaques. *International Journal of Primatology, 24*, 627-638.

Schweigert, W. A. (1994). *Research methods and statistics for psychology*. Belmont, CA: Brooks/Cole Publishing Company.

Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L. & Connor, R. C. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour, 142*, 21-44.

Setchell, J. M. & Dixson, A. F. (2001a). Arrested development of secondary sexual adornments in subordinate adult male mandrills (*Mandrillus sphinx*). *American Journal of Physical Anthropology, 115*, 245-252.

Setchell, J. M. & Dixson, A. F. (2001b). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behaviour, 39*, 177-184.

Setchell, J. M. & Kappeler, P. M. (2003). Selection in relation to sex in primates. *Advances in the Study of Behaviour, 33*, 87-174.

Setchell, J. M., Lee, P. C., Wickings, E. J. & Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (*Mandrillus sphinx*). *American Journal of Physical Anthropology*, *115*, 349-360.

Seyfarth, R. M. (1980). The distribution of grooming and related behaviours among adult female vervet monkeys. *Animal Behaviour*, *28*, 798-813.

Seyfarth, R. M. (1978a). Social relationships among adult male and female baboons I: Behaviour during sexual consortship. *Behaviour*, *64*, 204-206.

Seyfarth, R. M. (1978b). Social relationships among adult male and female baboons II: Behaviour throughout the female reproductive cycle. *Behaviour*, *64*, 227-247.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Animal Behaviour*, *24*, 917-938.

Seyfarth R.M. & Cheney, D. L. (1984). Grooming alliances and reciprocal altruism in vervet monkeys. *Nature*, *308*, 541-3.

Shimooka, Y. (2003). Seasonal variation in association patterns of wild spider monkeys (*Ateles belzebuth belzebuth*) at La Macarena, Colombia. *Primates*, *44*, 83-90.

Sicotte, P. (2002). The function of male aggressive displays toward females in mountain gorillas. *Primates*, *43*, 277-289.

Silk, J. (2002). Kin selection in primate groups. *International Journal of Primatology*, *23*, 849-875.

Silk, J. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, *57*, 1021-1032.

Silk, J. (1994). Social relationships of male bonnet macaques: male bonding in a matrilineal society. *Behaviour*, *130*, 271-291.

Silk, J. (1992). Patterns of intervention in agonistic contests among male bonnet macaques. In: A. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and* *alliances in humans and other animals* (pp 215-232). Oxford: Oxford University Press.

Silk, J. (1982). Altruism among female *Macaca radiata*: explanations and analysis of patterns of grooming and coalition formation. *Behaviour, 79*, 162-188.

Silk, J. (1980). Kidnapping and female competition in captive bonnet macaques. *Primates, 21*, 100-110.

Silk, J. B., Alberts, S. C. & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302, 1231-1234.

Silk, J., Cheney, D. L. & Seyfarth, R. M. (1996). The form and function of post-conflict interactions between female baboons. *Animal Behaviour, 52*, 259-268.

Silk, J., Kaldor, E. & Boyd, R. (2000). Cheap talk when interests conflict. *Animal Behaviour*, *59*, 423-432.

Silk, J. B., Rendall, D., Cheney, D. L. & Seyfarth, R. M. (2003). Natal attraction in adult female baboons (*Papio cynocephalus ursinus*) in the Moremi Reserve, Botswana. *Ethology*, 109, 627-644.

Smuts, B. B. (1987a). Sexual competition and mate choice. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 385-399). Chicago: The University of Chicago Press.

Smuts, B. B. (1987b). Gender, aggression and influence In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 400-412). Chicago: The University of Chicago Press.

Smuts, B. B. (1985). *Sex and friendship in baboons.* Chicago: Aldine.

Smuts, B. B. & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior*, *22*, 1-63.

Smuts, B. B. & Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (*Papio cynocephalus anubis*). *International Journal of Primatology*, *11*, 147-172.

Soltis, J., Mitsunaga, F., Shimizu, K., Yanagihara, Y., Nozaki, M. (1997). Sexual selection in Japanese macaques I: female mate choice or male sexual coercion? *Animal Behaviour*, *54*, 725-736.

