2014-04-17

Female Partner Preferences in Colobus vellerosus

Potvin-Rosselet, Edith

UNIVERSITY OF CALGARY

Female Partner Preferences in *Colobus vellerosus*

By

Edith Potvin-Rosselet

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

DEPARTMENT OF ANTHROPOLOGY

CALGARY, ALBERTA

APRIL, 2014

ABSTRACT

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Social relationships directly influence female fitness in primates. While females benefit from affiliating with other females and males, social constraints on females can lead to unequal distribution of affiliative behaviours. In *Colobus vellerosus*, where females are facultative dispersers and where infanticide pressure is high, do females prefer to affiliate with females or with the resident male? I identified females' social partners and investigated the influence of maternal relatedness and reproductive status on the rates of affiliation between females and their partners. The majority of females distributed affiliative behaviours towards one female top partner. The reproductive status of females consistently influenced the rates of affiliative interactions between females and their top partners whereas relatedness did not. Lactating females received grooming at higher rates. As relatedness was not a strong predictor of the strength of affiliative relationships between females, I suggest that natal attraction mainly influences partner preferences in this population.

ACKNOWLEDGEMENTS

The content of the next 100 pages is the outcome of many months of learning, thinking, and watching monkeys. Without the support of many people, this thesis would not exist. First, I want to thank my supervisor, Dr. Pascale Sicotte, for giving me the opportunity to become a graduate student in Anthropology. Thank you, Pascale, for believing in me and in this project. Drs. Mary Pavelka, Linda Fedigan, Steig Jonhson, Hugh Notman also invested time in reading my work, providing advice and lines of thinking, listening to my talks and marking my papers. Thank you for sitting on my proposal or defense committee, and thank you for being my professors. Thanks to Dr. Eva Wikberg, for teaching me how to differentiate one colobus from another colobus and how to be efficient while collecting data. Many thanks to Dr. Tak Fung; without your precious help, the only numbers in this thesis would have been page numbers. Special thanks to Juli Finlay for saving my life by giving me a computer after mine was stolen … Thanks to Dr. Tania Saj and Iulia Badescu for reading my thesis, correcting spelling mistakes and making useful suggestions. Thanks to Dr. Catherine Potvin, my role model, for being so supportive and inspiring; I want to be like you.

I am so lucky to have worked with the best field assistants ever and I am afraid that I don't have enough words to express my gratitude to them. Thank you Charles Kodom for being my most patient and precious friend, teacher and guide. Thank you Rustu Ataman for being so enthusiastic, positive, and hard-working. Thank you Tessy P. Paquin for becoming my friend on such short notice, for waking me up every morning, for having spent 24 hours a day with me for three months and for still being my friend

after all! I am also thankful to Alfred and Bea Annor-Donyina, Anthony N'Dassah, Robert Koranteng, Constance, Joyce and Diana, Joseph, Isaac, Gregory, William and all my friends in Ghana for teaching me how to prepare fufu, how to play soccer properly, and how to be happy like Ghanaians do. Medase pa !

I also want to thank Laure, Richard, Isabelle, Mark and the girls for being so welcoming and helpful, and for making me feel at home. Thanks to all my friends in Calgary for the sporadic escapes to the mountains, the good dinners and your support throughout this adventure. Thank you maman et papa for your unconditional support and love, for sending me chocolate wherever I am in the world, and for teaching me to not be afraid of the unknown. Finally, a special thank to the monkeys for being so beautiful and amazing, and for being so patient while I peeked into the privacy of your wild life. I miss you a lot.

Last but not least, thanks to the Management Committee of Boabeng-Fiema Monkey Sanctuary (BFMS), the Ghana Wildlife Division, and the chiefs and traditional priests of Boabeng and Fiema for the permission they granted us to walk into their forest and watch the monkeys. Financial support for my project was provided by the Natural Science and Engineering Research Council (NSERC) of Canada, and the Research Services of the University of Calgary.

À Robert et Yvonne

Et

À Thérèse et Romuald

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CHAPTER I: INTRODUCTION

I

1 – PROLOGUE

Imagine life without social interactions between animals of the same group. A lack of interactions implies that individuals do not communicate information about food resources or predator presence, and it also means no mating, no grooming, no physical contacts between a female and her offspring. Studying anti-social animals living together would be nonsense for ethologists. What makes the study of animal behaviours fascinating is the social complexity that emerges from the simple interactions among group members. One aspect that distinguishes primates from other mammals is the wide array of adaptive behaviours that primates exhibit in response to social and ecological pressures.

Most primates live in social groups (Clutton-Brock 1974; Hinde 1976; van Schaik 1983; Kappeler & van Schaik 2002; Swedell 2012). Especially in diurnal primates, individuals of the same group frequently interact with each other (van Schaik 1983). Social relationships among individuals are the expression of behavioural strategies that maximize inclusive fitness (Hamilton 1964; Trivers 1972). For instance, female social relationships directly influence female survivorship and reproductive success in some species (*Papio ursinus*: Silk *et al.* 2009; Silk *et al.* 2010a). Investigating the variability in the nature of social relationships among females can reveal the variation of adaptive strategies they exhibit. The overall goal of my study is to describe and quantify the social relationships that adult female black-and-white colobus (*Colobus vellerosus*: white-thighed colobus, ursine colobus or Geoffroy's colobus) form and maintain with other

adult members of their social group. The nature of female social relationships is a fundamental factor that has been used in the construction of models attempting to explain primate social systems (Wrangham 1980; van Schaik 1989; Isbell & van Vuren 1996; Sterck *et al.* 1997). As stated by Wrangham (1979), females' concerns in social life differ from those of the males. This comes from the sex differences in competitive strategies: males mainly compete for mates and females mainly compete for food (Trivers 1972). Because food competition among females can take different forms, according to the quality of food resources and their distribution, the nature of relationships among females varies across species and within populations (Wrangham 1980; Barton *et al.* 1996; Hinde 1983; Dunbar 1988; van Schaik 1989; Mitchell *et al.* 1991; Sterck *et al.* 1997; Cords 2002; Koenig 2002; Wikberg *et al.* in press). Therefore, it is relevant to study social relationships from the perspective of females in an attempt to understand the diversity of primate social systems.

In the following sections, I review literature about primate social relationships and the models predicting variation in primate social structures. Then, I review male-female and female-female associations and the resulting types of social relationships that females form and maintain. I will then briefly introduce my study species, the black-and-white ursine colobus, and my study site, the Boabeng-Fiema Monkey Sanctuary (BFMS).

2 - LITERATURE REVIEW

The complexity of primate sociality

Why do primates have such a complex social life and why does it take so many different forms between species? The parsimonious answer that comes to my mind is that primates display diverse social systems because they are gregarious animals. Being gregarious, or in other words, to live within a group and frequently interact with the other members of that group, generate a panoply of challenges that animals have to cope with every day. These challenges are diverse in nature and their accumulation force primates to adapt in various aspects of their lives. This is true for all animals, but what makes primates different is the large number of social strategies they exhibit to solve the same number of challenges other animals face. Another aspect of primate social life is the high proportion of taxa in which the sexes associate permanently in bi-sexual units (75% of species compared to 30% in other mammals: Hinde 1983; van Schaik & Dunbar 1990; van Schaik & Kappeler 1997). With the exception of the solitary orangutan (Schaller 1961; Galdikas 1979; Watts 2012) and all-male bands (that can be found in most colobines: Sterck 2012; gorillas: Harcourt & Stewart 2007; geladas and hamadryas baboons: Dunbar 1983) adult diurnal primates live permanently with at least one member of the other sex.

In 1976, Robert A. Hinde suggested a conceptual framework to explain the emergence of a social structure by looking at dyadic interactions. A social relationship between two individuals emerges from repeated interactions between these individuals.

Individuals can have social relationships with different members of their group. The social structure of that group directly emerges from the network of social relationships woven among the members of the group. Kappeler and van Schaik (2002) apply this framework to better describe non-human primate social systems, or primate societies, using three different aspects: social organization, mating system, and social structure. The dynamic combination of these three aspects for a given population results in its social system. The social organization refers to the spatiotemporal cohesion (i.e. degree of fission-fusion) of a group and its demographic composition (e.g. the number of males and females in a group). The mating system is the number of partners' males and females of a same group typically mate with (e.g. monogamous, polyandrous, polygynous, polygynyandrous). The social structure of a group is the resulting pattern of relationships that emerges from the social interactions among the members of that group (Hinde 1976; Kappeler & van Schaik 2002). The social structure answers the question: Who are the preferred partners and for how long are they? Hinde (1983) emphasizes that the outcome of repeated past interactions (i.e. social relationship) between two individuals influences future interactions between the same individuals. Therefore, variation in content and quality of affiliative (friendly) and agonistic (aggressive and submissive) interactions will shape the variation in the strength of social relationships. The different types of social relationships commonly discussed in the primate literature will be reviewed later.

For primatologists who had focused their research interests on sociality, a major component to the understanding of the emergence of social systems is the notion of intrasexual and intersexual competition for resources (Trivers 1972; Wrangham 1979, 1980; van Schaik 1989; Isbell 1991; Sterck *et al.* 1997). There is a sex difference in

social strategies males and females adopt to maximize their reproductive success. A social strategy refers to a set of behaviours that affect the formation and maintenance of relationships and the resulting grouping pattern (Wrangham 1979). Although males and females have the same goal, which is to reproduce, there is a fundamental difference in its behavioural expression because males and females are not competing over the same resources. The reproductive success of males and females is limited by access to their key resource, respectively fertile females and food sources (Trivers 1972; Wrangham 1979). Across species and among populations, social relationships reflect competitive and cooperative behaviours in which males and females engage to gain access to these key resources. Male and female social strategies entangle and interact, resulting in the observed diversity of primate social systems.

Primates are unique among the mammal kingdom for the diversity of social systems they exhibit, both within and between species. This complexity emerges from primates' gregariousness and the high behavioural flexibility they express to socially adapt to a vast range of ecological and demographic conditions.

Models of primate social structure

Most primates live in bisexual groups that vary in size, composition, and cohesiveness (van Schaik 1983, 1989, 1999; Sterck *et al.* 1997). Once groups are formed, many factors can influence their structure. Two social-ecological models attempt to predict the social structure of primate groups from the social and ecological pressures animals are facing. First, Sterck and colleagues (1997) model (refined from Wrangham

1980 and van Schaik 1989) suggests that the type of food competition (scramble or contest: Nicholson 1954) and its intensity (within or between group) are the two factors determining female dispersal patterns and thus, the nature of female-female relationships (presence or absence of a female linear hierarchy) in a group. There are four different social categories emerging from the competitive regime and females' social response to it: Dispersal-Egalitarian, Resident-Egalitarian, Resident-Nepotistic, and Resident-Nepotistic-Tolerant (Sterck *et al.* 1997). In colobines, where females show a combination of residency and egalitarian relationships, due to low within-group food competition, related females can express low levels of affiliation and aggression.

The second model was proposed by Isbell and colleagues (Isbell 1991; Isbell & van Vuren 1996; Isbell & Young 2002; Isbell 2004). It suggests that high locational and social costs of dispersal lead to female philopatry. When there is a high inbreeding or infanticide risk, females are more likely to disperse from their natal group. In such situation, females lose their connection with group members and, after they settle in a new group, are likely to form stronger relationships with males (acting as protectors) than with unrelated females. When the benefits of the knowledge of food supply location within the natal home range and the benefits of having potential allies (i.e. related members: Wrangham 1980; Chapais 1995) in the group outweigh the costs of dispersal, females may form philopatric groups. In that situation, the potential to form and maintain strong social relationships with other females of the group is high.

Because food is the most limiting resource for females (Trivers 1972), food availability and the type of food competition should predict female group size or

population density (van Schaik & van Hoof 1983; Chapman 1990). Leaves are thought to be a relatively evenly distributed resource, and therefore to be relatively equally accessible to all members of a group, which should allowed large social groupings. Janson & Goldsmith (1995) have called the "folivore paradox" the fact that folivore primates live in smaller groups than expected. Originally, the folivore paradox was resolved by suggesting that social factors, rather than ecological factors, were the primary determinants of folivore group size (Steenbeek & van Schaik 2001). The important infanticide risk reported in colobines species (Sterck *et al.* 1997; van Schaik 2000; Teichroeb & Sicotte 2008; Palombit 2012) was suggested to explain the formation of smaller groups (Crockett & Janson 2000; Steenbeek & van Schaik 2001; Teichroeb *et al.* 2012). It was also suggested that males and females both benefit from living in small groups to better resist male immigration attempts and infanticide (Teichroeb *et al.* 2012). Indeed, because infanticide is costly for females, the association with a good protector male is important. More recently, the folivore paradox has been resolved on ecological grounds as well, as several studies have demonstrated that folivores are selective of leaf quality (Chapman & Chapman 2002; Koenig & Borries 2006; Snaith & Chapman 2007; Chapman *et al*. 2012). Therefore, it is likely that folivorous primates live in relatively small groups for both ecological and social reasons. The factors involved in keeping groups small certainly shape the type of social relationships expected in these groups.

Primate association and affiliation

Male-female association

Male-female sexual associations, also known as "consortships", are usually short-lived and serve reproductive purposes whereas "male-female social associations" last longer and serve multiple purposes (Wrangham 1979; Hinde 1983; Smuts 1985; Harcourt & Stewart 2007; van Schaik & Janson 2000). From the female point of view, a long-term association with a male provides mating opportunities but also possible physical protection against predators and infanticidal males, and potentially home range defence.

Male-female long-term associations have been extensively studied in baboons (Hinde 1983; Smuts 1985; Palombit 1999). In savannah baboons, adult males and females form long-term “friendly” bonds that persist in the absence of any immediate sexual relationship (Hinde 1983; Smuts 1985). Multiple functions of intersexual friendship have been proposed: infanticide avoidance, predation protection, and access to mates (Hinde 1983; Smuts 1985; Palombit *et al.* 1997; Harcourt & Stewart 2007). From the male point of view, the later explanation is relevant if females are difficult to locate (Borries *et al.* 2011a): the male needs to remain close in order to ensure access to the females when they are in oestrus (Wrangham 1979; Hinde 1983). From the female point of view, association with a strong male provides predation and infanticide protection. Because females invest heavily in their offspring, infanticide is costly for them. Consequently, females develop different counterstrategies to infanticide (such as dispersal, territoriality, coalition formation, and polyandrous mating in an attempt to confuse paternity); long-term association with a male is one of them (Hrdy 1979;

Steenbeek 1996; van Schaik 2000; Palombit 2012). Males are more likely to defend infants whose mothers were mating partners because of the high paternity probability (Palombit *et al*. 1997; Borries *et al.* 2011a). A high incidence of infanticide in uni-male/multi-females groups has been documented in Hanuman and Thomas's langurs, as well as in gorillas, baboons, and several colobines (Struhsaker & Leland 1987; Newton 1988; Watts 1989; Borries 1997; Sterck *et al.* 2005; Teichroeb & Sicotte 2008b, review in van Schaik & Janson 2000).

The home range defence by males is another reason why females would associate with males. Males can potentially defend a home range to defend mates or to indirectly defend mates by defending food sources. For example, Williams *et al.* (2004) found that male chimpanzees defend a home range for the food sources that it contains and to protect females from sexual harassment. In at least two species of black-and-white colobus *(Colobus guereza* and *C. vellerosus*), males seem to engage in home range defence to directly defend the mates and to indirectly defend the food sources for the benefit of the females (Fashing 2001; Sicotte & MacIntosh 2004, Harris 2006).

Uni-male/multi-females groups

If a single male is able and sufficient to provide protection to several females, and to defend their home range, then one of the conditions for the emergence of a uni-male social group is met. This male also needs to be able to evict young natal males from his group, and resist male immigration. A uni-male/multi-females group is a social group where one reproductive male lives with multiple reproductive females and their offspring.

Different processes can lead to the formation of uni-male groups. In female dispersal species, a male needs to attract and retain females around him. In female philopatric species, a male needs to integrate within the females' affiliative network. The examples of hamadryas and gelada baboons are particularly instructive (Stammbach 1987). In hamadryas baboons, both females and males disperse from their natal social group when reaching sexual maturity. Groups are formed of unrelated females and one sexually mature male. In an effort to maintain group cohesiveness, the resident male aggressively herds them because secondary dispersal is an option for females (Kummer 1968, Hinde 1983; Swedell *et al.* 2011). Females live among unrelated individuals and female-female social interactions are reported to be weak (Kummer 1968; Hinde 1983; Swedell *et al.* 2011). Their main affiliation is with the resident male. In fact, Kummer (1968) found that female affiliative interactions were preferentially directed to the resident male, at least seven times more often than the ones directed to other females. Competition among females for access to the resident male can also occur (Swedell 2002) as seen in mountain gorillas (Watts 1994). If the silverback dies, the cohesion of the group is broken suddenly and females will disperse (Harcourt & Stewart 2007).

