

# Mating Tactics in Male Grey-Cheeked Mangabeys (*Lophocebus albigena*)

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## Abstract

Reproductive tactics of males can change with individual quality, relatedness and social structure. Here we describe the behaviours of male grey-cheeked mangabeys towards other males, and females and their offspring (*Lophocebus albigena*) in relation to male status (high-ranking/low-ranking/transient) and group composition in Kibale National Park, Uganda. High-ranking males had the highest mating success, frequency of loud calls, mate guarding and aggression towards females and males. Only transient males were often observed to be aggressive towards juveniles, while some high-ranking males provided infant care. Mating tactics of high-ranking males varied greatly among the five studied groups, probably as a function of the intensity of male–male competition. These results are discussed with regard to the role of male–male competition and behaviours that could affect female mate choice as tactics to obtain reproductive success.

## Introduction

Reproductive success of males is thought to depend mainly on access to receptive females, and therefore, males compete for females (Darwin 1859; Andersson 1994). In social species, evidence for this competition is found in the distribution of males among groups containing females (Eberle & Kappeler 2002), in male–male interactions and in their manipulation of females to increase mating opportunities (Smuts & Smuts 1993). As males vary in age, size, fluctuating asymmetry and energy reserves they can adopt different tactics or change their tactics as they grow or age to optimize their reproductive success (Waltz & Wolf 1984; Stockley et al. 1996; Cook et al. 1997; Thirgood et al. 1999; Sinervo et al. 2000; Kemp 2002; Shuster & Wade 2003; Isvaran 2005; Lidgarda et al. 2005; Saunders et al. 2005; Caillaud 2008; Lucas & Howard 2008). When male tactics are costly to females, these females can respond with counter

strategies, which may lead to an arms race in sexual strategies (Agrell et al. 1998; Soltis et al. 2001).

In multi-male groups of primate species, dominance among males is the most important factor determining a male's access to females (e.g. Altmann 1962; Suarez & Ackerman 1971; Janson 1984; Dunbar 1988; Dixon et al. 1993; Altmann et al. 1996; Nishida 1997; Gust et al. 1998). However, there are few exceptions (Tutin 1979; Berard et al. 1993; Bercovitch 1997; Nishida 1997; Strier 2002).

In most primate species that live in mixed-sex groups, males have a tendency to leave their natal group and move between groups as transient males (Pusey & Packer 1987; Isbell 2004). This behaviour has also been documented in our study species, grey-cheeked mangabeys (Olupot 1999; Olupot & Waser 2001). Olupot & Waser (2001) divided these males into two categories: dispersing males (here called transient), which mated in new groups after migration, and visiting males which were not

observed to mate in new groups. It is not known if resident males were once transient (because of lack of long-term data) and it is likely that most are not in their natal group. Visiting males stayed in their new groups for a short time (maximum 14 d), while dispersing (transient) males stayed longer. For males, transferring among groups may be part of a reproductive strategy if they can maximize their reproductive success (Dunbar 2000) joining groups with a female-biased operational sex-ratio, thus increasing the chances of more immediate reproductive success (Phillips-Conroy et al. 1992; Olupot & Waser 2001) and perhaps avoid inbreeding (Pusey & Packer 1987). These transient males are likely to use social and sexual tactics that differ from resident males, because they are not related to the other group members and are not part of the social network (Clutton-Brock 1988).

Apart from attempted monopolization by high-ranking males, a wide range of male tactics have been observed in multi-male groups, including coalitions by middle-ranking males (Noe & Sluifster 1990), friendships between males and particular females (Smuts 1983) and consortships (Packer 1979). Where it is impossible for a male to monopolize copulations, a single male may copulate with a high frequency and out-compete rivals with the amount of sperm produced (Birkhead 1996, 2000; Dixon 1998; Birkhead & Pizzari 2002).

Female sexual strategies can play an important role in mating systems and affect male strategies. Sexual swellings appear to play a role in female manipulation of males in many primate species. Advertising ovulation by sexual swelling may promote male competition, sperm competition or female mate choice. However, reliability of this signal varies across species (Pagel 1994; Whitten & Russell 1996; Dixon 1998; Nunn 1999; Van Schaik et al. 2000; Domb 2001; Reichert et al. 2002; Emery 2003; Deschner et al. 2004; Engelhardt 2005; Barelli 2007; Deschner 2007; Gesquiere et al. 2007).

Our study was based on five of the seven mangabey groups studied in Kibale National Park by Olupot & Waser (2001). Grey-cheeked mangabeys live in groups in which most of the adult males migrate between groups with varying frequencies (Olupot & Waser 2001) and males sometimes move alone (Struhsaker & Leyland 1979; Olupot 1999). Males tend to transfer into groups with higher numbers of oestrous females (Olupot & Waser 2001), which suggests that they do pursue reproductive success. Resident males typically follow females with sexual swellings (Wallis 1979),

however, different sexual tactics may be undertaken by transient males.