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X. & Takenaka, 0. (1997). Sexual selection in Japanese macaques II: female mate choice and male-male competition. *Animal Behaviour*, *54*, 737-746.

Soltis, J., Thomsen, R., Matsubayashi, K. & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioural Ecology and Sociobiology*, *48*, 195-202.

Soltis, J., Thomsen, R. & Takenaka, O. (2001). The interaction of male and female reproductive strategies and paternity in wild Japanese macaques, *Macaca fuscata*. *Animal Behaviour*, *62*, 485-494.

Sorensen, T. C. & Fedigan, L. M. (2000). Distribution of three monkey species along a gradient of regenerating tropical dry forest. *Biological Conservation*, *92*, 227-240.

Stanford, C. B. (1998). *Chimpanzee and red colobus: The ecology of predator and prey*. Cambridge: Harvard University Press.

Stanford, C. B. (1992). The costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioral Ecology and Sociobiology*, *30*, 29-34.

Steenbeek, R. (2000). Infanticide by males and female choice in wild Thomas's langurs. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 153-177). Cambridge: Cambridge University Press.

Steenbeek, R. (1999). Tenure related changes in wild Thomas's langurs: I: Between group interactions. *Behaviour*, *136*, 595-625.

Steenbeek, R. (1996). What a maleless group can tell us about the constraints on female transfer in Thomas's langurs. *Folia Primatologica*, *67*, 169-181.

Steenbeek, R., Piek, R. C., van Buul, M. & van Hooff, J. A. R. A. M. (1999). Vigilance in wild Thomas's langurs (*Presbytis thomasi*): The importance of infanticide risk. *Behavioural Ecology and Sociobiology*, *45*, 137-150.

Steenbeek, R. & van Schaik, C. P. (2001). Group size as a limiting factor in Thomas' langurs (*Presbytis thomasi*): The folivore paradox revisited. *Behavioural Ecology and Sociobiology*, *49*, 100-110.

Sterck, E. H. M. (1997). Determinants of female dispersal in Thomas' langurs. *American Journal of Primatology*, *42*, 179-198.

Sterck, E. H. M. & Korstjens, A. H. (2000). Female dispersal and infanticide avoidance in primates. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 293-321). Cambridge: Cambridge University Press.

Sterck, E. H. M. & van Hooff, J. A. R. A. M. (2000). The number of males in langur groups: monopolizability of females or demographic processes? In P. M. Kappeler (Ed.), *Primate males* (pp 120-129). Cambridge: Cambridge University Press.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. (1997). The evolution of female social relations in nonhuman primates. *Behavioural Ecology and Sociobiology*, *41*, 291-309.

Stevenson, P. R. (1998). Proximal spacing between individuals in a group of woolly monkeys (*Lagothrix lagotricha*) in Tingue National Park, Colombia. *International Journal of Primatology*, *19*, 299-311.

Stevenson, P. R., Quiñones, M. J. & Ahumada, J. A. (1999). Effects of fruit patch availability on feeding subgroup size and spacing patterns in tour primate species at Tinigua National Park, Colombia. *International Journal of Primatology*, *19*, 313-324.

Stewart, K. J. & Harcourt, A. H. (1987). Gorilla: Variation in female relationships. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 155-164). Chicago: The University of Chicago Press.

Strier, K. B. (2000). From binding brotherhoods to short-term sovereignty: the dilemma of male Cebidae. In: P. M. Kappeler (Eds.), *Primate males* (pp 72-83). Cambridge: Cambridge University Press.

Strier, K. B. (1997). Mate preferences of wild muriqui monkeys (*Brachyteles arachnoides*): reproductive and social correlates. *Folia Primatologica, 68,* 120-133.

Strier, K. B. (1994). Brotherhoods among atelins. *Behaviour, 130,* 151-167.

Strier, K. B. (1992). Causes and consequences on nonaggression in woolly monkeys. In J. Silverberg & J. P. Gray (Eds.), *Aggression and peacefulness in humans and other primates* (pp 100-116). New York: Oxford University Press.