In contrast, female gelada baboons do not disperse from their natal social group and form female-philopatric groups. They form consistent long-term kin-based social relationships, and individuals belonging to different matrilines interact according to a strict and stable linear dominance hierarchy (Dunbar 1979, 1980; Hinde 1983; Silk *et al.* 2006 a,b, 2010). In this species, a single male monopolizes reproductive access to three to five females (Dunbar 1979). In contrast with social relationships among hamadryas females, the frequency of gelada female interactions is high. Grooming is concentrated

among females and the resident male is often excluded from grooming cliques (Dunbar 1979, Hinde 1983; Henzi *et al.* 2000). When the resident male dies, females stay cohesive and continue to act as a social group; a new male can join them, leading to a new uni-male/multi-females group (Hinde 1983).

There are three processes theoretically leading to the dissolution of a stable uni-male/multi-females group: the death of the resident male, a male takeover, or females' simultaneous dispersal (Sterck 1997; Sterck *et al.* 2005). Whether females are related or not, the consequences for group cohesiveness of male death or takeover will differ (as described above for hamadryas and geladas baboons). Therefore, there is variation in the processes of formation and dissolution of the group, as well as on the frequency of social interactions between group members according to intrinsic (such as relatedness) and extrinsic (such as local ecological pressures) characteristics of a species. In folivores, where food is usually not defensible, females do not benefit from maintaining frequent and strong social relationships with other females (relatives or not) in an attempt make allies and cooperatively defend food sources. Female dispersal in folivorous primates is theoretically more likely to occur than in frugivorous species (Sterck *et al.* 1997). The formation of a new group will potentially resemble the one observed in gorillas, where females are seeking a good quality male in order to transfer to him. Once this male is found, females may associate with him for an average of ten years (mountains gorillas: Watts 1996), and reproduce with him. However, females may disperse again when the resident male's relative quality decreases or if there is a higher quality extra-group male available, as secondary dispersal is possible in gorillas (Sicotte 2001). Therefore, female dispersal can result from both ecological and social circumstances.

Uni-male/multi-females groups are the primary type of group in some species [e.g. many colobine species (for reviews see Fashing 2011; Kirkpatrick 2011), Hanuman langurs in some habitats (Sterck 1998; Kirkpatrick 2011), Thomas' langurs (Sterck & Steenbeek 1997), guerezas (Oates 1977; Fashing 1999), gorillas (Harcourt 1979), howlers (Crockett & Eisenberg 1987), guenons and patas monkeys (Cords 1987)] or they can be part of a multi-level society such as in hamadryas and gelada baboons, in mandrills and drills (Stammbach 1987), or in Yunnan snub-nosed monkeys (Kirkpatrick *et al.* 1998).

Female-female association

In the previous section, I reviewed the benefits females gain from associating with males. Females also benefit from the presence of other females and three main reasons have been proposed to explain female-female association: 1) predation protection (Hamilton 1971), 2) presence of a protector male (Wrangham 1979; Dunbar 1988; van Schaik 1983; Sterck *et al.*1997), and 3) cooperative defence of resources (Wrangham 1980; van Schaik 1989; Sterck *et al.*1997).

Predation protection

Predation pressure has been considered the main evolutionary force that leads females to form cohesive groups (van Schaik 1989). Alarm calls, and dilution and confusion effects are known to decrease the chances of a successful predator attack (Hamilton 1971; Milinksi & Heller 1978). Therefore, higher predation risk in a

population should lead females to aggregate in larger groups than those exposed to lower risk (van Schaik 1983).

Protector male

Females jointly benefit from the presence of a protector male (Smuts 1985; Harcourt & Stewart 2007). Males can defend females' home range and act as protectors against intra-specific aggressors (e.g. infanticidal male) or extra-specific aggressors (i.e. predators) if sexual dimorphism advantages them (Williams *et al.* 2004; Fashing 2001; Harris 2006; van Schaik and Janson 2000; Hartcourt & Stewart 2007). If one male is able to defend several females, then these females can aggregate around the same male and benefit from its protection. Females will thus travel together, share proximity, food sources and sleeping sites, and therefore form a group with a certain degree of cohesiveness as a result of their common association with the same male (gorillas: Harcourt & Stewart 2007, geladas: Dunbar 1979; Hinde 1983, hamadryas baboons: Kummer 1968, Hanuman langurs: Borries 1993, Thomas' langurs: Steenbeek 2000). Females living in uni-male groups may or may not develop strong social relationships with each other. From a different perspective however, male protection can be seen as a mate guarding strategy against other males in order to monopolize reproduction (Wrangham 1979; Sterck *et al*. 1997).

Cooperative defence of resources

Females also benefit from the presence of other adult females when cooperation is needed to find and protect food patches against other groups (between-group feeding competition: Wrangham 1980; Janson & van Schaik 1988, van Schaik 1989). When contest competition prevails, females can rely on coalitionary partners to defend their food resources. Therefore, the strength of the relationships unifying partners (or allies) is an important factor contributing to the success of the food source defence. Strong female relationships occur frequently among relatives living in female philopatric groups (cercopithecines: Cords 2012).

Factors influencing female-female relationships

To form and maintain affiliative relationships, individuals need to have access to social partners, the time to interact with them, and to be engaged in affiliative interactions. Many factors can potentially influence the nature of affiliative relationships between females. This section reviews some of these factors, and the following section reviews different types of affiliative relationships commonly discussed in the primate literature.

Relatedness

Maternal relatedness is thought to be the one of the main factors contributing to affiliation among females. The idea comes from the kin selection theory stating that an individual's fitness benefits from biasing affiliative and cooperative behaviors towards relatives (Hamilton 1964). Philopatric females live with their female relatives and thus

have the potential to develop strong relationships with them. Females in such group usually form differentiated relationship among themselves, where strong relationships with one or several preferred partners are expressed. In species where females disperse, females share their home range mostly with unrelated individuals (e.g.: gorillas: Harcourt & Stewart 2007) and therefore cannot rely on related individuals for cooperation (Langergraber 2012). Given the lack of access to cooperative maternal kin, females in female-dispersing species usually show undifferentiated relationships, which means that they do not have a distinct preference for one female social partner (Wrangham 1980; but see Langergraber *et al.* 2009 for exception in chimpanzees).

Dominance rank

Dominance rank of females also has an important influence on their relationships. According to the degree of tolerance, dominants and subordinates individuals engaged in more or less affiliative, aggression and reconciliation interactions (Sterck *et al.* 1997). In female philopatric species, females have the possibility to form nepotistic dominance hierarchies where females rank close to their relatives (van Schaik 1989; Sterck *et al.* 1997). Females in nepotistic dominance hierarchies inherit their rank from their mother (matrilineal dominance system) and rank above or below all females ranking above or below their mother (cercopithecines: reviewed in Chapais 1988). In a highly linear nepotistic dominance hierarchy, rank and relatedness co-vary, and thus it is difficult to assess the importance of one or the other factors on the relationships between females. This type of hierarchies characterizes cercopithecines (Kapsalis 2004). Individualistic dominance hierarchies characterize egalitarian species, and they are primarily influenced

by the age, size, reproductive status, and residency status of females (Hrdy & Hrdy 1976; Harcourt & Stewart 2007; Lu *et al*. 2013). Species experiencing low levels of within-group contest competition for food are expected to form "egalitarian relationships" where females exhibit low levels of agonistics behaviours (van Schaik 1989; Isbell 1991; Sterck *et al.* 1997). However, despite the general thought that female dominance hierarchy affects female-female relationships, it has recently been shown that female dominance hierarchy does not always affect grooming between females in species exhibiting low level of affiliative interactions (*Nasalis larvatus*: Matsuda *et al.* 2012*; Macaca assamensis:* Macdonald *et al*. 2013).

Reproductive status

It has been suggested that the reproductive status of females (cycling, pregnant, lactating) can influence female-female social relationships (Altman 1980). Lactating females in some species receive more grooming than cycling or pregnant females (*Macaca radiata*: Sugiyama 1971; *Papio ursinus*: Seyfarth 1976). Because lactating females are more attractive as grooming partners to other females in some species, the reproductive status appears to be an important factor contributing to affiliation among females (*Macaca mulatta:* Martel *et al.* 1994). The primary cause of this attraction could be the presence of a newborn. Female attraction to newborns is well documented in wild species (review in Badescu 2011) and may be sufficient to explain the fact that mothers with young infants receive more grooming than other females. Therefore, a female that is cycling or lactating can be engaged in different levels of affiliative interactions. Lu and colleagues (2013) showed that the reproductive status, but not the relatedness, of

Hanuman langur females affected their dominance rank: cycling females gained rank positions prior to conception and dropped in the hierarchy after given birth. The higher rank of females during cycling may partly be due to male's mating interest in the female during that period. Alternatively, cycling females may be more assertive than females immediately after parturition.

Co-residency

Co-residency is measured by the time two individuals have spent in the same group (Kulik *et al.* 2012). In female philopatric species, the effects of long-term co-residency and relatedness on female behaviours overlap. In female-dispersing species, long-term co-residents tend to interact together at higher rates than with immigrant females (bonobos: Idani 1991) and sometimes direct aggression to the newcomer (Pusey & Packer 1987; Watts 1991). However, some studies have shown that despite no access to related partners, co-resident unrelated females can exhibit high rates of grooming and strong social bonds (*C. polykomos*: Korstjens *et al.* 2002; chimpanzees: Langergraber *et al*. 2009; Langergraber 2012). Therefore, relatedness is not the only factor responsible for the establishment and maintenance of social relationships (Watts 2001; Wikberg *et al*. 2012). Also, it has been showed that co-residency is an important component of the sociality index (CSI: Composite Sociality Index measured by friendly approaches, grooming and sharing of limited resources, Silk *et al.* 2003) in male-female dyads of rhesus macaques.

Nature of female relationships

As the influence of the factors previously discussed varies between species, female social relationships also vary. In order to contrast the nature of affiliative relationship between females, I present examples of undifferentiated and differentiated female-female relationships in different species living in uni-male/multi-females groups. I also discuss the nature of female relationships with their resident male in the light of these factors.

Social relationships in species where females are usually unrelated can be summarized as undifferentiated: little female-female grooming, low rates of aggression, submission and affiliation, and an absence of coalitionary alliances (Wrangham 1980; Sterck *et al.*1997). In other words, dominance hierarchy related behaviours are poorly expressed, most likely because of the low within-group food competition (Wrangham 1980; Sterck *et al.* 1997). Mountain gorillas (*Gorilla beringei*), Thomas's langurs (*Presbytis thomasi*) and hamadryas baboons are examples of species where female-female relationships are relatively undifferentiated within uni-male groups. Because females are not related and do not form coalitions or express significant affiliative relationships with other females of their group, they have the option to transfer without high social costs.

Female philopatry allows females to find allies in related members. Species where females are mostly philopatric show differentiated females social relationships, as expressed in high frequency of grooming, physical proximity and more frequent agonistic interactions (Wrangham 1980; Sterck *et al.* 1997). Philopatry is female-based in cercopithecines, and therefore females have the potential to express strong and life lasting

social relationships with their relatives (Cords 2012). The Hanuman langur (*Semnopithecus entellus*), which lives in uni-male groups, is an example of a species where female exhibit differentiated social relationships despite the fact that they do not exhibit a matrilineal dominance hierarchy even if philopatry is female-based (Hrdy & Hrdy 1976; Borries *et al.* 1994). Borries *et al.* (1994) showed that females' favourite grooming partners are related female members, and that the resident male plays a secondary role in the grooming network.

In uni-male/multi-females groups, differentiated relationships can also be expressed within intersexual dyads. In gorillas and saki monkeys, male-female relationships can sometimes be the strongest ones in a group (Harcourt & Stewart 2007; Thompson & Norconk 2011). When females direct most of their affiliative behaviours towards the male, the resulting pattern is what Kummer (1968) called a "star-shaped" sociogram. Colmenares *et al.* (1994) have found that hamadryas baboons conform to this pattern. They also found that dominance rank in females, even if they are unrelated, affects male-female social relationships because females are competing to access to a limited social resource: the male. Swedell (2002) suggested that even if hamadryas society is characterized by stronger male-female relationships, the social dynamic in some groups was also driven by female-female relationships. In fact, the star-shaped pattern persisted even when males were experimentally removed or disappeared naturally, suggesting that the alpha female may become the preferred partner for most other females. Therefore, male-female interactions are likely to be affected by female residence patterns and the nature of female-female relationships.

Based on the review I presented here, it is clear that females gain benefits from affiliating with both sexes. Unknown is whether females have a preference for some social partners in species that form uni-male groups, where infanticide is an important selective pressure, and where females are facultative dispersers (i.e. females can choose to remain in, or disperse from, the natal group). *Colobus vellerosus* presents these characteristics and thus is an ideal candidate to investigate the affiliative preferences of females.

Colobus vellerosus at Boabeng-Fiema Monkey Sanctuary

Just a decade ago, *Colobus vellerosus* was a poorly known species. The results of thirteen years of research at the Boabeng-Fiema Monkey Sanctuary (BFMS) have allowed us to document various aspects of the socio-ecology and conservation status of these monkeys. Today, the knowledge researchers have collected, compiled and published about this species encourages the rethinking of social categorization primatologists are using. Most colobines are folivores, display scramble food competition, have low within- group feeding competition, and display egalitarian female relationships (Newton & Dunbar 1994). Colobus at BFMS is no exception. Although *C. vellerosus* mostly fit the predictions of Sterck *et al.* (1997) socio-ecological model (Saj *et al.* 2007), it turns out that it is not simple to classify it as a dispersal-egalitarian or as a resident-egalitarian species. In fact, these categories seem now obsolete to describe the reality of *C. vellerosus* at BFMS because of the important variation in social structure between groups within this population (Wikberg *et al.* 2012). For instance, although

philopatry is female-biased, females in this population show facultative dispersal and therefore the potential access to related females varies between groups (Teichroeb *et al.* 2009; Wikberg *et al.* 2012). Also, the non-usurpable and non-monopolizable nature of the food resources along with a low level of agonistic interactions over these resources (Saj & Sicotte 2007a,b) lead researchers to conclude that females *C. vellerosus* experience scramble competition (Teichroeb & Sicotte 2009). Yet individualistic dominance hierarchies are documented and their strength varies greatly from one group to the other (Wikberg *et al.* 2013). Additionally, Saj *et al.* (2007) documented a between-group variation in the strength of social relationships that females form with other adult members of their group. For instance, female-female affiliation was higher than male-female affiliation, but the degree of inter-sexual affiliation varied between the studied groups. The group composition in *C. vellerosus* also varies: some groups are uni-male and some are multi-males (Wong & Sicotte 2006). Teichroeb and Sicotte (2010) suggested that resident males in uni-male groups exhibit better quality traits because they are usually able to keep other males away. Considering the high incidence of infanticide in this population, it is of primary importance for a female to choose a good male partner (Teichroeb & Sicotte 2008; Teichroeb *et al.* 2012).

Although the population of colobus at BFMS has been studied since 2000, it is only since 2005 that adult members of the groups are individually recognized (Wikberg 2012). Therefore, it is now possible to document detailed dyadic interactions between known individuals. It allows the investigation of within-group variability in the nature of social relationships females form with other adult members.

3 - RESEARCH QUESTIONS, OBJECTIVES AND PREDICTIONS

The goal of my study is to contrast social relationships that females form with the resident male and with other adult females of their group. Previous studies of *C. vellerosus* at BFMS report variation in the patterning of association among adults (Saj *et al.* 2007; Wikberg *et al.* in press). In this species where levels of affiliative interactions are low, do females distribute their affiliation evenly or do they direct it towards specific preferred partners? If females do have preferred partners, are they the other females or the resident male of the group? I will answer these questions by describing and quantifying the social relationships between adults living in uni-male groups. As a consequence of their facultative dispersal, female *C. vellerosus* have access to both related and unrelated female social partners. The frequency of affiliative behaviours directed at social partners is expected to vary according to the relatedness degree females are sharing, and thus to vary between dyads. As the males of uni-male groups appear to be higher quality (Teichroeb & Sicotte 2010) than the males of multi-males groups, and are likely offering important services to females in terms of infanticide protection (Teichroeb *et al.* 2012), females' choices of social partners potentially has considerable effects on their reproductive success, and on the survival of the species. Therefore, according to their reproductive status and the availability of related females, *C. vellerosus females* should prefer different social partners (the male or the females). More specifically, I will:

1- Determine if female *C. vellerosus* have preferred social partners.

I expect females to unevenly distribute their affiliation among available social partners and thus to create differentiated social relationships (Wikberg *et al.* 2012). Females having access to related female partners will direct affiliative interactions towards them. Females having no access to related partners will direct their affiliative interactions towards the resident male of their group.

2- Determine the characteristics of females' preferred social partners.

