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The Effect of Potential and Actual Paternity on Positive Male-Infant Behaviour in Ursine Colobus

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The Effect of Potential and Actual Paternity on Positive Male-Infant Behaviour in Ursine

Colobus

by

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Abstract

I aimed to investigate the interplay between paternal care and male infanticide in primates. I examined the effects of potential and actual paternity on positive male infant interactions in wild ursine colobus. I collected behavioural data on 12 adult and sub-adult males. Infants that were conceived when a male was sexually active and present in the infant's group were considered potential offspring of that male. I used DNA from fecal samples to determine paternity for 12 of the 16 infants in my study groups. Positive male-infant behaviour occurred at higher rates between males and potential offspring than males and unlikely offspring, and occurred more with infants than juveniles. These findings support the hypothesis that positive male-infant behaviour reflects paternal care, which possibly evolved in response to male infanticide. Paternity did not predict positive male-infant behaviour, suggesting that females may be successfully confusing paternity through polyandrous mating in the current conditions.

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Dedication

To Afia Rose, for teaching me perspective.

To Krakatoa, for tolerating Iron Man and Villain day after day. To Iron Man, for chasing chickens and living your short life so fearlessly. To Villain, for vigorously practicing your tiny stiff leg displays. To Marx, for relentlessly poking Outlaw. To Outlaw, for grooming Celine, and for knocking some sense into Marx. To Crocodile, for pulling Tobasco and Bridgette onto your stiff leg display. To Steele, for so gently and curiously grabbing Sarkodi's nose.

To the monkeys of Boabeng-Fiema, for giving me data, joy, and inspiration.

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Chapter One: **Overview**

1.1 Introduction

In this thesis I investigate the interplay between paternal care and male infanticide. The evolution of paternal care in primates is tied to male and female reproductive interests, which are often conflicting (Stumpf *et al.* 2011, Arnqvist and Rowe 2005, Lessells 2012). Therefore, when evaluating the conditions under which paternal care is expected to evolve, it is necessary to consider how male reproductive strategies intersect with female reproductive strategies, and how these in turn also influence male reproductive strategies (Stumpf *et al*. 2011, Arnqvist and Rowe 2005, Alonzo and Klug 2012). Sexually selected male infanticide, where males kill unrelated infants to increase their own reproductive potential, is an example of a sexual conflict. In this context, selective pressures favour females to dilute paternity certainty by mating with multiple males; and favour males to distinguish and protect putative offspring (reviewed in Muller and Emery Thompson 2012, Palombit 2012). Thus, male infanticide presents a social context in which we can evaluate the role of sexual conflict in shaping patterns of paternal care.

I begin this literature review by examining paternal care as a hypothesized function of positive male-infant behaviour in primates, such as affiliation and tolerance. In this section I discuss the conditions under which paternal care is expected to evolve in mammals. In the second section, I briefly describe male infanticide and sexual conflict, before exploring how male infanticide can provide conditions that favour paternal care. The discrimination of offspring is important for the evolution of both male infanticide and paternal care, thus in the third section I discuss potential mechanisms by which males might be able to discriminate offspring from non-offspring. In the fourth section I introduce an alternative non-adaptive hypothesis that could

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also explain positive male-infant behaviours in group living primates. As a conclusion to the literature review, I discuss why *Colobus vellerosus*, a species of African colobus monkey, are a suitable species in which to examine these topics, and the hypotheses and predictions that I intend to evaluate in this thesis. Finally, in the penultimate section I highlight the relevance of studying the intersection of paternal care and infanticide in primates.

1.2 Literature review

1.2.1 Paternal care

Paternal care refers to any behaviour by a male that benefits the development, well-being or survival of an offspring or putative offspring that would not be performed in the offspring's absence (also termed 'direct care', Kleiman and Malcolm 1981; Sheldon 2002). The obligate biparental care hypothesis proposes that paternal care evolved to successfully rear offspring (Wright 1990, Hill & Hurtado 1996, van Schaik & Kappeler 1997, Tardif and Bales 1997, Key & Aiello 2000, Achenbach & Snowdon 2002, Tardif *et al*. 2005). In the animal kingdom, paternal care is widespread among birds and fish, where males help incubate and protect eggs and provision offspring (reviewed in Balshine 2012) and occurs occasionally among amphibians, insects and worms (reviewed in Trumbo 2012). Among mammals, the female role in gestation and postpartum lactation reduce the opportunity for fathers to impact their offspring's fitness through caring behaviour (Trivers 1972, Woodroffe and Vincent 1994, Balshine 2012). This is compounded by low paternity certainty due to internal fertilization (Trivers 1972, Woodroffe and Vincent 1994, Balshine 2012). Finally, caring behaviour is expected to involve some fitness cost for males, primarily in terms of missed mating opportunities (Trivers 1972, Woodroffe and Vincent 1994, Balshine 2012). These circumstances favour mammalian males to abandon their

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offspring in favour of mating effort, and thus paternal care is broadly unexpected in mammals (Trivers 1972, Maynard-Smith 1977, Clutton-Brock 1991).

The decrease in future reproductive effort that a sire experiences as the result of caring for a current offspring is specifically termed 'paternal investment', and should not be used interchangeably with the term 'paternal care' (Trivers 1972, Sheldon 2002). Paternal investment is difficult to measure because fitness costs and benefits are difficult to measure in natural settings, especially where the long life histories of primates are concerned. Studies are rarely able to measure and contrast these variables. Further, in some instances, positive male-infant interactions can benefit an offspring and simultaneously increase a male's future reproductive potential with the infant's mother (van Schaik and Paul 1998), as I explain in more detail below. Therefore, where paternal care and mating effort are simultaneously occurring, paternal investment could be non-existent or reduced (van Schaik and Paul 1998). Thus, for the purpose of this thesis, I prefer the broader term paternal care, as in most studies.

Paternal care is observed in less than 10% of mammals, yet it occurs in about 40 % of primate genera, the highest incidence for any single mammalian order (Kleiman and Malcolm 1981). Primate behaviours that are typically considered to reflect paternal care include transporting, feeding, sharing food, grooming, playing, huddling, "babysitting", defending, retrieving, and teaching infants (reviewed in Woodroffe and Vincent 1994, Fernandez-Duque *et al.* 2009, Muller and Emery-Thompson 2012). In cases where paternal care is a reflection of the trade-off between investing in current offspring and seeking other reproductive opportunities, paternal care should be expressed to varying degrees between and within taxa. Therefore, comparisons of the social and ecological correlates of paternal care can help clarify the

conditions under which paternal investment is favoured (Clutton-Brock 1991, Geary 2000). Two primary factors are repeatedly associated with the evolution of paternal care in animals: an opportunity for males to positively affect offspring fitness and a high degree of paternity certainty (Trivers 1972, Maynard Smith 1977, reviewed in Clutton-Brock 1991, Geary 2000, Muller and Emery Thompson 2012).

Paternal care may be adaptive when it contributes to an infant's survival or overall condition. In some primates, male care contributes to infant survival by aiding females with the energetic costs of reproduction. This is likely the case in the cooperatively breeding callitrichids, where the regular birthing of twins and female postpartum oestrous result in high costs of reproduction for females (reviewed in Wright 1990, Fernandez-Duque *et al.* 2012). Putative fathers aid in infant carrying, grooming and food provisioning, and allocare by any individual is associated with increased success of infant survival (Goldzein 1987, Snowdon 1996). The energetic cost of male care is reflected in male weight gain during their mates' pregnancy and weight loss following the birth of offspring (Achenbach and Snowdon 2002, Ziegler *et al.* 2006). In contrast, however, paternal care is absent in several other small-bodied primates that also exhibit high infant to maternal weight ratios (eg. *Galago sp.*, *Microcebus sp.*, *Tarsius sp.*, reviewed by Wright 1990). Further, owl monkey (*Aotus sp.*) and titi monkey (*Callecebus sp.*) males exhibit intense paternal care, including infant carrying and food sharing, despite the comparatively low weight of their single offspring. A similar contrast is seen between siamangs (*Symphalangus syndactylus*) and the phylogenetically closely related white handed gibbons (*Hylobates lar*). Siamang males can carry putative offspring more than females during the infant's second year of life, while in white handed gibbons, which have similar social systems

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and higher infant to maternal weight ratios, males do not carry infants (Lappan 2008, reviewed in Muller and Emery Thompson 2012). Therefore, the energetic demands of raising offspring only partially explain paternal care in primates.

Fathers can also contribute to offspring fitness by protecting infants from conspecifics and predators. In savannah baboons (*Papio cynocephalus*), males selectively defended juvenile offspring in conspecific disputes, and a father's presence in the group during infant development accelerated offspring maturity (Buchan *et al.* 2003, Charpentier *et al.* 2008a). This could be because of the reduced social stress or improved rank acquisition that offspring might obtain when their father is present (Buchan *et al.* 2003, Charpentier *et al.* 2008a). In some primates, fathers may also protect offspring from infanticidal males, which I discuss in section 1.2.2. Protection of putative offspring from predators has been recorded in a handful of primate species (eg. *Cheirogaleus medius, Indri indri, Sanguinus fuscicollis, Aotus azare, Callecebus molloch, Alouatta pigra*, reviewed in Muller and Emery Thompson 2012). However, the role of predation protection is not often emphasized regarding the evolution of paternal care in primates. This is potentially because predation events are rarely recorded in wild primates, limiting available data (Fitchel 2012). Further, researchers may overlook cases where protection of infants from predators is indirect, for example if the presence of a male in the group deters predators (Kleiman and Malcolm 1981, Muller and Emery Thompson 2012). Thus, the importance of predation pressure as a factor impacting the evolution of paternal care is likely undervalued in primate literature and needs investigation.

The second condition for the evolution of paternal care is high paternity certainty. Paternal care might therefore be expected in monogamous, pair-bonded social groups, and in

polygynous, uni-male multi-female groups, and is unexpected in polyandrous or polygynandrous mating systems, due to the respective high and low paternity certainty assumed to be associated with these mating systems. Paternal care is indeed recorded in the monogamously mating Azara's owl monkey (*Aotus azarai* Huck *et al.* 2014), some pair-bonded primate species (eg. *Callimico goeldii* Whitten 1987, *Hapalemur griseus* Wright 1990, *Cheirogaleus medius* Fietz and Dausmann 2003, *Callicebus moloch* Fragaszy *et al.* 1982, *Symphalangus syndactylus* Lappan 2008, *Homo sapiens* Marlowe 2000) and uni-male multi-female groups of mountain gorillas (*Gorilla beringei beringei* Stewart 2001). Further, Huck *et al.* (2014) show that across mammals, more intense paternal care correlates with lower rates of extra-pair copulations. Nonetheless, some pair-bonded primates do not exhibit paternal care (eg. *Avahi laniger, Hylobates sp.* Wright 1990). Furthermore, paternal care has been documented in species where females mate with multiple males (*Semnopithecus entellus* Borries *et al.* 1999, *Papio cynocephalus* Buchan *et al.* 2003, Charpentier *et al.* 2008a, *Macaca mulatta* Langos *et al.* 2013, *Pan troglodytes verus* Lehmann *et al.* 2006, and multi-male groups of *Gorilla beringei beringei* Rosenbaum *et al.* 2011). If these behaviours represent true paternal care, it is expected that males in these species rely on cues to recognize their own offspring, which I discuss in more detail in section 1.2.3. Thus paternity certainty should not be assumed based on mating systems or social organizations. While paternity certainty remains a condition for paternal care, high paternity certainty does not alone guarantee paternal care.

An alternative to the obligate biparental care hypothesis, the 'mating effort' hypothesis proposes that males could care for infants, including offspring, to increase their own reproductive success (Smuts and Gubernick 1992, van Schaik and Paul 1998, Muller and Emery Thompson 2012). This could occur if males increase their current mating opportunity with a

female, or by increasing future mating opportunities with a female by increasing her future

reproductive potential (reviewed in Muller and Emery Thompson 2012). Males can indeed gain

current mating opportunities after caring for a female's infant, both in cases where the infant is

and is not the male's offspring (eg. *Macaca sylvanus* Menard *et al.* 2001). This mechanism

provides a good explanation for male care that is targeted at neither putative nor actual offspring.

The idea of male care as longitudinal mating effort is supported by interspecific comparisons

showing higher birth rates in species with allocare compared to those without (Mitani and Watts

1997, Ross and McLarnon 2000, Hrdy 2009). Although these cases of allocare do not always

include males, the underlying idea supports the suggestion that male care can impact female

reproductive potential. Further, some intraspecific studies show reduced inter-birth intervals

when females receive more aid from males (*Symphalangus syndactylus*, Lappan 2008;

Callitrichidae sp., Bales *et al.* 2000) or from allocare-givers in general (*Cercopithecus aethiops*

sabaeus, Fairbanks 1990; *Saguinus oedipus*, Bardi *et al.* 2001). In addition, in some species

males might care for infants as both a courtship strategy and paternal care (van Schaik and Paul

1998). This may be the case in owl monkeys, where males are observed to care for non-offspring

after taking over a group and then later care for offspring (Fernandez-Duque *et al.* 2008). In

humans, Xhosa men (South Africa) provide more care to biological children of current mates

than biological offspring residing with past mates, suggesting some portion of paternal care is

motivated by mating effort (Anderson *et al.* 1999). It is also plausible that behaviours that

appear to act as paternal effort are actually benefiting the female more directly than the offspring,

for example by allowing the female to wean infants sooner and thus increase her lifetime

reproductive success (van Schaik and Paul 1998). Although I will not focus on mating effort in

this thesis, it is important to acknowledge that paternal care and mating effort are not necessarily mutually exclusive (van Schaik and Paul 1998, Muller and Emery Thompson 2012).

It is clear that the relationship between paternity certainty and paternal care is complex, and the expression of paternal care is a reflection of the interaction between paternity certainty, fitness costs to males, and fitness benefits to infants. In the next section, I will review how infanticide by males presents a scenario that intersects these three variables in a way that could select for paternal care.

1.2.2 Male infanticide

Hrdy and Hausfater (1984) define infanticide as "any behaviour that makes a direct and significant contribution to the immediate death of an embryo or newly hatched or born member of the perpetrators' own species". The killing of infants by conspecifics is a behaviour most prevalently recorded in three mammalian taxa: primates, carnivores, and rodents (reviewed by van Schaik 2000a). Observations of male infanticide in many primate species support the conditions of the sexual selection hypothesis of infanticide, in which Hrdy (1979) posited that the killing of an unrelated infant by a male could induce the affected mother back into ovarian cycling, and allow the male increased reproductive opportunity if he subsequently gained access to the female (reviewed by van Schaik 2000b; Palombit 2012). Thus, infanticide by males is an example of sexual conflict, where the interests of one sex result in fitness costs for the other, because females loose offspring in which they have heavily invested. The strategy of one sex becomes a selection pressure for counter strategies in the other sex, and therefore as both sexes evolve to maximize fitness, an 'arms race' arises (Arnqvist and Rowe 2005, Clarke *et al.* 2009, Palombit 2010, Stumpf *et al.* 2011). For example, infanticide can only be a successful male

reproductive strategy if males do not kill their own offspring, resulting in a conflict of interest between the sexes over the disclosure of paternity information to males (Stumpf *et al.* 2005, Ostner *et al.* 2006, Palombit 2010, Stumpf *et al.* 2011). To avoid killing their own offspring, males need to establish paternity certainty. Simultaneously, females should mate polyandrously so that potentially infanticidal males have a chance of paternity and do not kill the infant (Hrdy 1979, Wolff and MacDonald 2004). Indeed, polyandrous mating is well documented in primates where male infanticide is prevalent (van Schaik *et al.* 2000). Nonetheless, male infanticide must coevolve alongside traits that enable males to discriminate between probable offspring and non-offspring. Thus high paternity certainty is a condition that is important for the evolution of both paternal care and male infanticide.

Infanticide is expected to evolve in species where male-male competition for access to mates is high. As such, infanticide is prevalent in species where males maintain tenure in a group for a relatively short period compared to the length of female gestation and lactation (Hrdy 1979, van Schaik 2000a). Since males are likely to hold reproductive tenure in a group only once in their lifetime, current offspring hold high reproductive value for a male because chances of future reproduction are somewhat low (van Schaik 2000b). The most common context of infanticide is in the case of the disappearance or incapacitation of putative sires, suggesting that the role of a defending male has a strong impact on offspring survival (reviewed in van Schaik 2000b, Paul *et al.* 2000). Therefore, male defence of offspring against infanticide, a form of paternal care, might confer reproductive benefits to a male that outweigh the costs of lost mating opportunity, if paternity certainty is sufficiently high.

Thus, while seemingly opposite, infanticide and paternal care can occur within a single species and can be understood as two sides of the same coin (Paul *et al.* 2000). The suggestion

that male infanticide can select for paternal care is supported by studies showing that putative

sires exhibit protective behaviour in the context of increased infanticide threat. For example,

Hanuman langur males differentially defend putative offspring from infanticidal attacks (Borries

*et al.*1999). Males who have been defeated by an immigrant male may stay in their groups and

defend their vulnerable offspring until they can be weaned (*Thereopithecus gelada*, Dunbar

1984; *Semnopithecus entellus*, Borries *et al.* 2001; *Colobus vellerosus*, Saj and Sicotte 2005,

Teichroeb and Sicotte 2008a). Similarly, in some species males have been observed to interact

infrequently with infants during times of group stability, but increase affiliative interaction with

infants in the presence of a potentially infanticidal immigrant male (*P. cynocephalus ursinus*,

Busse and Hamilton 1981; *Cercocebus galeritus,* Busse and Gordon 1984; *Cercocebus atys*,

Gust 1994). Playback experiments show that likely fathers respond to distress calls simulating

potentially infanticidal attacks on mothers and infants more than other males (*P. cynocephalus*

ursinus, Palombit *et al.* 1997); likely fathers were more likely to respond to strange male calls in

the presence of vulnerable infants (*Allouatta pigra,* Kitchen 2004); and likely fathers were able

to differentiate between potentially infanticidal all-male-band calls and neighbouring male calls

(*Presbytis thomasi*, Wich *et al.* 2004).

A particularly well-studied example of anti-infanticidal paternal care is shown in

savannah baboons where lactating females form bonds, or 'friendships' with protective males

(Smuts 1985, Palombit 2009, Moscovice *et al.* 2010). This is best studied in chacma baboons,

where infanticide is an important source of infant mortality. Here, male-female friendships are

established after consortships and mating, and are primarily maintained by the female through

proximity and grooming. Male-female interactions intensify following the birth of an infant,

males are often observed to hold or carry these infants especially during agonistic encounters

with immigrant males, and friendships tend to terminate if infants die (Busse and Hamilton 1981, Palombit *et al.* 1997, Palombit 2009, Moscovice *et al.* 2011). These observations, in addition to the playback experiments mentioned above, suggest that a primary benefit of these friendships for males and females is the protection of putative offspring from infanticidal males.

All together, these observational and experimental studies show that behaviour of putative fathers changes in the context of increased threat of infanticide. This supports the idea that protection from infanticide can be a critical factor in explaining paternal care and male-infant interactions in primates.

1.2.3 Mechanisms of kin recognition

Male traits that enhance their ability to deduce paternity should be selected for in species where infanticide and/or paternal care are advantageous to the male (Ostner *et al.* 2006, Widdig 2007). Two potential mechanisms have been suggested as to how males could discriminate offspring: phenotypic matching and the use of behavioural cues. The hypothesis of phenotypic matching suggests that primates are able to evaluate relatedness based on how well their own phenotype matches that of another individual. Primates might use clues from odour, appearance, personality, and/or vocalizations (reviewed in Widdig 2007). Evidence for this mechanism has been put forward primarily in rodents and birds, where individuals use odour and vocalizations to differentiate kin (reviewed in Hauber and Sherman 2001, Mateo and Johnston 2003, Widdig 2007; McDonald and Wright 2011). Evidence to suggest that primate males are able to identify kin based on phenotypic traits remains sparse. Some recent studies show that phenotypic cues differ between individuals in a way that could convey relatedness. Humans were able to detect maternal and paternal kinship by observing faces of rhesus macaques (Kazem and Widdig 2013);

swiss mice differentiated age and sex differences in baboon body odours (Célérier *et al.* 2010); and semiochemical profiles of male ring-tailed lemurs reflect heterozygosity and genetic distance during the mating season (Charpentier *et al.* 2008b). Nonetheless, evidence that primates use phenotypic cues to differentiate kin is largely lacking. An experiment demonstrating phenotypic matching in captive chimpanzees (Parr and de Waal 1999) was later shown to be an artefact of the study design (Vokey *et al.* 2004, discussed in Rendall 2004). While some primates studies exclude a role for phenotypic matching (eg. *Mandrillus sphinx* Charpentier 2007, *Colobus vellerosus* Wikberg *et al.* 2014), others do not (eg. *Papio cynocephalus* Alberts 1999, *Macaca mulatta*, Langos *et al.* 2013). Thus it remains possible that males could use phenotypic cues to distinguish offspring.

The hypothesis that primate males use behavioural cues related to the timing and quality of mating with a female to evaluate the likelihood of paternity is better supported than phenotypic matching. Buchan et al. (2003) found that wild savannah baboon males selectively supported biological offspring during disputes between juveniles, and that the proportion of a female's consort time that a male monopolized during the time of conception was a significant predictor of this male behaviour. Hanuman langurs males that were resident in a group at the time of the infant's conception were likely to defend infants against attacks from strange males, and males seemed to only take copulations with fertile females, not already pregnant females, as clues for paternity (Borries *et al.* 1999). In addition, Japanese macaque males were eight times more likely to attack infants if they had not previously mated with the mother (Soltis *et al.* 2000). Manipulative experiments in rodents have provided insight into the fine grain details of how males might use cues from mating behaviour. House mouse males are cued by the timing of mating, where male infanticidal behaviour can be 'switched' on and off by manipulating light

and dark cycles to affect a male's perception of time since mating with the female (Perrigio *et al.* 1990). Thus, there is support for the hypothesis that males in polyandrous mating primate species could use behavioural cues to predict paternity.