Strier, K. B. (1990). New world primates, new frontiers: Insights from the woolly monkey, or muriqui (*Brachyteles arachnoids*). *International Journal of Primatology, 11,* 7-19.

Strier, K. B. (1989). Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). *Folia Primatologica, 52,* 70-77.

Strier, K. B. (1987). Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoids*). *American Journal of Primatology, 13,* 385-395.

Strier, K. B., Carvalho, D. S. & Bejar, N. O. (2000). Prescription for peacefulness. In: F Aureli & F. B. M. de Waal (Eds.) *Natural conflict resolution* (pp 106-128). London: University of California Press.

Strier, K. B., Dib, L. T. & Figueira, J. E. (2002). Social dynamics of male muriquis (*Brachyteles arachnoids hypoxanthus*). *Behaviour, 139,* 315-342.

Strier, K. B., Mendes, F. D. C., Rímoli, J. & Odalia Rímoli, A. (1993). Demography and social structure in one group of muriquis (*Brachyteles arachnoids*). *International Journal of Primatology*, *14*, 513-526.

Struhsaker, T. T. & Leland, L. (1987). Colobines: Infanticide by adult males. In: B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp 83-97). Chicago: The University of Chicago Press.

Swedell, L. (2002). Affiliation among female wild hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology*, *23*, 1205-1226.

Symington, M. M. (1990). Fission-fusion social organisation in *Ateles* and *Pan*. International *Journal of Primatology*, *11*, 47-61.

Symington, M. M. (1988a). Food competition and foraging party size in the black spider monkey *(Ateles paniscus chamek*). *Behaviour*, *105*, 117-134.

Symington, M. M. (1988b). Demography, ranging patterns, and activity budgets of the black spider monkey *(Ateles paniscus chamek*) in the Manu national park, Peru. *American Journal of Primatology*, *15*, 45-67.

Symington, M. M. (1987). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioural Ecology and Sociobiology*, *20*, 421-425.

Szykman, M., Engh, A. L., van Horn, R. C., Scribner, K. T., Smale, L. & Holekamp, K. E. (2003). Rare male aggression directed toward females in a female-dominated society: bating behaviour in the spotted hyena. *Aggressive Behavior*, *29*, 457-474.

Takahata, Y. (1982a). Social relationships between adult males and females of Japanese macaques in the Arashiyama B troop. *Primates*, *23*, 1-23.

Takahata, Y. (1982b). The socio-sexual behaviour of Japanese monkeys. *Zeitschrift für Tierpsychologie*, *59*, 89-108.

Takahata, Y. Ihobe, H. & Idani, G. (1996). Comparing copulations of chimpanzees and bonobos: Do females exhibit proceptivity or receptivity? In: W. C. McGrew, L. F. Marchant & T. Nishida (Eds.), *Great ape societies* (pp 146-158). Cambridge: Cambridge University Press.

Tardif, S. D., Carson, R. L. & Gangaware, B. L. (1986). Comparison of infant care in family groups of the common marmoset (*Callithrix jacchus*) and the cotton-top tamarin (*Saguinus Oedipus*). *American Journal of Primatology, 11*, 103-110.

Thierry, B. (2000). Conflict management patterns across macaque species. In: F Aureli & F. B. M. de Waal (Eds.) *Natural conflict resolution* (pp 106-128). London: University of California Press.

Thierry, B., Aureli, F., de Waal, F. B. M., & Petit, O. (1997). Variation in reconciliation patterns and social organisation across nine species of macaques. *Advances in Ethology, 32*, S39.

Thierry, B., Iwaniuk, A. N. & Pellis, S. M. (2000). The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology, 106*, 713-728.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.). *Sexual selection and the descent of man, 1871-1971* (pp 136-179). Chicago: Alpine.

Utami, S. A. & van Hooff, J. A. R. A. M. (2004). Alternative male reproductive strategies: male bimaturism in orangutans. In: P. M. Kappeler & C. P. van Schaik (Eds.) *Sexual selection in primates: New and comparative perspectives* (pp 196-207). Cambridge: Cambridge University Press.

