Living with males

– benefits and costs to females of resident males

in *Colobus vellerosus*

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ABSTRACT

Only in primates is permanent male-female association the most widespread social structure of all. The continuous presence of resident males in the social group can have significant impacts on female fitness, both in forms of costs and benefits. In this study I investigate particular short-term benefits and costs of resident males to females in a population of ursine colobus (Colobus vellerosus). I hypothesise that for females permanent association with males result in certain benefits and certain costs, exceeding those provided or imposed by other females. The results indicate that female derive greater benefits from males than from females during intergroup encounters and in the form of vigilance since males were the main participants in intergroup encounter and were more vigilant than females. I could not confirm any type of behaviour employed by resident males that is costly to females. However, the rarity and subtleness of some costly male behaviours imply that more data is needed before making a conclusion on their absence or occurrence in this population and I purpose that herding behaviour could occur at my study site. Moreover, multi-male groups (MM-groups) showed higher rates of vigilance than single-male groups (SM-groups) and had a tendency to experiencing fewer intergroup encounters than SM-groups. I interpret the former as a result of the demanding social conditions in the MM-groups. The latter indicate that females may benefit from MM-group living through a decrease in intergroup encounters.
INTRODUCTION

Almost all primate taxa live in groups and the reproductive strategies of females is considered to be the main determinant of primate gregariousness and the predominant factor that shapes primate social system as a whole (Emlen and Oring, 1977; Wrangham, 1980). While females are believed to be the founders of groups, aggregating in order to optimize resource utilization and to gain protection, male reproductive success is suggested to be most dependant on mating opportunities (Trivers, 1972; Smuts et al., 1987; van Schaik, 1996) resulting in a male allocation primarily based on the distribution of females (Altman, 1990). Unlike most group living mammals, male and female primates have a social relationship which make them truly unusually. Only in primates is permanent male-female association the most widespread social structure of all, reaching almost 100% in diurnal species (Smuts et al., 1987). The continuous presence of resident males in the social group has a significant impact on female fitness, resulting in situations that alternately are costly or beneficiary. Sexual coercion, aggression and resource competition (Wrangham, 1980; van Schaik, 1983; Dunbar, 1988; Smuts and Smuts, 1993) are examples when males may impose a cost on females and protection against infanticide, defence against predators and enhanced competitive ability of the group (Wrangham, 1980; Robinson, 1988; van Schaik, 1989; Nunn, 2000) are examples when males may provide a benefit to females.

Of the numerous types of costs resident primate males can place on females sexual coercion is perhaps the most conspicuous. Smuts and Smuts (1993) defined sexual coercion as the force or intimidation used by a male to increase the likelihood that a female will mate with him and to decrease the prospect that she will mate with other males. For females costs associated with sexual coercion include deprivation of active mate choice by forced copulations (Smuts and Smuts, 1993; Muller et al., 2007), inhibition of promiscuity and free migration brought on by herding (Watts, 1989; Smuts and Smuts, 1993; Steenbeek, 1999) and injuries and fatal wounds caused by physical punishment for promiscuity (Goodall, 1986). There are also stress-related effects of male sexual harassment and coercion; abortion (Pireira, 1983), disruption of oestrus cycle (Goodall, 1986), increased glucocorticoid secretion (Muller et al., 2007) and temporary infertility (Dunbar, 1987). However the predominant and most well-studied form of sexual coercion is infanticide, the killing of unweaned young by conspecifics (Wrangham, 1979; Smuts and Smuts, 1993; Borries et al., 1999; Kappeler, 1999). Infanticide constitute a enormous cost to females and the risk of being exposed to this form of male behaviour can have a substantial impact on female behaviour (Palombit 1999, Steenbeek 1999), but notably, it is not a behaviour typically exhibited by resident males (Struhsaker and Leland, 1987).

Other cost to females of a continuous association with males is resource competition. Males may divert resources that would otherwise accrue to females and their relatives and male presence in the group increases size and thereby possibly also resource competition (Wrangham, 1980; van Schaik, 1983; Dunbar, 1988; O’Brien, 1991). In white-faced capuchins as much as 75% of all male-female agonism takes place during feeding (Rose, 1994). Competition over food also exists between females, but because of sexual dimorphism in size, strength and weaponry males are the dominant sex in the majority of primate species and females are assigned a disadvantageous position when competing with the opposite sex, thus suffering higher costs in food competition with males (Crook and Gartland, 1966; Smuts, 1987; Rose, 1994; Strier, 1994; Campbell, 2003).

The risk of receiving aggression from males may oblige females to maintain vigilance towards potentially dangerous males (Smuts and Smuts, 1993; Alberts, 1994, Kutsukake 2007). Caine and Marra (1988) suggested that a high demand for social within-group surveillance may handicap individuals with respect to other types of vigilance, i.e. vigilance aimed at the detection of predators. Thus in species where females are compelled to engage in a high frequency of social surveillance, either directed towards males or indeed also other females, they may suffer costs of decreased vigilance directed towards predator detection (Caine and Marra, 1988) and also loose time and energy otherwise spent (Smuts and Smuts, 1993).

Balancing the disadvantages females may suffer from permanent male presence in the group are the many possible and important benefits males also provide. For instance, resident males can constitute a defence system against intrusion of infanticidal males and in species where
infanticide is a major threat female primates are known to associate with particular males for offspring protection (Wrangham, 1979; Watts, 1989; O’Brien, 1991; Smuts and Smuts, 1993; Sterck et al, 1997; Fashin, 2001; Sicotte and Macintosh, 2004; van Schaik et al, 2004; van Schaik, 1996). In one newly documented case, Vogel and Fuentes-Jiménez (2006) observed a wedge-capped capuchin male, in spite of high costs to himself, rescue an infant and its mother from an attack by strange males.

Furthermore females can benefit from of having more than one male in their group. Infanticide is expected to be less likely in a group containing multiple reproductively active males (MM-group) since potentially infanticidal intruders face several competitors, of whom all are possible sires of the infants and consequently will protect them and resist take-over (of course this assumes promiscuous matings in multi-male groups) (Hrdy, 1979; Struhsaker and Leland, 1987; van Schaik, 1996; Altmann, 1990; Janson and van Schaik, 2000; Borries et al, 1999).