1.2.4 The non-adaptive hypothesis

The possibility that positive male-infant interactions do not have an adaptive importance must be considered. For example, within literature examining primate male-infant relationships, Buchan *et al.* (2003) test the idea that baboon males intervene in juvenile disputes randomly as a result of proximity. Lehmann *et al.* (2006) controlled for the possibility that chimpanzee males chose play partners at random from available partners by standardizing measures of play behaviour by infant availability. Non-adaptive explanations for interactions exist in other areas of primate literature. For example, the 'independent attraction hypothesis' has been applied as a null hypothesis to explain associations between individuals in chimpanzee fission-fusion communities. This hypothesis suggests that two individuals may appear to be associated but only because of a common attraction to a location, such as a fruiting tree (Newton-Fisher 1999). Similarly, Harcourt (1979) suggests that female-female proximity in mountain gorillas is a result of a common attraction to the silverback male. In infant handling literature the idea that adult females interact with non-offspring infants as by-product of selection for good mothering also serves as a 'non-adaptive' hypothesis (e.g. *Macaca radiata*, Silk 1999).

Expanding on the suggestions of Buchan *et al.* (2003) and Lehmann *et al.* (2006), I propose a more general hypothesis that males could interact with infants as a by-product of group living, which could be motivated by other selective pressures. In this case, males are

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predisposed to be in proximity to infants. A propensity for social interaction could be a misdirected product of selective pressures for social behaviour in other contexts, such as male-female consorting. In theory, in these scenarios the interaction between the infant and the male represents neither a cost nor a benefit for either participant. In studies that do not attempt to measure the costs or benefits of male-infant interactions, one approach to resolving this issue is to eliminate the null hypothesis by showing that male-infant interactions are not occurring at random. Non-adaptive hypotheses need to be investigated before we can discuss potential factors underlying male-infant interactions.

1.3 Thesis aims

1.3.1 Paternal care in Colobus vellerosus

In *C. vellerosus*, infanticide occurs as a male reproductive strategy in association with male immigration and group takeovers (Teichroeb and Sicotte 2008a). Infanticide accounted for 38.5% of infant mortality during a five year study period, thus infanticide is likely a strong selective pressure (Teichroeb and Sicotte 2008a). *C. vellerosus* females mate polyandrously (Saj and Sicotte 2005). Resident males have been observed attempting to defend infants from newly immigrated infanticidal males, where protective males were suspected to be sires (Saj and Sicotte 2005, Teichroeb and Sicotte 2008a, Teichroeb and Sicotte 2008b). Positive male-infant affiliative relationships occurring outside of this context are poorly documented in *C. vellerosus*, leaving the impression that they occur rarely. Using observational data collected on wild male colobus monkeys and genetic paternity, I aim to describe positive relationships between males and infants in *C. vellerosus* and address how these relationships vary in association with male

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potential and actual sireship of infants. In doing so, I will address male infanticide and female

counterstrategies to infanticide as factors shaping the social dynamics of this species.

1.3.2 Hypotheses and predictions

This thesis involves some limitations and assumptions. First, given the high proportion of

infant mortality attributed to infanticide in *C. vellerosus*, I assume that the primary opportunity

for males to invest in offspring is when they can defend infants from attacking males. However,

similar patterns of paternal care might arise in response to both infanticide and predation threat.

Dr. Sicotte and her students have never recorded a predation event when observing the colobus at

Boabeng-Fiema Monkey Sanctuary, and currently predators are extirpated from the forest. This

does not exclude the possibility that paternal care evolved under conditions where predation was

important, however it does make it difficult to compare infanticide and predation as selective

pressures. Therefore, while I acknowledge the possibility that predation played a role in the

evolution of positive male-infant behaviour in this species, I focus on male infanticide as an

explanatory framework and do not endeavor to examine the potential effect of predation.

Second, the time frame over which the data for this thesis was collected is relatively short

compared to the estimated lifespan of a *C. vellerosus* individual (estimated at 20 years, Dr.

Sicotte personal communication). Therefore I make no attempt to measure the cost or benefit that

positive interactions might have for male and infant fitness. Instead I assume that positive

interactions hold some proximate benefit(s) for the participants, such as reduced social stress or

foraging benefits from associating with males, or a higher probability of successful defence by a

male against an attack as a result of maintained proximity to infants (Lehmann *et al.* 2006,

Charpentier *et al.* 2008a, Rosenbaum *et al.* 2011).

Third, I expect that male traits that enhance their ability to deduce paternity should be favoured by selection but I will not investigate the actual mechanism of kin recognition. I assume that if it occurs, it will be an outcome of behavioural cues (section1.2.3), which may be as broad as presence in the group at the time of an infant's conception because *C. vellerosus* females do not show external signs of oestrous. I will use this broad presence/absence cue to define 'potential' and 'unlikely' offspring.

Finally, I will include sub-adult natal males in the models comparing patterns of positive behaviours with males and infants. Natal males could be the siblings of infants due to some level of female philopatry, but likely with a lower potential degree of relatedness (likely half sibship or less) than sire-offspring dyads because of the short tenure periods of reproductive males. I describe these definitions in more detail in section 2.5. With these assumptions in mind, I test the following hypotheses:

The non-adaptive hypothesis

Interactions between males and infants are a non-adaptive by-product of social living and have no cost and no benefit for male and infant fitness. Under this hypothesis, I predict that males will interact with infants at an expected rate based on the proportion of infants available in a group compared to individuals in other age/sex categories.

The paternal care hypothesis

Paternal care is selected for because infant death due to male infanticide is costly for male sires, males have some paternity confidence, and paternal care benefits male fitness by increasing

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infant fitness. Paternal care occurs in the form of positive male-infant behaviours. Under this hypothesis, I predict:

a. males will bias positive behaviour towards infants who are potential offspring compared to unlikely offspring, and compared to potential siblings.

b. males bias positive behaviour towards infants who are still vulnerable to infanticide (not yet weaned) but have increasing independence from their mother, who would otherwise be the primary protector of the infant.

However, *C.vellerosus* females mate polyandrously and this could confuse paternity. Thus:

a. if males bias positive behaviour toward offspring, it will suggest that males are successfully distinguishing offspring from non-offspring and female polyandrous mating is not broadly confusing paternity.

b. if males are directing positive interactions toward potential offspring but not discriminating genetic offspring, it will suggest that females are broadly confusing paternity among males.

1.4 Relevance

The frequency of year round associations between male and female primates is strikingly high, with over 70% of species showing associations compared with less than 15% of species in most mammalian orders (Wilson 1975, Wrangham 1987, van Schaik and Kappeler 1997). Hypotheses to explain the evolution of primate social systems initially focused on ecological reasoning, such as predation and resource availability (Wrangham 1980, Terborgh and Janson 1986, van Schaik 1989). More recently the role of social factors, such as conspecific threat and

male coercion, as main, or additional factors influencing social systems have received more attention (van Schaik and Kapeller 1997, Sterck *et al.* 1997, Treves 1998, Nunn and van Schaik 2000, reviewed in Palombit 2012). Infanticide pressure has been suggested to explain group living for at least some primate species (van Schaik and Kappeler 1997, Janson 2000, Palombit 2000). Support for the hypothesis that male-female associations evolved to reduce infanticide risk is substantial, including van Schaik and Kappeler's (1997) phylogenetic study showing that the evolution of male-female associations coevolved alongside the evolution of female-infant associations (as opposed to infant parking), and ample evidence that infanticide risk intensifies dramatically when putative fathers are ousted (reviewed in Paul *et al.* 2000, Palombit 2012). An important avenue that lacks investigation, however, is how positive male-infant behaviours, including infanticide defence, vary with respect to potential and actual paternity within polyandrous mating species (Paul *et al.* 2000). Despite advances in genetic methods to resolve paternity using non-invasively collected samples, only a handful of studies have successfully applied these methods (e.g. Borries *et al.* 1999, Buchan *et al.* 2003, Lehmann *et al.* 2006, Charpentier *et al.* 2008a). In addition, most research on the evolution of paternal care in mammals focuses on between species comparisons. More studies focused on variation in male-infant behaviour within a species are needed to understand the ability for males to facultatively express paternal care in relation to proximate conditions, including paternity certainty (as has been done in some bird species, reviewed in Geary 2000). Male paternity certainty will vary depending on both male and female reproductive strategies; therefore studies on paternal care in polyandrous mating species make important contributions to our understanding of intersexual selection as a selective force in the social evolution of primates.

Studies on primate behaviour are informative when understanding the origins of human

behavior and for society's perception of the role of the father. Paternal care has been observed in every human culture studied as of the year 2000 (Marlowe 2000). The degree and type of paternal care varies with social and ecological factors, such as the society's subsistence mode and mating system (Marlowe 2000). Obligate bi-parental care has been implicated in explaining the evolution of human monogamy, however mate guarding likely also plays a role (Marlowe 2000, Hawkes 2004). Understanding the conditions for paternal care in different mating systems of non-human primates will lead to a better understanding of the evolution paternal care in humans.

On a more proximate level, studies on non-human primate fathers affect the perception of paternal roles in humans. Fathers in North America and Europe have become increasingly involved in direct care of their children over recent decades (Lamb 1987, Hewlett 1992). This has generated public and academic interest in the 'natural' role of the father, including the range of paternal behaviour in hunter-gatherer to highly industrial human societies, and in the evolutionary and biological factors impacting paternal behaviour in non-human primates (Hewlett 1992, Geary 2000). The perception of males as fathers influences the fields of pediatrics and child psychology, and has resulted in an array public policy changes (Hewlett 1992, Geary 2000, Lamb 2010). My study will contribute to literature on the range of male-infant interactions among primates, and therefore deepen our understanding of the diversity of 'natural' paternal roles in primates.

Chapter Two: **Methods**

2.1 Study site

Boabeng-Fiema Monkey Sanctuary (BFMS) is comprised of a 192ha (1.9km^2) fragment

of dry semi-deciduous forest in the Brong-Ahafo region of Ghana, West Africa. It is surrounded

mainly by farmland (Fargey 1992), but connected to other small fragments of forest that range

from 3 to 55 ha in size and are connected by a narrow strip of riparian forest. The rainy season

occurs annually between March-October and the dry season occurs between November and

February (Fargey 1992). Two diurnal primate species, *Colobus vellerosus* and *Cercopithecus*

campbelli lowei, live in this forest and are both protected from hunting through local religious

taboo, and the colobus are also protected under national Ghanaian law (Saj *et al*. 2005; Saj &

Sicotte 2013). The main forest fragment hosts a community-based eco-tourism initiative. Tour

groups are guided on walking tours to see both species of monkeys.

2.2 Study species

This study was conducted on wild white-thighed colobus, or ursine colobus, *Colobus*

vellerosus, one of the five species of black and white colobus (Saj & Sicotte 2013). *C. vellerosus*

are endemic to West Africa (Saj and Sicotte 2013). Dr. Pascale Sicotte has supervised ongoing

research on the behaviour and ecology of *C. vellerosus* at BFMS since the year 2000. A 2007

survey reported 275 individuals distributed in 19 groups at this site (Kankam and Sicotte 2013).

Although individuals may move between forest fragments, the population living among the

network of fragments at BFMS can be considered a closed population.

White-thighed colobus are diurnal, arboreal and primarily folivorous with an annual diet comprised of 74% young and mature leaves (Saj *et al.* 2005). This species lives in social groups that can be uni-male/multi-female or multi-male/multi-female, with some all-male bands. Previous groups were observed to range in size from 9-38 individuals (Saj *et al.* 2005; Wong and Sicotte 2006). Groups are primarily female philopatric with male-biased dispersal, although facultative female dispersal does occur (Teichroeb *et al.* 2009; Teichroeb *et al.* 2011; Wikberg *et al.* 2012). Females experience scramble food competition (Teichroeb & Sicotte 2009), exhibit low rates of aggression, and lack formal linear dominance hierarchies (Wikberg *et al.* 2013).

Male takeovers of groups occur through male incursions, where extra-group males (from other groups, solitary males or males from AMBs) attack or interact with bisexual groups and try to evict current resident males (Sicotte and MacIntosh 2004; Saj and Sicotte 2005; Teichroeb *et al.* 2011). Both male incursions and intergroup encounters are typically aggressive and can result in targeted aggression toward infants (Sicotte and MacIntosh 2004; Saj and Sicotte 2005; Teichroeb *et al.* 2011). Targeted aggression toward infants and death of infants by unrelated males has been repetitively observed following takeover events and follow the predictions of the sexual selection hypothesis for infanticide (Saj and Sicotte 2005; Teichroeb and Sicotte 2008a). The relative rate of infant death due to infanticide has been estimated at 38.5% in the study population between 2000 and 2005 (Teichroeb and Sicotte 2008a; Teichroeb *et al.* 2012). Infanticide has been observed to occur up to 4 months after a new male has immigrated to a new group (Teichroeb and Sicotte 2008a).

Behaviours to counteract infanticide observed in this species include female coalitions (although they do not seem to be effective; Saj and Sicotte 2005; Teichroeb and Sicotte 2008a), facultative female dispersal (Teichroeb *et al.* 2009; Sicotte *et al.* accepted), and resident males

protecting infants by attacking or chasing away new males or positioning themselves between new males and infants (Saj and Sicotte 2005, Teichroeb and Sicotte 2008a, Teichroeb and Sicotte 2008b). Further, females are known to mate polyandrously within multi-male groups and extra-group mating by females has been seen in both multi-male and uni-male groups (Sicotte and MacIntosh 2004; Teichroeb *et al.* 2005; personal observation), and it is possible that both polyandrous mating and extra-group mating might function to counteract infanticide.

2.2.1 Age-sex categories and identification of individuals

C.vellerosus exhibit variation in the white pelage on the underside of the tail base that is used to determine sex of individuals. Females have white pelage that is broken at the perineum and males have a white pelage that is continuous across the perineum (Saj and Sicotte 2013). For individuals whose birth dates are not known, estimation of developmental stages and age categories is determined based on their size and appearance relative to individuals whose birth dates are known. For this study, individuals were classified in the following categories (as per Teichroeb *et al*. 2009, Teichroeb *et al.* 2011, Wikberg *et al.* 2012):

i)   Infants: from birth until age of weaning, which typically occurs between 60 and 77 weeks of age (MacDonald 2011). Birth dates are used to determine age. I considered individuals weaned from the last time seen suckling if they are not witnessed suckling again until the end of my study period, or for at least a two-week time period before the end of my study.

ii) Juveniles: weaned individuals up until age 3

iii) Sub-adults: ages 3-5 for females, and ages 3-7 for males. Sub-adults are smaller and have a less sleek coat than adults.

iv) Adults: females age >5 and males age >7. Adults are full body size and have a sleeker coat than sub-adults.

Individuals in my study groups were identified based on variation in eyebrow shape, black-cap and white-ruff shape, facial features, distinct scars, and tail characteristics in addition to age and sex. I have included some photos illustrating variation in eyebrows and black caps in Figure 2.1. I was trained in monkey identification by Josie Vayro and Angela Crotty, and was able to confidently identify all individuals in my study groups and therefore also identify when new monkeys approached or immigrated into my groups. I was also able to identify neighbouring groups by recognizing a number of key individuals in those groups. Throughout my fieldwork, our long-term local research assistants, Robert Korentang and Charles Kudom, who also have a good knowledge of the individuals in our research groups, supported me.
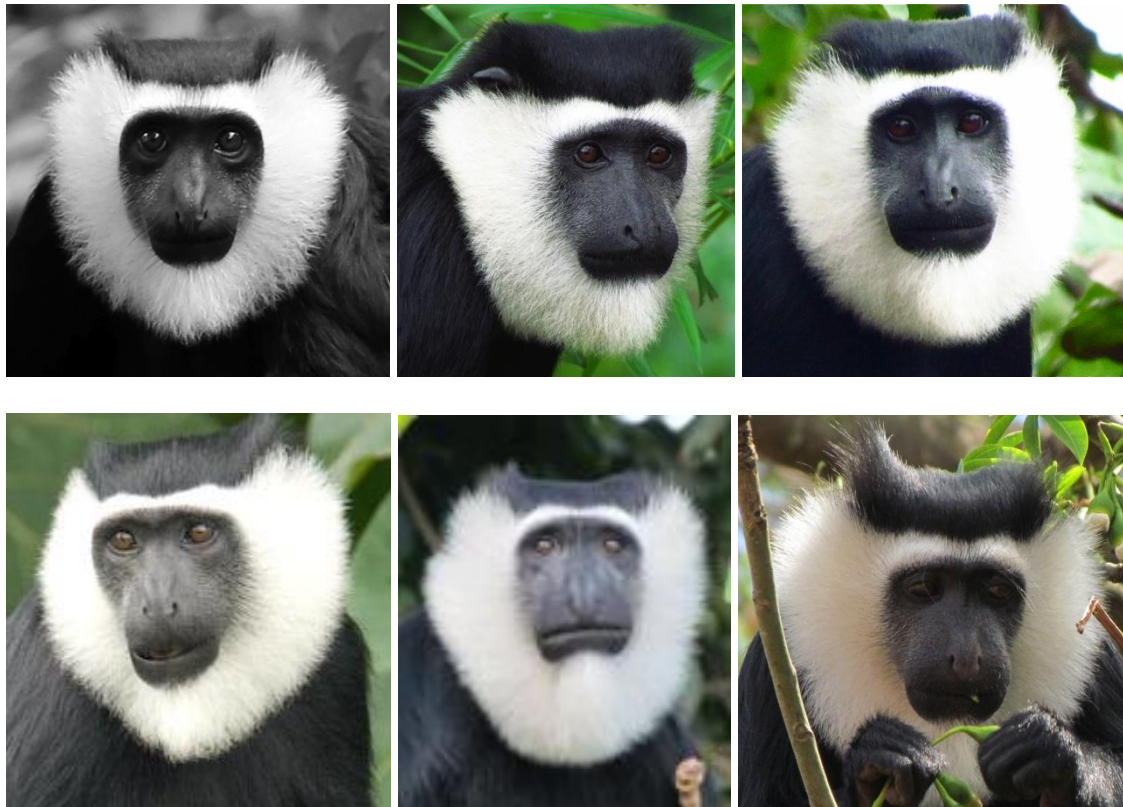
Figure 2.1. Photos exemplifying variation in eyebrow, black-cap and white-ruff shapes used for identification of monkeys. Photos are taken by Stephanie Fox and Patricia Homonylo.

2.2.2 Study groups and study subjects

I followed four study groups: redtail group (RT), splinter group (SP), wawa group (WW), and winter group (WT). Groups WT and WW were uni-male/multi-female groups where male tenure was stable during my field season. Groups RT and SP were multi-male/multi-female groups where male tenure changed across the course of my field season. The demographic composition of the study groups is listed in Table 2.1, where changes in demographic composition that occurred during my field season (May-November 2013) are detailed in Appendix A1. The total amount of time that I spent following each group (contact time) is listed per month in Table 2.2. Focal data was collected on all adult (N=7) and sub-adult males (N=5)

present in my study groups (Table 2.3). A total of 16 infants were available to interact with males across the study season.

I had some knowledge of long-term male tenure and kin relationships through observation of mother-infant dyads, genetic analyses completed by Dr. E. Wikberg, and long-term demographic contributed by Dr. E. Wikberg, J.Vayro, E. Potvin-Rosselet and A. Crotty. In addition, J.Vayro, E. Potvin-Rosselet and A.Crotty followed my study groups from June 2012 to April 2013, and therefore detailed demographic data and mating data was available for this time frame.

Table 2.1. Demographic composition of study groups

Group	Adult males*	Adult females	Subadult males	Subadult females	Juvenile males	Juvenile females	Infant males	Infant females
RT	1-2	5	3	0	4-5	3-4	1-2	1-3
SP	2-3	5	1-2	0-1	1-2	1-3	1-2	0-2
WT	1	3	0	0	0	0	0-1	1
WW	1	4	0	2	2	0-1	1-2	1-2

*A range indicates variation across the observation season. See appendix A1 for more detail.

Table 2.2. Total contact hours per group per month

Group	Jun	Jul	Aug	Sep	Oct	Nov	Total hours per group
RT	35.81	36.09	39.01	32.20	38.44	4.33	185.87
SP	38.51	46.84	45.07	36.04	32.69	8.38	207.53
WT	30.55	45.94	42.36	28.51	34.50	8.34	190.20
WW	28.82	45.20	37.28	39.64	36.96	4.31	192.22
Total hours per month	133.68	174.08	163.72	136.40	142.58	25.37	775.83

Table 2.3. Study subjects

ID	Group	Age class	Immigrant or natal	Dominance Status	Focal hours
KR	WT	adult	immigrant	alpha	31.44
OW	WW	adult	immigrant	alpha	29.56
CC	RT	adult	immigrant	alpha	18.09
MS	SP	adult	immigrant	alpha	25.08
KD	SP	adult	immigrant	non-alpha	20.51
TE	SP	adult	immigrant	non-alpha	11.28
JK*	RT	adult	immigrant	non-alpha	14.69
JK*	SP	adult	immigrant	non-alpha	1.80
MD*	SP	sub-adult	immigrant	non-alpha	15.71
MD*	WT	sub-adult	immigrant	non-alpha	1.00
JS	RT	sub-adult	natal	non-alpha	14.57
PE	RT	sub-adult	natal	non-alpha	18.68
SR	RT	sub-adult	natal	non-alpha	17.31
SB	SP	sub-adult	natal	non-alpha	6.83
				Total focal hours:	226.55

*MD and JK moved briefly between groups during my field season. I have listed a new line for each group in which they were observed.