If some females do prefer females as their social partners, I will investigate whether the reproductive status of social partners and focal females influences the distribution of affiliation, as documented in baboons (Seyfarth 1976; Altmann 1980). Because natal attraction has been documented in *C. vellerosus* and since lactation is associated with the presence of an infant, I expect females to prefer lactating females, compared to cycling or pregnant females (Brent *et al*. 2008, Badescu 2011). Also, because infanticide pressure is present in this population (Teichroeb & Sicotte 2008; Teichroeb *et al.* 2012), I expect lactating females to prefer the resident male.

3- Investigate the influence of these characteristics on the rates of interactions.

I will then investigate if the characteristics of the preferred social partners influence the rates of affiliative interactions exchanged between females and their preferred social partners. I will evaluate the mean rates of affiliative interactions between females and their preferred partners for the different characteristics females and their partners can exhibit. I expect that the relatedness degree and the reproductive status will positively influence the rates of affiliative interactions (approaches, proximity, grooming) between females and their preferred social partners.

CHAPTER II: METHODS

II

1 – The Study

Study site

This study was conducted at the Boabeng-Fiema Monkey Sanctuary (BFMS) located in the Nkoranza district of Brong-Ahafo region, in central Ghana (7°43′ N and 1°42′ W) (Fig. 2.1). The sanctuary is located at 350 meters above sea level and has a flat topography (Fargey 1992). This area is characterized by two rainy and two dry seasons. Detailed descriptions of the site are available in Saj *et al*. 2005 and Kankam *et al*. 2010.

Figure 2.1: Location of the study site. Source: ©2014 Google

The protected area was legally designated as a sanctuary in 1974 (Fargey 1992; Saj *et al.* 2005). Although the monkey population is protected, the forest itself faces the consequences of human activities (i.e. coal production, firewood extraction, medicinal and edible plant collection, bushmeat hunting, cattle foraging (sheep, pig, chicken), and public dump) (Kankam *et al.* 2010). The sanctuary covers an area of 5 km^2 containing a core forest fragment of 1.9 km^2 of dry semi-deciduous vegetation (Fargey 1992; Kankam *et al.* 2010). A fully closed canopy covers one third of the core fragment whereas open areas of the fragment are invaded by a weed (Siam weed: *Cromolaena odorata*) that prevents trees' seedlings to grow up, causing the forest to regenerate itself at a slow pace (Kankam *et al.* 2010). There are also nine smaller forest fragments in a 10 km radius from the core forest. The sanctuary's surrounding matrix mainly serves agricultural purposes (mainly cassava, yam, cocoyam, maize, groundnut and tomatoes) (Kankam *et al.* 2010). Along with farmlands, two villages, Boabeng and Fiema, border the core forest fragment. Otherwise, it is isolated from 50 km of any larger forest (Beier *et al.* 2002). In 2009, the estimated human population of the community (Boabeng and Fiema) was 2711 individuals (Kankam *et al.* 2010). Farming is the key economic activity of the human communities living in the area. Farmlands are distributed around the core fragment and a network of paths used by the villagers to reach the farmlands parcels out of the forest. These are the paths used by researchers to follow monkeys and also by visitors to enjoy a guided tour of the forest. As part of a community-based conservation program associated with the Ghana Wildlife Division, the local community has established a management committee that runs an ecotourism program including a guesthouse where tourists can spend a few nights and visit the sanctuary (Fargey 1992; Kankam *et al.* 2010).

National law and religious taboos perpetuated by the surrounding communities of Boabeng and Fiema protect the two diurnal monkey species living in the forest, the ursine colobus (*Colobus vellerosus*) and the Lowe's guenon (*Cercopithecus campbelli)* from hunting (Fargey 1992; Saj *et al*. 2005, 2006). Hunting taboos and religious beliefs at BFMS have been detailed in other studies (Saj *et al.* 2006; Kankam *et al.* 2010). The nocturnal Demidoff's bushbaby (*Galago senegalensis*) is also present in the forest fragments but is apparently hunted as bush meat (personal observation). Other large mammals are absent from the forest, however squirrels, bats and rodents are found. In 2000, the population of *C. vellerosus* was composed of approximately 200 individuals distributed in 14 groups (Saj *et al.* 2005), and it has been increasing to 275 individuals distributed in 19 groups in 2007 (Kankam *et al.* 2010). In contrast to other *C. vellerosus* populations, the BFMS population of colobus is increasing, likely due to the hunting taboo respected by the local people and to the successful eco-tourism program (Saj *et al.* 2005, 2006; Saj & Sicotte 2013).

Study species

Colobus vellerosus is endemic to West Africa and ranges from the eastern part of the Ivory Coast to southwestern Nigeria (Saj *et al.* 2005). This species belongs to the Old World monkey Colobinae subfamily. The African colobinea group includes three genera: red colobus (*Piliocolobus*: eight species), olive colobus (*Procolobus*: one species), and black-and-white colobus (*Colobus*: five species) (Groves 2001). Colobus monkeys are diurnal and arboreal, but they sometimes come to the ground to feed of travel between

forest patches (Wong & Sicotte 2006). *Colobus vellerosus* can live in wet, moist, riverine or dry forests (Chapman *et al.* 1999). Its diet is essentially composed of mature and young leaves (74%), but depending on the season, the percentage of leaves consumed varies from 97% (wet season) to 0% (dry season). Seeds and pods (8%), unripe fruits (8%), and flowers and buds (6%) are also consumed (Saj *et al.* 2005).

Colobus vellerosus lives in uni-male/multi-females groups or multi-males/multi-females groups, with some all-male bands. Group size ranges from 9 to 38 individuals (Wong & Sicotte 2006). Dispersal is male-biased (Teichroeb *et al.* 2011). Females tend to be philopatric but they can also disperse (Saj *et al.* 2007; Teichroeb *et al.* 2009; Wikberg *et al.* 2012). Scramble food competition occurs among females and aggression among them is low (Saj & Sicotte 2007; Teichroeb & Sicotte 2009; Wikberg *et al.* 2013). Consequently, female-female relationships have been classified as egalitarian, according to Sterck and colleagues' socio-ecological model (1997) (Marteinson 2003; Saj *et al*. 2007; Wikberg *et al.* 2013). Male incursions and takeovers as well as directed aggression towards infants by adult extra-group male during intergroup encounters occur (Saj & Sicotte 2005, Sicotte & McIntosh 2004; Teichroeb & Sicotte 2008a,b). Infanticide is an important cause of mortality in this population of colobus (Teichroeb & Sicotte 2008a).

Female C. *vellerosus* do not physically advertise their receptivity state. In uni-male groups, females presumably mate only with the resident male (Teichroeb *et al.* 2013) although a small proportion of extra-group copulations probably occurs (Teichroeb *et al*. 2005). In multi-male groups, females mate polyandrously and can solicit mating from several males (Teichroeb & Sicotte 2010). Births in *C. vellerosus* are aseasonal and

female give birth to a single infant (Teichroeb & Sicotte 2008; Saj & Sicotte 2013). The mean inter-birth interval, when infants survive to weaning, is approximately 22 months (N= 6; Teichroeb & Sicotte 2008a).

Study groups and study subjects

In May 2012, I conducted preliminary training observations in order to identify monkeys prior to start behavioural data collection. With the help of E.C. Wikberg, I learned to individually recognize adult and subadults monkeys belonging to three groups, based on age and sex categories (see Appendix A for definitions) using tail and body characteristics (ex. scars), head hair tufts shape, and facial features (shape of eye brow, the face and the eyes, presence and colour of facial hair). Distinguishing between individual monkeys, especially among adults, was an essential ability to develop in the context of this study in order to keep track of individual behaviours.

From June 4th to October 31st 2012, I collected behavioural data from ten adult females belonging to two different groups, Red Tail (RT) and Wawa (WW) (see Table 2.1 for details on individual females). RT was followed since 2004 and WW was followed since 2006 (Wikberg *et al.* 2013). Both groups were uni-male/multi-females during the data collection period (see Table 2.2 for group composition). Study groups were primarily selected on the basis of their composition, as my goal was to study social relationships in uni-male groups. The groups were also selected according to their level

of habituation to researchers presence, and for a matter of observation efficacy, on the location and accessibility of their home ranges.

Due to the extensive use of the forest by the villagers, many groups of *C. vellerosus* were habituated to human presence prior to the start of the long-term study at BFMS in 2000. The two study groups' home range overlap with the location of the nearby village (Boabeng) and monkeys occasionally get in proximity of villagers and tourists. The presence of researchers following and observing monkeys for many consecutive hours in the past years has lead the monkeys to minimally change their natural behaviours in our presence.

Table 2.1: Focal females' characteristics

Female ID	Grp ID	Res. Male ID	Infant ID	Age	Parity status	Res. status	# of focal sample *	Focal time (h)
TR	RT	CC	TE	A	Mu	Lt	83	11.47
BL	RT	CC	BD	A	Mu	Lt	90	14.20
BE	RT	CC	BG [a]	A	Mu	Lt	97	14.52
SU	RT	CC	SG [a]	A	Mu	Lt	85	12.28
FV	RT	CC	FN	A	Mu	Im	84	12.53
JI	RT	CC	n/a	S	Nu	Na	95	14.52
JN	WW	OW	JS	A	Mu	Lt	103	16.33
CR	WW	OW	CE	A	Mu	Lt	103	15.56
ML	WW	OW	n/a	A	Mu	Lt	113	17.61
IT	WW	OW	IB	A	Mu	Na	97	15.01

Legend:
Grp ID = Group identity
Res. Male ID = Resident male identity
A= Adult; S = Subadult
Mu = Multiparous; Nu= Nulliparous
Res. status = Residency status
Lt = Long-Term; Im = Immigrant; Na = Natal

[a] *BG and SG were weaned during the data collection period.*

***** *Used in the analyses*

Table 2.2: Group composition from June to October 2012

		Adults		Subadults		Juveniles		Infants	
Group ID	Group Size	F*	M	F	M	F	M	F	M
RT	21	5	1	1	4	3	3	1	3
WW	15-16	4	1	1	0	2	4-5	1[a]	2[b]

** F = Female; M = Male*
[a] A female infant (CE) was born in on August 21st
[b] A male infant (JS) disappeared and likely died around August 9th; A male infant (IB) was born on September 6th

2- DATA COLLECTION

Behavioural sampling

Behavioural data were collected from June 4th to October 31st 2012, from 6 am to 2 pm, during five complete days a week. A team made up of a trained research assistant (Tessy P. Paquin (TP) from June 4th to August 14th and Rustu Ataman (RA) from September 5th to October 31st), one experienced local field assistant (Charles Kodom (CK)) along with myself (EPR) followed the two study groups. Each group was visited at least every second day, but depending on their location, we sometimes collected behavioural data on both groups the same day. The difficulty of accessing certain areas of their home ranges and the reduced visibility of the monkeys due to leaf cover and height imposed flexibility in the data collection schedule. However, I attempted to obtain a similar numbers of observation hours in each group (≅ 94 hours RT, ≅ 71 hours in WW). In total, I spent 824 hours in the forest following the monkeys over 22 weeks. I decided not to include the data collected during the first two weeks of my data collection to avoid

uncertainty. Therefore, the dataset used for the analyses contains 149 hours of observations (≅ 85 h in RT, ≅ 64 h in WW).

No random order was set up to manage the observation sequence of the females because the visibility of the focal subjects was unpredictable. Therefore, focal subjects were chosen based on their visibility and on the overall time spent observing them in an attempt to collect a relatively equal amount of data for each focal female. A minimum of 30 minutes between each focal samples of the same female was respected.

Behavioural data were collected using a combination of continuous and instantaneous sampling methods (Altman 1974). CK responsibility was to track the study group and the focal females, as well as to watch for defecation events (see below). At the same time, my research assistant and myself were collecting behavioural data using 10-minute focal animal sampling with instantaneous point samples every 2.5 minutes. A stopwatch was used to keep track of the start and end of each 10-minute focal and to indicate each instantaneous point sample. Instantaneous samples were conducted to record proximity between the focal female and other group members as well as female's state behaviour. State behaviours were divided into four categories: resting, travelling, social, and foraging. Using the tail length of the monkeys as a visual reference, I recorded proximity among group members at distances of 0 meter, 1 meter, 3 meters, and 5 meters. I used the same distance categories to record approaches and leaves. I only used the non-agonistic approaches to 1 meter in the analyses because I consider that an approach to 3 meters or 5 meters does not represent a preference in the individual that is approached (Saj 2005).

During 10-minute focal samples, using a pair of 8 x 42 binoculars, I was calling out all the behaviours performed by or directed toward the focal female, the identification of actors and receivers, and the proximity between the focal female and any other colobus monkeys. Using a series of codes for each event and state behaviour, and ID codes for animal identification, the research assistant was recording them in a hand-held computer (PSION) (see codes and definitions of behaviours sections below). The PSION device automatically records the time at which a code is typed in. In that way, the duration of state behaviours can be calculated. On a few occasions during which I was on my own, I used a handheld dictaphone voice recorder to record the behaviours, using the exact same recording structure. In total, I recorded 1070 focal animal samples on ten study subjects in my two study groups (a mean of 107 focal samples per female, ranging from 89 to 123).

During focal sampling I collected affiliative, agonistic and mating behaviours directed by and to the focal female. More specifically, along with actors and recipients identity, I collected: 1) the direction of sexual solicitations, 2) the direction, frequency and duration of grooming bouts in females and male-female dyads, and 3) the frequency and duration of proximity bouts in females and male-female dyads (see Appendix A for definitions).

Faecal sampling

As part of a broader project (J. Vayro PhD project), I collected faecal samples on the same ten adult females. The goal was to extract reproductive hormonal data from these samples. Faecal samples were collected continuously from June 18th to October 31st 2012, from 6 am to noon, five days a week, and from 6 am to 8 am on Tuesdays. To avoid potential effect of daily variation in hormones concentrations, we systematically stopped collecting faecal samples at noon. As oestrous is thought to be three days long in female colobus (*Colobus guereza*: Harris & Monfort 2006), we attempted to collect a faecal sample from each study subject every second day. In doing this, we insure to collect faecal material that contained female reproductive hormones in a one-day window of the ovulation peak. In order to make a connection between the social and mating behaviours of a female and her hormonal cycle, behavioural and faecal samples were collected on the same day. While I was confirming the identity of the study subjects, my assistants were watching and waiting for the known females to defecate. When an identified female defecated and the faeces were found on the forest ground, we used a sterile 15 ml vial to collect a piece as big as a grape or at least to allow us to obtain 0.2 g of faeces. Because faecal sample collection for hormonal analysis was a priority every morning, the first six hours of work were focused on getting the needed faecal samples although behavioural and hormonal data collection were sometimes compatible. The time period between noon and 2 pm was exclusively devoted to behavioural data collection.

Results from hormonal analysis were not available at the time of analyzing behavioural data and presenting the results included in my dissertation. I will eventually use the hormonal data in order to pair them up with the behavioural data.

3 – DATA ANALYSIS

As an observer keeping track of wild animals travelling in their natural habitat, I sometimes was not able to obtain full ten-minute focal animal samples. I did not include in the data set the focal animal samples that were 10 % or less of the full ten minutes duration (following procedures in Saj 2005). The final data set contained 950 focal animal samples, ranging from 83 to 113 samples per focal animal (Table 2.1).

I extracted approaches, proximity bouts, and grooming bouts from the final data set. I only used data from continuous sampling because they provided fine details on the interactions between two individuals and the duration of these interactions. For the approaches and the grooming episodes, I divided the behaviours into two unidirectional categories: what the focal female gave and what the focal female received. I consider the proximity as a bidirectional interaction. I did not assess the responsibility for initiating and maintaining the proximity.

Determining the identity of top partners

I first determined if females were interacting with every adult in their group. In RT, each focal female had a total of six possible adult partners (five other females, one resident male). In WW, each focal female had four possible adult partners (three other females, one resident male). For each female, I compared the number of available partners with the number of partners I observed her interacting with ("observed partners") (Table 2.3).

Then, I determined if females had partners with whom they interacted at a higher rate than with other partners. If they did, I called that individual the "top partner". I used six measures of affiliation to calculate rates of interaction between the focal females and their social partners. The measures are: the frequency of given and received approaches, the duration and the frequency of proximity bouts, and the frequency of given and received grooming bouts. To calculate the rates of interaction between a focal female and her partners, I divided the frequency of interactions with each partner by the focal time of that female (in hours). The individual with the highest rate of interaction was "the top partner". In theory, each focal female could potentially have six top partners, one for each affiliative measure.