Accordingly, two case studies have shown that infanticide risk is greater in single-male groups (SM) than in MM-groups (Hanuman langurs: Newton, 1986; mountain gorillas: Robbins, 1995). Numerous reports confirm that primate males take greater responsibility for anti-predatory tactics than primate females, thus suggesting that continuous male presence in the group can decrease female mortality and consequently have a substantial beneficiary influence on female fitness (Wrangham, 1979, 1980; van Schaik, 1989). For example, there are reports of male group members being the first to confront predators (white-fronted capuchin and brown capuchin: van Schaik and van Noordwijk, 1989; vervet monkey: Baldellou and Henzi, 1992), the last to leave if the troop turns to flee (white-fronted capuchin and brown capuchin: van Schaik and van Noordwijk, 1989; Phayre’s leaf monkey: Lloyd et al, 2006) and the most prominent in attacking, mobbing or chasing predators off (chacma baboon: Busse, 1980; white-fronted capuchin and brown capuchin: van Schaik and van Noordwijk, 1989; spectral tarsier: Gursky, 2005; red colobus: Stanford, 2002). Also, in many species, males are more vigilant than females (de Ruiter, 1986; van Schaik and van Noordwijk, 1989; Baldellou and Henzi, 1992; Rose, 1994; Rose and Fedigan, 1995, Gould et al, 1997) and since there is a strong correlation between vigilance and predator detection (Caine, 1984; de Ruiter, 1986; Boinski, 1988; Caine and Marra, 1988; van Schaik and van Noordwijk, 1989; Fragaszy, 1990; Rose, 1994), male’s greater vigilance make them likely to detect predators sooner than females and thereby they may reduce the burden of staying alert for female group members (Eisenberg et al, 1972; van Schaik and van Noordwijk, 1989; Artiss and Martin, 1995). Furthermore, it is expected that the positive influence males may have on female safety lead to a covariance between threat increase and male group numbers, i.e. where predation risk is high groups should contain multiple males (Cheney and Wrangham, 1987; van Schaik and van Noordwijk, 1989). This potential connection was investigate and confirmed by Anderson (1986) and van Schaik and van Höstermann (1994) who preformed comparisons of predation pressure and male group numbers across taxa and found that where primate groups suffered from strong predation pressure they contained a lager number of males.

I will conclude this basic outline of benefits and costs of primate males to females by looking in to one final benefit males can provide females; competition potential. Because female reproductive success depends largely on access to food (Trivers, 1972; van Schaik, 1989), acquiring this resource is of utmost importance to female fitness. Whenever food is limited and, depending on the distribution and quality of it, females will compete within the group or between groups to increase their access to it. Intergroup encounters are situations that can act as means of contest competition over resources between neighbouring groups (Wrangham, 1979, 1980). Females are known to participate aggressively in these interactions (guereza: Fashing, 2001; ursine colobus: Sicotte and Macintosh, 2004; western black-and-white-colobus: Korstjens et al, 2002), i.e. for the reason of female resource defence (Cheney, 1987; Fashin, 2001), but males are usually the most active participators (guereza: Oates, 1977; Fashing 2001; Harris 2006; ursine colobus: Sicotte and Macintosh, 2004). Since male fitness is governed by mating opportunities not food (Trivers, 1972), males are assumed to engage in intergroup encounters for other reasons than females, principally mate defence (Cheney, 1987). But by excluding non-group conspecifics, either through direct mate defence (driving rival males away) (Cheney, 1987) or indirect mate defence (defending the groups resources or territory and thereby attracting females, e. g. resource defence polygyny) (Emlen and Oring, 1977), males provide female group members with benefits
of increased resource access (Wrangham, 1980; van Schaik, 1989; O’Brien, 1991) and ultimately increase female reproductive success.

In this study I will investigate the particular short-term benefits and costs that males place on females in a wild population of ursine colobus (Colobus vellerosus) (Fig. 1b) at Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana. I hypothesis that: I) For females permanent association with males result in certain benefits, exceeding those provided by other females; and II) For females permanent association with males result in certain costs, exceeding those imposed by other females.

The predictions associated with hypotheses I are; a) males are more vigilant than females, thereby relieving females of the burden of vigilance (van Schaik and van Noordwijk, 1989; Rose, 1994); b) females will have a tendency to scan less when males are in proximity than when other female group members are in proximity, suggesting that females rely more on male vigilance than on female vigilance (van Schaik and van Noordwijk, 1989); c) males are more active than females in intergroup encounters thus contributing more than females in between-group competition (van Schaik 1989; O’Brien 1991).

The predictions associated with hypotheses II are; a) during foraging females engage in aggressive interaction more often with males than with other females, suggesting that there is a greater resource competition between the sexes than within (Rose 1994); b) males will be aggressive towards female group members while females will tend to direct submissive signals towards males, suggesting that females are disadvantaged in antagonistic encounters with male group members (Rose, 1994; Smuts, 1987; Campbell, 2003), c) female foraging is more often interrupted by males than by other females, suggesting that female feeding success suffers in male presence, d) female foraging success decreases with increased time spent in close vicinity to males, implying that males inflict a negative influence on female foraging (O’Brien 1991).

In addition, since BFMS is an unusual study site in the sense that both MM and SM-groups exists within the same population, I will also examine if group type (i.e. the presence of one or several adult resident males in the group) can explain any observed difference between the groups in certain behaviours, namely vigilance, intergroup interaction and male aggression. As mentioned in the sections above, several researchers have found that the number of males per group influence a wide range of behaviours, conditions and phenomenon, such as female reproductive rate (Dunbar, 1987), infanticide risk (van Schaik, 1996), vigilance rates (Rose and Fedigan, 1995) and group competition potential (Wallace, 2007) to name a few. Consequently, I find group type an interesting additional parameter worth investigating in the context of benefits and costs of males to females.

**MATERIAL & METHODS**

**Study site**

This study was conducted at the Boabeng-Fiema Monkey Sanctuary (BFMS) in the Nkoranza District in the Brong-Ahafo region, central Ghana (7° 43’N and 1° 42’W) (Fig. 1a). BFMS encompasses 192ha of dry semi-deciduous forest in the forest-savanna transition zone in western Africa. The sanctuary lies on the border of the small twin-community of Boabeng-Fiema (Teichroeb et al 2008) and is surrounded by farmland separating it from the nearest large forest block by 50km (Beier et al, 2002). However, there are riparian forest strips and patches of secondary forest that links BFMS with surrounding smaller forest fragments (Wong and Sicotte 2006).

BFMS has two species of monkey; ursine colobus (Colobus vellerosus) and mona monkey (Cercopithecus campbeli). C. vellerosus is also present in the forest fragments surrounding BFMS and it is believed that migration occur between them (Kankam, 1997; Wong and Sicotte, 2006).

BFMS is a community-based conservation effort, founded in 1974 when the twin-community of Boabeng and Fiema passed a District Council by-law prohibiting harm to the monkeys in the area (Ghana Forestry Commission; Saj et al, 2005). Within the sanctuary it is not allowed to fell
large live trees but the hunting ban only incorporates the two species of monkey and villagers use the forest for medicinal plants, to graze sheep and to collect fire wood. The presence of exotic plant species and patches of regenerating farm land, the rarity of large predators and encroachment along the edges of the forest all bear witness to the long-term anthropogenic influence in the area (Teichroeb et al, 2008; Saj et al, 2005).

**Study Species**

Ursine colobus (Fig.1b) is an arboreal folivore with a diet consisting mainly of young and mature leaves, though seeds constitute a significant proportion when available (Saj and Sicotte, 2007a). The species is one of five representatives of the genus Colobus, of which all are generally restricted to the tropical rainforests of Africa (Struhsaker and Leland, 1987; Oates, 1994). *C. vellerosus* is the least known of all black and white colobus species (Sicotte and Macintosh, 2004).