2.3 Data collection

Collection of behavioural data and fecal samples (for genetic analyses) took place between May 9th and November 3rd 2013. I primarily dedicated observation during May and early June to learning identification of individual monkeys and data collection techniques from J. Vayro, A. Crotty and Dr. P. Sicotte. This included learning what traits to use to identify monkeys, how to collect focal follow, group scan and *ad libitum* data, and learning to identify the behaviours from the ethogram (Appendix B). Mating behaviour, changes in group composition and some weaning behaviours were noted *ad-libitum* as of May 9. From June 3rd until November 3rd behavioral data, ranging data, phenology data and fecal samples were collected for my study groups on a regular schedule that is detailed below. Ranging data was also collected from neighboring groups whose ranges met the periphery of the study groups' ranges to determine group overlap areas.

2.3.1 Behavioural data

I followed my study groups for five days per week, following each group for 4-hour periods every other day, alternating between 7-11am and 12-4pm. I used continuous focal animal sampling to record the behaviour of a focal male during a 10-minute period (Altmann 1974) using 12x42 Nikon Monarch binoculars when needed. In real time, I dictated the focal male's behaviour, interactions and the ID's of the receivers and initiators of interactions and my assistant A. Robas typed all dictation into the program "Behaviour" (Syscan International Inc. Montreal Quebec) on a PSION handheld digital device. A. Robas typed behaviours using a coding system; codes for all behaviours recorded are listed with the ethogram in Appendix B, which was established and built on by previous students supervised by Dr. Sicotte as well as by

myself. I collected point samples every 2.5 minutes during a 10-minute focal, including at the start, providing 5 point samples per focal. This provided additional instantaneous data recording proximities and state behaviour, which will mainly contribute to long-term data records. I used a digital watch to time focal follows, which was programmed to beep every 2.5 minutes to prompt point samples.

Focal subjects were chosen in a priority sequence in order to obtain the most data on the individuals of highest interest. Males were divided into three groups for focal samples: alpha males were sampled once an hour immediately following the group scan; immigrant non-alpha males were second priority and sampled following the alpha male, with the aim of obtaining one focal per hour each; and natal males were sampled as third priority if time permitted. Focal follows of immigrant non-alpha males and natal males were chosen by rotating through a set order; if the focal animal next in line was not available we moved onto the next male and returned back to the skipped male when he became available. Assistants RK and CK looked for the next focal male while I concentrated on the current focal, and the next male was skipped if RK and CK could not find him by the end of the current focal. Focals that followed this priority sequence were deemed 'scheduled focals', and will be used to determine rates of interactions in my analysis. I completed a maximum of one scheduled focal per hour per male. The total focal time that I observed per male is included in **Error! Reference source not found.**. The median ocal time per male in a single group was 16.51 hours, but the focal hours per male ranged widely between 1 and 31.44 hours as a result of the prioritized focal system, immigration, emigration, and deaths. It is worth noting that the intention of this non-random sampling method was initially to collect more data on males who we were more interested in at the outset of this project (alpha males). However, this lead to less data on males that later turned out to be of more interest. Thus

in retrospect, a randomized sampling of males would have been more beneficial.

I used 'opportunistic focals' to record male-infant interactions that occurred outside of scheduled focals. Opportunistic focals were never prioritized over scheduled focals and therefore were mainly used in one-male groups when I had extra time after completing scheduled focals on all available males. Opportunistic focals did not contribute to the rates used in my analysis, but were a useful means of recording interactions and their context in more detail than would be provided in *ad libitum* data collection, so that interactions could be used anecdotally to note the full range of behaviours witnessed during my season and their contexts. Opportunistic focals did not have a pre-determined duration. *Ad-libitum* data collection was used to note the presence of intergroup encounters and incursions by extra group males, occurrences of nursing and weaning behaviour used to determine infant or juvenile status of immatures (to contribute to MA student Angela Crotty's data collection), all observed occurrences of mating behaviour, male-male aggressive and submissive behaviour, male-infant interactions that occurred outside of scheduled and opportunistic focals, and any other rare and noteworthy events.

I performed a group-scan once every hour, where I recorded the state behaviour and individuals in proximity for all adult and sub-adult individuals that could be found. I alternated starting group-scans from left to right and right to left, and a 5 second delay was used before scanning an individual to avoid bias toward attention-grabbing behaviours such as travelling. Because the intention of the group scan was primarily to establish and track group composition, scans were not restricted to a set duration so as many individuals as possible could be found, however a 15-minute maximum was used as a rule of thumb. While group scans primarily allowed me to track group composition, they also provided instantaneous data on proximities and state behaviours that will contribute to long-term data records.

2.3.2 Phenology data

My assistant A. Robas and our local collaborator Anthony Dassah, who was previously an employee of the Ghana Wildlife Division, collected phenology data on a biweekly basis. Mr. Dassah has aided Dr. Sicotte's students with phenology data collection for over a decade and ensures consistency between researchers. Phenology routes were chosen previously by J. Teichroeb, T. Saj and E. Wikberg by randomly choosing 3-5 mapped trees per large tree species (depending on availability per study area) within the study groups' home ranges, for a total of 162 trees surveyed. Data was collected along two routes allowing each transect to be surveyed once a month. Mr. Dassah and A.Robas walked phenology routes between 8-12 am and always in the same order to reduce variation in lighting that might alter visibility. For each tree, flower, fruit and seedpod availability were each recorded as a raw count and leaf availability was recorded as bare, mid-full, or full. Next, young leaf, mature leaf, flower bud, flower, unripe fruit, ripe fruit, unripe seed pod, and ripe seed pod availability was recorded on a scale of 0 to 4 where 0=0%, 1=1-25%, 2=25-50%, 3=50-75%, and 4=75-100%. Phenology data has been collected since 2000 at BFMS. Data collected during my field season was not directly related to my research question but will contribute to long-term records.

2.3.3 Fecal sample collection

I opportunistically collected fecal samples from all members of my study groups for whom genetic information was not obtained in previous years. I pre-prepared vials with 5 mL of RNAlater (QIAGEN), a reagent that stabilizes cellular RNA and DNA until the sample is processed. To collect a sample, first the individual was identified, primarily by myself but occasionally by an assistant, and the individual monkey was monitored so we could be certain to

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collect the correct feces once it had fallen. The collector was equipped with a hat, mask and sterile gloves before pulling sterile sticks and the collection vial out of the collection kit (Figure 2.2). One to two milliliters of feces were picked up using the sterile sticks, placed inside the vial with care not to touch anything else, and then broken up inside the vial using the sticks. Once the vial was closed and sealed using paraffin wax the vial was labeled with the date, time of collection, sample number, individual ID code, and the initials of the person who identified and collected the sample. During my field season I collected a total of 111 fecal samples from 30 different individuals with the help of A. Robas, R. Korenteng, C. Kudom and M. Schlumpf. I aimed to obtain 3-5 samples per individual, however this was not always possible. A. Crotty collected an additional 47 samples from 13 individuals during May-November 2014 from new infants, new immigrant individuals, or individuals for whom I was not able to obtain enough samples. Samples were refrigerated until they could be shipped to Dr. Nelson Ting's Molecular Anthropology Laboratory at the University of Oregon where they were stored in a -20°C freezer.

Figure 2.2. Photo illustrating fecal collection procedure.

2.3.4 DNA extraction and STR genotyping

I processed the fecal samples for nDNA analysis at Dr. Nelson Ting's laboratory at the University of Oregon between September and December 2014. In addition to being guided and supported by Dr. Ting, I was trained on extraction and amplification protocols by Dr. Ting's PhD student N.Simons, received support on lab protocols and spectrogram analysis by Dr. E.C. Wikberg and Dr. Ting's postdoctoral researcher Dr. M.J.Ruiz-López, and received assistance with preparing amplification reactions and plating reaction products from Dr. Ting's MA student Diana Christie.

I extracted nDNA from thawed fecal samples using a QIAamp® DNA stool mini kit. The precise extraction protocol that I followed is included in Appendix C, which is modified from the QIAamp® protocol based on suggestions from Dr. M.J. Ruiz-Lopez and Dr. E. Wikberg for

optimal extraction. I quantified the amount of DNA in each extract using Qubit® fluorometric

quantification, which quantifies all DNA (not just species specific DNA), to check if there was

any DNA in the sample extract before proceeding with PCR.

To genotype samples, I used a panel of ten MapPairs® microsatellite markers that Dr. E.

Wikberg had previously successfully applied in this population of *C. vellerosus* (Table 2.4;

Coote and Bruford 1996, St. George *et al.* 1998, Bradley *et al.* 2000, Yamane *et al.* 2003,

Arandjelovic *et al.* 2009). As determined by Dr. Wikberg (2012), these markers are not sex

linked, do not deviate from Hardy-Weinberg equilibrium, are in linkage equilibrium, are co-

dominant, and shows a pattern of Mendelian inheritance. These markers had high rates of

amplification success in Dr. Wikberg's data set, had low rates of allelic drop out relative to other

markers, and were sufficiently polymorphic to determine parentage (Table 2.4, Wikberg 2012). It

was necessary to use a panel of markers that completely overlapped with the markers that Dr.

Wikberg used so that I could make use of previously determined genotypes, especially for the

mothers of the infants in my data set.

I amplified DNA using the polymerase chain reaction (PCR). I amplified up to three

microsatellite regions simultaneously using multiplex groups that are listed in Table 2.4.

Reactions were prepared in a 10μL final volume containing either 1.2μL template DNA, 1μL

BSA (New England BioLabs Inc.®), 1.8μL molecular grade water, 1μL primer dilution, and 5μL

QIAGEN Multiplex PCR Master Mix; or, for markers run not in a multiplex, 1.2μL template

DNA, 5μL GoTaq Green, 1μL BSA, 2.48μL molecular grade water, 0.16μL each of the forward

and reverse primer. All reactions were run for 35 cycles in an Eppendorf Mastercyler® Nexus or

Nexus Gradient. Annealing temperatures were optimized for each multiplex group and are listed

in Table 2.4. All other amplification cycling settings were set according to QIAGEN Multiplex

PCR Handbook's suggested protocols for microsatellite loci using multiplex PCR. I gel electrophoresed PCR products to test for amplification success and contamination and then plated samples for capillary electrophoresis. Capillary electrophoresis was carried out on an ABI3730 DNA Analyzer (Applied Biosystems) by staff at the CORE Facilities in Oregon State University's Department for Genome Research and Biocomputing. Florescence from HEX, FAM and NED labels on 5' forward primers allowed allele sizes to be determined, which were compared to the GeneScan™ 500 ROX™ size standard for interpretation. I called all allele sizes in GeneMapper 3.7 software (Applied Biosystems) and confirmed each call with visual inspection of the spectrograms.

Table 2.4. Microsatellite markers and multiplex groups.

Multiple x Group	Primers	Number of alleles	Amplification success (%)*	Dropout rate (%)*	Annealing Temp. (°C)
1	D3s1766	5	97.83	27.34	58
	D6s311	6	78.52	24.16	
2	D6s474	7	83.61	22.54	58
	D10s676 (Nested)	10	89.55	24.67	
	C19a	4	82.92	22.21	
3	D4s2408 (Nested)	7	88.36	21.29	48
	D1s207	7	84.65	21.72	
4	D7s503	9	82.95	20.29	56
	D4s243	8	80.13	14.06	
5	D11s2002	7	77.87	24.25	56

*Amplification success and dropout rates are calculated from Dr. Wikberg's dataset.

Heterozygote loci were confirmed with at least two replicates, and homozygotes were confirmed with 5-7 replicates. To confirm homozygous results, Morin *et al.* (2001) recommends using a different number of replicates depending on the quality of the sample extract. To confirm low quality extracts (25-100 pg/reaction) Morin *et al.* (2001) recommends 7 replicates are needed. This method relies on using quantitative PCR (QPCR) to determine extract quality. I was unable to apply QPCR to my samples and therefore aimed for 7 replicates when time permitted. Extracts that amplified inconsistently, and were therefore likely poor quality (<25pg/reaction), were not used in my analysis. In addition, Dr. Wikberg's genotyping of quantified *C.vellerosus* extracts using locus-specific dropout rates showed that a mean of 4 replicates were required to confirm a homozygote (Wikberg *et al.* in preparation). Therefore, I considered cases where I was able to repeat homozygous results at least 5 times to be a confirmed genotype and included these in my paternity analysis.

To confirm an individuals' identity, I matched genotypes from two separately collected samples for each individual, or checked that infants shared at least one allele at each locus with their known mother when using genotypes obtained from one sample. I worked with samples from 49 individuals, which are listed in Appendix A2, along with the number of loci successfully genotyped, who collected the sample, an indication of which samples were partly genotyped by myself and partly by Dr. Wikberg, and which individuals' genotypes were used in this thesis. The genotypes not used in this thesis contribute toward Dr. Sicotte's long-term dataset.

2.4 Data analysis

I used three primary behavioural categories to quantify positive male-infant relationships: affiliative interactions, male tolerance for infant play, and the time that an infant and a male spent in proximity. These measures were defined as the following:

Affiliative interactions: included any friendly behaviours between males and infants, which are listed in detail in section 3.1, and could either be instantaneous or have a start and end time denoted.

Male tolerance of infant play: recorded when infants were making continuous, fast-paced, small movements, often attributed to social or solitary play behaviour, within three tail lengths proximity of the male.

Time spent in proximity: measured using the proportion of total point samples (during focal follows of the male) where the infant was present within 3 tail lengths of a male.

For affiliative interactions and male tolerance of infant play, I considered affiliative behaviours to be distinct from each other if they occurred more than one minute apart from each other, or if there was more than one minute between the end of one bout and the beginning of the next bout. A one minute cut-off was chosen because infants move between activities faster than adults and the average duration of interactions was 17.56 seconds. Therefore during a one minute period between interacting with a male, an infant could have interacted with one or more other individuals or partaken in another activity, denoting a change of motivation between interactions or between individuals.

I quantified affiliative interactions and male tolerance based on rates of behaviours per male-infant dyad, per focal hour that both the male and infant were present in the group. For example,

for infants born during my field season, only focal samples of a male that occurred after the infant's birth were included when calculating rates for that dyad. Although I aimed for focal samples that lasted 10 minutes, it was not always possible to track an animal for this full duration. I included in my analysis focal samples that were ≥ 2.5 minutes in length, because interactions with infants were short in duration, and I felt that this time frame was likely to catch a complete interaction and therefore also the absence of an interaction. I excluded from all analyses any affiliative interactions that occurred between a male, a mother, and an infant simultaneously (N=6 out of N=1036 total affiliative behaviours between males and all individuals) because it was not clear what the choice of partner was in these triadic interactions. I acknowledge that this biases the analysis away from interactions with very young infants (0-2.9 months), because mothers primarily determine interactions and social proximities for very young infants, as these infants depend heavily on their mothers to travel and feed. I also excluded two males with less than 2 hours of total focal data in a group (Table 2.3), and therefore excluded the six dyads connected to these males, leaving a total of 53 dyads in the analysis.

One of my independent variables is 'dyad type', which refers to the potential kinship between a male and an infant. I used three dyad-type categories, which are labeled from the male's perspective: potential offspring dyads (PO dyads), unlikely offspring (UO dyads), and potential sibling dyads (PS dyads). PO dyads (N=22) involved infants that were conceived when the male was present in the infant's group and sexually active; UO dyads (N=13) involved infants that were conceived when the given male was not present in the infant's group; and PS dyads (N=18) involved infants and males born in and still resident in the same group, who could therefore share some degree of kinship, such as half or full sibling. Males in PS dyads were not

sexually active at the time of the infant's conception. The demographic data necessary to determine male dyad type was available from long-term data collection by Dr. P. Sicotte's students, primarily J. Vayro and Dr. E. Wikberg.

In models where it was appropriate to consider the number of infants available to a male, I used a weighted average of the number of infants available during a time period because the number of infants changed due to births, deaths and weaning. I computed this number for each male using the following equation:

$$I = i_1 \left(\frac{t_1}{T}\right) + i_2 \left(\frac{t_2}{T}\right) \ldots + i_n \left(\frac{t_n}{T}\right)$$

where I is the weighted average of infants available to the male; i is the number of infants during time period $1, 2$ and n; t is the number of focal hours during time periods $1, 2,$ and n; and T is the total focal hours during time periods $1, 2$ and n. For some models, I used this same calculation process to compute the total number of juveniles or all group members available to a male.

In models where it was important to control for the unequal availability of male and female infants, I computed a similar weighted value based on the relative proportion of male and female infants available for a given amount of time. Given that the proportion of female infants is directly related to the proportion of male infants, I included only the relative proportion of female infants available as a covariate in the models pertaining to infant sex. I computed this covariate for each male using the following equation:

$$F = \left(\frac{f_1}{A_1}\right)\left(\frac{t_1}{T}\right) + \left(\frac{f_2}{A_2}\right)\left(\frac{t_2}{T}\right) \ldots + \left(\frac{f_n}{A_n}\right)\left(\frac{t_n}{T}\right)$$

where F is the proportion of female infants available to the male; f is the number of female infants available during time periods *1, 2,* and *n*; A is the total number of infants available during time periods *1, 2,* and *n*; t is the focal hours during time periods *1, 2,* and *n*; and T is the total focal hours.

For several of my analyses I used Generalized Linear Mixed Models (GLMM) ('genlinmixed' function in SPSS), which are appropriate for analyzing dyadic data because the repeating of male and infant IDs can be controlled for as random effects. When analyzing data using a GLMM, too many variables or too many levels within each variable relative to the amount of data in the model can reduce the accuracy of the model results. Therefore, for my main analyses of the 53 dyads, I included a maximum of one target variable and one covariate variable in each model, where there was a maximum of five levels between these variables. Each model was first run with the covariate, target variable, and an interaction term between the covariate and factor. In all cases, I confirmed that there was no interaction between the covariate and the factor, which meant that the model could be considered valid and subsequently run without the interaction term. For models comparing more than two groups that showed a significant effect ($p \leq 0.05$) or a statistical trend ($0.05 < p \leq 0.10$)(Stoer 1999, Langos *et al.* 2013) , pairwise comparisons were justified to investigate if differences between groups were driving the pattern (as recommended by Tak Fung, statistical consultant, University of Calgary Information Technologies). For all models I applied a normal distribution, identity link function and adjusted p values using an LSD correction where multiple comparisons were being made.

2.4.1 Testing the null hypothesis

To test the possibility that males interacted affiliatively with infants as by-product of living in a social group, I compared expected and observed rates of affiliative interaction using a Wilcoxon sign rank test in SPSS. I calculated the expected rate of interaction for each male as the number of affiliative social interactions, between the male and all individuals per hour, and standardized this by the weighted average number of individuals available. The observed value was calculated as the number of affiliative interactions between a male and all infants per hour, standardized by the number of infants available. Although infants move between activities, including social interactions, faster than adults, I upheld the one-minute cut-off time when counting interactions between males and adults to create comparable values. Given that I measure the rate of tolerance based on 'small movements' made by infants, it was inappropriate to use compare this measure between infants and other members of the social group. For example, adult females probably do not engage in this behaviour frequently. In cases where individuals could not be identified, I included interactions between males and unidentified individuals if their age class was identified.

2.4.2 The effect of infant sex

I tested for the effects of infant sex on male-infant relationships using three GLMMs, where the rate of affiliative interaction between a male and an infant, rate of male tolerance for infant play, and proportion of time a male and an infant spent in proximity were the dependent variables. I compared the variable of infant sex to each dependent variable in a separate model because my sample size (number of dyads) was small and therefore I had to restrict the number of variables in a model. I controlled for the proportion of female infants available as a covariate,

and asked if the rate of affiliative interaction (GLMM #1), rate of tolerance for infant play (GLMM #2), and time that males and infants spend in proximity (GLMM #3) varied by infant sex.

To determine if differences in behaviour between sexes were attributable to male biases for male or female infants, or attributable to variation in male and female infant behaviour, I used two GLMMs to ask if infant sex had an effect on the rate of male approaches to infants (GLMM #4) or the rate of infant approaches to males (GLMM #5).

2.4.3 The effect of age

I broadly analyzed the effect of age of by comparing the rate of affiliative interaction between male and infants and males and juveniles using a Wilcoxon sign rank test. Rates of affiliative interaction were calculated per male rather than per dyad because not all juveniles could be easily identified. However, because age category (juvenile or infant) was easily recorded I could calculate a rate per male of affiliative interaction with all juveniles, and a rate with all infants. I excluded one male who had access to only infants and no juveniles, leaving N=11 males in the analysis. The rate of affiliative interaction per focal hour per male (not per dyad) was standardized by the weighted average number of infants or juveniles available.

2.4.4 The role of mothers

To examine the role of the mother in mediating interactions where the infant was not in contact with the mother, I analyzed the mothers' presence at the time of the interaction between the male and the infant, and the global relationship between a male and a mother during the infant's lifetime. Mothers were considered present during an interaction if they were within 3 tail

lengths of the male at the time that the male interacted with the infant. I calculated the proportion

of interactions where the mother was present and the proportion of interactions where the mother

was absent. As a proxy for the global relationship between a male and female, I measured the

amount of time that a mother and a male spent in proximity using the proportion of total point

samples (during focal follows of the male) where the female was present within 3 tail lengths of

the male. I used a GLMM (#6) to ask if the time that males and mothers spent together could be

predicted by the dyad relationship (PO, UO, PS) between a female's infant and a male. Although

the number of females in a group could affect the amount of time that any male spent with a

female, it was not necessary or possible to control for this effect because the number of females

did not vary across time and did not vary substantially enough between groups (females per

group ranged from 3 to 5).