Table 2.3: Number of available and observed partners per focal female

			RT						WW			
			TR	**BL**	**BE**	**SU**	**FV**	**JI**	**JN**	**CR**	**ML**	**IT**
Number of available partners		**F**	5	5	5	5	5	5	3	3	3	3
		M	1	1	1	1	1	1	1	1	1	1
Number of observed partners	Approaches G**	**F**	5	***4****	***4***	5	5	5	3	3	***2***	3
		M	***0***	1	1	1	1	1	1	1	1	1
	Approaches R	**F**	5	5	5	5	***4***	***4***	3	3	3	***2***
		M	1	1	1	1	1	1	1	1	1	1
	Proximity D	**F**	*1*	***0***	*2*	*2*	*2*	*3*	3	***2***	***2***	***2***
		M	***0***	***0***	***0***	***0***	1	1	1	1	***0***	1
	Proximity F	**F**	5	5	***4***	5	***4***	5	3	3	3	3
		M	1	1	1	1	1	1	1	1	1	1
	Grooming G	**F**	***0***	***4***	***2***	5	***2***	***3***	***2***	3	***1***	3
		M	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***
	Grooming R	**F**	***0***	***4***	***0***	***3***	***3***	***3***	3	***2***	3	***1***
		M	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***	***0***

**Italicized bold numbers indicate a difference between the number of available partners and the number of partners a female has been observed interacted with.*

***G = Given; R = Received; D = Duration; F = Frequency*

Determining the top partners' profile

Some females had two or more partners with an equal rate of affiliative interactions per affiliative measure (N= 8). Some females had no top partner: there was no interaction directed from that female towards other individuals or vice-versa (N=1). I identified the top partners for each female in each reproductive status (as defined in the following section). I also reported the identity and characteristics of the top partners (Table 2.4). When a female had more than one top partner, I reported the identity and characteristics for all of them. When the top partner was the resident male of the group, I also provided the information about the second adult top partner who was always a female. In order to build the typical profile of the females' top partners, I combined data on the sex, the parity, the relatedness category and the reproductive status of focal females' top partners. I used the identity of the top partner as a stability measure to assess if females were consistently engaged in affiliative interactions with the same individual or not.

To assess if females' pairing with top partners was simply a reflection of the availability of partners or if females' pairing was skewed towards partners with certain characteristics, I calculated, for each focal female, the proportion of available: male and female, multiparous and nulliparous females, cycling, pregnant, and lactating females, and related and non-related partners. Because the availability of cycling, pregnant and lactating partners could change over the data collection period, I used the number of days in which partners of a particular category were available to calculate the proportion. For the other characteristics, I calculated the proportion using the number of partners

available for each characteristic. Then, for each focal female and for each characteristic, I compared the proportion of available partners with the proportion of top partners exhibiting this characteristic (Table 2.5). If the proportion of top partners was higher than the proportion of available partners (10 % or more) I considered that the focal female skewed her interactions towards partners exhibiting this characteristic. Once I did that comparison for each of the ten focal females, I combined the results and divided by ten focal females to have the proportion of focal females skewing or not their preference for top partners. In the following paragraphs, I describe how I determined the parity status, the relatedness category and the reproductive status of the females and their top partners. These variables were used as the independent variables in the statistical analyses.

Table 2.4: Identity of females' top partners and their characteristics per affiliative measure

			Approaches Given					Approaches Received					Proximity Duration				
	FF ID	FF Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status
RT	TR	**L**	SU	F	M	NR	P	CC	M	-	-	-	SU	F	M	NR	P
	TR	**L**	-	-	-	-	-	FV	F	M	NR	L	-	-	-	-	-
	BL	**L**	BE	F	M	R	P	SU	F	M	R	P	SU	F	M	R	P
	BL	**L**	SU	F	M	R	P	-	-	-	-	-	-	-	-	-	-
	BL	**L**	JI	F	N	-	C	-	-	-	-	-	-	-	-	-	-
	BE	**P**	SU	F	M	NR	P	JI	F	N	-	C	CC	M	-	-	-
	BE	**P**	-	-	-	-	-	CC	M	-	-	-	FV	F	M	-	L
	SU	**P**	JI	F	N	-	C	TR	F	M	NR	L	JI	F	N	-	C
	SU	**P**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	FV	**L**	CC	M	-	-	-	CC	M	-	-	-	JI	F	N	-	C
	FV	**L**	JI	F	N	-	C	TR	F	M	NR	L	-	-	-	-	-
	FV	**L**	-	-	-	-	-	BE	F	M	NR	P	-	-	-	-	-
	FV	**L**	-	-	-	-	-	JI	F	N	-	C	-	-	-	-	-
	JI	**C**	BE	F	M	-	P	CC	M	-	-	-	SU	F	M	-	P
	JI	**C**	FV	F	M	-	L	FV	F	M	-	L	-	-	-	-	-
WW	JN	**L**	CR	F	M	NR	P	CR	F	M	NR	P	IT	F	M	R	P
	JN	**L**	ML	F	M	R	C	ML	F	M	R	C	-	-	-	-	-
	JN	**C**	IT	F	M	R	P	IT	F	M	R	P	IT	F	M	R	P
	JN	**P**	IT	F	M	R	L	IT	F	M	R	L	IT	F	M	R	L
	CR	**P**	JN	F	M	NR	L	JN	F	M	NR	L	OW	M	-	-	-
	CR	**P**	-	-	-	-	-	-	-	-	-	-	ML	F	M	R	C
	CR	**L**	JN	F	M	NR	P	IT	F	M	NR	L	ML	F	M	R	C
	CR	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	ML	**C**	CR	F	M	R	L	JN	F	M	R	L	IT	F	M	R	P
	ML	**C**	-	-	-	-	-	IT	F	M	R	P	-	-	-	-	-
	IT	**P**	CR	F	M	NR	P	JN	F	M	R	C	ML	F	M	R	C
	IT	**P**	ML	F	M	R	C	-	-	-	-	-	-	-	-	-	-
	IT	**L**	JN	F	M	R	P	JN	F	M	R	P	JN	F	M	R	P

Table 2.4: *continues …*

			Proximity Frequency					Grooming Given					Grooming Received				
	FF ID	FF Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status	TP ID	TP Sex	TP Parity	TP Rel.	TP Repr. status
RT	TR	**L**	SU	F	M	NR	P	-	-	-	-	-	SU	F	M	NR	P
	TR	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BL	**L**	SU	F	M	R	P	SU	F	M	R	P	SU	F	M	R	P
	BL	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BL	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	BE	**P**	CC	M	-	-	-	BL	F	M	R	L	SU	F	M	NR	P
	BE	**P**	SU	F	M	NR	P	-	-	-	-	-	-	-	-	-	-
	SU	**P**	JI	F	N	-	C	BL	F	M	R	L	JI	F	N	-	C
	SU	**P**	TR	F	M	NR	L	-	-	-	-	-	-	-	-	-	-
	FV	**L**	CC	M	-	-	-	JI	F	N	-	C	JI	F	N	-	C
	FV	**L**	JI	F	N	-	C	-	-	-	-	-	-	-	-	-	-
	FV	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	FV	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	JI	**C**	SU	F	M	-	P	SU	F	M	-	P	SU	F	M	-	P
	JI	**C**	FV	F	M	-	L	-	-	-	-	-	-	-	-	-	-
WW	JN	**L**	CR	F	M	NR	P	ML	F	M	R	C	IT	F	M	R	P
	JN	**L**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	JN	**C**	IT	F	M	R	P	CR	F	M	NR	L	IT	F	M	R	L
	JN	**P**	IT	F	M	R	L	-	-	-	-	-	-	-	-	-	-
	CR	**P**	JN	F	M	NR	L	IT	F	M	NR	P	IT	F	M	NR	P
	CR	**P**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	CR	**L**	ML	F	M	R	C	JN	F	M	NR	C	JN	F	M	NR	C
	CR	**L**	-	-	-	-	-	IT	F	M	NR	L	-	-	-	-	-
	ML	**C**	CR	F	M	R	L	JN	F	M	R	L	IT	F	M	R	P
	ML	**C**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	IT	**P**	JN	F	M	R	C	JN	F	M	R	L	CR	F	M	NR	P
	IT	**P**	-	-	-	-	-	CR	F	M	NR	P	-	-	-	-	-
	IT	**L**	JN	F	M	R	P	JN	F	M	R	C	-	-	-	-	-

Legend: FF = Focal females; TP = Top partner; Rel. = Relatedness category; NR = Non-related; R = Related; M = Multiparous; N=Nulliparous; C = Cycling; P = Pregnant; L = Lactating. IN PINK = ID and characteristics of the second top partner when first top partner is a male.

Table 2.5: Proportions of top partners and available partners for each characteristic

		Characteristics of top partners								
		F	**M**	**Mu**	**Nu**	**R**	**NR**	**C**	**P**	**L**
JN	% TP	100	0	100	0	78	22	17	50	33
	% Av. P	75	25	100	0	67	33	33	35	32
CR	% TP	92	8	100	0	17	83	33	25	42
	% Av. P	75	25	100	0	33	67	46	27	27
ML	% TP	100	0	100	0	100	0	0	43	57
	% Av. P	75	25	100	0	100	0	9	47	44
IT	% TP	100	0	100	0	77	23	38	54	8
	% Av. P	75	25	100	0	67	33	43	27	30
TR	% TP	80	20	100	0	0	100	0	100	0
	% Av. P	83	17	80	20	0	100	20	40	40
BL	% TP	100	0	88	12	100	0	12	88	0
	% Av. P	83	17	80	20	50	50	20	40	40
BE	% TP	57	43	75	25	33	66	25	50	25
	% Av. P	83	17	80	20	25	75	20	20	60
SU	% TP	100	0	43	57	33	67	57	0	43
	% Av. P	83	17	80	20	25	75	20	20	60
FV	% TP	50	50	0	100	n/a	n/a	100	0	0
	% Av. P	83	17	80	20	0	100	20	40	40
JI	% TP	88	12	100	0	n/a	n/a	0	71	29
	% Av. P	83	17	80	20	n/a	n/a	0	40	60

Legend:
% TP = % of top partners; % Av. P = % of available partners
F = Female; M = Male
Mu = Multiparous; Nu = Nulliparous
R = Related, NR = Non-Related
C = Cycling; P = Pregnant; L = Lactating

Parity status

To assess the parity status of each focal female, I used the long-term demographic data from BFMS and information provided by E.C. Wikberg, who is long-term observer of the population. Out of the ten focal females, nine were multiparous and one was nulliparous. The parity status was always associated with age: multiparous females were always adults. Because my sample only contained one nulliparous female, the results concerning the parity variable need to be carefully interpreted. Focal females in WW were all multiparous females, thus they only have the possibility to have a multiparous female as top partners. In RT, five females out of six were multiparous and one female was nulliparous. When the top partner was the resident male (n = 8), I looked at the parity status of the second top partner. In one case, three females were equally representing the second top partner position and I thus considered all of them in calculating the proportion of multiparous and nulliparous top partners.

Relatedness category

I used published data on relatedness (Wikberg *et al.* in press) to assess if focal females and their top partners were related or not. Related female dyads included mother-daughter, full sister, half-sister, full aunt-niece, and grandmother-granddaughter dyads ($r \geq 0.28$). Non-related females dyads include half aunt-niece, cousin, and unrelated dyads ($r \leq 0.28$). The availability of related partners varied between the two study groups. In RT, three females had access to both related and non-related partners, two females had

only access to non-related partners and one female' relatedness relationships haven't been assessed. Therefore, this female has been removed from the analysis aiming to assess if females biased their interactions towards related females or not. In WW, three females had access to both related and non-related partners and one female had only access to related partners. I used females that had access to both related and non-related partners as a subgroup to test the effect of relatedness on the rate of affiliative interactions with the top partner. I collected all my data blindly, prior to knowing the relatedness between females.

Reproductive status

The different reproductive statuses of females (cycling, pregnant, lactating) are often perceived as non-overlapping exclusive categories (Altman 1980). However, recent work suggested that this might not be the case, particularly in colobines (Borries *et al.* 2011b). In *C. vellerosus*, I observed that these categories could indeed overlap. For example, two females (BE and SU) were lactating throughout the data collection period and gave birth a few weeks after the end of my data collection. Knowing the approximate date of birth and considering pregnancy to last six months in this species (Saj *et al*. 2005), I backtracked the approximate date of conception. I found that both females were lactating and pregnant at the same time for the whole duration of my data collection. However, ongoing work suggests that this may not be the case for all females (J. Vayro in prep).

Until we know more about this phenomenon, I treated the different statuses as exclusive categories using the following rules: 1) pregnancy lasts six months in female *C. vellerosus* (Teichroeb & Sicotte 2010), 2) weaning can occur as early as seven months after birth (Saj *et al.* 2005), and 3) cycling resumes after weaning or death of an infant. This means I consider a female "pregnant" for the six months during which she carries her unborn infant, whether she lactates or not. I consider a female "lactating" for the first seven months after birth, and I consider a female as cycling at the end of the seven months of lactation, whether she is lactating or not. I realize that this categorization is not ideal, since pregnancy and lactation can have different consequences on the nature and the frequency of females' interactions.

Table 2.6: Focal females' reproductive status over the data collection period

Group	Female	Reproductive Status *	Reason of the change from previous status	Duration (days)	Start Date	End Date
RT	TR	L	n/a	135	Jun 19	Oct 31
	BL	L	n/a	135	Jun 19	Oct 31
	BE	P	n/a	135	Jun 19	Oct 31
	SU	P	n/a	135	Jun 19	Oct 31
	FV	L	n/a	135	Jun 19	Oct 31
	JI	C	n/a	135	Jun 19	Oct 31
WW	JN	L	n/a	51	Jun 19	Aug 9
	JN	C	Infant death	36	Aug 10	Sep 14
	JN	P	Conception	46	Sep 15	Oct 31
	CR	P	n/a	63	Jun 19	Aug 20
	CR	L	Infant birth	71	Aug 21	Oct 31
	ML	C	n/a	135	Jun 19	Oct 31
	IT	P	n/a	79	Jun 19	Sep 6
	IT	L	Infant birth	55	Sep 6	Oct 31

** C = Cycling; P = Pregnant; L = Lactating*

Co-residency

In WW, all focal females were long-term residents and thus there was no variation in the residency status on which to base investigation of female partners preference. In RT, three of the six focal females were long-term residents, two natal females and one was immigrant. The immigrant female (FV) was giving grooming to and receiving grooming from the same top partner (JI) who is one of the natal female of this group. This immigrant female had the same top partner whether she was receiving approaches or herself approaching, and this partner was the resident male of the group (CC). Therefore, I was unable to investigate the effect of this variable on females' preferences for top partners.

Determining the factors influencing the rate of affiliation

I investigated the effect of the group identity, the parity status of the top partners, the relatedness relationship between the focal females and their top partners, the reproductive status of focal female, and the reproductive status of the top partners on the rates of affiliative interaction. I used data on approaches, proximity and grooming to construct six types of affiliative measures (dependent variables). Specifically, I investigated the effect of the independent variables on: 1) the hourly rate of approaches given to the top partner, 2) the hourly rate of approaches received from the top partner, 3) the proportion of time spent in proximity to the top partner, 4) the hourly rate of proximity bouts with the top partner, 5) the hourly rate of grooming given to the top partner, and 6) the hourly rate of grooming received from the top partner. In the

following paragraphs, I first described the affiliative interactions and how I converted them into rates, and then I described the statistical tests I performed using these rates.

Approaches

An approach refers to a non-agonistic approach to one meter between adults outside of the mating context. All approaches immediately preceding (10 sec or less (following procedures in Saj 2005)) a grooming interaction were not considered approaches because I wanted to obtain the rate of strict approaches independently from grooming. I made a distinction between two types of approaches to zero meters: a passive body contact and an instance of active body contact like gentle touching or grooming. All approaches to zero meter immediately preceding (10 sec or less) a grooming interaction were not considered approaches but fell into the grooming category. I recorded three cases of active approaches to zero meter and they all happened within the same dyad, involving infant transfer between a mother and another adult female. I observed intersexual active body contact between the resident male and the females of his group in only one context: mating. In RT, the resident male (CC) has been observed touching a female's hips (JI) twice (once in June, once in July). In WW, *ad libitum* data provide one example of mating between the resident male (OW) and one adult female (JN). I did not record evidences of approaches to zero meter from a female to a male.

I calculated an hourly rate of approaches given from the focal female to her top partner, and an hourly rate of approaches received by the focal female from her top partner. For each focal female, I calculated the hourly rate of approaches given and received by dividing the number of approaches given or received by the total focal time

for that female. I did that calculation for every dyad and then used the highest rate to determine the focal female's top partner.

Proximity

I used approaches and leaves to determine the occurrence and the length of proximity bouts. Since I wanted to investigate proximity independently from other social interactions, grooming was not part of what I defined to be proximity between two individuals. I counted the establishment of a proximity bout as an occurrence of proximity. I also reported the duration of proximity using a subset of bouts for which I had an approach and a leave corresponding to the beginning and the end of the bout.

I calculated the proportion of time a focal female and her top partners spent in proximity by dividing the time spent in proximity by the total focal time for that particular female. I also calculated an hourly rate of proximity establishments between a focal female and her top partners by dividing the number of proximity bouts a female or her top partner established by the total focal time for that particular female.