Throughout most of its range in, *C. vellerosus* seems to be declining and the species is listed as Vulnerable by IUCN (2007). However, BFMS appears to be an exception; here the population has been growing in the past 15 years and increasing as much as 78,9% between 1991 and 2003 (Wong and Sicotte, 2006; Saj et al, 2005). According to the latest population census of *C. vellerosus* at BFMS conducted in 2003, the sanctuary inhabits 217-241 individuals in 15 groups (Wong and Sicotte, 2006). There is considerable variation (4-32) in group size in the area (Saj et al., 2004) and groups are both uni- and multi-male (Saj et al, 2005), with female transfer known to occur (Sicotte and Macintosh, 2004).

Intergroup encounters are frequent and often aggressive at BFMS and home ranges are small and overlap with neighbouring groups’ (Sicotte and MacIntosh, 2004). Incidents of infanticide, male take-over, extra-group matings and occurrence of all-male-bands have been documented in the population. Female dispersal is presumably facultative and individuals are known to stay and breed in their natal groups (Saj and Sicotte, 2005; Teichroeb et al, 2005; Saj et al, 2007; Sicotte et al, 2007).
Table 1. Sex and age-class composition of study groups.

<table>
<thead>
<tr>
<th>Group name</th>
<th>Group type</th>
<th>Total group size</th>
<th># adult ♀</th>
<th># subadult ♀</th>
<th># adult ♂</th>
<th># subadult ♂</th>
<th># juven. &amp; infants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nippy, NP</td>
<td>SM</td>
<td>11</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>4</td>
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<td>Bentesua, BS</td>
<td>SM</td>
<td>11</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Splinter, SP</td>
<td>SM</td>
<td>13</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Red tail, RT</td>
<td>MM</td>
<td>15</td>
<td>6</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Dadie, DA</td>
<td>MM</td>
<td>19</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Wawa, WW</td>
<td>MM</td>
<td>20</td>
<td>9</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Odum, OD</td>
<td>MM</td>
<td>21</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>11.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>

The first column lists all names used for the study groups during data collection in the field. In the data set the names were shortened to a two-letter code, also seen in the table, and I will only use these codes when referring to the different groups. Group type refers to the number of males present in the group, SM-groups being single-male (NP, BS, SP) and MM-groups being multi-male (RT, DA, WW, OD). A mean group size is presented for both group types (11.7 for SM-groups and 18.8 for MM-groups). Adult denotes individuals known to be sexually mature, subadult denotes individuals that are fully grown or nearly fully grown and believed to be sexually mature or very soon sexually mature, juv. denotes juvenile individuals not yet fully grown nor sexually mature and infants denotes individuals that are not yet fully grown nor sexually mature and that are very dependant on their mothers. The symbol ♀ represents females and ♂ represents males. No sex difference is considered for juveniles or infants.

Study Groups

Behavioural data was collected for seven study groups (DA, BS, NP, OD, RT, SP, WW) of *C. vellerosus* (Table 1). All groups had been under observation before and three (BS, RT, WW) since the beginning of Pascal Sicotte’s research at the site in 2000. All groups were more or less habituated and were not disturbed by human presence as long as a distance of at least 10 meters between observer and the nearest individual was maintained.

Three of the seven research groups were single-male (NP, BS, SP) and four were multi-male (RT, DA, WW, OD). The group NP was part of DA in 2006, but split off from DA between August 2006 and May 2007. The group OD was the least known of the seven groups and was at the time of this study subject of a major influx of new males. All members of the seven groups could be identified individually by facial characteristics, size, scars and/or tail shape. In addition to the seven study groups, three additional groups (SK, VI, BO) could be identified on group level and were included in the analysis on occasions when they participated in intergroup encounters with any of the study groups.

Data collection

Data were collected through May to the beginning of August 2007 and observations took place between sunrise (06:30-07:30) and sunset (17:00-19:00).

Group scans were executed once every hour. Each group scan included the behaviours of five randomly sampled adult or subadult individuals of the same group. Since there could be a risk of sampling the same individuals several times in a row if the animals stayed stationary, sampling changed directionality every other sampling occasion, going left to right or right to left. Some groups had only one adult male and to avoid low male representation in the data, efforts were made to include a male in each scan even if this meant diverting from the sampling scheme.

Focal observations of the duration of 10 minutes (Altmann, 1974) were conducted on adult and subadult females. All exhibited and received behaviours of the focal individual were documented. Also, for each focal observation five point samples (one every 2.5 minute) were
taken, registering the focal animal’s behaviour at that precise moment and the proximities of all other individuals within 5 meters. Three different proximity categories were used to assign distance between the focal animal and other individuals; within 1 tail length, within 3 meters and within 5 meters.

To ensure independence, focal observations on one individual were never collected twice in one hour and a 10 minute interlude was also used to separate samples of individuals that had been closer than 1 meter of the last sampled individual. The dense terrain did not allow for a strict sampling scheme; valuable time would have been lost waiting for the next animal in turn to appear. However, the aim was to finish all females in one group before resampling any of the females from that group or before moving on to the next study group.

When considered to be foraging, focal feeding follows (Altmann, 1974) of the duration of 1 minute were conducted on adult and subadult females. All exhibited and received behaviours of the focal individual were noted as well as the proximity of all other individuals within 5 meters of the focal animal. Feeding follows were also extracted from focal observations. To be considered a valid feeding follow for extraction, the foraging period had to include the ingestion of at least 2 items within a one minute period. To ensure independence no more than one feeding follow was extracted from each focal observation.

Intergroup encounters were documented ad libitum and were defined as occasions where one or several groups came in 50 meter of the focal group (Oates, 1977; Fashing, 2001; Sicotte and Macintosh, 2004). Encounters in which none of the involved groups exhibited agonistic behaviours were excluded from the analysis on sex difference in intergroup behaviour but kept for calculation on the hourly rate of intergroup encounters per group. Agonistic behaviours were characterized as low intensity only or high intensity, where low intensity aggression include; jump display, open mouth display or stiff leg display (Oates, 1977) and high intensity aggression include; chase or contact aggression (Sicotte and Macintosh, 2004). During encounters, participants (aggressors and targets) were individually identified as often as possible, but otherwise categorized as male or female. The hourly rate of intergroup encounters per group was calculated by dividing the number of intergroup encounters per group with the hours spent observing the group.

All observations were conducted with binoculars (8x42) and behavioural data was registered with behaviour codes on hand-held computer (Psion Organizer, model LZ64). During intergroup encounters or other highly eventful situations observations were documented by tape recorder and later transcribed into behaviour codes.

**Data Analysis**

Data on vigilance behaviour was extracted from group scan observations and expressed as occasions of scans versus occasions of other observed behaviours and tested for sex, group and group type (SM or MM) differences using a generalized linear model.

Differences in female vigilance depending on the sex of a neighbouring individual was extrapolated from two different data localities; point samples and focal follows and both calculations were done using a linear mixed-effects model. Data from point samples were expressed as occasions of scans versus occasions of other observed behaviours when the focal animal was alone or in the vicinity of males or other females. Three proximity classes were used to assign vicinity of neighbours: within 1 meters, within 3 meters and within 5 meters. Data from focal follows were expressed as hourly rate of scanning per individual, i.e. proportion of time spent vigilant out of the total observation time with a female or a male neighbour or any neighbour irrespective of sex.