2.4.5 Maintenance and establishment of proximity

To explore how male-infant interactions function, I analyzed the maintenance of

proximity between males and infants using Hinde's index (Hinde and Atkinson 1970), and I

compared the establishment of proximity bouts by males with that of infants. Hinde's index is

used to measure responsibility in the maintenance of proximity between two individuals. The

index gives a higher value to the individual who is approaching more frequently and leaving less

frequently, and therefore shows the extent to which an individual is responsible for maintaining

proximity. The index is calculated by subtracting the proportion of total leaves given by the same

individual from the proportion of total approaches given by that individual. I computed this value

using the following equation:

$$A'\text{s responsability for maitaining proximity} = \frac{U_A}{(U_A + U_B)} - \frac{S_A}{(S_A + S_B)}$$

where A and B are the individuals comprising the dyad; U_A is the number of events where a proximity bout was established by A's actions; U_B is the number of events where a proximity bout was initiated by B; S_A is the number of events where a proximity bout was ended by A's actions; and S_B is the number of events where a proximity bout was ended by B's actions (Martin and Bateson 1993). Therefore the index provides a number on a scale of -1 to 1, where if calculating the index for individual A, a number closer to -1 reflects that individual B was more responsible for maintaining proximity, and a number closer to 1 indicates that individual B was more responsible for maintaining proximity. For my analysis, -1 indicates that proximity was maintained entirely by the male and +1 indicates proximity was maintained entirely by the infant. I only calculated an index for dyads with a minimum of 15 interactions (approaches and leaves combined) to minimize the effect of random extreme variation in small sample.

To examine the establishment of proximity I used a matched pair Wilcoxon sign rank test to ask if infants approached males more, or if males approached infants more. For each male, I calculated the rate of approaches from males to 1 tail length of an infant and a rate of approaches received to one tail length of a male from an infant. Rates were calculated per focal hour and standardized by the weighted average number of infants available during the focal time for that male.

2.4.6 Male-infant dyad type

I tested for the effects of male-infant dyad type using three GLMMs, where the rate of affiliative interaction between a male and an infant, rate of male tolerance for infant play, and proportion of time a male and an infant spent in proximity were the dependent variables. Similar to my analysis of the effect of infant sex, I compared these dependent variables against dyad types in three separate models. I controlled for the number of infants available as a covariate, and asked if the rate of affiliative interaction (GLMM #7), rate of tolerance for infant play (GLMM #8), and time that males and infants spend in proximity (GLMM #9) varied by dyad type.

2.4.7 Paternity testing

Paternity was assigned in Cervus v3.0.7 (Marshall *et al.* 1998, Kalinowski *et al.* 2006) based on comparing genotypes of infants, candidate sires, and known mothers. Cervus calculates a 'likelihood ratio' (also called a Paternity Index) to compare the probability that a male is a sire with the probability that a male is not the sire. The probability of either case being true is calculated from the allele frequencies in the population and the likelihood of obtaining the observed infant genotype given the mother genotype and the candidate sire genotype (Edwards 1972). Likelihood ratios are advantageous over exclusion-based methods that use allele sharing only because Cervus takes into account how common the infant and male genotypes are in the population to determine the likelihood that each non-excluded male (i.e. male that shares at least one allele per locus with the infant) is the true sire. It is more likely that a male shares a rare allele with an infant by descent than by chance while the opposite is true for common alleles. Based on this information, Cervus calculates a 'LOD' score (Kalinowski *et al.* 2007). Positive LOD scores indicate a male who is more likely to be the true sire than not the true sire, and a

negative LOD scores indicate that the male is more likely to not be the true sire than the true sire. Parentage assignments were based on the delta score, which is the difference in LOD scores between the most likely and the second most likely candidate sire. This way, I minimized the risk of incorrectly assigning a male as the true sire when a second male also had a high LOD. To determine how large the delta has to be to assign sires at the 95% confidence level, Cervus calculates a probability distribution based on a parentage assignment simulation. The simulation takes into account population allele frequencies, the number and sampled proportion of candidate sires, the number and confirmed proportion of loci, and the overall genotyping error.

I used a standard genotyping error of 0.01, and set the confidence level at 95%. The number of minimum matching markers I used ranged between five and eight, which I determined for each analysis based on the lowest number of marker overlap for each dyad that would allow me to include as many genotyped candidate sires as possible. As candidate sires, I included all males who were over the age of three and present in the infant's group during my field season or at the probable time of conception. Although this is a broader group of males than those that I have considered as potential sires in my behavioural data, I have chosen to be conservative in not pre-emptively ruling out any males. I ran five separate paternity assignment analyses that included a total of 12 infants, where each analysis included a cohort of infants who had the same candidate sires. A list of the cohorts is included in Table 2.5, which also includes the number of candidate sires, the proportion of sampled sires, and the minimum matching markers used for each cohort analysis. For cohorts where I sampled all of the known candidate sires, the proportion of sampled sires was set at a maximum of 0.90 to account for the possibility of females mating with extra group males.

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It is useful to note that I conducted my laboratory analyses after having conducted my behavioural data collection, which means that I collected my behavioural data without prior knowledge of the paternity status of the males.

Table 2.5. Cohorts and parameters for paternity analysis in Cervus.

Group (Cohort)	Infant ID	Loci typed	Mother ID	Loci typed	Number of candidate sires	Proportion of candidates sires sampled	Minimum loci matched
WT	VN	9	VM	9	9	0.89	7
	I9	8	IS	9			
SP Cohort 1	XA	9	XE	9	11	0.82	5
	SW	8	SE	9			
	CK	9	CT	9			
SP Cohort 2	S7	8	SA	9	14	0.86	8
RT	S9	9	SU	6	5	0.90	6
	F9	9	FV	9			
	B9	9	BL	9			
	BO	9	BE	9			
WW	IB	9	IT	8	8	0.90	4
	CX	9	CR	9			

2.4.8 Combining paternity and behavioural data

I combined behavioural data on male-infant affiliation with genetic paternity testing to ask if males accurately directed positive behaviour toward offspring. Based on paternity tests, I categorized each male-infant dyad was defined as either offspring or non-offspring dyads. I used three GLMMs to ask if genetic paternity predicted the rate of affiliation (GLMM #10), tolerance (GLMM #11) or time spent in proximity (GLMM #12) observed within a dyad. Because sub-adult natal males were considered potential siblings, and therefore neither potential sires nor unlikely sires, I did not find it biologically meaningful to label infants as 'non-offspring' in these dyads and instead excluded these males from this analysis. In addition, I could only include infants that I was able to genotype. Therefore, eight immigrant males and twelve infants were included in this analysis, comprising a total of 26 dyads (N=7 sire-infant dyads, N=19 non-sire-infant dyads).

Chapter Three: **Results**

3.1 Description of positive male-infant behaviour

I observed interactions between males and infants in my four study groups that ranged from affiliation to tolerance to aggression. Affiliative behaviours included: approaches to contact, friendly touches, grabs, nose grabs, pulls or reaching for an individual, sniffing, hugs, kisses, friendly inspections, playing, play presenting or play faces, grooming, groom presenting, grabbing onto tails and swinging on males' tails, climbing on or jumping on males, and infants squealing at males. I recorded a total of 180 affiliative interactions between males and infants during focal time. Of the 53 possible dyads between males and infants in my study groups, 27 dyads did not interact affiliatively. Of the 26 dyads that did interact affiliatively, the rate of affiliation ranged from 0.05 to 1.90 interactions per focal hour, where the median rate was 0.27 interactions per focal hour. Appendix A3 presents the rates of affiliation, tolerance and proportion of time in proximity for each dyad.

During focals, the top three most common affiliative behaviours that I observed between males and infants were approaches to contact (N=94 events), friendly touches (N=50 events) and infants jumping on males (N=37 events). These three behaviours remain the most common behaviours if *ad libitum* data is also included. Infants climbing on males, grabbing males' tails and play behaviour were also relatively common behaviours. I observed a male grooming an infant on three occasions, and I observed four bouts of infants grooming males. I have incorporated photos of some of these behaviours in Figure 3.1.

Figure 3.1. Photos of some positive male-infant behaviours. Clockwise from left: an infant climbing up an adult male's tail; a sub-adult natal male playing with an infant; and an adult male and infant in close proximity.

I observed males protecting infants from attacking males on two occasions. The first occasion occurred in group WW, during an incursion by an extra-group male (July 1, 2013, 8:06-8:14 AM). The male ran directly towards and infant JJ, who was located in proximity to her mother and another adult female. The resident male, OW, reacted frantically, however, the tree that OW was in was separated from JJ's tree by a road. After running back and forth in his tree, OW ran to another tree, in the opposite direction of the intruding male, in order to cross the road. During this time the intruding male attacked JJ, who was defended by her mother and another adult female. JJ's mother and the other female engaged in contact fighting with the male. Once

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OW was in proximity, he engaged in short bout of contact fighting with the male, before chasing him away. JJ, who did not incur any visible injuries from the attack, was a potential offspring of OW. I was not successful at genotyping JJ, so paternity is unresolved.

The second example of a male defending an infant occurred in the group WT (July 13, 2013, 2:09-2:26 PM). An extra group male, who was initially assisted by additional extra-group individuals, had successfully chased the entire WT group out of their feeding spot. As the group fled, infant VN, who was not being carried by her mother, fell behind the rest of the group. The extra-group male lunged at VN and pounced on her. She fell a short distance out of the tree but appeared uninjured. The resident male KR stopped fleeing, turned around, and slightly approached VN and the intruding male. He looked at the attacking male, who then haulted. Infant VN was able to catch up to KR, looking at and squealing at him. As KR and VN continued to flee, KR positioned himself between VN and the attacking male. VN was a potential but not genetic offspring of KR.

Infants often interacted with males in the context of male-male confrontations, during which males performing stiff-leg displays targeted at extra-group males, in addition to other types of displays (Teichroeb *et al.* 2010, Fox *et al.* 2015). Infants sometimes reacted to these displays by jumping, climbing and grabbing onto the displaying male while squealing intensely at him (Fox *et al.*2015). Males and infants both initiated interactions, where sometimes a male would pull the infant towards himself onto his lap. I recorded 136 cases (15.5%) of infant involvement during 878 displays that occurred during focal and *ad libitum* data collection. I have included photos of infant involvement in a male display in Figure 3.2. Although male display can

escalate to contact aggression, I only saw infants involved during male display behaviour, not during male-male contact fighting.

Figure 3.2. Photos of an infant jumping on, squealing at and grabbing onto an adult male who is stiff-leg and open mouth displaying. Photography by Patricia Homonylo.

I considered males to demonstrate tolerance of infants when infants were making frequent small movements in close proximity to a male. As explained earlier, this usually occurred when infants were engaged in social or solitary play. A good example of male tolerance is illustrated by a series of events I observed between infants I9 and VN and male KR (Aug. 14, 2013, 8:20-8:27 AM). The infants were engaged in social play and making frequent movements in proximity to the male, who was resting. The infants periodically moved onto a branch that was positioned above the male, such that when their body weight was added to the branch, the branch bounced down and hit the male on the head. KR was hit on the head 9 times during the span of the play bout. KR did not react and continued to rest, which I interpreted as convincing evidence for tolerance for the infants' play.

Although this thesis is focused on the positive interactions between males and infants, it is worth noting that I also observed agonistic interactions between males and infants. I did not observe a male from my study group attack an infant; agonistic behaviours were mild and included males aggressively lunging at, pulling, pushing, swiping at, and hitting infants. I also observed infants avoiding, fleeing, cowering from males, and submissively presenting toward males. Male-infant agonistic behaviours were generally rare. I recorded 40 agonistic behaviours during focal time, and 45 additional behaviours were recorded in *ad libitum* data. When including ad-libitum data, the most commonly recorded male-infant agonistic behaviours were infants fleeing males (N=16 events), infants avoiding males (N=15 events), and males hitting infants (N=15 events). A good example of an agonistic interaction occurred between male MS and infant XA in group SP (Sept. 28, 2013, 10:02-10:03 AM). XA pant grunted at MS, who responded with 3 open mouth displays. XA responded with 2 open mouth displays, another pant grunt, and then submissively presented at MS. XA fled from MS and then MS moved into XA's previous space.

Males occasionally showed intolerance toward infants, but generally I observed males being intolerant of juveniles more than infants. An example of male intolerance for a juvenile occurred between male OW and juvenile MW (Sept. 27, 2013, 10:44-10:45 AM). MW friendly touched OW, who swiped at and grunted at MW. MW cowered, open mouth displayed at OW 3 times, and then friendly touched OW 5 times before cowering again. MW open mouthed at OW 2 more times and then began to groom OW. OW hit MW twice, and MW cowered after each hit. MW open mouth displayed 2 more times friendly touched OW 3 three more times. OW hit MW again, and MW cowered.

Within my focal groups, I recorded affiliative interactions approximately 4.5 times as often as I recorded agonistic interactions. Male-infant agonistic interactions within my focal groups were never as intensely aggressive as the interactions observed between extra-group males and infants. Thus, within-group male-infant interactions in *C.vellerosus* are generally positive.

3.2 Testing the null hypothesis

I observed a total of 338 affiliative interactions between males and all individuals. Of these, 180 (53.25%) were between males and infants and 158 (46.74%) were between males and other individuals within their social group. A Wilcoxcon sign rank test showed that males interacted with infants significantly more than expected when considering each males' overall rate of affiliative interaction with all group members, and the proportion of available social partners that are infants ($Md_{observed}$=0.15, $Md_{expected}$= 0.08, *N*=12, T=10, p=0.02).

3.3 The effect of infant sex

Infant sex did not significantly influence the rate of affiliation ($F_{(1, 50)}$=2.79, p=0.10), rate of tolerance ($F_{(1, 50)}$=3.35, p=0.07) or the proportion of time spent in proximity ($F_{(1,50)}$=1.05, p=0.31) between males and infants. The proportion of female infants available, which was included as a covariate, significantly predicted rates of affiliation ($F_{(1, 50)}$=6.43 p=0.01) and tolerance $F_{(1,50)}$=4.63, p=0.04) between males and infants. Infant sex was a significant predictor of the rate of approaches by a male to an infant ($F_{(1,50)}$=4.16, p=0.05) and the rate of approaches from an infant to a male ($F_{(1,50)}$=8.00, p=0.01), where focal males

approached infant males more than infant females, and infant males approached focal males more than infant females approached focal males (Figure 3.3, Figure 3.4). In both models the proportion of female infants available (covariate) had a significant effect ($F(1,50)=5.52$, $p=0.02$, $F(1,50)=11.13$, $p=0.00$ respectively). The results of these five GLMMs, including estimated means and standard errors, are available in Table **3.2** at the end of this chapter.
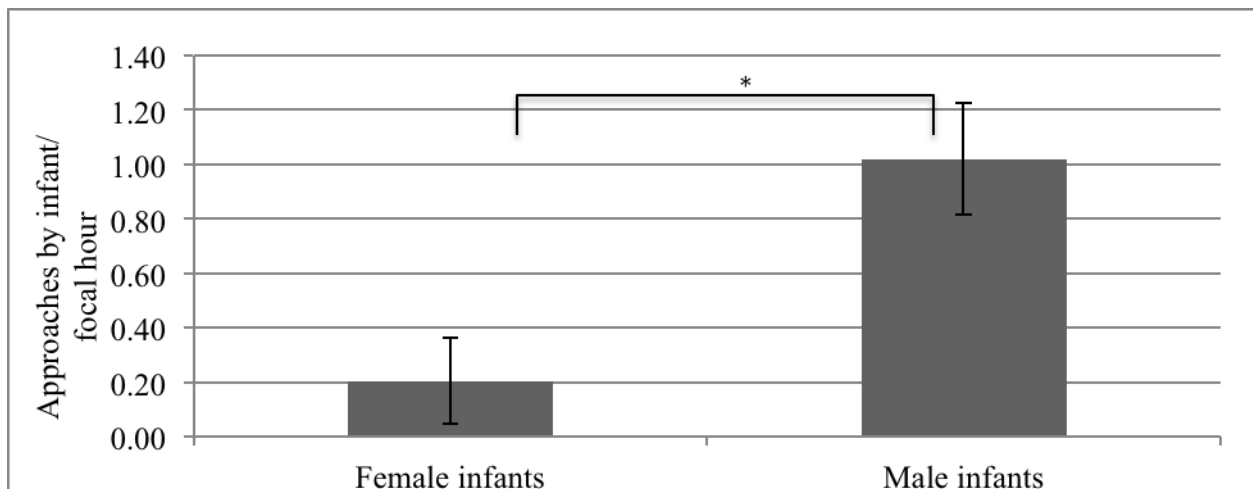
Figure 3.3. Estimated mean rates (± SE) of approaches by male and female infants to focal males. * denotes significant differences between groups (GLMM, $p \leq 0.05$).
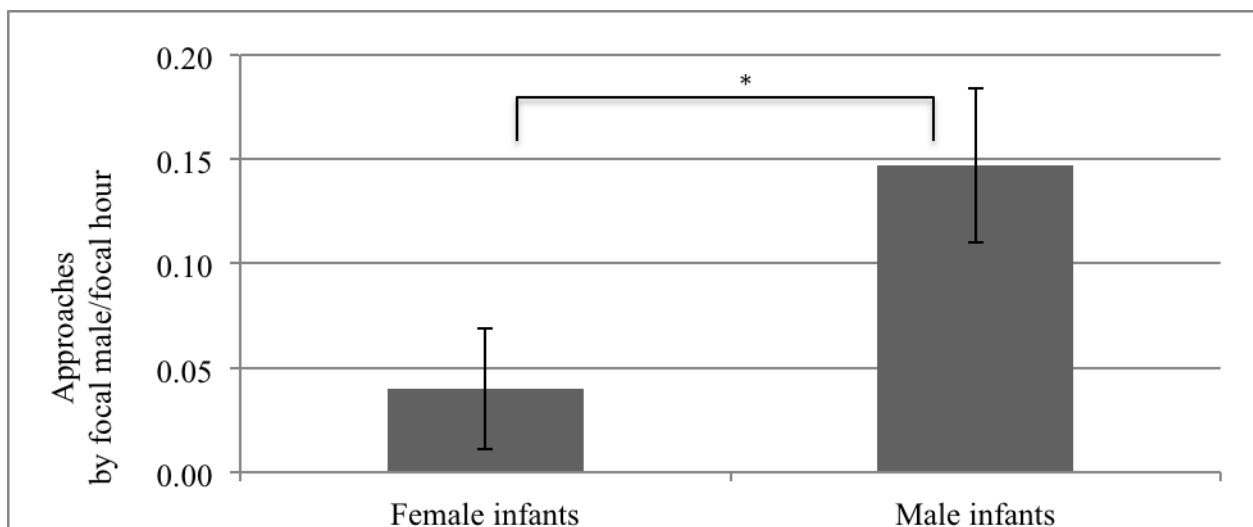
Figure 3.4. Estimated mean rates (± SE) of approaches by focal males to male and female infants. * denotes significant differences between groups (GLMM, $p \leq 0.05$).

3.4 The effect of age

I included a total of 198 affiliative interactions in the analysis comparing interactions between males and infants, and males and juveniles. Of these, 118 occurred between males and infants and 78 occurred between males and juveniles. A Wilcoxon sign rank test comparing rate of affiliative interactions per male showed that males interacted significantly more with infants than with juveniles ($Md_{infants}=0.12$, $Md_{juveniles}=0.08$, $N=11$, $T=11$, $p=0.05$). To illustrate the dependence of very young infants on their mothers and other adult females, and therefore acknowledge the inherent bias in excluding interactions between males and non-independent infants, Figure 3.5 compares the proportion of infant approaches to other individuals when infants are with their mothers to when approaches when infants are independent, according to infant age category.
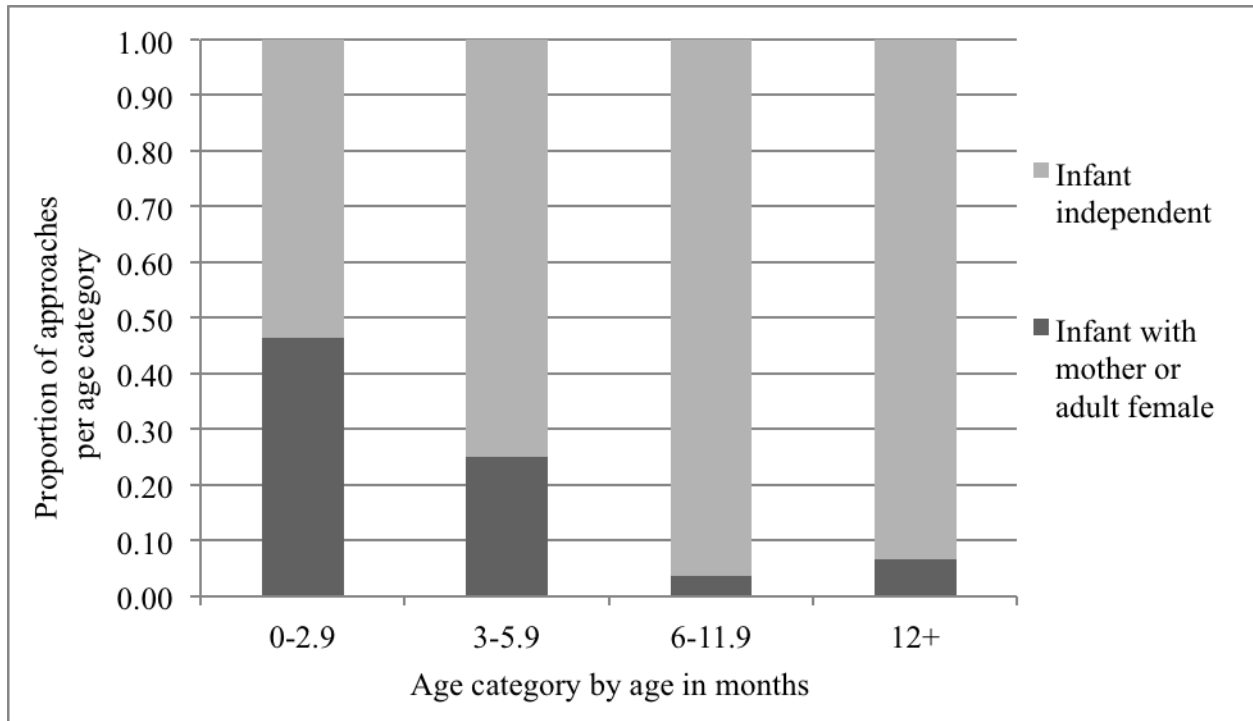
Figure 3.5. Infant dependence on mothers and adult females according to infant age category.