Grooming

I recorded the start and the end of a grooming interaction along with the identity of the groomer, the groomee (i.e. the receiver of grooming), the instigator and the individual ending the grooming interaction. I reported descriptive statistics on the duration and the frequency of grooming bouts. In the main analysis, however, I only used the frequency of

grooming bouts. The establishment of a grooming bout was thus counted as an occurrence of grooming and was used in calculating the hourly rate of grooming.

I calculated an hourly rate of grooming given by the focal female to her top partner and an hourly rate of grooming received by the focal female from her top partner. For each focal female, I divided the number of grooming bouts given or received by the total focal time for that female.

Generalized Estimating Equations

I used Generalized Estimating Equation (GEE) models (Liang & Zeger 1986) to test the effect of five independent variables on the rates of affiliative interactions between the focal females and their top partners. I did employ a GEE approach because it is a type of statistical tool that takes into account repeated measures on the same individual (i.e. interdependence of the data) and thus a possible unknown correlation of the data (Hanley *et al.* 2003). In my case, the different units of analysis (i.e. female per reproductive status) were not independent from each other since some females appeared more than once in the data set. In contrast to Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM), GEE models do not violate the independence assumption (Zuur *et al.* 2009).

I first looked at the effect of the independent variables using the ten focal female per reproductive status as the unit of analysis (N=14) ("full analysis"). Then, to control for the variation in the access of related and non-related partners, I use a subgroup of

females that had access to both categories of partners (N=10) ("kin subgroup analysis"). I tested the effect of the variables on the six types of affiliative measures I described, using the rate of interaction with the top partner as the dependant variable. I repeated the tests on the "kin subgroup". I included in the tests females that had no top partner, and thus for which the rate of interaction was zero, because this value represents an absence of interaction and not a lack of data.

I included in the models potential covariates in order to control for the variation in the availability of partners between focal females. I calculated the proportions of multiparous and nulliparous females, of related and non-related females, and the proportions of cycling, pregnant, and lactating females that each focal female had access to. Since the proportion of a category of females (e.g. related) is inversely proportional to the other category (e.g. non-related), I only introduced, in the models, one of the proportions as the covariate. Therefore, I used the percentage of available multiparous partners as a covariate of the parity status in order to control for the variation of available partners of each parity status on the rate of affiliative interactions, and the percentage of available related partners as a covariate of the relatedness relationship between the focal females and their top partner in order to control for the variation of available partners of each relatedness category on the rate of affiliative interactions.

Because I could only introduce a maximum of two covariates at once for the same variable, I tested the effect of the top partners' reproductive status using three different models, each one including a pair of covariates controlling for the variation of available partners of each reproductive status on the rate of affiliative interactions. The first model

included the percentage of cycling partners and the percentage of pregnant partners; the second model included the percentage of cycling partners and the percentage of lactating partners; and the third model included the percentage of lactating partners and the percentage of pregnant partners.

Each model, testing the effect of a covariate on a variable, produced three types of values I needed to consider: the statistical interaction between the variable and its covariates, the effect of the variable on the rate sof affiliative interactions, and the effect of the proportion of available partners (i.e. the covariate) on the rates of affiliative interactions. I tested the effect of the variables and their covariates on both the full sample and the "kin subgroup". If the interaction between a variable and its covariate was significant, I could not use this covariate as a control variable. When the interaction was not significant, I reported the tests' values of the variable and the covariate when they had a significant effect on the rates of affiliative interactions.

When several correlation types (autoregressive, unstructured, exchangeable) were tested on a set of data, I always reported the results for the best fitting model (smaller-is-better fit) according to the quasi likelihood under independence model criterion. All tests are two-tailed and were conducted using SPSS 21.0. The significance level was set at $p < 0.05$.

CHAPTER III: RESULTS

III

1 – FEMALES DO HAVE TOP PARTNERS

I observed a between-group variation in the number of partners females interacted with. In WW, all four females interacted with all other adult females, except for the time spent in proximity and the establishment of proximity bouts where focal females concentrated their time towards one or two partners. All females of that group were the top partner of every other female at least once during the data collection period. Only one female in the group (CR) had the resident male as her top partner for one affiliative measure (duration of proximity bouts). In RT, some pairs of females never interacted. Out of 15 possible pairs of females for each affiliative measure, one pair never established proximity; eight pairs never spent time in proximity; and five pairs never exchanged grooming. Unlike WW females, some females in RT were never top partners for other females. In this group, four females (TR, BE, FV, JI) had the resident male as their top partner for at least one affiliative measure.

For each focal female, I calculated the proportion of the identities of her top partners throughout the data collection period. I found that seven females out of ten had the same top partner in 50 % or more of the six affiliative measures. The rest of the time, focal females affiliated with different social partners and their identity was not consistent between the different affiliative behaviours.

I used the total number of focal female in each reproductive status per affiliative measure (unit of analysis) to calculate the number of females having zero, one, or more than one top partner. Most females had one top partner per affiliative measure; this was the case in 82 % of the cases (N = 84). Some females had no top partner and some females had more than one top partner per affiliative measure (Figure 3.1). I found that seven of the focal females had more than one top partner for at least one affiliative measure. I found a similar pattern of variation when looking at the second top partner.

I determined if females were engaged in significantly more interactions with their top partners than with other social partners. I used six types of affiliative measures to compare the rate of affiliative interactions between a female and her top partner and a female and her second top partner. I found a significant difference between the mean rates of affiliative interactions between focal females and their top partners and the mean rates of affiliative interactions between focal females and their second top partners (t = 5.383, df = 2, mean difference = 0.2741, std. error = 0.0509, $p < 0.05$). This difference indicated that females interacted significantly more with their top partners than with other social partners.

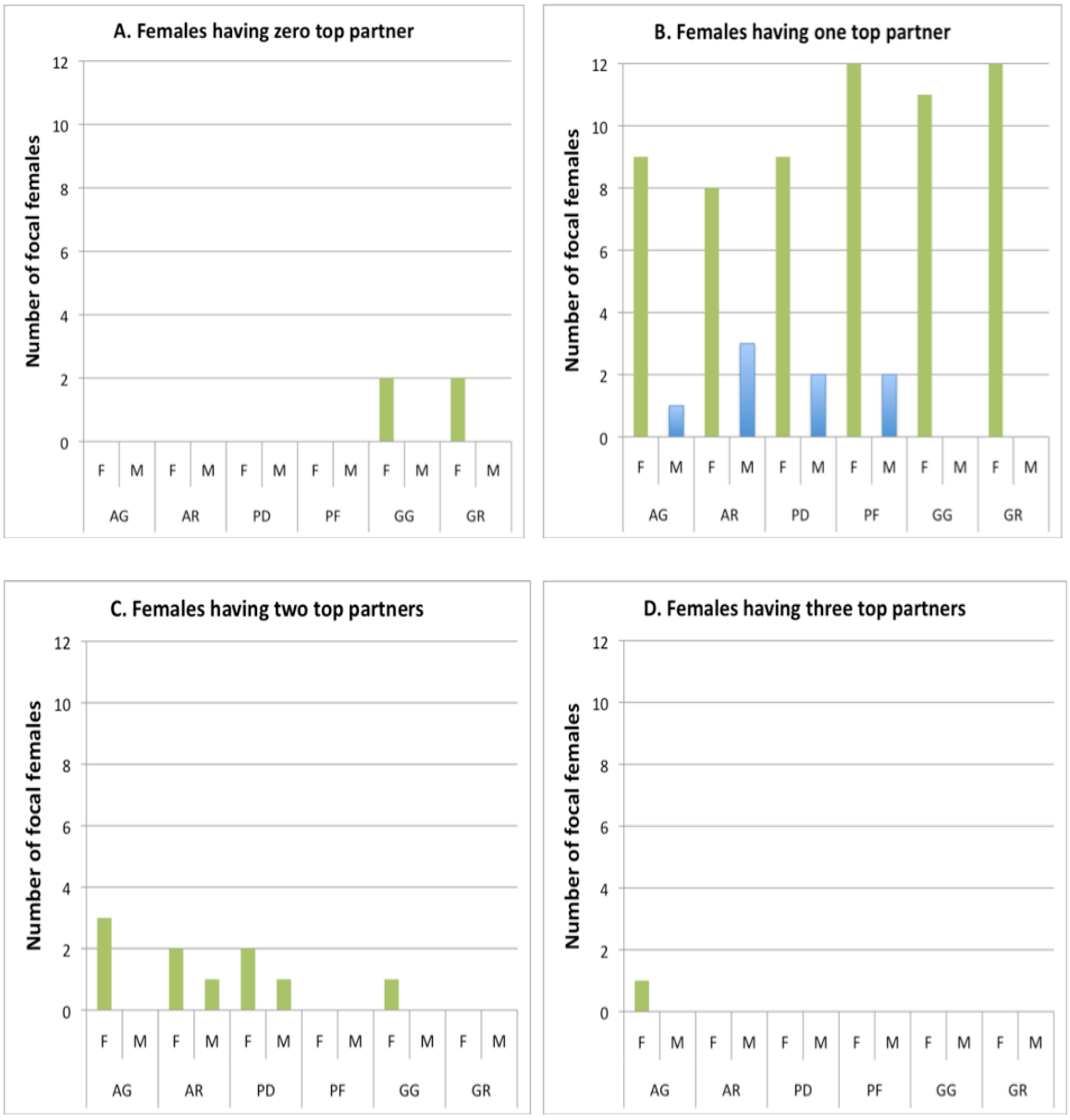

Figure 3.1: Number of females having different number of top partners per sex category per affiliative measure

Legend:
F = Females (in green); M = Males (in blue)
AG = Approaches Given; AR = Approaches Received
PD = Proportion of time spent in proximity; PF = Proximity bouts
GG = Grooming Given; GR = Grooming Received

2 – TOP PARTNERS' CHARACTERISTICS

To determine if females interacted with their partners according to their availability or if they biased their interactions towards partners having particular characteristics, I compared the proportion of available partners per characteristic with the proportion of top partners having the same characteristic.

Comparison based on sex

Combining the top partners for each focal female per reproductive status per affiliative measure, I found 92 instances of top partners. Overall, in 90 % of these instances, the focal females' top partner was a female. In the remaining 10 % (n = 9) of these instances, the resident male was the top partner. Globally, this probably does not vary for the expected distribution of partner choice based on the availability of males and females. However, these choices did not appear to be distributed equally among the different affiliative measures. When looking at grooming, none of the females had the resident male as her top partner. When looking at proximity, four females had the resident male as their top partners. When looking at the approaches, four females received approaches from a male top partner and one female gave approaches to a male top partner.

When comparing the proportion of available male and female partners with the sex of the top partners, I found that 60 % of the focal females had females as their top partner in a higher proportion than what was available in their group. Only 20 % of the focal females were top partner with the resident male of their group in a higher proportion than what was available. The remaining 20 % of the focal females were top partner with females and the male in the same proportion as each sex was available in their group (Figure 3.2).

Comparison based on the parity status

In RT, 79 % of the top partners (N = 42) were multiparous females. In WW, females only had access to multiparous female partners. When comparing the proportion of available multiparous and nulliparous partners with the parity status of the top partners, I found that 40 % of the focal females, that had access to these two categories (N = 5), had multiparous and nulliparous top partners in the same proportion as each parity status was available. For 40 % of the focal females, the top partner was nulliparous in a higher proportion than what was available. The remaining 20 % of the focal females had multiparous top partners in a higher proportion than what was available.

Comparison based on the relatedness category

Combining the number of top partners for focal females having access to both related and non-related partners (N = 6), I found 48 instances of top partners. In 54 % of these instances, the focal females' top partner was a related female. When comparing the proportion of available related and non-related partners with the relatedness category of the top partners, I found that 83 % of the focal females having access to both categories had related individuals as their top partners in a higher proportion than what was available in their group. Only 17% of the focal females were top partner with a non-related individual in a higher proportion than what was available.

Comparison based on the reproductive status

In both study groups, focal females had access, at some point during the data collection period, to cycling, pregnant and lactating partners. Only one female in RT never had access to a cycling partner. The availability of partners from each category varied between focal females. Combining the number of top partners for each focal female per reproductive status per affiliative measure, I found 93 instances of top partners. In 45% of these instances, the focal females' top partner was pregnant. In 28 % and 27 % of these instances, the top partner was lactating and cycling, respectively. When comparing the proportions of available cycling, pregnant, and lactating partners with the reproductive status of the top partners, I found that 60 % of the focal females had a pregnant top partner in a higher proportion than what was available in their group. I also found that 20 % of the focal females had a pregnant top partner in a smaller

proportion than what was available and that the remaining 20 % of the focal females had pregnant partners as much as they were available. For 70 % of the focal females, the top partner was a lactating female in smaller proportion than what was available. For 20 % of the focal females, the top partner was lactating in a higher proportion than what was available and 10 % of the focal females had a lactating top partner as much as they were available. Finally, I found that 22 % of the focal females had a cycling partner in a higher proportion than what was available. Also, 44 % of the focal female had a cycling top partner in a smaller proportion than what was available, and 33 % of the focal females had a cycling top partner as much as they were available.

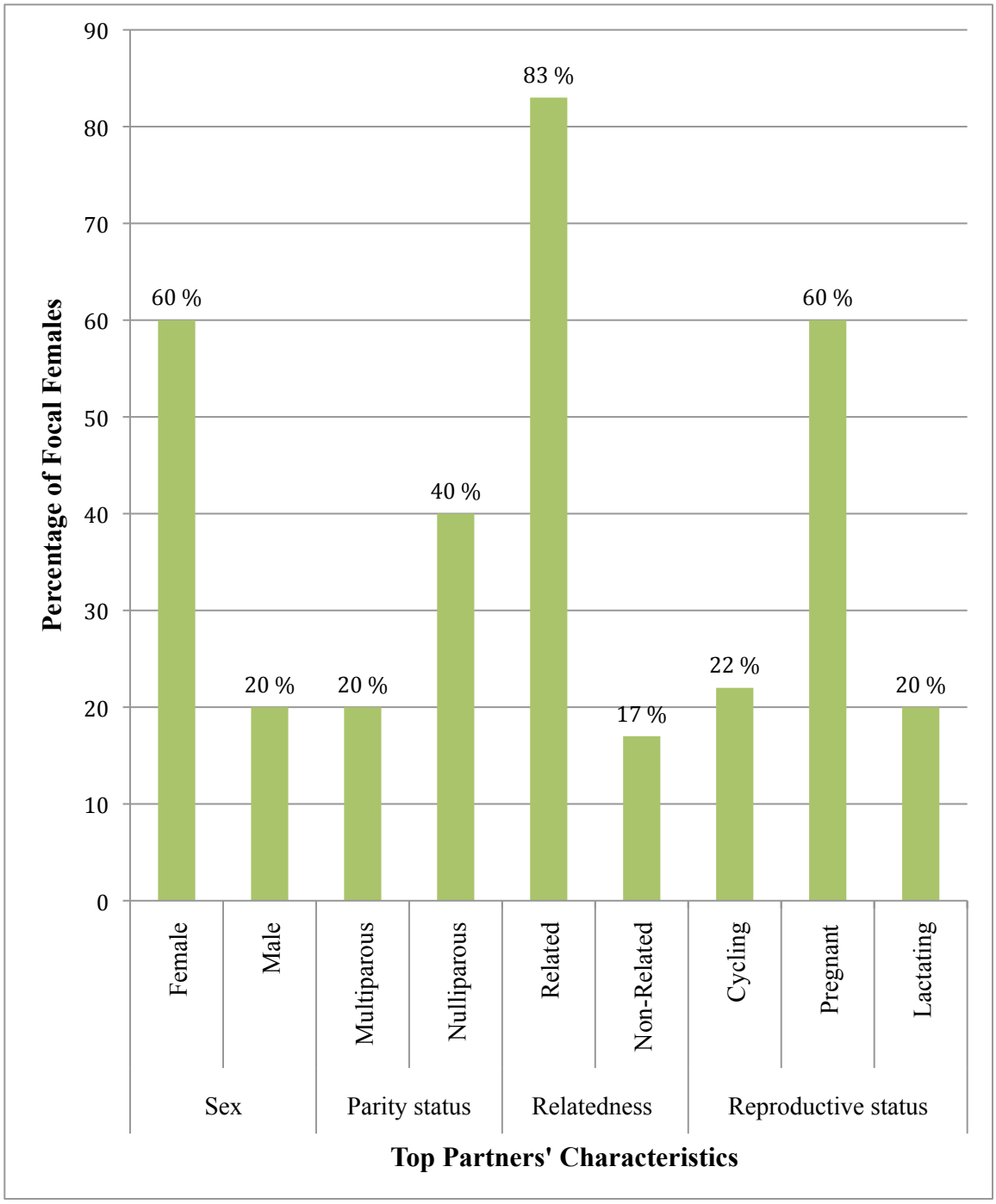

Figure 3.2: Percentage of focal females in RT and WW having a higher proportion of top partners than the proportion of available partners for each characteristic

In the following section, I first describe the different types of affiliative interactions I observed in female *C. vellerosus*. I focus on the frequency of approaches, proximity and grooming bouts, and on the duration of proximity and grooming. I distinguish between the affiliative interactions females had with other adults and the affiliative interactions females had with their top partner for each type of behaviours. Then, I report the results of the statistical analyses that I used to investigate the effect of the group identity, the parity status of the top partners, the relatedness between the focal females and their top partners, the reproductive status of the focal females, and the reproductive status of the top partners on the rates of affiliative interactions.