Intergroup encounters were divided into low intensity and high intensity classes. Sex differences in participation was tested for all encounters as well as for the two intensity categories, using Fisher’s exact test. Participation differences between groups and group types (SM or MM) were also tested using Fisher’s exact test.

Since no occasions of male aggression, female submissive signals or male interruption of female feeding was witnessed, data analyses on these predictions were not needed.
Differences in foraging success when the focal was in the vicinity of males or females or alone were documented in two ways; foraging success and feeding efficiency and tested using linear mixed-effects model. Foraging success was expressed as proportion of foraging time spent ingesting food and feeding efficiency was expressed as ingested items per minute. No distinction on the type of item (fruit, leaf or seed) ingested was made and neither on the quality (young or mature leaf).

All statistical analyses were done in the statistical computer program R and statistical significance was set at the 5% level.

RESULTS

In total, 478 observation hours and 63 days were spent in the field. I collected 40.5 hours of focal data (N = 243), 83 (39 + 44) feeding follows and observed 49 intergroup encounters. Mean observation time per study group was 68 hours, but varied between groups (Table 2).

<table>
<thead>
<tr>
<th>Groups</th>
<th>NP</th>
<th>BS</th>
<th>SP</th>
<th>RT</th>
<th>DA</th>
<th>WW</th>
<th>OD</th>
<th>mean</th>
</tr>
</thead>
<tbody>
<tr>
<td># of days / group</td>
<td>16</td>
<td>9</td>
<td>17</td>
<td>11</td>
<td>14</td>
<td>23</td>
<td>9</td>
<td>14</td>
</tr>
<tr>
<td># of hours / group</td>
<td>77</td>
<td>41</td>
<td>68</td>
<td>61</td>
<td>105</td>
<td>87</td>
<td>34</td>
<td>68</td>
</tr>
</tbody>
</table>

I) Benefits of males to females

Vigilance.

A comparison between female and male vigilance level showed a significant difference in the proportion of vigilance behaviour of each sex. Males were considerably more vigilant than females (P<0.001). However, an intragroup comparison revealed a more variable situation. In two of the seven study groups, one being MM (DA) and one SM (NP), males were significantly more vigilant than females (P<0.05 resp. P<0.001), but in the remaining five the distinction was no longer statistically different even if male vigilance showed a tendency to exceed female vigilance in all but one (BS) group (Fig.2). There was no significant difference in vigilance between the seven groups when all adult and subadult individuals were considered, and likewise, no significant difference in vigilance between the different groups’ females or between the different groups’ males. However, when comparing MM and SM-groups there was a significant difference in vigilance; members of MM-groups scanned more than individuals in SM-groups (P< 0.05). However, the difference disappeared in a sex dependent analysis; i.e there was no difference in vigilance between females from MM groups and females from SM groups or males from MM groups and males from SM-groups.

Vigilance and neighbours

Results from focal follows and point samples were unanimous. There was no statistical difference in the amount of time a female spent scanning depending on the sex of her neighbours. However, if no regard was taken to the sex of the neighbour, females spent significantly more time scanning alone (P<0.05) than when in company of another group member. Data was not comprehensive enough to allow for an analysis on group type differences.

Intergroup encounters

A total of 49 intergroup encounters were documented and all were used for calculating the hourly rate of intergroup encounters experienced by each study group. SP had the highest frequency of
Fig 2. Sex and group differences in the proportion (%) of vigilant behaviour observed during group scans. Percentages represent vigilance in relation to all other types of behaviour sampled. All groups are represented with one bar for each sex (♀ = females, ♂ = males). In all groups, except BS, males showed a higher percentage of vigilant behaviour than females.

intergroup encounters (0.265 encounters per hour) and DA experienced the lowest frequency (0.105 encounters per hour) (Table 3). MM-groups generally experienced fewer intergroups encounters than SM-groups. The hourly rate of intergroup encounters for MM-groups was 0.157 compared to 0.223 for SM-groups, however, the difference was not statistically significant.

For the analysis on sex differences in intergroup behaviour 12 of the 49 observed cases of intergroup encounters had to be removed since they continued without any indication of particular intergroup related behaviours or aggressiveness and an additional 8 cases had to be excluded because of uncertainties concerning the sex of the participating individuals. Of the remaining 29 cases 18 were categorized as high intensity encounters and 11 as low intensity encounters. The result showed that males were more active in intergroup encounters than females. While males participated in all 29 between-group encounters, females were active in a significantly lower proportion \((P < 0.05)\) (Table 4). Males were also the most active sex in intergroup encounters of high intensity, participating with high intensity behaviours in 94.44% of all cases, significantly more than the 61.11% for females \((P < 0.05)\) (Table 4). Male predominance prevailed in intergroup encounters of low intensity, where male participation was 100%, against the female participation at 63.63%. However, the difference was not statistically significant in encounters of low intensity.

Table 3. The hourly rate of intergroup encounters per group. The approximate hourly rate of intergroup encounters (IGE) was calculated by dividing the number of IGE per group with the observation hours (Table 2) per group. The mean hourly rate of IGE for SM-groups (NP, BS, SP) was 0.223 and the mean hourly rate of IGE for MM-groups (RT, DA, WW, OD) was 0.157. There was no statistically significant difference between the mean hourly rate of IGE of SM and MM-groups. Note that the IGE presented in this table \((N=49)\) are not fully equivalent to the encounters \((N=29)\) used for the analysis of sex differences in intergroup behaviour (see Table 4).

<table>
<thead>
<tr>
<th>Groups</th>
<th>NP</th>
<th>BS</th>
<th>SP</th>
<th>RT</th>
<th>DA</th>
<th>WW</th>
<th>OD</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td># of IGE / group</td>
<td>16</td>
<td>8</td>
<td>18</td>
<td>7</td>
<td>11</td>
<td>20</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Hourly rate of IGE / group</td>
<td>0.208</td>
<td>0.195</td>
<td>0.265</td>
<td>0.115</td>
<td>0.105</td>
<td>0.230</td>
<td>0.176</td>
<td>0.185</td>
</tr>
<tr>
<td>Hourly rate of IGE for SM-groups</td>
<td>0.223</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hourly rate of IGE for MM-groups</td>
<td>0.157</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Sex differences in intergroup behaviour. A total of 29 intergroup encounters (IGE) were included in the analysis on sex differences in intergroup behaviour. The number of IGE with female participants (N = 22, 75.86%) were significantly fewer (P < 0.05) than the number of IGE in which males participated (N = 29, 100%). A total of 18 encounters were categorized as being of high intensity and of these females participated with high intensity behaviours in 11 (61.11%) and males in 17 (94.44%). Eleven of the IGE were categorized as being of low intensity and of these females participated with low intensity behaviours in 7 (63.63%) and males in 11 (100%).