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3.5 The role of mother mediation

Mothers were present for 30.6% of affiliative interactions that I observed between males and infants and were not present for 70.4% of interactions. Dyad type significantly predicted the amount of time that a male and a mother spent in proximity ($F_{(2, 50)}=7.04$, p=0.00). Pairwise comparisons showed that males spent more time with mothers of potential offspring than mothers of potential siblings ($t_{(50)}=3.71$, p=0.00), and more time with mothers of unlikely offspring than with mothers of potential siblings ($t_{(50)}=2.26$, p=0.03). There was no difference between the amount of time that males spent with mothers of potential and unlikely offspring ($t_{(50)}=1.03$, p=0.31). Thus females spent more time around adult males (potential sires and unlikely sires of their offspring) compared to sub-adult males. This pattern is illustrated in Figure 3.6 and estimated means and standard errors are reported in Table **3.2**.
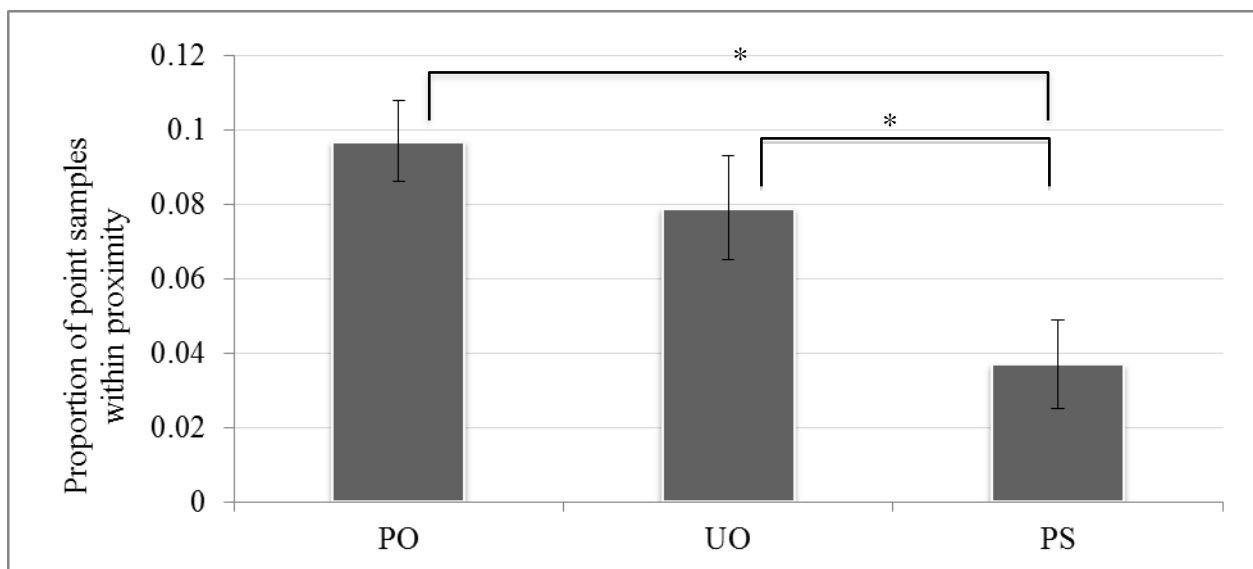
Figure 3.6. The estimated mean proportion of time (± SE) that males and mothers spent in proximity compared by male-infant dyad type. * denotes significant differences between groups (GLMM, $p \leq 0.05$).

3.6 The maintenance and establishment of proximity

For the 17 dyads (N_{PO}=9, N_{UO}=1, N_{PS}=7) that I was able to calculate Hinde's index, indexes ranged from -0.19 to 0.31, where the median index was 0.00. Indexes are presented in Figure 3.7, arranged according to dyad type. Given the reduced dataset for which I could calculate indexes and the narrow variation within these scores, I did not analyze indexes by dyad type. I analyzed of the establishment of proximity using 648 approaches and 639 leaves recorded between males and infants during focal sampling. Infants were responsible for 86.3% of approaches and 87.8% of leaves. A Wilcoxon sign rank test indicates that the rate of approaches given by a male (Mdn= 0.08) was significantly different from the rate of approaches received from an infant (Mdn= 0.43) (N=12, T=12, p= 0.00).
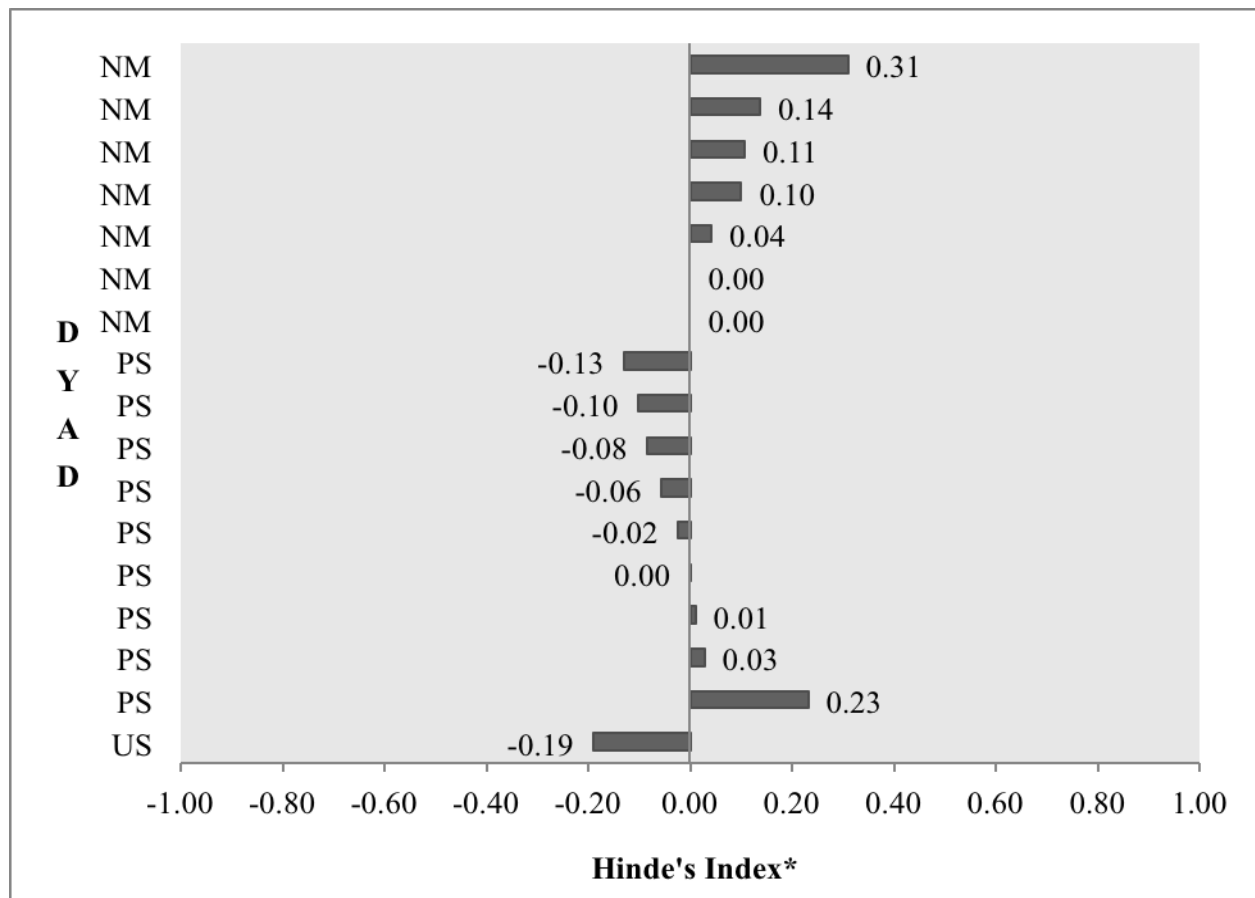
Figure 3.7. Hinde's indexes for the N=17 male-infant dyads with sufficient approach/leave data. *An index value of -1 indicates that proximity was maintained exclusively by the male and a value of +1 indicates proximity was maintained exclusively by the infant.

3.7 Male-infant dyad type

Dyad type did not significantly predict the rate of affiliative interaction between males and infants when controlling for the number of infants available, but a trend was detected $(F_{(2,49)}= 2.74, p=0.07)$. Pairwise comparisons carried out to investigate the trend showed that potential sire dyads had higher rates of affiliation than unlikely sires dyads $(t(49)=2.32, p=0.03)$. Neither potential offspring dyads nor unlikely offspring dyads interacted at a significantly different rate than potential sibling dyads $(t(49)=3.14 \; p=0.75; t(49)=1.76, p=0.08$ respectively).

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Dyad type significantly predicted the rate of male tolerance for infant play ($F_{(2, 49)}=$ 3.59, p=0.04). Males were more tolerant toward potential offspring than toward unlikely offspring ($t_{(50)}=2.39$, p=0.02). There was no difference in the amount of tolerance observed between potential offspring dyads and potential sibling dyads ($t_{(50)}=1.84$, p=0.07), or between unlikely offspring dyads and potential sibling dyads ($t_{(50)}=0.61$, p=0.55).

Finally, dyad type did not significantly predict the proportion of time that a male and infant spent in proximity, although a trend was detected again ($F_{(2,49)}=2.98$, p=0.06). Pairwise comparisons showed that potential offspring dyads spent more time in proximity than unlikely offspring dyads ($t_{(50)}=2.37$, p=0.02), but no significant difference emerged between potential sibling dyads and potential sire dyads ($t_{(50)}=1.281$, p=0.23) or between unlikely offspring dyads and potential sibling dyads ($t_{(50)}=1.03$, p=0.02).

The results of these three GLMMs are illustrated in Figure 3.8. Estimated means and standard errors for each GLMM are presented in Table **3.2**. For all pairwise comparisons, the number of infants available was held constant at 3.184.
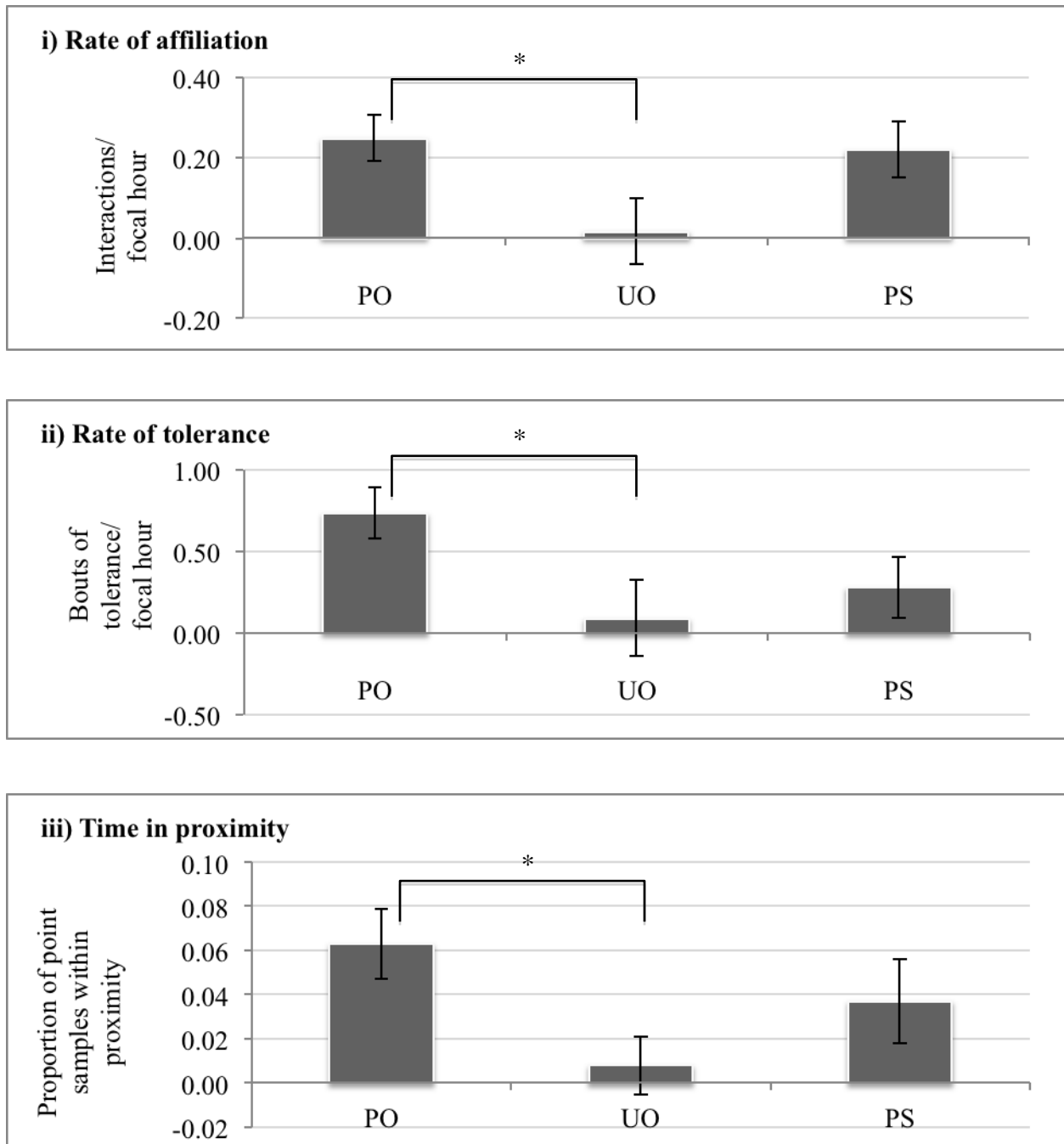
Figure 3.8. Estimated mean (± SE) rates of affiliation, tolerance, and proportion of time in proximity between males and infants compared by male-infant dyad type. * denotes significant differences between groups (GLMM, $p \leq 0.05$). Note that y-axis scales differ between graphs.

3.8 Paternity testing

I obtained genotypes for 12 of 16 infants that were present in the four study groups during my field season. For all 12 of these infants I was able to confirm paternity to 95% confidence. The most likely candidate sires for each infant are listed in Table 3.1 with the paternity testing statistics. Infant S7 appeared to have a mutation at one locus. It was likely a mutation because the allele followed the stutter pattern typical at this locus, there was no contamination at this locus or other loci, the allele size was within the range for this species, and the allele size followed the repeat pattern for this microsatellite, and this allele size had never been recorded in this population before. Paternity was assigned at a 95% confidence level despite this mutation.

3.9 Combining paternity results and behavioural data

Paternity relationships did not predict rates of affiliation ($F(1, 24)=1.11$, $p=0.30$), tolerance ($F(1,24)=1.34$, $p=0.26$), or the proportion of time spent in proximity ($F(1,24)=0.25$, $p=0.62$) between males and infants. These relationships are illustrated in Figure 3.9. Estimated means and standard errors for these three GLMMs are presented in Table 3.2.

Table 3.1. Results of paternity testing.

Group	Infant ID	Most likely sire*	Trio** loci compared	Trio loci mismatches	Trio LOD score	Trio Delta score	Trio confidence
WT	VN	JA	9	0	6.04	6.04	≥ 95%
Cohort	I9	LS	8	0	6.56	0.92	≥ 95%
SP	XA	**KD**	9	0	7.70	6.11	≥ 95%
Cohort	SW	**KD**	8	0	7.65	7.64	≥ 95%
1	CK	**KD**	9	0	3.99	3.99	≥ 95%
SP Cohort 2	S7	JA	8	1	2.23	2.23	≥ 95%
	S9	**CC**	9	0	6.57	5.23	≥ 95%
RT	F9	**CC**	9	0	8.50	8.50	≥ 95%
Cohort	B9	**CC**	9	0	7.47	7.47	≥ 95%
	BO	**CC**	9	0	5.15	5.15	≥ 95%
WW	IB	**OW**	9	0	7.23	7.23	≥ 95%
Cohort	CX	HA	5	0	4.64	2.16	≥ 95%

*Bolded sires are males that were present during my field season (my focal males).
** Trio values refer to comparisons made between male, mother, and infant genotypes simultaneously.
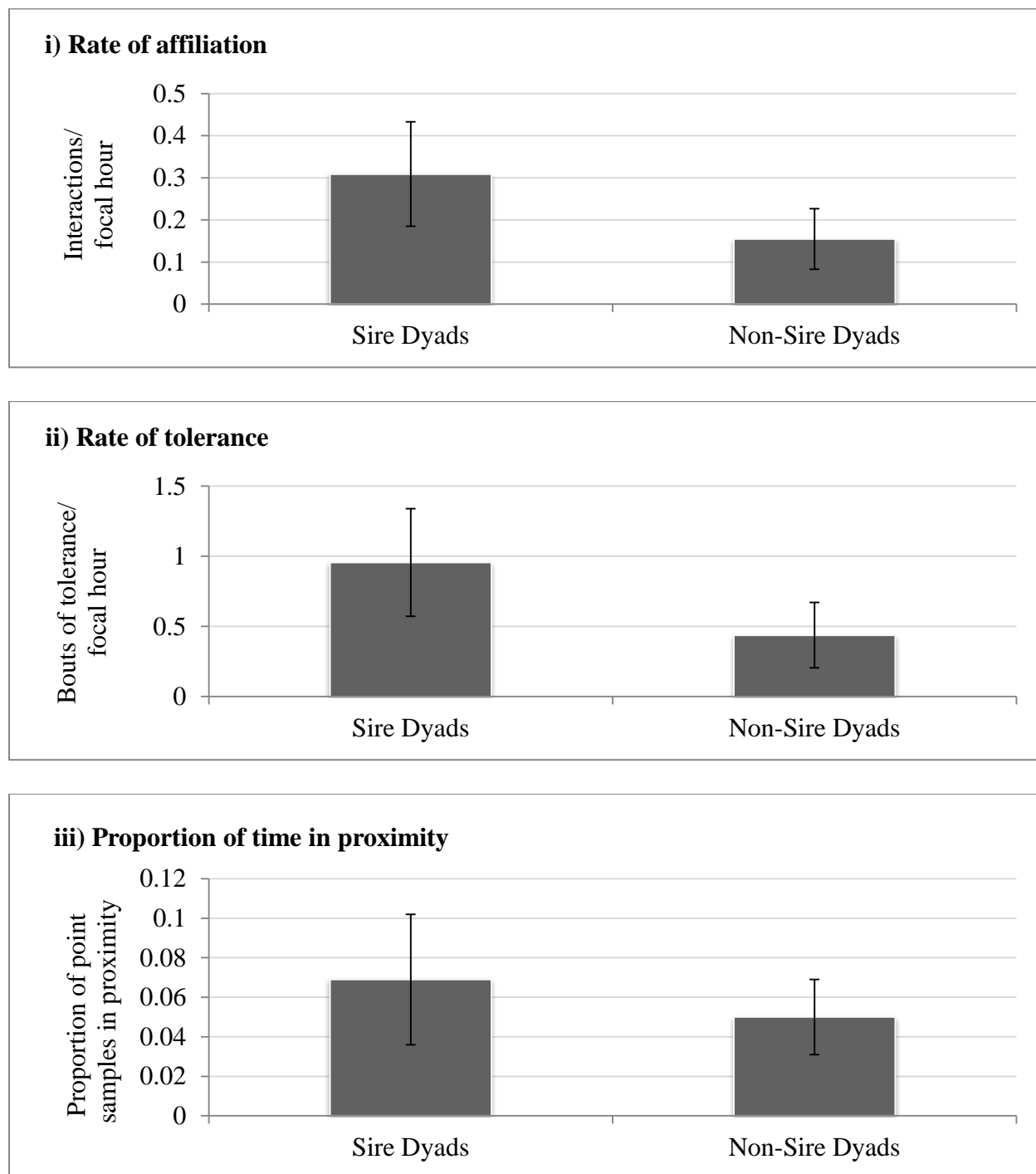
Figure 3.9 Estimated mean (± SE) rates of affiliation, tolerance, and proportion of time in proximity observed between sires and offspring and non-sires and infants. No significant differences were detected when comparing these two dyad types (GLMM, $p \leq 0.05$). Note that y-axis scales differ between graphs.

Table 3.2. Detailed results of all GLMMs.