Affiliative interactions

Approaches

Approaches to one meter represent 51 % of all approaches (including three and five meters, N = 1266). Of these, 153 approaches happened in female dyads (64 in RT, 89 in WW), and 51 in intersexual dyads (31 in RT, 20 in WW). In intersexual dyads, 72.5 % of the approaches were performed by the resident male towards a female (22 out of 31 in RT, 15 out of 20 in WW). I observed 114 approaches between the focal females and their top partners (44 in RT, 70 in WW) (Table 3.2).

Proximity

I recorded 116 establishment of proximity in female dyads (48 in RT, 68 in WW), and 44 in intersexual dyads (25 in RT, 19 in WW). I observed 65 of these proximity establishments between the focal females and their top partners (31 in RT, 34 in WW).

I observed 42 complete proximity bouts between adults (22 in RT, 20 in WW). Of these bouts, 29 were recorded in female dyads (13 in RT, 16 in WW), and 13 in intersexual dyads (9 in RT, 4 in WW). The duration of all proximity bouts varied from 3 seconds to 1237 seconds, with a mean of 278 seconds. In RT, the 22 complete bouts ranged from 3 seconds to 1237 seconds with a mean of 273 seconds, and in WW the 20 complete bouts ranged from 6 seconds to 818 seconds, with a mean of 203 seconds. Of these complete bouts, 25 were recorded between the focal females and their top partners (12 in RT, 13 in WW). In RT, their duration ranged from 3 seconds to 1237 seconds with a mean of 201 seconds per bout. In WW their duration ranged from 67 seconds to 818 seconds with a mean of 153 seconds per bout.

Grooming

I observed 255 grooming bouts among individuals (185 in RT, 70 in WW), and 239 of them took place in female dyads (173 in RT, 66 in WW). I never observed grooming in intersexual dyads involving the resident male. I observed 104 of these grooming bouts between the focal females and their top partners (72 in RT, 32 in WW).

I observed 98 complete grooming bouts between females (69 in RT, 29 in WW). Overall, the duration of grooming bouts ranged from 2 seconds to 207 seconds with a mean of 43 seconds per bout. In RT, the 69 complete bouts ranged from 2 seconds to 145 seconds with a mean of 47 seconds per bout. In WW, the 29 complete bouts ranged from 2 seconds to 124 seconds with a mean of 34 seconds per bout. Of these complete bouts, 77 were recorded between the focal females and their top partners (53 in RT, 24 in WW). In RT, their duration ranged from 2 seconds to 145 seconds with a mean of 48 seconds per bout. In WW their duration ranged from 2 seconds to 124 seconds with a mean of 28 seconds per bout.

Table 3.1: Frequency and mean duration of affiliative interactions per group

		RT			**WW**		
		F-F*	**F-M**	**F-TP**	**F-F**	**F-M**	**F-TP**
Approaches		64	31	44	89	20	70
Proximity	Number of establishment	48	25	31	68	19	34
	Number of complete bouts	13	9	12	16	4	13
	Mean duration (s/bout)	**273**		**201**	**203**		**153**
Grooming	Number of establishment	173	0	72	66	0	32
	Number of complete bouts	69	0	53	29	0	24
	Mean duration (s/bout)	**47**		**48**	**34**		**28**

* *F = Female, M = Male, TP = Top Partner*

Variables influencing the rates of affiliative interactions

In this section, I report the results of the GEE analyses for each dependant variable in the following order: the group identity, the reproductive status of the focal females, the parity status of the top partners, the relatedness relationship between a focal female and her top partners, and the reproductive status of the top partners. In each section, I first report the GEE results of the analysis on the full data set (full), followed by the results of the analysis on the "kin subgroup" (kin). I report in the text the statistical values for the significant effects only. Appendix C includes the detailed GEE results and all statistical values.

<u>The group identity partially influenced the rates of affiliative interactions.</u>

For both analyses, the group identity had an effect on the hourly rate of approaches given to the top partners (full: Wald $\chi^2 = 10.025$, df = 1, $p < 0.05$; kin: Wald $\chi^2 = 11.949$, df = 1, $p < 0.05$), the hourly rate of approaches received from the top partners (full: Wald $\chi^2 = 23.052$, df = 1, $p < 0.05$; kin: Wald $\chi^2 = 44.055$, df = 1, $p < 0.05$), and the hourly rate of proximity bouts between the focal females and their top partners (full: Wald $\chi^2 = 30.483$, df = 1, $p < 0.05$; kin: Wald $\chi^2 = 30.483$, df = 1, $p < 0.05$). For both analyses, the hourly rates' means of approaches given and received and the mean hourly rate of proximity bouts were higher in WW than in RT, meaning that adult females in WW were engaged in more approaches and in more proximity bouts with their top partners than did RT females (pairwise comparisons reported in Table 3.3). The group identity did not have an effect on the proportion of time focal females spent in proximity to their top

partners, neither on the hourly rate of grooming given to the top partners and the grooming received from the top partners.

Table 3.2: Significant differences in the means of affiliative interactions between WW and RT

Direction of the significance		Affiliative measure **	Mean difference	Std. error	df	p-value
FULL	**WW > RT**	Approaches G	0.362	0.143	1	0.011
		Approaches R	0.533	0.159	1	0.001
		Proximity F	0.788	0.230	1	0.001
KIN *	**WW > RT**	Approaches G	0.517	0.165	1	0.002
		Approaches R	0.690	0.095	1	0.000
		Proximity F	1.002	0.184	1	0.000

**Kin = "Kin subgroup" analysis*
***G = Given; R = Received; D = Duration; F = Frequency*

The reproductive status of the focal females influenced the rates of affiliative interactions.

For both analyses, the reproductive status of the focal females had an effect on the six types of affiliative measures (all p values = 0.000, see Appendix C). The differences in the hourly rates' means of affiliative interactions between cycling, pregnant, or lactating focal females and their top partners varied between types of affiliative measures and between the full analysis and the "kin subgroup" analysis (Table 3.4). The general pattern of variation is the following: cycling focal females gave more approaches than lactating or pregnant females; pregnant focal females received more approaches than cycling females; pregnant females spent more time in proximity with their top partners

than did cycling and lactating females; cycling focal females gave more grooming than lactating females; lactating females received more grooming than pregnant females (Figure 3.3).

Table 3.4: Significant differences in the means of affiliative interactions between cycling (C), pregnant (P), and lactating (L) focal females

	Affiliative measure	Direction of the significance	Mean difference	Std. error	df	p-value
Full	Approaches G *	C > L	0.428	0.139	1	0.006
		C > P	0.472	0.112	1	0.000
	Approaches R	P > C	0.302	0.097	1	0.005
	Proximity D	P > C	0.019	0.005	1	0.000
		P > L	0.013	0.006	1	0.048
		L > C	0.006	0.002	1	0.005
	Grooming G	C > L	0.394	0.016	1	0.000
	Grooming R	L > P	0.821	0.232	1	0.001
Kin	Approaches G	C > L	0.521	0.131	1	0.000
		C > P	0.574	0.126	1	0.000
	Approaches R	P > C	0.336	0.091	1	0.001
	Proximity D	P > L	0.004	0.001	1	0.004
		P > C	0.015	0.005	1	0.004
	Grooming G	C > L	0.441	0.099	1	0.000
	Grooming R	L > P	0.821	0.233	1	0.001

** G = Given, R = Received, D = Duration, F = Frequency*

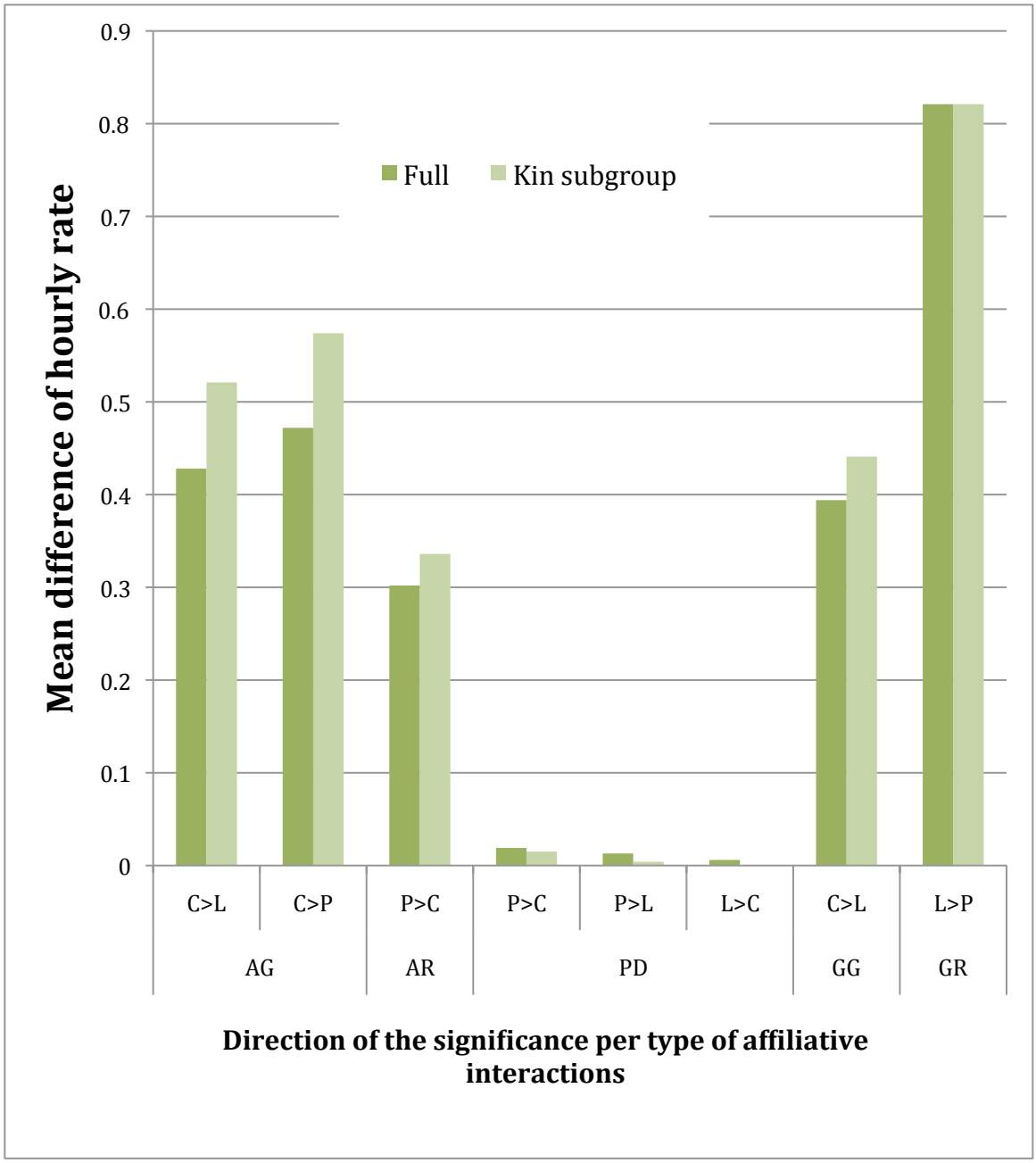

Figure 3.3: Significant differences in the means of affiliative interactions between cycling (C), pregnant (P), and lactating (L) focal females per type of affiliative measure

Legend:
AG = Approaches Given; AR = Approaches Received
PD = Proportion of time spent in proximity; PF = Proximity bouts
GG = Grooming Given; GR = Grooming Received

The parity status of the top partner partially influenced the rates of affiliative interactions.

The significance of the interaction between the parity status and its covariate (i.e. the percentage of available multiparous partners) varied between the full analysis and the "kin subgroup" analysis and between the different affiliative measures (see Appendix B for a summary of the effect of the variables and covariates and Appendix C for GEE values). For the full analysis, the parity status of the top partner had an effect only on the duration of proximity bouts (Wald $\chi^2 = 5.812$, df = 1, mean = 0.011, se = 0.227, $p < 0.05$). Despite this overall effect, the difference in the means of time focal females spent with multiparous top partners or nulliparous top partners was not significant.

For the "kin subgroup" analysis, the parity status of the top partner had an effect on the hourly rate of approaches received from the top partners (Wald $\chi^2 = 15.719$, df = 1, $p < 0.05$), the proportion of time focal females spent in proximity of their top partners (Wald $\chi^2 = 8.986$, df = 1, $p < 0.05$), and on the hourly rate of proximity bouts between the focal females and their top partners (Wald $\chi^2 = 4.081$, df = 1, $p < 0.05$). In these cases, despite the overall significant effect of the parity status on the approaches received and the proximity, the difference in the means of affiliative interactions were not different between focal females and their multiparous top partners or between focal females and their nulliparous top partners. In summary, both analyses indicated that females do not affiliate more or less with multiparous or nulliparous top partners.

Relatedness partially influenced the rates of affiliative interactions.

The significance of the interaction between the relatedness relation and its covariate (i.e. the percentage of available related partners) varied between the full analysis and the "kin subgroup" analysis and between the different affiliative measures. The relatedness between the focal females and their top partners had an affect only on the rates of grooming given to the top partners and of grooming received from the top partners for the "kin subgroup" (given: Wald $\chi^2 = 8.133$, df = 1, $p < 0.05$; received: Wald $\chi^2 = 5.718$, df = 1, $p < 0.05$). For the "kin subgroup" analysis, the percentage of available related partners was contributing to the variation of the proportion of time females and their top partners spent in proximity (Wald $\chi^2 = 5.903$, df = 1, B = 0.057, se = 0.024, $p < 0.05$), meaning that when the availability of related partners increased, the time females and their partners spent together increased as well. The percentage of available related partners was also contributing to the variation in the hourly rates of grooming received from the top partners in an inversely proportional way (Wald $\chi^2 = 6.546$, df = 1, B = -0.024, se = 0.0096, $p < 0.05$), indicating that when the availability of related partners decreased, the rates of grooming received from the top partners increased. Despite the effect of the covariate on the variation of the rates between females, there was never a significant difference in the mean rates of affiliative interactions between females and their related top partners and the females and their non-related top partners.

For the full analysis, the relatedness between the focal females and their top partners affected the rate of grooming given from the focal females to their top partners (Wald $\chi^2 = 5.585$, df = 1, $p < 0.05$). Because the interaction of the variable (i.e.

relatedness) and its covariate (i.e. percentage of available related partners) was significant, I could not use the covariate to control for the effect on the relatedness relation in the model. However, the percentage of available related partners was contributing to the variation of time females and their top partners spent in proximity (Wald $\chi^2 = 3.970$, df = 1, B = 0.017, se = 0.009, $p < 0.05$), indicating that when the percentage of available related partners increased, females and their top partners spent more time in proximity. Despite this significant effect of the covariate on the proportion of time females and their top partners spent in proximity, there was no significant difference in the mean rates of affiliative interactions between the females and their related top partners and the females and their non-related top partners.

<u>The top partners' reproductive status partially influenced the rates of affiliative interactions.</u>

For the full analysis, the significance of the interaction between the reproductive status of the top partners and the percentage of available top partners in each reproductive status varied between affiliative measures. When the percentage of available cycling, pregnant or lactating partners was controlling for the effect of top partners' reproductive status on the rates of affiliative interactions, the covariate was never significant, indicating the absence of a contribution of the partners' availability on the rates of affiliative interactions. The top partners' reproductive status influenced the rates of affiliative interactions for all affiliative measure except for the grooming received (Table 3.5). Despite the overall effect of the top partners' reproductive status on the rates of affiliative interactions, there was never a significant difference in the means of affiliative

interactions between focal females and their top partners, whichever the reproductive status of the top partners.

For the "kin subgroup" analysis, the significance of the interaction between the top partners' reproductive status and the percentage of available top partners per reproductive status varied between affiliative measures. When the percentage of available cycling, pregnant or lactating partners was controlling for the effect of top partners' reproductive status on the rates of affiliative interactions, the covariate "percentage of available pregnant partners" was contributing to the variation of the hourly rates of approaches received by the females from their top partners (Wald $\chi^2 = 22.669$, df = 1, B = 0.041, se = 0.009, $p < 0.05$), indicating that when the percentage of available pregnant partners increased, the hourly rate of approaches received from the top partners increased as well. The top partners' reproductive status influenced the hourly rates of approaches given and grooming received, and the proportion of time females and their top partners spent in proximity (Table 3.5). Despite the effect of the top partners' reproductive status on these three affiliative measures, there was never a significant difference in the means of affiliative interactions between focal females and their top partners, whichever the reproductive status of the top partners.