<table>
<thead>
<tr>
<th></th>
<th>Total #</th>
<th>Female participation (#)</th>
<th>Female participation (%)</th>
<th>Male participation (#)</th>
<th>Male participation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IGE</td>
<td>29</td>
<td>22</td>
<td>75.86</td>
<td>29</td>
<td>100</td>
</tr>
<tr>
<td>High intensity IGE</td>
<td>18</td>
<td>11</td>
<td>61.11</td>
<td>17</td>
<td>94.44</td>
</tr>
<tr>
<td>Low intensity IGE</td>
<td>11</td>
<td>7</td>
<td>63.63</td>
<td>11</td>
<td>100</td>
</tr>
</tbody>
</table>

II) The costs of males to females

Male aggression
No aggressive interactions between male and female group members were observed. The only documented form of male aggression towards females occurred when individuals from different groups intermingled, i.e. during instances of intergroup encounters and male incursions.

Female submissive signals
No observations of female submissive signals toward male group members were observed.

Foraging and male interruption.
The degree of within-group aggression during foraging was very low in all of the seven study groups and there were no documentation of male interruption of female feeding. However, there were some rare occasions of female-female agonism in foraging context.

Feedings success and neighbours
There was no statistical indication of a difference in foraging success for females depending on the sex of the neighbouring group member and neither did the female ingestion rate (items ingested per hour) differ significantly depending on whether the female was feeding in the proximity of males or other females.

DISCUSSION

Benefits of males to females

Vigilance
The result of this study confirmed my prediction that ursine colobus males are more vigilant than females. An intragroup comparison revealed a corresponding situation, where males tended to be the most vigilant sex in all groups except one, BS-group and since all other groups had noticeably higher male vigilance BS-group stands out as an inconsistency. One possible explanation for BS-group’s dissimilarity with the other study groups is insufficient data. I spent a mean observation time of 68 hours per group, but BS was only observed for 41 hours and it is possible that additional time spent with this group would generate data that would be more in line with that of the other groups.

This is the first study on sex difference in vigilance behaviour in a black and white colobus species. Greater male than female vigilance has been confirmed in several other primate species, but notably not in many old world species and in very few colobines (New world species: redbacked squirrel monkey (Boinski, 1988); white-fronted capuchin and brown capuchin (van Schaik and van Noordwijk, 1989); wedge-capped capuchin (Fragaszy, 1990); white-faced capuchin (Rose, 1994; Gould et al, 1997); Old world species: vervet monkey (Baldellou and
Henzi, 1992); colobine species: Thomas’s langur (Steenbeek et al, 1999a). Since vigilance behaviour is positively correlated with predator detection (Caine, 1984; Caine and Marra, 1988; de Ruijter, 1986; van Schaik and van Noordwijk, 1989; Rose, 1994), this study indicates that females may derive greater benefits from males than from other female group members in the form of vigilance and that males may provide superior anti-predatory services compared to females in this sense. This is particular interesting since predation risk could be the major force behind gregariousness in primates (Alexander, 1974; van Schaik, 1983; van Schaik and van Hooff, 1983; Terboorgh and Janson, 1986; Dunbar, 1988; Janson, 1992; Sterck et al, 1997). Thus greater male than female vigilance suggest, as Rose (1994) noted in her study on white-faced capuchin monkeys, that females derive the greatest benefit of group living from males. However, it would be precipitated to assume that male vigilance is exclusively, or even primarily, aimed towards discovering potential predators in light of the fact that vigilance also can serve as within-group surveillance (Caine and Marra 1988, Alberts 1994, Treves 1999, Jack 2001), a component of male mate defence (Treves 2000) and to detect conspecific groups (Balduellou and Henzi 1992, Rose and Fedigan 1995). So even if male vigilance surpasses female vigilance, the male motive may not be predator detection but enhancing male reproductive success. In the case of the latter, could male vigilance still be beneficiary for females? Yes and no. Yes since it would be highly unlikely that a vigilant male scanning for competitors would ignore an approaching predator if he spotted it and also because strange males are not just competition for the group’s resident male, they also pose a threat of infanticide. The benefit for females could thus still stand even if the motive of male vigilance is aimed towards other males. However, if the male in question is a member of a MM-group, the motive for his vigilance behaviour could be monitoring competitors within the group. In such circumstances male vigilance would be of lesser value for females, partly because males already part of the group pose little threat of infanticide and partly because vigilance used for within-group surveillance takes time from vigilance aimed at external threats, such as predators (Caine and Marra, 1988). Additionally, on occasions when males are monitoring competitors for the purpose of mate defence, male vigilance may in fact inhibit female mate choice and constitute a cost (Treves, 1999). Consequently, the aim of male vigilance is of significance to primate females; when males effectively spot danger and relieve females from requirements of vigilance they provide a benefit, but when the purpose of male vigilance is within-group surveillance or mate defence, it is less valuable to females and could even be costly to them.

The directionality and purpose of male vigilant behaviour is a noteworthy issue for other reasons. When I examined group type differences in vigilance I found that when no regard to sex was taken individuals from MM-groups were statistically more vigilant than SM-group individuals. This is surprising for two reasons. First, you would expect individuals of MM-groups to be less vigilant than individuals of SM-groups since the greater number of resident males in MM-groups means that there are more animals of the more vigilant sex present and that this in turn should lower requirements on individual vigilance in MM-groups (van Schaik and van Noordwijk, 1989; Rose and Fedigan, 1995; but see Balduellou and Henzi, 1992). Secondly, at BFMS all MM-groups were larger in size than the SM-groups which according to the “group size effect” is another reason to expect a decrease in individual scanning rate in MM-groups (Burger and Gochfeld, 1992; for review on vigilance group size effect see Bednekoff and Lima, 1998). However I propose that the tendency for MM-group individuals to be more vigilant than individuals of SM-groups can be clarified if focusing on the directionality and purpose of vigilance. When performing a group scan I made a distinction between long-distance scanning behaviour and close-range scanning behaviour since these two actions could serve different functions. The function of long-distance scanning / non-social vigilance is presumably predator detection (or detection of other threats such approaching groups) whereas the function of close-range scanning is food-related or social, for example used for within-group surveillance (Caine and Marra 1988, Treves 1999, Jack 2001). Subsequently, I only used long-distance scanning in my analysis on vigilance. Though, in retrospect, it may have been arbitrary to generalise the function of an individual’s vigilance behaviour based on the distance of the object the animal seemed to be watching without actually confirming what this object was. There is a possibility that a certain amount of the vigilance I denoted long-distance in fact could have been caused by
social conditions within the group, i.e. even though individuals did not seem to be watching a group member or food item in close proximity they could still have been looking at another group member further away. Chapman and Pavelka (2005) have argued that larger groups in black-and-white colobus (*C. guereza*) are unstable since an increase in the number of resident males (a result of the increase of females) cause an increase in aggression. In fact, three of the four MM-groups (but non of the SM groups) in this study experienced intense male-male interactions (DA, WW) or exceptional male related conditions (OD) that could increase the entire group’s uneasiness and with it it’s group member’s tendency to be vigilant towards individuals within the group. DA-group was followed by an extra-group male that on several occasions was engaged in high-intensity interactions with the group’s resident males, in WW-group one of the two resident males was repeatedly seen attacking and even wounding the other male and OD-group had within the previous 8 months acquired 6 new males. Females have good reason for increasing their vigilance in these conditions since high-intensity male-male competition can induce certain costs (Chapman and Pavelka, 2005) such as stress (Dunbar, 1987) and the presence of strange males increase the risk of infanticide (Struhsaker and Leland, 1987; Kappeler, 1999). Additionally, for males competitive conditions can be a reason to increase alertness towards other male group members (Baldellou and Henzi, 1992; Treves, 1999). Subsequently I believe that the social situations could be the reason behind the higher vigilance rates of the individuals of MM-groups.