Valero, A. Schaffner, C. M., Vick, L. G., Aureli, F. & Ramos-Fernandez, G. (2006). Intragroup lethal aggression in wild spider monkeys. *American Journal of Primatology, 68*, 732-737.

van Hooff, J. A. R. A. M. (2000). Relationships among non-human primate males: a deductive framework. In P. M. Kappeler (Ed.), *Primate males* (pp 183-191). Cambridge: Cambridge University Press.

van Hooff, J. A. R. A. M. & van Schaik, C. P. (1994). Male bonds: Affiliative relationships among non-human primate males. *Behaviour, 130*, 309-337.

van Hooff, J. A. R. A. M. & van Schaik, C. P. (1992). Cooperation in competition: The ecology of primate bonds. In H. A. Harcourt & F. B. M. de Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp 357-389). Oxford: Oxford University Press.

van Noordwijk, M. A. (1985). Sexual behaviour of the Sumatran long-tailed macaques. *Zeitschrift für Tierpsychologie, 70*, 277-296.

van Roosmalen, M. G. M. & Klein, L. L. (1988). The spider monkey genus *Ateles*. In: R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. da Fonseca (Eds.), *Ecology and behaviour of neotropical primates* (pp 455-537). Washington DC: World Wildlife Fund.

van Schaik, C. P. (2000a). Infanticide by males: The sexual selection hypothesis revisited. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 21-60). Cambridge: Cambridge University Press.

van Schaik, C. P. (2000b). Social counterstrategies against infanticide by males in primates and other animals. In: In P. M. Kappeler (Ed.), *Primate males* (pp 34-52). Cambridge: Cambridge University Press.

van Schaik, C. P. (2000c). Vulnerability to infanticide by males: Patterns among mammals. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 61-72). Cambridge: Cambridge University Press.

van Schaik, C. P. (1996). Social evolution in primates: The role of ecological factors and male behaviour. *Proceedings of the British Academy, 88*, 9-31.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V Standen & R. A. Foley (Eds.), *Comparative socioecology* (pp 195-218). Oxford: Blackwell Scientific Publications.

van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour, 87*, 120-144.

van Schaik, C. P. & Aureli, F. (2000). The natural history of valuable relationships. In F. Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp 307-333). London: University of California Press.

van Schaik, C. P., Hodges, J. K. & Nunn, C. L. (2000). Paternity confusion and the ovarian cycles of female primates. In: C. P. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp 361-387). Cambridge: Cambridge University Press.

van Schaik, C. P. & Kappeler, P. M. (1997). Infanticide risk and the evolution of male-female associations in primates. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *264*, 1687-1694.

van Schaik, C. P., Pradhan, G. R. & van Noordwijk, M. A. (2004). Mating conflict in primates: Infanticide, sexual harassment and female sexuality. In: P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp 131-150). Cambridge: Cambridge University Press.

van Schaik, C. P. & van Noordwijk, M. A. (1988). Competition among female long-tailed macaques (*Macaca fascicularis*). *Animal Behaviour*, *35*, 557-589.

van Schaik, C. P. & van Noordwijk, M. A. (1986). The hidden costs of sociality: Intra-group variation in feeding strategies in Sumatran long-tailed macaques (*Macaca fascicularis*). *Behaviour*, *99*, 296-315.

van Schaik, C. P., van Noordwijk, M. A. & Nunn, C. L. (1999). Sex and social evolution in primates. In: P. C. Lee (Ed.), *Comparative primate socioecology* (pp 204-231). Cambridge: Cambridge University Press.

van Schaik, C. P. & van Hooff, J. A. R. A. M. (1996). Toward an understanding of the orangutan's social system. In: W. C. McGrew, L. M. Marchant and T. Nishida (Eds.), *Great ape societies* (pp 3-15). Cambridge: Cambridge University Press.

van Schaik, C. P. & van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour*, *85*, 91-117.

Vigilant, L., Hofreiter, M., Siedel, H. & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Science*, 98, 12890-12895.

Wallis, (1997). A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park, *Journal of Reproduction and Fertility, 109*, 297-307.