Model #	Variables		Results			
	Dependent	**Independent**	**Estimated means ± standard error**	**F**	**df1, df2**	**p**
1	Male-infant rate of affiliation	Infant sex	Male=0.28 ± 0.07, Female=0.11 ± 0.06	2.86	1, 50	0.01
		Proportion of infants that are female (covariate)		6.43	1, 50	0.01
2	Male-infant rate of tolerance	Infant sex	Male=0.73 ± 0.20, Female=0.22 ± 0.15	3.35	1, 50	0.07
		Proportion of infants that are female (covariate)		4.63	1, 50	0.04
3	Male-infant time in proximity	Infant sex	Male=0.06 ± 0.02, Female=0.03 ± 0.01	1.05	1, 50	0.31
		Proportion of infants that are female (covariate)		2.99	1, 50	0.09
4	Rate of approaches by infant to male	Infant sex	Female=0.20 ± 0.16, Male=1.02 ± 0.20	8.00	1,50	0.01
		Proportion of infants that are female (covariate)		11.13	1,50	0.00
5	Rate of approaches by male to infant	Infant sex	Female=0.04 ± 0.03, Male=0.15 ± 0.04	4.16	1,50	0.05
		Proportion of infants that are female (covariate)		5.52	1,50	0.02
6	Proportion of time male and	Dyad type	PO=0.10 ± 0.01, UO=0.08 ± 0.01,	7.04	2, 50	0.00

	mother are in proximity		PS= 0.04 ± 0.01			
7	Male-infant rate of affiliation	Dyad type	PO=0.25 ± 0.06, UO=0.02 ± 0.08, PS=0.22 ± 0.07	2.74	2, 49	0.07
		Number of infants available (covariate)		2.93	1,49	0.09
8	Male-infant rate of tolerance	Dyad type	PO=0.73 ± 0.16, UO=0.09 ± 0.22, PS=0.28 ± 0.19	3.59	2,49	0.04
		Number of infants available (covariate)		0.44	1,49	0.51
9	Male-infant time in proximity	Dyad type	PO=0.06 ± 0.01, UO=0.01 ± 0.02, PS= 0.04 ± 0.02	2.98	2,49	0.06
		Number of infants available (covariate)		3.95	1,49	0.05
10	Male-infant rate of affiliation	Paternity	Sire=0.31 ± 0.12, Non-Sire=0.16 ± 0.07	1.11	1,24	0.30
		Number of infants available (covariate)		1.02	1,24	0.32
11	Male-infant rate of tolerance	Paternity	Sire=0.96 ± 0.38, Non-Sire=0.44 ± 0.23	1.34	1,24	0.26
		Number of infants available (covariate)		1.03	1,24	0.32
12	Male-infant time in proximity	Paternity	Sire=0.07 ± 0.03, Non-Sire=0.05 ± 0.02	0.25	1,24	0.62
		Number of infants available (covariate)		2.51	1,24	0.13

Chapter Four: **Discussion**

4.1 Summary of key results

This is the first study to analyse positive interactions between males and infants in an African colobine. Males and infants interacted affiliatively more than expected when considering group composition, supporting the idea that these interactions may have an adaptive function. In support of the paternal care hypothesis, positive behaviours were observed at higher rates between males and potential offspring than between males and unlikely offspring, and more affiliative interactions were observed between males and infants than males and juveniles. The expression of positive behaviour did not differ between potential offspring dyads and potential sibling dyads. Males did not bias positive behaviour toward genetic offspring compared to non-offspring. Infant sex did not predict rates of positive behaviour. Mothers of these infants were not important in mediating interactions. Infants were primarily responsible for the establishment and termination of proximity bouts. There was some sex bias in the establishment of proximity by males and infants.

4.2 The non-adaptive hypothesis

To address the hypothesis that male-infant interactions could be non-adaptive, I tested whether affiliative male-infant interactions occurred more than expected based on infant availability in the group. Males interacted with infants significantly more than expected based the proportion of infants in the group. This result contradicts my prediction for the non-adaptive hypothesis, and thereby indicates that males and/or infants are making a choice to interact with

each other. This supports the idea that interactions are not a by-product of social living and are likely motivated by an adaptive function. This validates the testing of adaptive hypotheses.

4.3 Paternal care in *C. vellerosus*

4.3.1 Effect of potential and actual paternity

Positive behaviours occurred more within potential offspring dyads than within unlikely offspring dyads, which follows my first prediction of the paternal care hypothesis. Males did not, however, bias positive behaviour toward genetic offspring more than non-offspring. It is important to clarify that this does not necessarily undermine the paternal care hypothesis. This pattern suggests that males are relying on cues, such as their presence or absence at the time of conception, to estimate paternity and bias affiliation and tolerance. Ursine colobus males' apparent inability to accurately estimate paternity suggests that males do not have definite clues indicating paternity. This is possibly because female polyandrous mating is successfully confusing paternity. However, this suggestion hinges on the assumption that male-infant interactions are not also serving an alternative purpose (Borries *et al.* 1999). It is also possible that indiscriminate care could result if interactions are so low-cost that selection has not favoured elaborate paternity discrimination mechanisms in males, as might be the case with infant care by alpha male mountain gorillas (Rosenbaum *et al.* 2011). However, my anecdotal report of male KR protecting a non-offspring infant from an attacking male suggests that male ursine colobus express even costly behaviours toward potential but not genetic offspring. Nonetheless, the basis of this argument could still be relevant, if modified slightly to consider the relativity of costs and benefits. Sheldon (2002) articulates that the degree of paternity certainty necessary to favour paternal care depends on male future breeding potential, and these variables together affect the

value of the current potential/actual offspring to the male. Thus, while it is likely that polyandrous mating is effectively reducing paternity certainty, males might be favoured to 'cast their net wide' because of the complex intersection of paternity confusion, factors affecting access to future mates (eg. tenure length, male dominance status, number of females in the group, potential for secondary dispersal), and the cost of infant death.

My findings contrast studies that have used genetic data to demonstrate that males in polyandrous mating species can distinguish genetic offspring, implying that female polyandrous mating is not broadly confusing paternity in these species (*Papio cynocephalus* Buchan *et al.* 2003, *Pan troglodytes verus* Lehmann *et al.* 2006, *Mandrillus sphinx* Charpentier *et al.* 2007, *Macaca mulatta* Langos *et al.* 2013). My findings are more similar to the pattern reported by Borries *et al.* (1999) in hanuman langurs, where potential and actual sires defended infants from male attacks, indicating that hanuman langur males may also be casting their net wide. Lehmann *et al.* (2006) discuss the idea that polyandrous mating could be a conserved female strategy even if successful paternity confusion is only occasional. Polyandrous mating is proposed as a counterstrategy to male infanticide, and although I have not tested the effect of polyandrous mating on rates of infanticide, my findings contribute to this debate by supporting the hypothesis that polyandrous mating can confuse paternity on some level.

One problem with testing hypotheses about the conditions for paternal care is that researchers can never directly measure a male's paternity certainty. In this thesis, I imposed the criterion of presence or absence at the time of conception. The significant difference in positive behaviour between potential and unlikely offspring dyads suggests that this categorization holds some biological significance. Simultaneously, the observation that some males did not express any positive behaviour with potential offspring suggests that my criterion may not completely

capturing the cues that males might be using (i.e. males MS and MD with potential offspring S7 and V8, male KD with offspring XA, SW, and CK). This is similar to Borries *et al.*'s (1999) report that males who copulated with pregnant females did not defend the subsequent infants, and sometimes attacked them. In some cases, the discrepancy in my findings could relate to infant age, because I was only able to capture the first few months of life for infants that were born late in my field season (i.e. infants S7 and V8). During this time, these infants would have been more dependent on their mothers, leading to a skewed representation of their rates of positive behaviours with males. It is also possible that males vary in their ability to recognize and use cues, that males use more specific cues relating to the timing and quality of mating (e.g. *Semnopithecus entellus* Ostner *et al.* 2006), or that males use even broader cues to estimate paternity. For example, in species with high reproductive skew, male dominance rank could function as a simple cue for male paternity certainty (e.g. *Gorilla gorilla beringei* Rosenbaum *et al.* 2011, *Cebus capucinus* Seargant 2014. Preliminary data suggest that reproductive skew can be high in *C.vellerosus* (Teichroeb *et al.* 2013 report 6/7 infants sired by the alpha male in one multi male group). Male dominance rank should best tested in a larger dataset that includes more multi-male groups. Male tenure phase, or how long a male has been present in a group, could also be a broad but useful cue to a male. In general, testing the predictive value of fine and coarse grain cues that males could be using could lead to a better understanding of the cues that males may be using to determine paternity certainty. Finally, although it was not my intention to test mechanisms of kin recognition, it is not likely that males are using phenotypic matching to identify kin because genetic paternity was not a better predictor of positive behaviour than potential paternity. Alternatively, this could mean that they phenotypic cues are also an imperfect cue.

4.3.2 The effect of age

Following my second prediction of the paternal care hypothesis, higher rates of affiliative interactions were recorded between males and infants than males and juveniles. Further, there was only 6 occasions where males interacted with infants while they were with their mothers, suggesting that males are interacting with infants who are more independent from their mothers. This contrasts with Badescu's (2011) finding that males exhibited higher rates of attraction and handling of white or grey infants compared to black and white infants, although Badescu does not compare these values statistically. A more thorough analysis of infant age might reveal that rates of positive male-infant behaviours follow a bell-shaped curve, where interactions are infrequent with very young infants who are heavily dependent on their mothers; rates of interaction increase as infants gain independence but remain vulnerable to infanticide; and then drop off as infants near the age of weaning. This pattern is reported in rhesus macaques (Langos *et al.* 2013).

4.4 Positive male-infant behaviour

I have shown in this study that male ursine colobus show an array of low-intensity affiliative behaviours with infants and are generally tolerant. Intense care of infants occurs in the form of grooming behaviour and protection of infants from attacking extra-group males, but is expressed rarely. This is consistent with Badescu's (2011) finding that adult and sub-adult males in this population exhibit attraction to infants and handling of infants. My observations of males protecting potential offspring from extra-group male attacks are similar to previous reports in this population by Saj and Sicotte (2005) and Teichroeb and Sicotte (2008a, 2008b), and in

another colobine, *Semnopithecus entellus* (Borries *et al.*1999).

Among old world monkeys, the presence of positive male-infant behaviour has primarily been reported in macaques and baboons (reviewed in Paul *et al.* 2000, Muller and Emery Thompson 2012; Langos *et al.* 2013). Within colobines, records of positive interactions between infants and non-mothers have focused heavily on female-infant and juvenile-infant interactions, giving the impression that positive behaviour between adult or subadult males and infants is rare or absent (reviewed in McKenna 1979, Ross and MacLarnon 2000, MacKinnon 2011, Muller and Emery Thompson 2012, but see Xiang *et al.* 2009, Borries *et al.* 1999). My thesis contributes to the expanding body of evidence that positive male-infant interactions are more widespread in primates than initially thought.

4.4.1 Benefits of positive behaviour to infants

Before concluding that paternal care is occurring in *C. vellerosus*, it is necessary to revisit the potential benefits that positive behaviours might hold for colobus infants. I observed intense paternal care rarely, in the form of grooming and active defence of infants. Positive male infant behaviours were primarily comprised of affiliative interactions and tolerance by males that appear low-cost to the male. These behaviours could benefit offspring by providing a zone of reduced social conflict or lower foraging competition (*Gorilla beringei beringei*; Stewart 2001, Rosenbaum *et al.* 2011; *Papio cynocephalus*; Buchan *et al.* 2003, Onyango *et al.* 2013), by impacting infant development through play behaviour (Loizos 1967, Spinka *et al.* 2001), or through teaching skills (e.g. juvenile males trying stiff leg displays after displaying adult males, SF personal observation; Lonsdorf *et al.* 2004, reviewed in Lonsforf and Ross 2012). Among old world monkeys, proximity is arguably the most common form of paternal care, thought to

provide a 'safe zone', where infants suffer reduced threat from conspecifics, including

infanticidal males (Buchan *et al.* 2003, Charpentier *et al.* 2008b, Rosenbaum *et al.* 2011,

Onyango *et al.* 2013). Male tolerance and affiliation with infants might lead to greater

probability of male protection from infanticide if needed. Therefore, seemingly low cost

behaviours by a male could have high impact benefits for infants. The anecdotal reports of a

male attack on infant JJ while male OW was distant, and the effort made by male KR to maintain

proximity during the attack on infant VN both support the idea that proximity is valuable

paternal care in *C.vellerosus*. Maintaining proximity could also increase the chance that a male is

able to protect potential offspring from predators. In this thesis I have focused on mapping

patterns of positive male-infant behaviour onto conditions associated with male infanticide, and a

similar study should be done for predation pressure. For example, encountering predators that

differ in characteristics such as relative body size, predation tactic, or habitat use could result in

varying predictions for male behaviour toward potential offspring. In either case, more specific

measures of infant fitness benefits are needed to confirm the effect that male proximity might

have on infant fitness. While the precise benefits to infant fitness remain to be measured, I

suggest that these interactions globally reflect care by males.

4.4.2 Mechanics of male-infant spatial proximity

To understand the mechanics of male-infant spatial proximity, I analysed the pattern of

responsibility in the establishment and termination of proximity between adult males and infants.

Infants established and terminated bouts of proximity more than adult males; however, Hinde's

index showed variation between dyads in the degree of infant and male maintenance of

proximity. Although no dyad had a particularly strong index value in either direction, the dyads

where males maintained proximity more than infants were predominantly potential offspring dyads. More data is needed to test the idea that males are more concerned with maintaining proximity to their potential offspring compared to unlikely offspring or potential siblings. Despite not being able to calculate Hinde's index for many dyads, the index provides a useful point of quantitative comparison between species. For example, the variation in Hinde's index that I report differs from those found in mountain gorillas, where infants are primarily responsible for maintaining proximity to putative sires (Stewart 2001). Few studies describing male-infant interactions have reported Hinde's index. This may be because infants typically move between activities faster than adults, resulting in a skewed and less telling comparison. Future studies may be able to calibrate the relative rate of movement by infants and males using focal data, before analysing the establishment and termination of proximity. Nonetheless, for the purpose of this thesis, these measurements illustrate that although infants are likely making faster movements than males, in some cases males are still primarily responsible for the maintenance of proximity.

4.4.3 Triadic male-infant-male interactions

An interesting interaction that I observed was the tendency for infants to react to male displays by jumping and climbing on the displaying male while squealing intensely at him ('jump-on' interactions, Fox *et al.* 2015). Male colobus displays are typically targeted at extra-group males (Teichroeb and Sicotte 2010), qualifying 'jump-on' interactions as a component of a triadic male-infant-male interaction. Triadic male-infant-male interactions have been observed in various forms in a handful of other primate species, in both agonistic and affiliative contexts ('agonistic buffering': *Macaca sylvanus* Deag and Crook 1971, *Theropithecus gelada* Dunbar

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1984; 'bridging': *Macaca arctoides* Estrada 1984, *Macaca thibetana* Ogawah 1995, Bauer *et al.* 2014; 'interposition': *Gorilla beringei beringei* Sicotte 1995; 'passport': *Macaca fuscata* Itani 1959;'progeny protection': *Papio cynocephalus ursinus* Busse and Hamilton 1981, *Cercocebus atys* Busse and Gordon 1984). With the exception of the progeny protection hypothesis, interactions are thought to reduce social tension or facilitate male-male affiliative relationships and do not reflect potential or actual sireship. In all of these species, male-infant-male interactions occur within groups, in contrast to the between group interactions that I observed in ursine colobus. As an avenue for future research, it may be interesting to make a more thorough comparison of male-infant-male interactions in *C.vellerosus* with that observed in other primate species.

4.5 Potential sibling dyads

Although it was not my intention to test adaptive explanations for positive behaviours between males and infants who are potential siblings, the high rate of positive behaviours in these dyads that did not differ from rates of positive behaviours in potential offspring dyads necessitates some discussion. There are two primary hypotheses in primate literature that speak to interactions between sub-adult natal males and infants. First, natal males might interact with infants as means of forming social bonds with individuals who could be future allies, such as partners for dispersal. If this hypothesis is valid, we would expect natal males to bias affiliation toward male infants, as I discussed in more detail in section 4.6. Second, the 'maternal kin bias' hypothesis proposes that males might interact with infants who are maternal kin as a means of increasing their inclusive fitness (Reidman 1982, Nicolson 1987, reviewed in Langergraber 2012). The focus on maternal kin comes from the assumption that males are able to recognize

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maternal kin through associating with a common mother, but that individuals are unable to recognize paternal kin. Recent evidence challenging this assumption is beginning to surface (reviewed by Widdig 2007, Langergraber 2012), suggesting that maternal and paternal kin bias should both be considered. In either case, males could increase inclusive fitness by reducing their mother's burden of parental care, thereby increasing their mother's allocation of energy and resources to future offspring (eg. *Callitrichidae,* reviewed in Fernandez-Duque *et al.* 2012). In addition, sibling interaction with infants is associated with acceleration of infant transition to independence (*Macaca fuscata,* Hiraiwa 1981; *Macaca mulatta*, Berman 1982, Suomi 1982; *Pan troglodytes,* Brent *et al.* 1997). It can be adaptive for males to contribute to the success of their siblings if there is a low chance of successfully reproducing on their own, such as when they are still sexually immature. This hypothesis is uncommonly discussed in male-infant literature and is more commonly applied to female infant handling (eg. *Colobus vellerosus* Badescu *et al.* 2014). This hypothesis could, however, just as easily explain infant handling by male older siblings. An analysis of kin bias using coefficients of relatedness (r-values) was beyond the scope of this thesis, but is worth future investigation.

4.6 The effect of infant sex

Infant sex did not have a pronounced effect on the expression of positive behaviours in *C.vellerosus*. Infant males did, however, approach adult and sub-adult males more than infant females did; and adult and sub-adult males approached infant males more than they approached infant females. Nonetheless, it seems that this bias in attraction between males and male infants did not materialize in a difference of positive behaviours.

The variation in infant approaches that I observed is reflected in other studies, which found that juvenile and infant male primates tend to engage in play more than females, including rough-and-tumble and chasing play. These behaviours are thought to prepare infant males for mating competition later in life (reviewed in Brown and Dixson 2000, Lonsdorf and Ross 2012). Therefore, the differences in male and female infant approaches that I observed could reflect a broader trend in male and female infant development. Male colobus infants transition coat colours faster than female infants (Badescu *et al.* 2015), but whether males and females differ in behaviour or when they establish independence from their mothers is unknown.

Male preference for male infants is recorded in some other primate species. This is interpreted as an alliance building mechanism in male philopatric spider monkeys (Evans *et al.* 2012), and in white-faced capuchins, where males frequently disperse in parallel (Schoof *et al.* 2009). Male preference for male infants is also observed in *Macaca sylvanus* (Paul *et al.* 1996), *Macaca thibetana* (Zhao 1996) and *Macaca mulatta* (Langos *et al.* 2013) but is not well understood. Male colobus monkeys are known to disperse in parallel (Teichroeb *et al.*2011). Although this is seen more among sub-adult males than adult males, in one case a father and son were observed to disperse together (Teichroeb *et al.* 2011). Adult female colobus handle male infants more than female infants (Badescu *et al.* 2014). Badescu *et al.* (2014) suggest that this might reflect an increased need to protect male infants from infanticide, because infanticidal males have targeted male infants more than female infants (Teichroeb and Sicotte 2008a). Therefore, it may be of interest to investigate if male bias for male infants becomes a significant pattern in a larger data set, and examine if the bias is stronger in sub-adult male dyads compared to adult male dyads, or potential offspring dyads compared to unlikely offspring dyads.

4.7 Mother mediation

The finding that mothers are not important mediators of male-infant interactions is important for two reasons. First, female colobus did not associate with males based on potential paternity, thus instantaneous cues from females were probably not functioning as an indicator of paternity for males. This contrasts behaviour seen in chacma baboons, where females seek out and maintain 'friendships' with protective males who are likely sires (Palombit 2009). Second, the absence of mothers in the majority of interactions suggests that male-infant interactions are probably not a tactic for males to gain current mating access to females. This does not rule out the possibility that mating effort is occurring through male-infant interactions. There could be a time lag between when males interact with infants and when they gain access to females, or interactions could increase female reproductive rates by accelerating infant transition to independence.

4.8 Conclusion

This thesis makes important contributions to primate literature in two immediate ways. First, my findings contribute to the building evidence that paternal care can and does occur in polyandrous mating primates, and suggests that high paternity certainty may not be as important a prerequisite for paternal care as initially thought. Second, my findings contribute to the discussion of sexual conflict in primate reproductive strategies by supporting the hypothesis that polyandrous mating could be confusing paternity in *C.vellerosus*. This contrasts the pattern that has emerged in some other primate species where males do differentiate offspring. On a more global scale, these findings speak to the pervasive importance of infanticide as a selection pressure in primate social evolution; to the range of conditions under which paternal care might

evolve in human and non-human primates; and to the range of paternal roles that males can play in their offspring's lives.

A.1. Demographic changes in group composition

	Individual ID	Age/Sex	Group	Date (2013)
Births	T2	IM	RT	June 26
	B9	IF	RT	May 23
	F9	IM	RT	September 9
	S7	IM	SP	September 13
	V8	IF	SP	October 9
	C7	IM	WW	October 23
Deaths	19	IM	WT	September 13
	CK	IF	SP	September 15
	CC	IM	RT	September 19
	T2	IF	RT	September 19
	PK	JM	RT	October 5
Immigration	KD	AM	SP	June 21
Emigration	AB	SM	SP	June 21
	KO	SF	SP	June 5
	SB	SM	SP	Aug 28
Weaning	CK	JF	SP	August 17
	XA	JF	SP	August 30
	CX	JF	WW	September 14
	SW	JM	SP	September 26
	BO	JF	RT	October 16

A.2. Fecal samples that I worked on in Dr. Ting's lab, listed by monkey ID.

Monkey ID*	Number of samples used	Number of loci confirmed by SF	Samples collected by?	Started by Dr. Wikberg?
B9	1	10	AC	N
BB	2	6	EW	Y
BO	1	10	SF	N
BY	1	9	SF	N
CC	2	10	SF	N
CI	1	3	EW	Y
CK	1	10	SF	N
CO	1	6	EW	Y
CX	1	10	SF	N
DU	2	10	SF	N
EA	2	2	EW	Y
ET	1	8	EW	Y
F9	1	10	AC	N
FV	2	10	SF	N
GI	3	9	EW	Y
GO	2	8	EW	Y
I9	1	9	SF	N
IB	2	10	SF	N
IS	1	7	EW	Y
IT	1	5	EW	Y
JA	1	6	EW	Y
JJ	2	0	AC	N
JK	2	10	AC	N
JS	2	10	SF	N
KD	2	10	SF	N

Monkey ID*	Number of samples used	Number of loci confirmed by SF	Samples collected by:	Started by Dr. Wikberg?
LI	1	10	EW	Y
LS	2	10	EW	Y
LY	1	9	SF	N
MD	2	9	SF	N
MS	2	10	SF	N
NS	2	10	EW	Y
OW	3	10	SF	N
PE	2	10	SF	N
PG	1	3	EW	Y
S7	1	8	AC	N
S9	1	10	SF	N
SB	1	10	SF	N
SC	2	9	EW	Y
SH	2	8	EW	Y
SR	1	10	EW	N
SU	2	5	EW	Y
SW	1	9	SF	N
TE	2	10	SF	N
V8	1	0	AC	N
VM	1	10	AC	N
VN	2	10	SF	N
WH	1	8	EW	Y
WO	2	9	EW	Y
XA	1	10	SF	N

* Genotypes of individuals whose ID is bolded were used in the analysis for this thesis.