In another analysis on group type, I found that there was no statistical difference in the vigilance rates between females or between males when comparing SM and MM-groups. This implies that neither males nor females reduce their vigilance rates in response to the number of resident males in the group. This is surprising since males proved to be the most vigilant sex and more male group members imply lowered requirements on individual vigilance. It is possible that in order to significantly influence vigilance behaviour in all group members, the number of resident males in the group needs to be greater than it was in any of my study groups, i.e. >7. This being said, even though there was no difference in vigilance rates within the sexes depending on group type, there might still be other vigilance-dependent differences between group types, namely the purpose of the vigilance behaviour. For instance, and as exemplified in the previous section, males of MM-groups have competitors present continuously and are therefore potentially more exposed to male-male interactions than males of SM-groups. This might force them to engage in with-group surveillance more frequently than males of SM-groups (Treves, 1999; Cameron and du Toit, 2005). Conversely, males of SM-groups might show more vigilance directed towards neighbouring groups than males in MM-groups because of the slightly greater frequency of inter-group encounters SM-groups experience (this study, further discussed in the section on intergroup encounters). Hence, the motive for male vigilance might differ depending on group type and as noted earlier, for females the motive of male vigilance can be of importance. If SM-group males tend to direct more vigilance outwards the group than MM-group males, females in SM-groups may derive greater benefits from male vigilance than females in MM-groups. To be able to distinguish male vigilance directionality and consequently the motive, a more detailed sampling method than group scans is required, for example continuous focal sampling of males.

**Vigilance and male neighbours**

In contrast to my predictions, female vigilance did not differ depending on the sex of the nearest group member. This contradicts a previous study by van Schaik and van Noordwijk (1989) who found that vigilance in capuchin monkeys was lower when one or more of the neighbours of the focal animal were adult males. It is indeed surprising that I did not find indications attesting that male presence influence female vigilant behaviour since males proved to be the more vigilant sex. There is the possibility that this study is not extensive enough. Since all study groups contained more females than males data points of male presence were underrepresented in the analysis. To evaluate whether this unevenness could have biased the result more data needs to be collected and the analysis repeated with the added sample. Still, presuming that data deficiency is not the reason for my results there are other conditions and variables that can deliver possible answers as to why my prediction could not be confirmed.

Firstly there could be a need for supplementary parameters. In addition to looking at sex differences when evaluating differences in vigilance, several authors have also considered age
(Alberts, 1994) and rank (Alberts, 1994; Gould et al, 1997), existence of offspring (Alberts, 1994; Steenbeek et al, 1999a; Treves, 1999; Kutsukake, 2007), closeness to neighbouring group’s home range (Steenbeek et al, 1999a), the individuals’ position in relation to the rest of the group and height above ground (van Schaik and van Noordwijk, 1989; Steenbeek et al, 1999a). Not all of these factors are of interest to this study, but a few of them deserve further attention. Note for example, that females without depending infants could be the only females that would regulate their vigilance rates depending on the proximity and sex of neighbours since females that have infants have much more to lose and would maintain the same level of vigilance irrespective of the sex of neighbouring individuals. Thus, separating vigilance data from females in different life history stages might render other results then those presented here. Similarly, the threat towards an individual differs depending on spatial factors. For example, on occasions when foraging is taking place near ground or in the periphery of the group the animal is potentially subjected to higher levels of danger and should thus regulate vigilance rate accordingly. Changes in vigilance caused by the position of the focal might then obscure an analysis on the importance of the focal’s neighbours.

Secondly there is yet again the issue of vigilance directionality. As mentioned in the precious section on vigilance, there are difficulties in separating social from non-social vigilance when the object of the focal animals’ vigilance is not known. Hence, the lack of difference in vigilance rate between females with female neighbours and females with male neighbours, might not necessarily mean a lack of importance of male vigilance to the females, but could simply reflect the possibility that I mistook some social vigilance and visual foraging for non-social vigilance. In fact, since within-group surveillance is expected to increase with group size (Treves, 1999; Treves and Baguma, 2002), the overall higher vigilance rate in the larger MM-groups may indicate that within-group surveillance might be an issue at BFMS, which I also noted earlier. In opposition, female ursine colobus suffer a very low risk of aggression from other group members (Saj and Sicotte, 2007b; this study) so with the exception of the high-intensity male-male interactions in MM-groups, there should be little cause for within-group surveillance in this species (agression rates will be further discussed in the section on the cost of males to females). In accordance, females did spend significantly more time scanning alone than when in company of another group member when no regard to the sex of the neighbour was taken, thus implying that the purpose of female vigilance is non-social vigilance. These contradictions might have been entangled if the data would have permitted an analysis on group type differences in female vigilance and neighbours, but unfortunately a comparison of this sort could not be preformed without an addition in datapoints.

**Intergroup encounters**

As predicted, males were the main participants in inter-group encounters and were active in all low intensity cases and 94.44% of all high intensity cases. Sicotte and Macintosh (2004) also found that males were the most active sex in inter-group encounters in their study on one C. vellerosus group at BFMS (BS/B2). My data underlines their findings, confirms that males are more active in between-group encounters in an additional five groups at this site and further strengthen the notion that male predomination in inter-group encounters is the norm in this population.

Female primates can derive great benefits from having male group members participating extensively in intergroup encounters. If a group is successful during agonistic interactions with neighbouring groups it can increase its inter-group dominance. In turn, a raised position in the inter-group hierarchy could grant the group extended access to resources such as food and water and may also serve to intimidate extra-group males from performing incursions or take-overs, instances where the group’s infants are at risk of Infanticide. Benefits for females of extensive male participation in intergroup encounters thus include increased resource access and infant safety (Wrangham 1980). Whether or not these particular benefits are made available to females of ursine colobus at BFMS is another matter, which will be discussed further in the following part of this section where I also will address the competitive ability of the study groups and the implications of group type in inter-group hierarchies.

Sicotte and Macintosh (2004) found indications of male resource defence in their study of ursine colobus’ inter-group behaviour at BFMS. This would indicate that resource competition
occurs between groups in this population and that males take part in defending the group’s resources during intergroup encounters. Hence one of the female benefits I suggested is implied. However, the theory that extensive male involvement in between-groups interactions lead to a reduction in infanticide risk has to remain speculative. Infanticide is known to occur at BFMS (Sicotte et al, 2007), and thus means of reducing it would be of great importance for females (Steenbeek et al, 1999a), but it is a rare and difficult phenomenon to study (van Schaik and Jansen, 2000) and at this point there is no available data confirming whether inter-group dominance lessens infanticide risk or not.