Watts, D. P. (2000). Grooming between male chimpanzees at Ngogo, Kibale National Park 1: partner number and diversity and grooming reciprocity. *International Journal of Primatology, 21*, 189-210.

Watts, D. P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behavioural Ecology and Sociobiology, 44*, 43-55.

Watts, D. P. (1997). Agonistic interventions in wild mountain gorilla groups. *Behaviour, 134*, 23-57.

Watts, D. P. (1996). Comparative socioecology of gorillas. In: W. C. McGrew, L. M. Marchant and T. Nishida (Eds.), *Great ape societies* (pp 16-28). Cambridge: Cambridge University Press.

Watts, D. P. (1995). Post-conflict social events in wild mountain gorillas I: Social interactions between opponents. *Ethology, 100*, 139-157.

Watts, D. P. (1994). Agonistic relationships between female mountain gorillas (*Gorilla gorilla beringei*). *Behavioural Ecology and Sociobiology, 34*, 347-358.

Watts, D. P. (1992). Social relationships of immigrant and resident female mountain gorillas I: Male-female relationships. *American Journal of Primatology, 28*, 159-181.

Watts, D. P. (1991). Harassment of immigrant female mountain gorillas by resident females. *Ethology, 89*, 135-153.

Watts, D. P. (1990). Ecology of gorillas in its relation to female transfer in mountain gorillas. *International Journal of Primatology*, *11*, 21-45.

Watts, D. P. (1989). Infanticide in mountain gorillas: New cases and review of evidence. *Ethology*, *8*, 1-18.

Watts, D. P., Colmenares, F. & Arnold, K. (2000) Redirection, consolation and male policing. In: F Aureli & F. B. M. de Waal (Eds.), *Natural conflict resolution* (pp 281-301). London: University of California Press.

Weingrill, T. Lycett, J., Barrett, L., Hill, R. A. & Henzi, S. P. (2003). Male consortship behaviour in chacma baboons: The role of demographic factors and female conceptive probabilities. *Behaviour*, *140*, 405-427.

White. F. J. (1988). Party composition and dynamics in *Pan paniscus*. *International Journal of Primatology*, *9*, 179-193.

Whiten, A., Byrne, R. W. & Henzi, S. P. (1987). The behavioural ecology of mountain baboons. *International Journal of Primatology*, *8*, 367-388.

Wittig & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology*, *24*, 847-867.

Wong, B. B. M. & Candolin, U. (2005). How is female mate choice affected my male competition? *Biological Review*, *80*, 559-571.

Wrangham, R. W. (2002). The cost of sexual attraction: id there a trade-off in female *Pan* between sex appeal and received coercion? In: C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp 204-215). Cambridge: Cambridge University Press.

Wrangham, R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: P. M. Kappeler (Ed.), *Primate Males* (pp 248-258). Cambridge: Cambridge University Press.

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262-300.

Wrangham, R. W., Chapman, C., Clark, A. P. & Isabirye-Basatu, G. (1996).

Wrangham, R. W., Clark, A. P. & Isabirye-Basatu, G. (1992). Female social relationships and social organisation of Kibale Forest chimpanzees. In: T. Nishida, W. C. McGrew, P. Marler, M. Pickford & F. B. M. de Waal (Eds.), *Topics in primatology: Human origins* (pp 81-98). Tokyo: University of Tokyo Press.

Yeager, C. P. & Kirkpatrick, R. C. (1998). Asian colobine social structures: Ecological and evolutionary constraints. *Primates*, *39*, 147-155.

Youlatos, D. (2002). Positional behaviour of black spider monkeys (Ateles paniscus) in French Guiana. *International Journal of Primatology*, *23*, 1071-1093.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology*, *53*, 205-214.

Zahavi, A. & Zahavi, A. (1975). *The handicap principle*. Oxford: Oxford University Press.

Zinner, D. P., Nunn, C. L., van Schaik, C. P. & Kappeler, P. M. (2004). Sexual selection of exaggerated sexual swellings of female primates. In: P. M. Kappeler & C. P. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp 71-89). Cambridge: Cambridge University Press.