A.3. Rates of affiliative interaction (RA), male tolerance (RT), and time in proximity (TP) per male-infant dyad.

Group	Male	Infant	Infant Sex	Dyad Type	Paternity*	RA[1]	RT[2]	TP[3]
RT	CC	S9	M	PO	Y	0.61	2.54	0.02
		BO	F	PO	Y	0.22	1.38	0.10
		B9	F	PO	Y	0.66	1.05	0.10
		T2	F	PO	no data	0.12	0.87	0.10
	JK	S9	M	PO	N	0.00	0.07	0.01
		BO	F	PO	N	0.00	0.00	0.01
		B9	F	PO	N	0.00	0.00	0.01
		T2	F	PO	no data	0.00	0.00	0.00
		F9	M	PO	N	0.11	0.00	0.00
	PE	S9	M	PS	N	0.37	0.64	0.07
		BO	F	PS	N	0.31	0.25	0.03
		B9	F	PS	N	0.32	0.54	0.03
		T2	F	PS	no data	0.09	0.09	0.02
		F9	M	PS	N	0.00	0.00	0.00
	SR	S9	M	PS	N	0.00	0.12	0.02
		BO	F	PS	N	0.26	0.07	0.03
		B9	F	PS	N	0.00	0.23	0.02
		T2	F	PS	no data	0.00	0.21	0.00
		F9	M	PS	N	0.00	0.00	0.00
	JS	S9	M	PS	N	0.14	0.21	0.01
		BO	F	PS	N	0.39	0.46	0.05
		B9	F	PS	N	0.21	0.96	0.03
		T2	F	PS	no data	0.00	0.24	0.02
		F9	M	PS	N	0.00	0.15	0.01

Group	Male	Infant	Infant Sex	Dyad Type	Paternity*	RA[1]	RT[2]	TP[3]
WW	OW	IB	M	PO	Y	0.47	1.12	0.17
		CX	F	PO	N	0.10	0.73	0.11
		JJ	F	PO	no data	1.08	1.83	0.13
		C7	M	PO	no data	0.00	0.00	0.00
SP	MS	XA	F	UO	N	0.00	0.00	0.03
		CK	F	UO	N	0.00	0.00	0.01
		SW	M	UO	N	0.06	0.11	0.03
		S7	M	PO	N	0.00	0.00	0.00
		V8	F	PO	no data	0.00	0.00	0.00
	MD	XA	F	UO	N	0.00	0.00	0.03
		CK	F	UO	N	0.00	0.21	0.01
		SW	M	UO	N	0.21	0.31	0.04
		S7	M	PO	N	0.00	0.12	0.00
		V8	F	PO	no data	0.00	0.00	0.00
	TE	XA	F	UO	N	0.00	0.00	0.06
		CK	F	UO	N	0.28	0.00	0.01
		SW	M	UO	N	0.26	0.00	0.04
		S7	M	UO	N	0.00	0.83	0.01
		V8	F	UO	no data	0.00	0.00	0.00
	SB	XA	F	PS	N	0.44	0.00	0.07
		CK	F	PS	N	0.18	0.00	0.02
		SW	M	PS	N	0.44	0.00	0.03

Group	Male	Infant	Infant Sex	Dyad Type	Paternity*	RA1	RT2	TP3
SP	KD	XA	F	PO	Y	0.00	0.00	0.00
		CK	F	PO	Y	0.00	0.00	0.00
		SW	M	PO	Y	0.00	0.00	0.02
		S7	M	UO	N	0.10	0.42	0.04
		V8	F	UO	no data	0.00	0.00	0.00
WT	KR	VN	F	PO	N	1.08	2.83	0.32
		I9	M	PO	N	1.09	3.72	0.31

*paternity was not confirmed for infants T2, V8 and JJ because samples were unobtainable, identified incorrectly, or got contaminated.

[1] Interactions/focal hour

[2] Bouts of tolerance/focal hour

[3] Proportion of point samples in proximity

APPENDIX B: ETHOGRAM USED DURING BEHAVIOURAL DATA COLLECTION

This ethogram includes the codes used for all long term data collection at BFMS.

CODE	USAGE
TYPE OF DATA	
A	adlib interaction. Followed by behavior code, actor, receiver, and then "other" ID (if it's a triadic interaction)
F	dyadic interaction where focal is actor. Followed by behavior, then recipient ID
R	dyadic interaction where focal is the recipient of the behavior from other; followed by behavior, then other ID
M	mutual initiation of interaction; followed by behavior and other ID in focal follows
S	self-directed behavior or non-directed behavior by focal
PROXIMITY CLASSES	
0	in body contact
1	within one tail length (approximately one meter)
3	within three tail lengths
5	within 5 tail lengths
W	in view, can be used during intergroup interactions
N	nursing (in contact)
V	ventral
/	if infant is in V or N of another (usually mother) during another individual's group scan/focal
PROXIMITY RELATED BEHAVIOURS	
AL	follow
AR	run towards
A	approach
L	leave
D	dorsal (approach/leave/follow)
SELF DIRECTED BEHAVIOURS	
AB	defecate
AE	piloerect
AF	fecal rub
AG	autogroom
AH	touch
AI	inspect
AL	bug slap

AM	masturbate
AME	masturbate end
AN	erection
ANE	erection end
AP	autoplay
AS	scratch
AU	urinating
AV	vigilant
AY	yawn

DISPLAY BEHAVIOURS

DB	stiff leg, both legs on branch
DE	display end
DH	display hop
DI	stiff leg, one leg only
DJ	jump display
DL	stiff leg, one leg on branch
DM	small open mouth
DO	open mouth
DR	run display/run through
DS	stiff leg, two legs

AFFILIATIVE BEHAVIOURS

FB	tail grab - usually by an infant
FE	end groom
FE S	grooming at end of follow
FF	play face
FG S	grooming at start of follow
FG	start groom
FH	hug
FI	inspect
FJ	jumps on top of other individuals (often infant jumps on male when stiff legs)
FK	kiss/mouth to mouth/face sniff/face inspect
FL	play present
FM	grooming open mouth, not as wide as normal open mouth
FO	over the head mount
FP	groom present
FQ	tail hits another individual
FR	each for
FS	sniff

FT	touch
FU	friendly pull
FY	play

AGGRESSIVE AND SUBMISSIVE BEHAVIOURS

GA	avoid
GB	bite
GC	chase
GD	displace. Includes approach of displacer to 2 m and a leave by the displaced animal within 5 seconds of the approach (sensu Palombit et al 2001., p1161). (F food, S social partner, R resting spot)
GE	aggressive end
GF	flee
GG	fear grin
GH	hit
GJ	bounce
GL	lunge
GM	moving displace. One individual leaves before the second one approaches to one but the second one takes the spot of the first one
GN	pinch
GO	cower
GP	pounce on
GQ	small displace; the displayed individual stays in one
GV	push, shove
GR	grab
GS	snap at
GT	submissive present.
GU	pull
GW	swipe at
GX	contact fighting (when I don't see exact behaviors I use contact fighting)
GY	delayed displace
GZ	nose grab

INFANT RELATED BEHAVIOURS

IA	attempted transfer
IB	infant climb
IC	carry
ID	infant dorsal
IE	end nursing
IE S	nursing at end of follow

IF	failed nursing attempt or attempt to get to nursing position
II	ride invite
IL	infant waves its tail
IN	start nursing
IN S	nursing at start of follow
IO	try to get infant off nipple
IR	restrain, hold back, resist transfer, retrieve infant, i.e. pull infant to body contact.
IS	infant swings on another individuals tail (during play)
IT	transfer infant
IV	infant in ventral position
IW	want to get infant off ventral/dorsal position

SOCIAL FOOD RELATED BEHAVIOURS

MA	attempted theft
MC	co-feeding (in the same spot, within 1 tail length from the same cluster of leaves/food patch)
MI	food interest
MO	tolerated theft
MS	steal food
MT	touch others food

SEXUAL BEHAVIOUR

SA	attempted mount
SD	dismount
SE	sex end
SJ	ejaculate
SG	sex grin
SH	hip touch
SI	inspect anogenital area
SL	sexual slap. Ie female reaches around a hits male during copulation
SM	mount
SN	sniff anogenital area
SP	present
SR	resist mount
SS	stop thrust without dismount
ST	mount with thrust
SW	watches sex, looks at couple copulating with or without interference.
SH	sexual harassment

VOCALIZATIONS

VA	click-alarm call

VC	click before loud call
VG	grunt
VF	fast grunt
VH	cough, the vocalization not just coughing
VI	intense grunt
VK	click when open mouth
VL	loud call
VP	pant grunt
VQ	squeal, normal - followed by space I for intense or space W for weak.
VR	fight roar
VS	scream
VT	intense pant grunt
VU	unhappy vocalization
VY	yelp
VX	unknown vocalization
*D or Group Name	if vocalization is coming from distance

FOOD RELATED BEHAVIOURS

B	bite
H	handle
I	ingest

FOOD ITEMS

A	sap
B	bark
D	water/drink
E	flower bud
F	fruit
G	grass
H	pith
I	stem of the fruit
K	stick
L	leaf
M	mature leaf
O	other
P	seed pod
Q	leaf bud
R	flower
S	seed
T	petiole (leaf stem?)

U	bud
V	vine
W	wall
X	unknown
Y	young leaf

TRAVEL

TT	start travelling
TE	end travelling
TD	travel distance, e.g. TD5 for travelling 5 tail lengths
TTS	start travelling before start of follow
TES	end travelling after the end of the follow
TS	small movements – often when individuals are playing (with another conspecific or solitary play) next to the focal individual. Eg. RTSJJ
TSE	small movement end. Eg. RTSJJE. (I put E at end of line to reduce errors in parsing)
TSS	small movement is continuing at end of focal. Eg. RTSJJS (put S at end to reduce error in parsing.

GROUP SCANS AND POINT SAMPLES

X	proximity data within focal samples, followed by distance code and all IDs within that category.
Y	activity at point sample

ACTIVITY CODES FOR POINT SAMPLES AND GROUP SCANS

AA	other self-directed behavior
AG	autogroom or scratch
FB	foraging in bark
FD	drink
FF	foraging fruit
FL	foraging leaf
FO	foraging 'other'
FT	foraging and locomoting simultaneously
OT	other
RE	rest lying or sitting, sleep, standing still
SA	aggressive behavior
SD	social display
SF	social friendly, affiliative other than grooming
SG	groom
SM	social food-related behavior
SP	play (social)
SS	sexual behavior

ST	triadic/coalitionary behavior
SU	submissive behavior
TT	travelling
TV	travelling and vigilant
VF	visually foraging, scanning close range for food (conspecifics)
VV	vigilant, scanning longer range

CODES TO ID CONSPECIFICS

XX	unidentified
XM	unidentified male
XF	unidentified adult female
XJ	unidentified juvenile
XB	unidentified infant
NM	new male

OTHER ANIMALS

OO	observer
OH	other human besides observers
ZM	mona monkey
ZB	bird
ZS	snake
ZP	sheep
ZG	pig
ZC	other colobus

OTHER CODES

F	food
S	social partner
R	resting spot
I	infant
D	in distance
R	reply
M	mutual
X	sexual harassment
OG	gunshot
OV	out of view
OVF	face out of view
IV In view	in view
IVF Face in view	face in view
D	focal subject ignores whatever happened on the previous line

FAV	focal subject looks at whatever happened on the previous line or looks at monkey if followed by ID code (e.g. FAVPO) or looks at jumps (FAV JUMP)

LOCATION POINTS

CL	Location when tree is not on the map
L	Location when tree is on the map, e.g. 150DA1
LG	Location taken on the GPS
LM	Centre of mass (use tree location point from on the map)

INTERGROUP BEHAVIOURS

IS	Intergroup start EG. ISSWT
ISS	Intergroup started before observer arrived
IE	Intergroup end
IES	Intergroup still going on when observer leave
IL	Location of encountered group or focal group if taking other location points than those scheduled on the hour
IW	Winner
IR	Contested resource
IY	Activity before, during, after intergroup
IM	Main participant

COMMENTS

C	comments general
CA	allomothering
CB	comment birth/death/disappearances
CC	conditions (weather, visibility etc)
CE	comment for data editing and analyses
CF	food (e.g. descriptions of plants)
CG	group ID, group composition etc
CI	intergroup
CM	group movement, animals relative position, leader of progression
CN	comment nursing
CP	focal animal's location during follow
CS	focal animal's relative position during follow, followed by C/I/P
CR	reaction to vocalizations
CT	triadic interactions
CV	description of vocalizations
CW	wounds
CX	comment sex/consorts
CY	comment play/games
CZ	interspecific interactions

APPENDIX C: PROTOCOL FOR DNA EXTRACTION FROM FECAL SAMPLES

This protocol is based on the QIAamp DNA Stool Mini Kit (Qiagen cataolog 51504) with modifications as suggested by Dr. M.J. Ruiz-Lopez and Dr. E.C. Wikberg for optimal extraction success.

To lyse DNA samples, I pipetted 800µl of the fecal sample (feces mixed with RNAlater) into a 2ml tube with 1ml of ASL buffer and 1 mg (50µl) of proteinase K. This lysate solution was shaken in an incubator overnight at 55°C and 300rpm in a dark room. The next day, I centrifuged samples at full speed for 1 minute to pellet stool particles, and then pipetted 1.4ml of the supernatant into a new 2ml tube. I added ½ of an InhibitEx tablet to each sample and then vortex the sample continuously for 1-minute until the table was completely suspended. I incubated this suspension for 1 minute at room temperature to allow inhibitors to absorb to the InhibitEx matrix. I centrifuged the sample at full speed for 5 minutes to pellet stool particles, and I pipetted all of the supernatant into a new 1.5ml microcentrifuge tube. I discarded the pellet and repeated this process centrifuging the sample at full speed for 3 minutes. I then pipetted 600µl of supernatant into new 2ml microcentrifuge tube, and added 600µl of buffer AL. I vortexed the sample for 15 seconds, to ensure that the sample and buffer AL were thoroughly mixed to form a homogenous solution, and then incubated this mixture at 70°C for 10 minutes. I added 600µl of ethanol (96-100%) to the solution, mixed by vortexing, and then applied 600µl of the lysate to a QIAamp spin column spin column. I centrifuged the spin column at full speed for 1 minute, and discarded the filtrate. This was repeated two more times until all of the lysate solution was passed through the spin column. Next I applied 500µl of buffer AW1 to the spin column filter, and centrifuged the column at full speed for 1 minute, and discarded the filtrate. This was

repeated with 500μl of buffer AW2, but centrifuged for 3 minutes. I eluted DNA from the spin column filter by applying 75μl of buffer AE directly on filter, leaving this to incubate at room temperature for 30 minutes, and then centrifuge at full speed for 2 minutes. I kept DNA extracts refrigerated at 4°C to avoid freeze-thaw cycles while carrying out PCR reactions.

References

Achenbach G, Snowdon C. 2002. Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. Int J Primatol 23:179–189.

Alberts SC. 1999. Paternal kin discrimination in wild baboons. Proc Biol Sci 266:1501–1506.

Alonzo SH, Klug H. 2012. Paternity, maternity and parental care. In Royle NJ, Smiseth PT, Kolliker M (Eds), The evolution of parental care. 2012. Oxford University Press, UK. p.189-205.

Altmann J. 1974. Observational study of behavior - sampling methods. Behaviour 49:227–267.

Anderson KG, Kaplan H, Lam D, Lancaster JB. 1999. Paternal care by genetic fathers and stepfathers II: reports by Xhosa High School students. Evol Hum Behav 20:433–51

Arandjelovic M, Guschanski K, Schubert G, Harris T, Thalmann O, Siedel H, Vigilant L. 2009. Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. Mol Ecol Res 9:28-36.

Arnqvist G, Rowe L. 2005. Sexual Conflict. Princeton University Press, USA.

Badescu I. 2011. The effect of female kinship and relatedness on infant handling in ursine colobus. Masters Thesis. University of Calgary, Calgary.

Badescu I, Sicotte P, Ting N, Wikberg EC. 2014. Female parity, maternal kinship, infant age and sex influence natal attraction and infant handling in a wild colobine (*Colobus vellerosus*). Am J Primatol.77:376-387.

Badescu I, Wikberg EC, Macdonald L, Fox SA, Vayro J, Sicotte P. 2015. Infanticide pressure and group size affect natal coat development in wild *Colobus vellerosus* at Boabeng-Fiema Monkey Sanctuary, Ghana. 84th Annual Meeting of the American Association of Physical Anthropologists, St. Louis, USA.

Bales KL, Dietz JM, Baker AJ, Miller KE, Tardif SD. 2000. Effects of allocare-givers on fitness of infants and parents in callitrichid primates. Folia Primatol. 71:27–38

Balshine S. 2012. Patterns of parental care in vertebrates. In Royle NJ, Smiseth PT, Kolliker M (Eds), The evolution of parental care. 2012. Oxford University Press, UK. p.62-80.

Bardi M, Shimizu K, Fujita S, Borgognini-Tarli S & Huffman M. 2001. Hormonal correlates of maternal style in captive mcacques (*Macaca fuscata* and *M. mulatta*). Int J Primatol 22:647-662.

Berman CM. 1982. The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys: social networks and differentiation. Anim Behav 28:860-873.

Bauer B, Sheeran LK, Matheson MD, Li J-H, Wagner SR. 2014. Male Tibetan macaques (*Macaca thibetana*) choice of infant bridging partners. Zool Res 35:222–230.

Borries C, Koenig A, Winkler P. 2001. Variation in life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). Behav Ecol and Sociobiol 50:391-402.

Borries C, Launhdart K, Epplen C, Epplen JT, and Winkler P. 1999. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups – defense pattern, paternity and sexual behavior. Behav Ecol and Sociobiol 46:350-356

Bradley BJ, Boesch C, Vigilant L. 2000. Identification and redisgn of human microsatellite markers for genotyping wild chimpanzee (*Pan troglodytes*) and gorilla (*Gorilla gorilla gorilla*) DNA from faeces. Conser Genet 1:289-292.

Brent L, Bramblett CA, Bard KA, Bloomsmith MA, Blangero J. 1997. The influence of siblings on wild chimpanzee social interaction. Behaviour 134:1189-1210.

Brown GR, Dixson AF. 2000. The development of behavioural sex differences in infant rhesus macaques (*Macaca mulatta*). Primates 41:63–77.

Buchan JC, Alberts SC, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. Nature 425:179–181.

Busse CD, Gordon TP. 1984. Infant carrying by adult male mangabeys (*Cercocebus atys*). Am J Primatol 6:133–141.

Busse CD, Hamilton WJ. 1981. Infant carrying by male chacma baboons. Science 212:1281–1283.

Célérier A, Huchard E, Alvergne A, Féjan D, Plard F, Cowlishaw G, Raymond M, Knapp LA, Bonadonna F. 2010. Detective mice assess relatedness in baboons using olfactory cues. J Exp Biol 213:1399–1405.

Charpentier MJE, Boulet M, Drea CM. 2008b. Smelling right: the scent of male lemurs advertises genetic quality and relatedness. Mol Ecol 17:3225–3233.

Charpentier MJE, VanHorn R, Altmann J, Alberts SC. 2008a. Paternal effects on offspring fitness in a multimale primate society. PNAS 105:1988–1992.

Charpentier MJE, Peignot P, Hossart-McKey M, Wickings EJ. 2007. Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. Anim Behav 73:9–9.

Clarke P, Pradhan G, van Schaik CP. 2009. Intersexual conflict in primates: infanticide, paternity allocation, and the role of coercion. In Muller M, Wrangham RW (Eds), Sexual coercion in primates and humans. Harvard University Press, USA. p.42-80.

Clutton-Brock TH. 1991. The Evolution of Parental Care. Princeton University Press, USA.

Coote T, Bruford MW. 1996. Human microsatellites applicable for analysis of genetic variation in apes and old world monkeys. J Hered 87:406-410.

Deag J, Crook J. 1971. Social behaviour and 'agonistic buffering' in the wild Barbary macaqus *Macaca sylvana*. Folia Primatol 15:183–200.

Dunbar R. 1984. Infant-use by male gelada in agonistic contexts: Agonistic buffering, progeny protection or soliciting support? Primates 25:28–35.

Edwards AWF. 1972. Likelihood. An account of the statistical concept of likelihood and its application to scientific inference. Cambridge University Press, London-New York.

Estrada A. 1984. Male-infant interactions among free-ranging stumptail macaques. In Taub DM (Ed), Primate Paternalism. Van Nortrand Reinhold, New York. p. 56-87.

Evans K, Pavelka M, Hartwell K, Notman H. 2012. Do adult male spider monkeys (*Ateles geoffroyi*) preferentially handle male infants? Int J Primatol 33:799-808.

Fairbanks L.1990. Reciprocal benefits of allomothering for female vervet monkeys. Anim Behav 40:553-562.

Fargey PJ. 1992. Boabeng-Fiema Monkey Sanctuary – an example of traditional conservation in Ghana. Oryx 26:151-156.

Fernandez-Duque E, Di Fiore A, Huck M. 2012. The behaviour, ecology, and social evolution of New World monkeys. In Mitani, JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds), The Evolution of Primate Societies. The University of Chicago Press, Chicago. p.43-64.

Fernandez-Duque E, Juárez CP, Di Fiore A. 2008. Adult male replacement and subsequent infant care by male and siblings in socially monogamous owl monkeys (*Aotus azarai*). Primates 49:81–84.

Fernandez-Duque E, Valeggia C, Mendoza SP. 2009. The biology of paternal care in human and nonhuman primates. Annu Rev Anthropol 38:115-130.

Fietz J, Dausmann KH. 2003. Costs and potential benefits of parental care in the nocturnal fat-

tailed dwarf lemur (*Cheirogaleus medius*). Folia Primatol 74:246-258.