Table 3.4: Tests' p-values of the effect of the top partners' reproductive status on the rate of affiliative interactions per affiliative measure *

	Affiliative measure	χ^2	df	p-value
FULL	Approaches G	21.031	2	0.000
	Approaches R	10.757	2	0.005
	Proximity D	19.235	2	0.000
	Proximity F	20.367	2	0.000
	Grooming G	23.660	2	0.000
	Grooming R	1.684	2	0.431
KIN	Approaches G	7.812	2	0.020
	Approaches R	3.536	2	0.171
	Proximity D	10.433	2	0.005
	Proximity F	1.331	2	0.514
	Grooming G	27.732	2	0.000
	Grooming R	0.005	2	0.997

** Each test of the effect of the top partners' reproductive on the affiliative measure has been repeated three times, once with each pair of covariates (% of available cycling partners, % of available pregnant partners, % of available lactating partners). Because the best-fitting models were consistently the same per affiliative measure for each pair of covariates, the values of the 36 tests are reduced to one set of values per affiliative measure.*

CHAPTER IV: DISCUSSION

IV

The main goals of this study were to: 1) determine if females *C. vellerosus* are selective in their social relationships by examining whether they engage in social interactions with top partners or if they interact with all adults available, 2) identify the characteristics of the top partners, and 3) determine if some of these characteristics influence the rates of affiliative interactions between females and their top partners. Based on previous studies (Altmann 1980; Kapsalis 2004; Sterck *et al.* 1997; Brent *et al.* 2008; Wikberg *et al.* 2012; Lu *et al.* 2013), I predicted that 1) females living in uni-male groups will have top partners, 2) that their top partners will be related females and lactating females, and that lactating females' top partners will be the resident male, and 3) that the reproductive status and the relatedness degree between females and their top partners will positively influence the rates of affiliative interactions (approaches, proximity, grooming) between them. In the following sections, I summarize and discuss the key results.

1 - SUMMARY OF KEY RESULTS

The results of this study indicate that female *C. vellerosus* living in uni-male groups in the BFMS population do have a social partner that they either approach, stay in proximity or groom at a higher rates compared to other social partners. These top partners are adult females in most cases. Related females and pregnant females are more often top partners than what would be predicted on the basis of their availability. The reproductive status of focal females consistently influences the frequency of affiliative interactions between the females and their top partners, whereas the reproductive status of the top partners does not. Even if related and pregnant females are overrepresented as top partners, the rates of affiliative interactions between focal females and their top partners are not affected by the relatedness degree or by the pregnant state of the top partners.

Although the composition of my two research groups was similar, the groups varied in the number of partners focal females interacted with and the frequency of affiliative interactions exchanged between females and their top partners. Females in RT were more selective of their social partners and interacted with the resident males more often than did females in WW. The means rates of approaches given and received, and the number of proximity bouts between females and their top partners were higher in WW than in RT.

In summary, the results support the first prediction but give only partial support to the second and third sets of predictions. Lactating females were not more attractive as social partners than cycling or pregnant females, and the resident male was not the top partner of lactating females. Also, the reproductive status of females partially influenced the rates of affiliative interactions but the relatedness degree never did (Table 4.1).

Table 4.1: Research questions and predictions

Question	Prediction	Prediction supported?
1. Do females have top partners ?	**1.1.** Females do have top partners.	Yes
2. What are the characteristics of the top partners ?	**2.1.** Top partners are related females.	Yes
	2.2. Top partners are lactating females.	No
	2.3. Lactating females' top partners are the resident male.	No
3. Which characteristics influence the rates of affiliation between females and their top partners ?	**3.1.** The reproductive status influences the rates of affiliation.	Partially
	3.2. The relatedness degree influences the rates of affiliation.	No

2 – HOW IS AFFILIATION DISTRIBUTED ?

Compared to colobines, cercopithecines generally feed on more scattered food, travel further to fulfil their energy requirements, and consequently spend less time resting. Cercopithecines also spend more time socializing, mainly through the exchange of grooming, an activity observed in colobines as well but to a lesser extent (Lawrence & Cords 2012; Grueter *et al.* 2013). Activity budgets in Asian and African colobines are well documented and consistently show that colobines devote little of their time to social activities (Asian colobines: 0.1 – 6.5 %; African colobines: 1 - 15 %, review in Kirkpatrick 2011; Fashing 2011) in comparison with most cercopithecines (e.g.: Papionins (baboons, drills, mandrills, mangabeys): 5 - 24 %, review in Swedell 2011; Macaques: 8.4 – 23.5 %, review in Sussman & Garber 2011). This is also true of female *C. vellerosus* who engaged in few affiliative interactions with other adults of their group (2.6 % of their activity budget: Teichroeb *et al.* 2003). My study showed, however, that the little affiliation colobus females expressed was not distributed evenly between their possible social partners. Therefore, females seemed to manifest a preference for some partners.

Variation between females and groups

Females in both study groups directed and received approaches from all possible adult partners, male or female, but this was not observed for proximity and grooming interactions: some pairs of females never maintained proximity and some never groomed.

Approaches are probably less specific interactions, compared to the time spent in proximity and grooming, because the approaches received from an individual can be due to the proximity with a third individual (i.e. the target of the approaches). Therefore, approaches probably give little information on potential preferences for social partners. However, when looking at the distribution of the time spent in proximity and grooming, a pattern of preference is discernible. I found that most females spent time in proximity to all other females and that all females spent some time in proximity to the resident male, but the mean duration of proximity bouts between females and the male was shorter than the mean duration of proximity bouts between females. This is consistent with Wikberg and colleagues (2012) who found that the majority of females (87%) had higher proximity scores with females than with males. Therefore, even if females spent some time around the resident male, they preferred the proximity of other females. Also, I found that females were engaged in grooming interactions with adult females (even if some pairs of females never engaged in grooming interactions), but never with the resident male.

Grooming is thought to be the most important behaviour used by primates to maintain social relationships (Henzi & Barrett 1999; Schino 2001). Grooming has been used as a measure of affiliation because it appears to be a friendly behaviour (Kummer 1968; Dunbar & Dunbar 1975; Seyfarth 1977). In several species, grooming is usually non-randomly distributed among members of a social group (vervets: Seyfarth 1980; baboons: Silk *et al.* 1999; blue monkeys: Cords 2002; Japanese macaques: Nakimichi & Shizawa 2003; wild tufted cacpuchins: Tiddi *et al.* 2012). Indeed, in my population, most females groomed one top female and did not engage in much grooming with others. My

results also suggest a between group variation in the number of grooming partners: in WW, all females were engaged in grooming interactions with all other adult females, but still had one top partner, and in RT, five pairs of female never exchanged grooming.

Saj *et al.* (2007) documented between-group variation in intersexual affiliation: male-female affiliation was stronger than female-female affiliation in certain groups. In these groups, infanticide risk was higher, due to male take-over, suggesting that females would potentially reinforce male protection by grooming them more. In the same study, under male take-over conditions, females were the ones directing grooming to the males and thus being responsible for maintaining the relationship. During my study period, takeover attempts did not occur in my two study groups. This means that there was stability in male membership, and thus low infanticide pressure. This could explain why I did not observe intersexual grooming. It can also possibly explain why lactating females did not prefer the resident male as their top social partner. Stability of group membership in this population could have a direct influence on female affiliative relationships and therefore explain variation in patterns of intersexual affiliation between groups.

Taken together, my results suggest a between-group variation in the number of social partners females interacted with, but also a variation in the number of partners per type of affiliative interactions. It seems that females were choosier of their grooming partner than of their approaches and proximity partners. This is consistent with the fact that grooming networks in females *C. vellerosus* are differentiated in more groups than approaches networks are (Wikberg *et al.* 2012). As I indicated earlier, approaches and proximity between two individuals can be the outcome of an individual interaction with a

third party and therefore not always reflect a choice, for either the actor or the receiver (Hartcourt 1979). Since both individuals are actively participating in a grooming interaction and that the outcome of the interaction can have consequences on one's fitness (enhance longevity: Silk *et al.* 2010a); removal of ectoparasites, release of endorphins, and reduction of tension: review in Schino & Aureli 2008), I suggest that females choose their grooming partners more carefully than their approaches or proximity partners.

Females in my study groups expressed a preference for three kinds of social partners: females, related females, and pregnant females. But does having top partners mean that females actually formed differentiated relationships? My results suggest that it is the case. However, because the nature of female *C. vellerosus* social relationships at BFMS is variable between groups, sometimes characterized as differentiated or, when undifferentiated between females, as male-female bonded (Wikberg *et al.* 2012), care in formulating generalizations is required. The focal females I observed exhibited characteristics expected of females who form differentiated relationships: these females were mostly philopatric, and thus the groups were female kin-based, with very few interactions with the resident male. Differentiated relationships also suggest that the affiliative partners are not randomly chosen, as I observed for grooming.

The effect of reproductive status

I expected lactating females to be more attractive as top partners than cycling or pregnant females because lactating females carry their infant with them most of the time, and infant attraction is quite strong in primates in general (baboons: Silk *et al.* 2003;

macaques: Silk 1999; Schino *et al.* 2003, capuchins: Manson 1999) and in *C. vellerosus* in particular (Brent *et al.* 2008; Badescu 2011). This prediction was not supported by the results. In fact, pregnant females seemed to be the favourite top partners: about half of the focal females (45%) had a top partner that was pregnant and the majority of females (60%) had a pregnant top partner in higher proportions than the proportion of available pregnant partners. Even if the reproductive status was a good predictor of the identity of the top partners, it was only partially influencing the rates of affiliative interactions. The reproductive status of the top partners had an effect on most of the rates of affiliative interactions, but there was no difference in the mean rates between females and their top partners of each category (cycling, pregnant, lactating). This means that females and their pregnant top partners did not approach, stay in proximity, or groom one another at higher rates than females and their cycling top partners and females and their lactating top partners.

The reproductive status yielded contrasting results when analyzed from the focal females' perspective. For both the full and the "kin subgroup" analyses, the reproductive status of the focal females had an influence on all six affiliative measures. The direction of the difference followed a similar pattern with some variations, notably in three circumstances: 1) for the time focal females spent in proximity to their top partners, where lactating females spent significantly more time in proximity compared to cycling females for the full analysis whereas this difference was not significant for the "kin subgroup" analysis; 2) when pregnant females established proximity bouts at higher rates with their top partners than did cycling females for "kin subgroup" analysis whereas no difference between cycling, pregnant, and lactating females was found in the full

analysis; 3) when pregnant females groomed at higher rates their top partners than cycling females for the "kin subgroup" analysis whereas this difference was not significant for the full analysis. Overall, however, cycling females gave approaches at higher rates, pregnant females received approaches at higher rates, pregnant females spent more time in proximity to their top partners, cycling females gave grooming at higher rates, and lactating females received grooming at higher rates.

These sets of results support the prediction that the reproductive status influences the rate of affiliative interactions. This is true for the reproductive status of both the focal females and the top partners. It needs to be stated again, still, that the statistical models did not detect significant variations in the mean rates of affiliative interactions between females and their top partners, whichever the reproductive status of the top partner was. However, the mean rates of affiliative interactions varied with the reproductive status of the focal females in interpretable directions. Here, my interest focuses on the fact that lactating females received significantly higher rates of grooming than pregnant females.

Lactation and natal attraction

Natal attraction has been documented in most non-human primate species (review in Badescu 2011). Infants are the target of curiosity and handling behaviours by conspecifics, mostly juveniles and subadults females, but by adult females as well (Maestripieri 1994). Because younger infants are more attractive than older ones (Paul

1999), lactating females can become the target of disproportional social attention due to the physical proximity with their infant. Some studies have demonstrated that females with newborn receive more grooming compared to other females (baboons: Henzi & Barrett 2002; capuchins: Tiddi *et al.* 2010; mangabeys and vervets: Fruteau *et al.* 2011). My results indicate that lactating females are the primary receivers of grooming in *C. vellerosus;* this is a significant trend I identified when looking at the focal females reproductive status. Therefore, reproductive status impacted the distribution of affiliation in my study groups.

The "relatedness paradox"

The effect of maternal relatedness on social behaviours is an important topic in the non-human primate literature. Social relationships are influenced by relatedness and the distribution of affiliation is often biased towards related individuals living in the same group (review in Gouzoules & Gouzoules 1987). In egalitarian species, as in most colobines (Sterck *et al.* 1997), this tendency to engage in affiliative interactions with related females is noticeable but to a lesser extant than in most matrilocal cercopithecines (Gouzoules & Gouzoules 1987; Kapsalis 2004). The pattern seen in colobines resembles the one observed in mountains gorillas, where females do live with related and non-related females (Stewart & Harcourt 1987; Watts 2001) and where there is a variation in the degree of affiliation between female dyads. I found that a majority of females had top partners that were related females instead of non-related females. This supports part of

the second prediction and is consistent with previous findings at BFMS revealing that relatedness influences females' social network, particularly in groups formed of long-term female residents (Wikberg *et al.* 2012). As my two study groups were composed of natal and long-term resident females (except one immigrant female in RT), it was difficult to distinguish the effect of familiarity due to long-term co-residency and relatedness on females' preferences for social partners. Co-residency is another factor influencing variation in female relationships (gorillas: Watts 2001), especially for females living with unrelated individuals and where secondary transfer is a possibility (Stewart & Harcourt 1987). Familiarity among females, not only the relatedness degree they share, is therefore a source of variation in female social relationships. My results show that even if the degree of relatedness was a predictor of the identity of top partners, it did not consistently generate differences in the rates at which females interacted with their related or non-related top partners: Females and their related top partners did not exchange more grooming than females and their non-related partners. Among the three types of affiliative interactions, the rates of grooming were the only ones being affected by relatedness. This partially supports the prediction that the relatedness degree between females and their top partners influences the rate of affiliative interactions. Therefore, in contrast with previous findings at BFMS, I argue that relatedness is a good predictor of the identity of the top partner but does not influence the rates of approaches, proximity bouts and the time spent in proximity between females and their related top partners, hence the idea of the paradox. However, because grooming was biased towards related top partners, it confirms that grooming is more a "sensitive" behaviour, useful to measure preferences in social partners.

Is affiliation friendship?

Following Hinde's framework (1976) on the emergence of social structure, I suggest that the link between affiliation and friendship can be draw this way: since "affiliative" is an adjective that characterizes the interactions between two individuals and "friendship" is qualifying their relationship, repeated bi-directional affiliative interactions can result in a friendship. Therefore, the definition of a "top partner" I have been using is compatible with the notion of friendship. Many studies in non-human primates suggest an adaptive value to friendship between males (e.g. chimpanzees (Mitani 2009)), between females (e.g. rhesus macaques: Kapsalis 2004, blue monkeys: Cords 2002) and between males and females (e.g. baboons: Smuts 1985; Nguyen *et al.* 2009). Long-term cooperative relationships (i.e. strong social relationships: Seyfarth & Cheney 2012) have been studied in mammals, including feral horses (Cameron *et al.* 2009), macaques (Schülke *et al.* 2010) baboons (Silk *et al.* 2003, 2006a,b, 2009, 2010a,b) and chimpanzees (Wittig *et al.* 2014). Silk and colleagues investigated the effect of the strength of social bonds in female chacma baboons on their longevity and infant survival. They found that strong, long-term, and consistent social bonds between females positively influenced female longevity and the number of infants. In humans, social isolation has been identified as a risk factor of morbidity and mortality (myocardial infarction, stroke, cancer, diabetes) (Cacioppo & Hawkley 2003). Some studies also suggested that women with stronger social networks are less likely to get depressed (Berkman & Syme 1979; Cacioppo & Hawkley 2003; Noble 2005). Even if a clear positive influence of social integration on ones' fitness has been demonstrated, few studies actually considered the number of social partners in the equation. The size of a

social network, and the strength of the bonds within that network are likely to vary between individuals, especially when relationships are differentiated. In non-human primates, the number of individuals in a group has been used as a measure of social network size (Dunbar 1998) but this definition does not apply to humans who can maintain relationships with individuals outside of their immediate everyday social life. Is having a few strong bonds more beneficial than having many moderately strong social bonds? The answer to this question does not emerge clearly from the literature and further research is needed to determine if the size of social network in primates has an effect on fitness.