Shifting the focus to group type, did the number of males in the group influence competition potential of the group? Unfortunately, the dense vegetation often made it difficult to determine which group “won” an encounter and I could not comprise an intergroup hierarchy based on the data I collected. But assuming that males have the ability to increase the competitive capacity of their group, groups containing more than one adult male would have greater competitive ability than groups having just one male. A group’s position within the group hierarchy would thus reflect group type (SM or MM). A similar relationship between the number of males per group and group rank have been previously predicted by Wrangham (1980) and Nunn (2000) and confirmed in a study on wedge-capped capuchin monkeys (Robinson, 1988). Thus if intergroup encounters function as a way of between-group competition over resources in C. vellerosus, which is possible (Sicotte and Macintosh, 2004), and male group numbers influence the outcome of such competitive interactions, females can benefit from MM-group living. In light of this hypothesis it is regrettable that I could not establish a group hierarchy of the study groups at BFMS and investigate whether group rank was predisposed by group type. However, in the few cases where a winner of an inter-group encounter could be established, no clear-cut tendency concerning group type emerged. For instance, the SM-group BS was observed retreating several times when approached by a MM-group, but in at least one occasion the SM-group SP was observed driving away the MM-group WW. It is possible that a potential intergroup hierarchy existing at BFMS is not fixed and linear as in guerezas (Harris, 2006) but depending on the groups that meet and when, as in Japanese macaques (Sugiura et al, 1999). If this is the case, female benefits of group type in between-group interaction are less distinct.

As previously mentioned, all MM-groups were larger than the SM-groups (Table 1). Hence it is difficult to distinguish whether a behaviour expressed by individuals of MM-groups is associated with the greater number of males or the greater number of individuals of the group, or perhaps a combination of both. This complication being noted, there is still some debate on the importance of group size in between-group ranking (Harris 2006).

Even though I was unsuccessful in extracting any data on group hierarchy from my observations, it was possible to calculate the frequency of inter-group encounters per group type. MM-groups experiences a slightly lower frequency of between-groups encounters than SM-groups, a tendency which is in line with the four studies compiled by van Schaik (1996) indicating that groups containing multiple adult males are less likely to suffer conflicts with neighbouring groups. van Schaik suggested that this could be explained by between-group avoidance. For females, the advantages of a decrease in, or low rate of, inter-group encounters would be facilitated infant defence and perhaps a reduction of infanticide risk and injuries. However, the difference in intergroup encounter frequency between SM and MM-groups was not statistically significant and I suggest that this is might be a prolonged consequence of population density. There are examples among several species suggesting that density is the critical factor affecting between-group aggression (lion: Heinoth, 1997; Japanese macaque: Saito et al, 1998; bonnet macaque: Cooper et al, 2004; but see mantled howler monkey: Cristóbal-Azkarate et al, 2003) and intergroup encounter frequency (mungo: Gilchrist and Otali, 2002). BFMS is a small reserve with a population of colobus monkeys that have been growing for at least 15 years (Beier et al, 2002; Wong and Sicotte, 2006). The higher density of individuals could be increasing intergroup encounters and in turn, an overall augmentation in intergroup encounters could dilute the significance of group type. Strengthening this explanation is an example from one of the study groups, BS. This group has seen an increase in the hourly rate of intergroup encounters since 2001, from 0.099 (34 encounters in 343 hours: Sicotte and Macintosh, 2004) to 0.195 (8 encounters in 41 hours, this study).
Costs of males to females

I did not expect to find extensive or severe within-group aggression between the sexes since this is mainly common in species socially and/or ecologically different from black and white colobus species (e.g., orang-hutan: Mitani, 1985; Fox 2001; Japanese macaques: Eaton, 1984; Matsubara and Sprague, 2004; hamadryas baboon: Smuts, 1995; chimpanzee: Goodall, 1986; Muller et al., 2007; wedge-capped capuchin: O’Brien, 1991; Rose, 1994). I did, however, wish to investigate whether aggression, when it did occur, was more frequent between than within the sexes. Nevertheless, the results of this study did not support any of the predictions I put forward; there was a total absence of male aggression towards female group members, males did not interrupt female foraging and male presence did not have a negative influence on female feeding or foraging success. In short, this study suggests that ursine colobus males do not impose costs on females in form of aggression nor constitute a cost component in resource competition with females. It is possible that within-group agonistic interaction between the sexes still occur even though I did not observe it, but even so, most definitely at a very low rate.

The implications of my findings result in two questions; i) why did I not observe any male aggression towards females within the groups? and ii) if resident ursine colobus males do not impose cost to females in the form of aggression or feeding competition, is there any other way in which they impose costs on females?

The answer to the first question is linked to the ecology and social life of C. vellerosus. If we start by looking at the ecology of ursine colobus we find that it is primarily a folivorous species (Saj et al., 2005) and folivores usually depend on food resources that are evenly distributed and plentiful, i.e., hard to monopolize. A resource that is not monopolizable does usually not generate direct competition (within-group contest competition, WGCC) (Wrangham, 1980; van Schaik, 1989), thus rates of agonistic interactions over food should be infrequent in folivorous populations. Just recently Saj and Sicotte (2007a) presented results indicating that the potential for WGCC at BFMS indeed is low and in another study (2007b) they also found that female-female aggression during feeding within the group is rare. The result of this study, that male-female aggression during feeding also is rare, is added evidence for absence of WGCC at BFMS.

Besides feeding competition, the other major circumstance in which female-directed male aggression is observed in primates is sexual coercion. Herding, intimidation, physical punishment and forced copulations are all variant types of sexual coercion exhibited by male primates (Smuts and Smuts 1993). Why were not any of these forms of male aggression observed at BFMS?

Firstly, it is important to remember that sexual coercion can occur at a very low rate. This study is based on seven study groups and only occasionally were we able to have more than one group under surveillance and even then dense cover prevented us from a clear view of all individuals. Hence there were several opportunities for males to exhibit certain rare aggressive behaviours without our knowing. To take an example, infanticide was only recently documented in the black-and-white colobus genus (Harris and Monfort, 2003; Onderdonk, 2000) even though these species have been studied extensively since before the 1970s and at BFMS it was officially confirmed as late as in 2007 (Sicotte et al., 2007).