Fitchel C. 2012. In Mitani, JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds), The Evolution of Primate Societies. The University of Chicago Press, Chicago. p.169-194.

Fox SA, Vayro J, Potvin-Rosselet E, Crotty A, Sicotte P. 2015. Infant involvement in male agonistic displays in black and white colobus monkeys (*Colobus vellerosus*). 84th Annual Meeting of the American Association of Physical Anthropologists, St. Louis, USA.

Fragaszy DM, Schwarz S, Shimosaka D. 1982. Longitudinal observations of care and development of infant tit-monkeys (*Callicebus moloch*). Am J Primatol 2:191-200.

Geary DC. 2000. Evolution and Proximate Expression of Human Paternal Investment. Psychological Bulletin 126:55–77.

Goldzein AW. 1987. Tamarins and Marmosets: Communal Care of Offspring. In Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Strusaker TT (Eds), Primate Societies. University of Chicago Press, Chicago. p.34-43.

Gust D. 1994. A brief report on the social behavior of the crested mangabey (*Cercocebus galeritus galeritus*) with a comparison to the sooty mangabey (*C. torquatus atys*). Primates 35:375-383.

Harcourt AH. 1979. Social relationships between adult male and female mountain gorillas in the wild. Anim Behav 27:325-342.

Hauber ME, Sherman PW. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. Trends Neurosci 24:609–616.

Hawkes K. 2004. Mating, parenting, and the evolution of human pair bonds. In Chapais C and Berman CM (Eds), Kinship and Behavior in Primates. Oxford University Press, Oxford. p.443–73.

Hewlett BS. 1992. Introduction. In Hewlett BS (Ed), Father-child relations, cultural and biosocial contexts. Aldine, New York. p. xi-xix.

Hill KR, Hurtado AM. 1996. Ache Life History: The Ecology and Demography of a Foraging People. Aldine de Gruyter, New York.

Hinde R, Atkinson S. 1970. Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in rhesus monkeys. Anim Behav18:169-176.

Hirawa M. 1981. Maternal and alloparental care in troop of free-ranging Japanese monkeys. Primates 22:309-329.

Hrdy SB. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13-40.

Hrdy SB. 2009. Mothers and Others: The Evolutionary Origins of Mutual Understanding. Harvard University Press, USA.

Hrdy SB, Hausfater G. 1984. Introduction and overview. In Hausfater G, Hrdy SB (Eds.) Infanticide: comparative and evolutionary perspectives. Aldine, New York. p. xiii-xxxv.

Huck M, Fernandez-Duque E, Babb P, Schurr T. 2014. Correlates of genetic monogamy in socially monogamous mammals: insights from Azara's owl monkeys. Proc Biol Sci 281:20140195.

Itani J. 1959. Paternal care in the wild Japanese monkey, *Macaca fuscata fuscata*. Primates. 2:61-93.

Janson C. 2000. Primate socio-ecology: The end of a golden age. Evol Anthropol 9:73-86.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16:1099–1106.

Kalinowski ST, Wagner AP, Taper ML. 2006. ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Mol Ecol Notes 6:576–579.

Kankam BO, Sicotte P. 2013. The effect of forest fragment characteristics on abundance of *Colobus vellerosus* in the forest-savanna transition zone of Ghana. Folia Primatol (Basel) 84:74–86.

Kazem AJN, Widdig A. 2013. Visual phenotype matching: cues to paternity are present in rhesus macaque faces. PLoS ONE 8:e55846–e55846.

Key C, Aiello LC. 2000. A Prisoner's Dilemma model of the evolution of paternal care. Folia Primatol (Basel) 71:77–92.

Kitchen DM. 2004. Alpha male black howler monkey responses to loud calls: effect of numeric odds, male companion behaviour and reproductive investment. Anim Behav 67:125–139.

Kleiman DG, Malcolm JR. 1981. The evolution of male parental investment in mammals. In Gubernick DJ, Klopfer PH (Eds), Parental Care in Mammals. Plenum Press, New York. p.347-388.

Lamb ME. 1987. Father's role: cross cultural perspectives. Erlbaum, New York.

Lamb ME. 2010. How to fathers influence children's development? Let me count the ways. In Lamb ME (Ed), The Role of the Father in Child Development. John Wiley and Sons Inc, New Jersey. p. 1-26.

Langergraber KE. 2012. Cooperation among kin. In Mitani, JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds), The Evolution of Primate Societies. The University of Chicago Press, Chicago. p. 491-514.

Langos D, Kulik L, Mundry R, Widdig A. 2013. The impact of paternity on male-infant association in a primate with low paternity certainty. Mol Ecol 22:3638–3651.

Lappan S. 2008. Male care of infants in a siamang (*Symphalangus syndactylus*) population including socially monogamous and polyandrous groups. Behav Ecol Sociobiol 62:1307–1317.

Lehmann J, Fickenscher G, Boesch C. 2006. Kin biased investment in wild chimpanzees. Behaviour 143:931-955.

Lessels CM. 2012. Sexual Conflict. In Royle NJ, Smiseth PT, Kolliker M (Eds), The Evolution of Parental Care. Oxford University Press, UK. p.150-170.

Loizos C. 1967. Play behavior in higher primates: a review. In D. Morris (Ed), Primate Ethology. Aldine, New York. p.176-218.

Lonsdorf EV, Pusey AE, Eberly L. 2004. Sex differences in learning in chimpanzees. Nature, 428: 715-716.

Lonsdorf EV, Ross SR. 2012. Socialization and development. In Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds), The Evolution of Primate Societies. The University of Chicago Press, Chicago. p.245-268.

MacDonald L. 2011. Infant development in *Colobus vellerosus*. Masters Thesis. University of Calgary, Calgary.

MacKinnon KC. 2011. Social beginnings: the tapestry of infant and adult interactions. In Campbell CJ, Fuentes A, MacKinnon KC, Bearder SK, Stumpf RM (Eds), Primates in Perspective. Oxford University Press, Oxford. p.440-454.

Marlowe F. 2000. Paternal investment and the human mating system. Behav Process 51:45–61.

Marshall TC, Slate J, Kruuk LE, Pemberton JM. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Mol Ecol 7:639–655.

Martin P, Bateson P. 1993. Measuring behaviour : an introductory guide. Cambridge University Press, Cambridge and New York.

Mateo JM, Johnston RE. 2003. Kin recognition by self-referent phenotype matching: weighing the evidence. Anim Cogn 6:73–76.

Maynard-Smith J. 1977. Parental investment: a prospective analysis. Anim Behav 25:1–9.

McDonald PG, Wright J. 2011. Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. Proc Biol Sci 278:3403–3411.

McKenna JJ. 1979. The evolution of allomothering behavior among colobine monkeys: function and opportunism in evolution. Am Anthropol 81:818–840.

Ménard N, Segesser von F, Scheffrahn W, Pastorini J, Vallet D, Gaci B, Martin RD, Gautier-Hion A. 2001. Is male-infant caretaking related to paternity and/or mating activities in wild Barbary macaques (*Macaca sylvanus*)? C R Acad Sci III 324:601–610.

Mitani J, Watts D. 1997. The evolution of non-maternal caretaking among anthropoid primates: do helpers help? Behav Ecol Sociobiol 40:213–220.

Morin PA, Chambers KE, Boesch C, Vigilant L. 2001. Quantitative polymerase chain reaction analysis of DNA from non-invasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Mol Ecol 10:1835–1844.

Moscovice LR, Di Fiore A, Crockford C, Kitchen DM, Wittig R, Seyfarth RM, Cheney DL. 2010. Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. Anim Behav 79:1007–1015.

Muller MN, Emery-Thompson M. 2012. Mating, Parenting, and Male Reproductive Tactics. In Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds), The Evolution of Primate Societies. The University of Chicago Press, Chicago. p.387-411.

Newton-Fisher N. 1999. Association by male chimpanzees: a social tactic? Behaviour 136:705–730.

Nicolson NA. 1987. Infants, Mothers and Other Females. In Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Strusaker TT (Eds), Primate Societies. University of Chicago Press, Chicago. p 330-342.

Nunn CL, van Schaik CP. 2000. Social evolution in primates: the relative roles of ecology and intersexual conflict. In van Schaik CP, Janson CH (Eds), Infanticide by males and its implications. Cambridge University Press, Cambridge. p.388-412.

Ogawah H. 1995. Bridging behavior and other affiliative interactions among male tibetan macaques (*Macaca thibetana*). Int J Primatol 16:707–729.

Onyango PO, Gesquiere LR, Altmann J, Alberts SC. 2013. Testosterone positively associated

with both male mating effort and paternal behavior in Savanna baboons (*Papio cynocephalus*). Horm Behav 63:430–436.

Ostner J, Chalise MK, Koenig A, Launhardt K, Nikolei J, Podzuweit D, Borries C. 2006. What Hanuman langur males know about female reproductive status. Am J Primatol 68:701–712.

Palombit RA. 2000. Infanticide and the evolution of male-female bonds in animals. In van Schaik CP, Janson CR (Eds), Infanticide by Males and Its Implications. Cambridge University Press, Cambridge. p. 239-268.

Palombit RA. 2009. "Friendship" with males: a female counterstrategy to infanticide in chacma baboons of the Okavango Delta. In Muller M, Wrangham RW (Eds), Sexual coercion in primates and humans: An evolutionary perspective on male aggression against females. Harvard University Press, USA. p.377-409.

Palombit RA. 2010. Conflict (and bonding) between the sexes. In Kappeler PM, Silk JB (Eds), Mind the Gap—Tracing the Origins of Human Universals. Springer, Berlin. p.53-84.

Palombit RA. 2012. Infanticide: Male Strategies and Female Counter Strategies. In Mitani, JC, Call J, Kappeler PM, Palombit RA, Silk JB (Eds) The Evolution of Primate Societies. Chicago: The University of Chicago Press. p. 432-469.

Palombit R, Seyfarth R, Cheney D. 1997. The adaptive value of "friendships" to female baboons: experimental and observational evidence. Anim Behav 54:599–614.

Parr LAL, de Waal FBF. 1999. Visual kin recognition in chimpanzees. Nature 399:647–648.

Paul A, Kuester J, Arnemann J. 1996. The sociobiology of male-infant interactions in Barbary macaques, *Macaca sylvanu*s. Anim Behav 51:155–170.

Paul A, Preuschoft S, van Schaik CP. 2000. The other side of the coin: infanticide and the evolution of affiliative male-infant interactions in Old World primates. In van Schaik CP, Janson CH (Eds), Infanticide by Males and Its Implications. Cambridge University Press, Cambridge, Massachusetts. p. 269 –292.

Perrigo G, Bryant W, and vom Saal F. 1990. A unique neural timing system prevents male mice from harming their own offspring. Anim Behav 39:535-539.

Reidman ML. 1982. The evolution of allparental care and adopting in mammals and birds. Q Rev Biol 57:405-435

Rendall D. 2004. "Recognizing" kin: mechanisms, media, minds, modules, and muddles. In Chapais B, Berman CM (Eds), Kinship and Behaviour in Primates. Oxford University Press, Oxford UK. p. 295-316.

Rosenbaum S, Silk JB, Stoinski TS. 2011. Male-Immature relationships in multi-male groups of mountain gorillas (*Gorilla gorilla beringei*). American Journal of Primatology. 73:356-365.

Ross C, MacLarnon A. 2000. The evolution of non-maternal care in anthropoid primates: a test of the hypotheses. Folia Primatol. 71:93–11

Saj TL, Sicotte P. 2005. Male takeover in *Colobus vellerosus* at Boabeng-Fiema Monkey Sanctuary, central Ghana. Primates 46:211–214.

Saj TL, Sicotte P. 2013. *Colobus vellerosus* white thighed colobus (Geoffroy's pied colobus, Ursine colobus). In Kingdon J. (Ed), Mammals of Africa Volume II: Primates. A&C Black. p.109-111.

Saj TL, Teichroeb JA, Sicotte P. 2005. The population status of the ursine colobus (*Colobus vellerosus*) at Boabeng-Fiema, Ghana. In Paterson JK, Wallis J (Eds), Special topics in primatology, Vol 4: commensalism and conflict: the human primate interface. Norman, American Society of Primatologists. p.350-375.

Sargeant E. 2014. Infant handling and allonursing in white-faced capuchins (*Cebus capucinus).* Masters Thesis. University of Calgary, Calgary.

Schoof VAM, Jack KM, Isbell LA. 2009. What traits promote male parallel dispersal in primates? Behaviour 146:701–726.

Sheldon B. 2002. Relating paternity to paternal care. Philos Trans R Soc London B Biol Sci 357:341-350.

Sicotte P. 1995. Interpositions in conflicts between males in bimale groups of mountain gorillas. Folia Primatol (Basel) 65:14–24.

Sicotte P, MacIntosh AJ. 2004. Inter-group encounters and male incursions in *Colobus vellerosus* in central ghana. Behaviour 141:533–553.

Sicotte P, Teichroeb JA, Vayro JV, Fox SA, Badescu I, Wikberg EC. Accepted. The Influence of Male Takeovers on Female Dispersal in *Colobus vellerosus.* American Journal of Primatology, AJP-14-0222.R1.

Silk J. 1999. Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. Anim Behav. 57:1021-1032.

Smuts, B. 1985. Sex and friendship in baboons. New York: Aldine.

Smuts B, Gubernick D. 1992. Male-infant relationships in nonhuman primates: paternal investment or mating effort? In Hewlett BS (Ed), Father-child relations, cultural and biosocial contexts. Aldine, New York. p.1– 30.

Snowdon CT. 1996. Infant care in cooperatively breeding species. In Rosenblatt, JS and Snowdon CT (Eds), Parental Care: Evolution, Mechanisms and Adaptive Significance. Academic Press, San Diego. p. 643–689.

Soltis J, Thomsen R, Matsubayashi K, Takenaka O. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). Behav Ecol and Sociobiol 48:490–490.

Spinka M, Newberry RC, Bekoff M. 2001. Mammalian play: training for the unexpected. Quarterly Review of Biology 76:141–168.

Sterck E, Watts DP, vanSchaik CP. 1997. The evolution of female social relationships in nonhuman primates. Behavioral Ecology and Sociobiology 41:291–309.

Stewart KJ. 2001. Social relationships of immature gorillas and silverbacks. In Robbins MM, Sicotte P, Stewart KJ (Eds), Mountain gorillas: Three decades of research at Karisoke. Cambridge University Press, UK. p.184-213.

St. George D, Witte SM, Turner TR. Weiss ML, Phillips-Conroy J, SMith EA, Rogers J. 1998. Microsatellite variation in two populations of free-ranging yellow baboons (*Papio hamadryas cynocephalus*). Int J Primatol 19: 273-285.

Stoer AM. 1999. Are significance thresholds appropriate for the study of animal behaviour. Anim Behav 57:F22-F25.

Stumpf RM, Boesch C. 2005. Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*) of the Tai National Park, Cote d'Ivoire. Behav Ecol and Sociobiol 57:511–524.

Stumpf RMR, Martinez-Mota RR, Milich KMK, Righini NN, Shattuck MRM. 2011. Sexual conflict in primates. Evol Anthropol 20:62–75.

Suomi SJ. 1982. The development of social competence by rhesus monkeys. Ann Ist Super Sanita 18:193–202.

Tardif SD, Bales KL. 1997. Is infant-carrying a courtship strategy in callitrichid primates? Anim Behav 53:1001-1007.

Tardif SD, Ziegler TE, Power M, Layne DG. 2005. Endocrine changes in full term pregnancies and pregnancy loss due to energy restriction in the common marmoset (*Callithrix jacchus*). J Clin Endocrinol Metab 90:335–39.

Teichroeb JA, Sicotte P. 2008a. Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new cases and a test of the existing hypotheses. Behaviour 145:727–755.

Teichroeb JA, Sicotte P. 2008b. Social correlates of fecal testosterone in male ursine colobus monkeys (*Colobus vellerosus*): The effect of male reproductive competition in aseasonal

breeders. Horm Behav 54:7–7.

Teichroeb JA, Sicotte P. 2009. Test of the ecological-constraints model on ursine colobus monkeys (*Colobus vellerosus*) in Ghana. Am J Primatol 71:49–59.

Teichroeb JA, Sicotte P. 2010. The Function of Male Agonistic Displays in Ursine Colobus Monkeys (*Colobus vellerosus*): Male Competition, Female Mate Choice or Sexual Coercion? Ethology 116:366–380.

Teichroeb JA, Wikberg EC, Bădescu I, Macdonald L. 2012. Infanticide risk and male quality influence optimal group composition for *Colobus vellerosus*. Behav Ecol 23:1348-1359.

Teichroeb JA, Wikberg EC, Sicotte P. 2009. Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important. Behaviour 146:551-582.

Teichroeb JA, Wikberg EC, Sicotte P. 2011. Dispersal in male ursine colobus monkeys (*Colobus vellerosus*): influence of age, rank and contact with other groups on dispersal decisions. Behaviour 148:765–793.

Teichroeb JA, Wikberg EC, Ting N, Sicotte P. 2013. Factors influencing male affiliation and coalitions in a species with male dispersal and intense male–male competition, *Colobus vellerosus.* Behaviour 151:1045–1066.

Terborgh J, Janson CH. 1986. The socioecology of primate groups. *Annu Rev Ecol Sys* 17:111-136.

Treves A. 1998. Primate social systems: con- specific threat and coercion-defense hypotheses. Folia Primatol 69:81–88.

Trivers R. 1972. Parental investment and sexual selection. In Campbell B (Ed), Sexual selection and the descent of man. Chicago: Aldine Publishing Co. p.136-179.

Trumbo ST. 2012. Patterns of parental care in invertebrates. In Royle NJ, Smiseth PT, Kolliker M (Eds), The evolution of parental care. Oxford University Press, UK. p.81-100.

van Schaik CP. 1989. The ecology of social relationships amongst female primates. In Standen V, Foley R (Eds), Comparative socio- ecology of mammals and humans. Black- well Publications, Oxford. p.195–218.

van Schaik CP. 2000a. Vulnerability to infanticide by males: patterns among mammals. In van Schaik CP, Jansen CH (Eds), Infanticide by Males and its Implications. Cambridge University Press, Cambridge, Massachusetts. p.61–71.

van Schaik CP. 2000b. Infanticide by male primates: the sexual selection hypothesis revisited. In van Schaik CP, Jansen CH (Eds), Infanticide by Males and its Implications. Cambridge

University Press, Cambridge, Massachusetts. p.27-60.

van Schaik CP, Hodges JK, Nunn CL. 2000. Paternity confusion and the ovarian cycles of female primates. In van Schaik CP, Janson CH (Eds), Infanticide by males and its implications. Cambridge University Press, Cambridge, Massachusetts. p.361–387.

van Schaik CP, Kappeler PM. 1997. Infanticide risk and the evolution of male/female association in primates. P Roy Soc Lond A Bio 264: 1687-1694.

van Schaik CP, Paul A. 1998. Male care in primates: does it ever reflect paternity? Evol Anthropol 5: 152-156.

Vokey JR, Rendall D, Tangen JM, Parr LA, de Waal F. 2004. Visual kin recognition and family resemblance in chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 118:194–199.

Whitten P.L. 1987. Infants and Adult Males. In Smuts B, Cheney DL, Seyfarth RM, Wrangham RW, Strusaker TT (Eds), Primate Societies. University of Chicago Press, Chicago. p.343-357.

Wich S, Assink P, Sterck E. 2004. Thomas Langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: a factor in avoiding infanticide? Behaviour 141:41–51.

Widdig A. 2007. Paternal kin discrimination: the evidence and likely mechanisms. Biol Rev Camb Philos Soc 82:319–334.

Wikberg EC. 2012. Relationships, relatedness and residency patterns in female *Colobus vellerosus*. Doctoral Thesis. University of Calgary, Calgary.

Wikberg EC, Sicotte P, Campos FA, Ting N. 2012. Between-group variation in female dispersal, kin composition of groups, and proximity patterns in a black-and-white colobus monkey (*Colobus vellerosus*). PLoS ONE 7:e48740.

Wikberg EC, Teichroeb JA, Badescu I, Sicotte P. 2013. Individualistic female dominance hierarchies with varying strength in a highly folivorous population of black-and-white colobus. Behaviour 150:295–320.

Wikberg EC, Ting N, Sicotte P. 2014. Familiarity is more important than phenotypic similarity in shaping social relationships in a facultative female dispersed primate, *Colobus vellerosus*. Behavioural Processes 106:27–35.

Wilson EO. 1975. Sociobiology. Cambridge: Belknap Press. UK.

Wolff JO, Macdonald DW. 2004. Promiscuous females protect their offspring. Trends Ecol Evol

(Amst) 19:127–134.

Wong SNP, Sicotte P. 2006. Population size and density of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary and surrounding forest fragments in Ghana. Am J Primatol 68:465–476.

Woodroffe R, Vincent A. 1994. Mothers Little Helpers - Patterns of Male Care in Mammals. Trends Ecol Evol (Amst) 9:294–297.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262-300.

Wrangham RW. 1987. Evolution of social structure. In Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (Eds), Primate societies. University of Chicago Press, Chicago. p.282-297.

Wright P. 1990. Patterns of paternal care in primates. Int J Primatol 11:89-102.

Xiang ZF, Sayers K, Grueter CRC. 2009. Direct paternal care in black-and-white snub-nosed monkeys. Journal of Zoology. 278:157–162.

Yamane A, Shotake T, Mori A, Boug AI, Iwamoto T. 2003. Extra-unit paternity of hamadryas baboons (*Papio hamadryas*) in Saudi Arabia. Ethol Ecol Evol 15:379-387.

Zhao Q-K. 1996. Male-infant-male interactions in Tibetan macaques. Primates 37:135–143.

Ziegler TE, Prudom SL, Schultz-Darken NJ, Kurian AV, Snowdon CT. 2006. Pregnancy weight gain: marmoset and tamarin dads show it too. Biology Letters 2:181-183.