In a comparative perspective, the size of social network is a variable that has been linked to the size of neocortex in primates. Dunbar and colleagues (Dunbar 1992; 1998, Aiello & Dunbar 1993; Kudo & Dunabr 2001; Lehmann & Dunbar 2009) suggested a positive correlation between the size of the neocortex and the ability to use social skills to maintain cohesion in large groups: as the number of individuals in a group demands more memory and information processing, the neocortex, the seats of cognitive processes, would increase proportionally. This is the premise of the social brain hypothesis. Large groups are usually fragmented into smaller units, thus the social connectivity value is lower than in smaller groups. However, for social cohesion to be maintained between units of a same group, social flexibility is required (Lehmann & Dunbar 2009). Dunbar (1998) insisted on the fact that social flexibility is not just about remembering the information, but is about the ability to manipulate it. If there is truly a correlation between group size and neocortex size, a small number of social relationships can be associated with a smaller relative neocortex size in primates. It has been showed that

folivores, and therefore colobus, have smaller neocortex relative size than frugivores (Clutton-Brock & Harvey 1980). The fact that female C. *vellerosus* have small social network and form a limited number of important social relationships (i.e. top partners) is thus congruent with the social brain hypothesis.

3 – LIMITATIONS AND RESEARCH PERSPECTIVES

This is the first study to examine the effect of female reproductive status on the distribution of affiliative interactions in a wild population of colobus. I found that the reproductive status of females is a major factor in the expression of preferences for social partners, and this can probably be explained by natal attraction exhibited by females in this population. However, I did not find a consistent pattern explaining the distribution of female affiliation as neither the reproductive status, the relatedness degree or the parity status fully predict the identity of top partners and the frequency of affiliative interactions. Due to a small sample size and variation in the group composition, the results of this study do not provide insights on the effect of long-term co-residency on females' partner preferences, a potential factor influencing female social relationships. Comparing related long-term co-resident dyads and non-related long-term co-resident dyads would allow future researchers to distinguish the effects of relatedness and long-term co-residency on the rates of affiliative interactions between females.

Also, a more detailed analysis of affiliation exchange between the focal females and their social partners would have allowed the investigation of the consistency of

female-top partner relationships over time. The effect of life events (birth, death of infant, changes in group composition) paired with the identity of the top partner before, during, and after these events would have informed us on the consistency of preferred relationships as well as on the potential factors influencing these relationships. In fact, a bigger sample size and long-term data are needed to assess if these preferred relationships are long-term preferences or not, and if they affect the reproductive success of females. To fully address the question of females' fitness, I will be interested in looking at females' reproductive success (i.e. number of living and fertile offspring), the number of social partners females have, and the consistency of their preferred relationships over time.

4 – CONCLUSION

This study shows that females do not affiliate equally with all adult members of their group, but instead express a preference for some social partners. In *C. vellerosus* at BFMS, where females are facultative dispersers and where males play an important role as protector against infanticide, females still prefer to direct most of their affiliation towards other females. However, there is no clear pattern of affiliation in this population, even though the relatedness seems to influence the identity of female top partners. The reproductive status of the females partially influences the frequency at which affiliative interactions are exchanged: I identified trends in the exchange of affiliation when looking at the effect of the focal females status, but these trends did not appear when I looked at the effect of the top partners reproductive status on the rates of affiliation. This absence of a pattern can be in fact the exhibition of behavioural plasticity, revealing females' capacity to adapt to different social settings if the benefits of affiliation with different partners change over time.

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APPENDIX A

AGE AND SEX CLASSES DEFINITIONS

The following definitions are derived from Marteinson (2003), MacDonald (2011), and Badescu (2011).

Sex

- Males are identifiable by a continuous white rump patch.
- Females are identifiable by a discontinuity in the white rump patch.

Age

- Infants (0 to ±1 year old) are identifiable by their natal coats, which gradually change in colour from white, to grey, to adult black and white pelage. Infants are unweaned and have a small body size.

- Juveniles (1 to 2 years old) are distinguishable from older black-and-white infants based on their larger body size and sleeker coats, and independence from their mothers. Juvenile females do not have elongated nipples.
- Subadult females (2 to 4 years old) are larger than half the size of an adult female and do not have elongated nipples. Subadult males (2 to 6 years old) are about the size of an adult female, but still smaller than an adult male.

- Adult males and females are the largest individuals. Adult females that have elongated nipples are either primiparous or multiparous, while adult females without elongated nipples are nulliparous. Relative to males, adult females have rounder snouts and a slightly smaller body size.

Parity status

- Primiparous: Females with elongated nipples that have given birth once.
- Multiparous: Females with elongated nipples that have given birth more than once.
- Nulliparous: Females without elongated nipples that have not given birth.

BEHAVIOURAL DEFINITIONS

The following definitions are derived from Saj (2005) and Marteinson (2003) unless specified otherwise.

- An **approach** is when an individual approach another one within a distance of one meter or less and without agonistics, affiliative or sexual behaviours happening in a time period of ten seconds or less.

- A **leave** is when an individual leave another one from a distance of at least one meter without agonistics, affiliative or sexual behaviours happening in a time period of ten seconds or less.

- A **grooming bout** is an event of continuous grooming between the same two individuals with breaks of less than 30 seconds. When partner switching occurred with breaks of less than 30 seconds, the bout is counted twice for the focal individual, once as groomed and once as grooming (Schino *et al.* 1988).

- A **proximity bout** between two individuals is when these individuals are resting, feeding, or travelling together at a distance of at least one meter, without grooming each other. An approach and a leave are corresponding to the beginning and the end of a proximity bout.

- **Sexual solicitations** include behaviours such as: sexual presentation (turning the back or lifting rump towards another animal), hip touching or grabbing, inspection of genital area, or a grab (one individual lightly grabs the back or the legs of another one).

APPENDIX B

Table B.1: Effect of the variables on the affiliative measures for the full analysis

	App. G	App. R	Prox. D	Prox. F	Gro. G	Gro. R
Group identity	✓	✓	×	✓	×	×
Focal females' reproductive status	✓	✓	✓	✓	✓	✓
Top partners' parity	×	×	✓	×	×	×
% multiparous partners	✓	✓	×	✓	×	×
Relatedness relationship	×	×	×	×	✓	×
% kin partners	×	×	✓	S	S	×
Top partners' reproductive status	✓	✓	✓	✓	✓	×
% of cycling partners	S	S	×	S	×	×
% of pregnant partners	×	S	×	S	×	×
% of lactating partners	×	S	×	S	S	×

Legend:
✓ *indicates a significant effect of the variable*
× *indicates the absence of an effect of the variable*
S *indicates a significant interaction between the variable and its covariate*
App. G = Approaches Given; App. R = Approaches Received
Prox. D = Proximity by Duration; Prox. F = Proximity by Frequency
Gro. G = Grooming Given, Gro. R = Grooming Received

Table B.2: Effect of the variables on the affiliative measures for the kin subgroup analysis

	App. G	App. R	Prox. D	Prox. F	Gro. G	Gro. R
Group identity	✓	✓	×	✓	×	×
Focal females' reproductive status	✓	✓	✓	✓	✓	✓
Top partners' parity	×	✓	✓	✓	×	×
% multiparous partners	✓	✓	×	✓	×	×
Relatedness relationship	×	×	×	×	✓	✓
% kin partners	S	S	✓	×	S	✓
Top partners' reproductive status	✓	×	✓	×	✓	×
% of cycling partners	×	×	×	×	×	×
% of pregnant partners	×	✓	×	×	×	×
% of lactating partners	×	×	×	×	×	×

Legend:
✓ *indicates a significant effect of the variable*
× *indicates the absence of an effect of the variable*
S *indicates a significant interaction between the variable and its covariate*
App. G = Approaches Given; App. R = Approaches Received
Prox. D = Proximity by Duration; Prox. F = Proximity by Frequency
Gro. G = Grooming Given, Gro. R = Grooming Received

APPENDIX C

Table C.1: Results of GEE examining the effect of the group identity (RT, WW) on the rates of affiliative interactions

		Affiliative measure	χ^2	df	Estimated marignal means	Std. error	p-value
FULL	**RT**	Appr. G	10.025	1	0.284	0.043	0.002
		Appr. R	23.052	1	0.274	0.032	0.000
		Prox. D	0.014	1	0.013	0.004	0.907
		Prox. F	30.483	1	0.359	0.024	0.000
		Groo. G	0.128	1	0.489	0.139	0.721
		Groo. R	0.674	1	0.687	0.062	0.412
	WW	Appr. G	10.025	1	0.647	0.136	0.002
		Appr. R	23.052	1	0.807	0.156	0.000
		Prox. D	0.014	1	0.013	0.004	0.907
		Prox. F	30.483	1	1.147	0.229	0.000
		Groo. G	0.128	1	0.411	0.163	0.721
		Groo. R	0.674	1	0.548	0.143	0.412
KIN	**RT**	Appr. G	11.949	1	0.262	0.065	0.001
		Appr. R	44.055	1	0.298	0.048	0.000
		Prox. D	0.039	1	0.012	0.007	0.844
		Prox. F	61.966	1	0.331	0.038	0.000
		Groo. G	0.333	1	0.635	0.207	0.564
		Groo. R	1.334	1	0.752	0.096	0.248
	WW	Appr. G	11.949	1	0.780	0.152	0.001
		Appr. R	44.055	1	0.988	0.082	0.000
		Prox. D	0.039	1	0.013	0.005	0.844
		Prox. F	61.966	1	1.332	0.180	0.000
		Groo. G	0.333	1	0.475	0.182	0.564
		Groo. R	1.334	1	0.533	0.144	0.248

Legend:
Appr. = Approaches; Prox. = Proximity; Groo. = Grooming
G = Given; R = Received; D = Duration; F = Frequency

Table C.2: Results of GEE examining the effect of the focal female reproductive status (C, P, L) on the rates of affiliative interactions

		Affiliative measure	χ^2	df	Estimated marignal means	Std. error	p-value
FULL	C	Appr. G	85.917	2	0.824	0.150	0.000
		Appr. R	87.700	2	0.315	0.078	0.000
		Prox. D	49.474	2	0.006	0.003	0.000
		Prox. F	79.326	2	0.522	0.128	0.000
		Groo. G	75.760	2	0.635	0.124	0.000
		Groo. R	1186775.953	2	0.600	0.349	0.000
	P	Appr. G	85.917	2	0.353	0.168	0.000
		Appr. R	87.700	2	0.617	0.137	0.000
		Prox. D	49.474	2	0.025	0.007	0.000
		Prox. F	79.326	2	0.760	0.222	0.000
		Groo. G	75.760	2	0.677	0.202	0.000
		Groo. R	1186775.953	2	0.290	0.243	0.000
	L	Appr. G	85.917	2	0.393	0.138	0.000
		Appr. R	87.700	2	0.471	0.133	0.000
		Prox. D	49.474	2	0.011	0.007	0.000
		Prox. F	79.326	2	0.613	0.171	0.000
		Groo. G	75.760	2	0.240	0.075	0.000
		Groo. R	1186775.953	2	1.111	0.475	0.000
KIN	C	Appr. G	102.406	2	1.064	0.175	0.000
		Appr. R	55.576	2	0.383	0.123	0.000
		Prox. D	43.257	2	0.003	0.002	0.000
		Prox. F	45.342	2	0.626	0.200	0.000
		Groo. G	101.181	2	0.747	0.131	0.000
		Groo. R	1836370.986	2	0.600	0.349	0.000
	P	Appr. G	102.406	2	0.491	0.167	0.000
		Appr. R	55.576	2	0.719	0.164	0.000
		Prox. D	43.257	2	0.018	0.006	0.000
		Prox. F	45.342	2	0.895	0.273	0.000
		Groo. G	101.181	2	0.792	0.209	0.000
		Groo. R	1836370.986	2	0.290	0.243	0.000
	L	Appr. G	102.406	2	0.544	0.171	0.000
		Appr. R	55.576	2	0.557	0.190	0.000
		Prox. D	43.257	2	0.007	0.002	0.000
		Prox. F	45.342	2	0.731	0.252	0.000
		Groo. G	101.181	2	0.307	0.080	0.000
		Groo. R	1836370.986	2	1.111	0.475	0.000

Table C.3: Results of GEE examining the effect of the top partners' parity (M, N) status on the rates of affiliative interactions

		Affiliative measure	χ^2	df	Estimated marignal means	Std. error	p-value
FULL	**M**	Appr. G	0.204	1	0.444	5.967	0.652
		Appr. R	3.600	1	0.497	5.821	0.058
		Prox. D	5.812	1	0.011	0.227	0.016
		Prox. F	0.625	1	0.657	8.175	0.429
		Groo. G	14639.873	1	0.511	9.806	0.000
		Groo. R *					
	N	Appr. G	0.204	1	0.444	5.967	0.652
		Appr. R	3.600	1	0.376	4.433	0.058
		Prox. D	5.812	1	0.039	0.862	0.016
		Prox. F	0.625	1	0.657	0.175	0.429
		Groo. G	14639.873	1	0.411	9.929	0.000
		Groo. R *					
KIN	**M**	Appr. G	1.376	1	0.517	6.488	0.241
		Appr. R	15.719	1	0.747	5.040	0.000
		Prox. D	8.986	1	0.009	0.321	0.003
		Prox. F	4.081	1	0.794	6.536	0.043
		Groo. G *					
		Groo. R	1.681	1	0.810	6.385	0.195
	N	Appr. G	1.376	1	0.572	7.134	0.241
		Appr. R	15.719	1	0.448	3.072	0.000
		Prox. D	8.986	1	0.075	2.716	0.003
		Prox. F	4.081	1	0.868	7.176	0.043
		Groo. G *					
		Groo. R	1.681	1	0.657	5.283	0.195

* *No statistical values: model was unable to compute the data.*

Table C.4: Results of the GEE examining the effect of the percentage of multiparous partners (% M) on the rates of affiliative interactions

		Affiliative measure	χ^2	df	B	Std. error	p-value
FULL	% M	Appr. G	4.588	1	0.031	0.015	0.032
		Appr. R	15.073	1	0.049	0.013	0.000
		Prox. D	6.223	1	0.058	0.023	0.013
		Prox. F	13.125	1	0.048	0.013	0.000
		Groo. G	0.225	1	-50.945	0.011	0.635
		Groo. R *					
KIN	% M	Appr. G	16.958	1	0.056	0.014	0.000
		Appr. R	48.541	1	0.053	0.008	0.000
		Prox. D	3.205	1	0.070	0.039	0.073
		Prox. F	65.820	1	0.071	0.009	0.000
		Groo. G	0.114	1	-0.008	0.023	0.735
		Groo. R	0.008	1	0.001	0.008	0.930

***** *No statistical values: model was unable to compute the data.*

Table C.5: The results of the GEE examining the effect of the relatedness (R, NR) on the rates of affiliative interactions

		Affiliative measure	χ^2	df	Estimated marignal means	Std. error	p-value
FULL	**R**	Appr. G	0.013	1	0.499	3.435	0.911
		Appr. R	0.164	1	0.559	5.955	0.685
		Prox. D	0.531	1	0.009	0.113	0.466
		Prox. F	.334	1	0.699	7.860	0.334
		Groo. G **	5.585	1	0.401	6.021	0.018
		Groo. R	1.925	1	1.000	12.736	0.165
	NR	Appr. G	0.013	1	0.499	3.435	0.911
		Appr. R	0.164	1	0.537	5.727	0.685
		Prox. D	0.531	1	0.014	0.183	0.466
		Prox. F	.334	1	0.804	7.856	0.334
		Groo. G **	5.585	1	0.897	13.576	0.018
		Groo. R	1.925	1	0.659	8.593	0.165
KIN	**R**	Appr. G **	.036	1	0.587	4.738	0.849
		Appr. R **	.011	1	0.779	5.522	0.918
		Prox. D	2.890	1	0.007	0.158	0.089
		Prox. F *					
		Groo. G **	8.133	1	0.477	5.999	0.004
		Groo. R	5.718	1	1.216	10.319	0.017
	NR	Appr. G **	.036	1	0.580	4.686	0.849
		Appr. R **	.011	1	0.781	5.532	0.918
		Prox. D	2.890	1	0.033	0.767	0.089
		Prox. F *					
		Groo. G **	8.133	1	0.974	12.343	0.004
		Groo. R	5.718	1	0.559	4.924	0.017

** No statistical values: model was unable to compute the data.*

*** Significant interaction between the variable and its covariate*

Table C.6: The results of the GEE examining the effect of the percentage of related partners (% R) on the rates of affiliative interactions

		Affiliative measure	χ^2	df	B	Std. error	p-value
FULL	% R	Appr. G	0.879	1	0.005	0.005	0.348
		Appr. R	1.179	1	0.007	0.007	0.278
		Prox. D	3.970	1	0.017	0.009	0.046
		Prox. F **	1.585	1	0.007	0.006	0.208
		Groo. G **	0.830	1	-0.011	0.012	0.362
		Groo. R	2.459	1	-0.014	0.009	0.117
KIN	% R	Appr. G **	10.252	1	0.029	0.009	0.001
		Appr. R **	4.913	1	0.017	0.008	0.027
		Prox. D	5.903	1	0.057	0.024	0.015
		Prox. F*		1			
		Groo. G **	.017	1	-0.002	0.015	0.897
		Groo. R	6.546	1	-0.024	0.010	0.011

* *No statistical values: model was unable to compute the data.*

** *Significant interaction between the variable and its covariate (refer to Table A.5)*