Secondly, the majority of these types of male sexual coercion are reported in primate species socially and physically different from ursine colobus. For example; orang-utan (Pongo pygmaeus), Japanese macaque (Macaca fuscata), hamadryas baboon (Papio hamadryas) and chimpanzee (Pan troglodytes). In orang-utans, forced copulations are common, but unlike ursine colobus orang-utan females are solitary and therefore lack protection from other group members (Mitani, 1985; Fox, 2002). In Japanese macaques, female-directed male aggression and violence is common, but unlike ursine colobus, Japanese macaques are seasonal breeders and male aggression escalate and intensify especially during the breeding season (Eaton, 1984; Matsubara and Sprague, 2004). In hamadryas baboons, male aggression towards females occurs at a regular basis, but unlike ursine colobus hamadryas males form tightly held harems through abducting child brides. By continuous threats and intimidation the hamadryas males are able to lay claim to females long before they are sexually mature and thus make sure that the females will reproduce with their harem master and not solicit matings with another male (Smuts, 1995). In chimpanzees, male aggression against females occurs frequently, but unlike ursine colobus chimpanzee females...
have sexual swellings that provoke high intensity male-male competition and it is believed that male aggression against females in this species is augmented by this physical attribute (Goodall, 1986; Muller et al, 2007). This being said, ursine colobus also have fair similarities, such as a folivorous diet and female dispersal, with species in which male aggression is common, e.g. mountain gorilla (Gorilla gorilla beringei). However, since female-female affiliation is greater than female-male affiliation in ursine colobus it is likely that female dispersal is more facultative in ursine colobus than in mountain gorilla (Saj et al, 2007). In the latter the male-female bond is stronger than the female-female bond and the frequent displays of female-directed aggression from silver-back males has been proposed to constitute a male demonstration of strength, exhibited in order to influence female mate choice and female dispersal as well as to keep female within-group competition from escalating (Watts, 1992; Sicotte, 2002). Also, the considerably greater sexual dimorphism in seize in mountain gorillas make male dominance maintenance less costly for males and females more vulnerable to male force than in ursine colobus (Sicotte, 2002; Slater et al, 2008). Summarizing the above, ursine colobus lack various social and physical traits, such as solitary living (Saj et al, 2005), seasonal breeding (Teichroeb and Sicotte, 2008), tightly held harems of unrelated females (Saj et al, 2005; Wong and Sicotte, 2006), sexual swellings (personal observation) and generalized female dispersal (Saj et al, 2007) present in other species that exhibit intense forms of sexual coercion and frequent male aggression.

Answering the second question, I propose the possibility that there is one particular phenomenon of male coercive behaviour I might have overlooked; male herding behaviour. Herding is a form of male mate defence employed by males in order to keep female group members from leaving the group (Steenbeek, 1999; Sicotte, 1993) or getting in contact with extra-group males for copulation (Steenbeek, 1999). Males can achieve this either through leading his group of females, i.e. herding them, away from other males or other groups, or through displays of aggression towards female group members when these approach or attempt to interact with other males (Majolo et al, 2005). Herding is considered to be a form of sexual coercion since it aims to manipulate mating opportunities.

Herding can be difficult to distinguish from general group movement, especially since it usually is associated with intergroup encounters, situations typically involving many rapidly moving individuals. This may be the major reason as to why I overlooked it. Herding is found in primates species socially or ecologically different from C. vellerosus (chimpanzee: Muller et al, 2007; Japanese macaque: Majolo et al, 2005) and in species living in a different (more open) habitat (hamadryas baboon: Swedell, 2002) but has also been suggested in black and white colobus species (C. guereza: Fashing, 2001). Since herding is male tactic designed to keep females from moving freely and engage in promiscuity it should only exist in species where female dispersal and extra-group matings occur. At BFMS, both female dispersal (Saj et al, 2007) and extragroup copulation attempts (Sicotte and Macintosh, 2004) have been documented. Also, males at BFMS are known to be the main aggressors during intergroup encounters (Sicotte and Macintosh, 2004; this study), which suggests existence of male mate defence. In light of these facts I propose the possibility that herding behaviour occurs in my study population of ursine colobus. At this time the only evidence I can present to support this theory is an observation of one possible herding attempt witnessed in the group SP. At this occasion the resident male of SP, ED, was observed following one of the group’s females as she approached members of OD during an intergroup encounter. The female later returned to SP tailed by ED. The purpose of the female’s behaviour will not be discussed here, but interestingly, one year later the female IO (possibly the female seen approaching OD) was missing from SP (Ewa Wikberg, personal comm.). Had IO been investigating dispersal opportunities in 2007 and than sometime between August 2007 and May 2008 decided to leave SP? Assuming this to be the case it is possible that ED had been employing herding behaviour when following IO. For females the costs associated with male herding behaviour include impediment of free female dispersal and free mate choice (Watts 1989; Smuts and Smuts, 1993; Steenbeek, 1999).

Finally I would like to address group type and cost of males to females. Since the results in this study could not confirm any form of cost to females linked to the presence of resident males I also lack data for a comparison depending on group type. However, if one broadens the view and includes results and settings other than those of this study, infanticide is often mentioned in
relation to male group numbers. This since infanticide and male takeovers (that can lead to infanticide) is expected to be more likely in groups with low male group number (Watts, 1989; Sommer, 1994; Rose and Fedigan, 1995; van Schaik, 1996; Perry, 1998). Thus females can reduce the risk of infanticide in MM-groups and are also known to prefer MM-groups if given the choice (Steenbeek et al. 1999b; Watts, 1999). A further negative consequence of SM-groups is an increase in female-female reproductive competition and restrained mate choice (Smuts, 1987; Altmann, 1990; Kappeler, 1999). Alternately, female members of MM-group experience a higher risk of intense sexual coercion (Smuts and Smuts, 1993) and a possible increase in food competition (Wrangham, 1980; van Schaik, 1983; Dunbar, 1988). MM-groups are also more likely to experience demanding social situations because of the coexistence of several competing males, which can induce stress-related cost on females (Dunbar, 1987; Chapman and Pavelka, 2005). To add a further level to the issue, all benefits and all costs of males to females are not of the same magnitude or importance for female fitness and different females would differ in their susceptibility to certain cost or benefits depending on their age, rank, sexual maturation and if they have offspring or not. Nevertheless, it is plausible to conclude that it would be in the interest of all females of all life history stages to manipulate male numbers to their advantage or at least not be passive in their choice of group if given the opportunity to choose.

CONCLUSIONS

The results of this study suggest that female ursine colobus can derive greater benefits from male than from female group members when it comes to vigilance and intergroup encounters. However, no indication of a male behaviour costly to females could be found. Thus, two of the predictions associated with my first hypothesis, that female’s permanent association with males result in certain benefits exceeding those provided by other females, was confirmed. However, my second hypothesis, that female’s permanent association with males result in certain costs exceeding those imposed by other females, could not be confirmed. I found no clear cut indication that group type could explain any differences in benefits or costs of males to females, other than a tendency for SM-groups to experience higher rates of intergroup encounters than MM-groups and that members of MM-groups appeared to be more vigilant than members of SM-groups. The first I interpret as an indication of group avoidance, beneficiary to the females of MM-groups, and the latter as a mere consequence of social conditions within the MM-groups. The absence of obvious costly male behaviour, such as aggression and resource competition, does not mean that female permanent association with male ursine colobus has to be entirely without costs but just that the costs may be of a very subtle nature (herding behaviour). For the future, I request more studies on this species, the least known of all black and white colobus, and emphasise that by evaluating benefits and costs of resident males to females we may increase the knowledge of basic female behaviours such as vigilance, foraging and intergroup behaviour as well as ultimately contribute to the understanding of the underlying motives for female dispersal and migratory behaviour.

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