The aim of this study was to compare the reproductive tactics used by high-ranking, low-ranking resident and transient males of grey-cheeked mangabeys. Firstly, we described patterns of migration during the study. Secondly, we examined across high-ranking, low-ranking, and transient males the relationship between rate of mating and aggression towards other males, females, and juveniles, the frequency of loud calls, and the probability of mate guarding. Loud calls (whoop-gobbles) could be used to signal male maturity or quality and could therefore be relevant to this study. Many of the measured parameters could be expected to relate to dominance and thus vary with both rank and group composition. Therefore, the relationship between rate of mate guarding and loud calls by high-ranking males were also correlated with an estimate of the amount of competition experienced in the group.

## Methods

### Study Site and Subjects

After a pilot study in 1999, data were collected for 6 mo (Jan.–Jun. 2001) in five social groups and supplemented with observations in 2002 in Kibale National Park, western Uganda (0°13′–0°41′N and 30°19′–30°32′E). Kibale (766 km<sup>2</sup>) is a moist, evergreen medium altitude forest (around 1500 m) with a mosaic of swamp, grassland, thicket, colonizing forest and softwood plantations (Chapman et al. 2000). Mangabeys in Kibale live in multi-male groups of on average 14 individuals (Waser 1977a; Wallis 1979; Olupot 1999). In total, we observed 26 sub-adult and adult males and 35 females (sub-adult and adult; Table 1). Recent work revealed that the grey-cheeked mangabeys in Uganda are morphologically distinct from more western populations and, therefore Groves (2007) proposed to grant them species status. As a result, the mangabeys in Kibale that were once called *Cercocebus albigena*, then *Lophocebus albigena*, may now be called *L. ugandae* by some.

Fourteen males were recognized by the unique colour combination of their collars or attached radios placed on them in an earlier study (Olupot 1999). Males without a collar were classified as adult male (AM, n = 7), or sub-adult male (SAM, n = 5) and were recognizable on the basis of their relative sizes and other distinguishing features. In each of the groups, there were at least two individual males present in the same group during Jan.–Jun. 2001.

**Table 1:** Group composition of grey-cheeked mangabeys in Kibale per observation period based on 236 d of direct observations

Group	Statistic	No. individuals in the category						Group size
		AF	OAF	AM	SAM	JUV	INF	
Butanzi	Min	5.00	1.15	1.00	0.00	3.00	3.00	16.00
	Max	6.85	3.00	5.00	1.00	3.00	3.00	20.00
	Mean	6.01	1.98	3.40	0.80	3.00	3.00	18.20
	SD	0.59	0.59	1.36	0.40	0.00	0.00	1.32
CC	Min	5.00	0.60	3.00	0.00	3.00	2.00	16.00
	Max	7.00	2.99	5.00	1.00	3.00	2.00	19.00
	Mean	6.12	1.88	4.20	0.40	3.00	2.00	17.60
	SD	1.03	1.03	0.75	0.49	0.00	0.00	1.01
Lower Camp	Min	3.60	0.40	2.00	0.00	4.00	3.00	15.00
	Max	5.60	2.40	5.00	1.00	4.00	3.00	19.00
	Mean	4.50	1.49	2.60	0.60	4.00	3.00	16.20
	SD	0.80	0.80	0.80	0.49	0.00	0.00	0.75
Mikana	Min	3.00	0.40	2.00	0.00	3.00	2.00	12.00
	Max	5.00	2.40	5.00	1.00	3.00	2.00	13.00
	Mean	3.69	1.49	2.60	0.60	3.00	2.00	12.60
	SD	0.85	0.80	0.80	1.49	0.00	0.00	0.49
Upper Camp	Min	5.69	0.20	4.00	0.00	5.00	5.00	22.00
	Max	7.80	2.31	7.00	1.00	5.00	5.00	26.00
	Mean	6.69	1.30	4.80	0.20	5.00	5.00	23.00
	SD	0.88	0.88	1.17	0.40	0.00	0.00	1.55

AF, adult females; AM, adult males; OAF, oestrus adult females; SAM, sub-adult males; JUV, juveniles; INF, infants.

These males were regarded as resident males ( $n = 16$ ). Males that emigrated at least once from a group or that immigrated into a group and then dispersed during these 6 mo were called transient males ( $n = 10$ ). These transient males typically spend between several weeks and several months with a particular group (Olupot & Waser 2001). This excluded visiting males that were sighted only briefly (<2 d) in groups. Unfortunately, age, rank and natal status could not be distinguished during this study, and males probably go through stages of residency and migration throughout their life, while adjusting their mating tactics.

Females with sexual swellings were present throughout the year as this species has no seasonal reproduction or synchronized oestrus. The swelling increases in size and colours gradually, deepening to pink (oestrous adult female inflating) until the maximum stage of swelling is reached (oestrous adult female peak). As oestrous passes, the swelling becomes less turgid and the colour changes to dark purple (oestrous adult female deflating; Danjou 1972; Deputte 1991; Wallis 1983). Average durations reported range from 17 to 31 d of sexual swelling; the phase from quiescence to peak swelling is 4–14 d long, the peak size of sexual swelling lasts 2–4 d, and the deflating stage lasts 7–14 d (Rowell &

Chalmers 1970; Danjou 1972; Wallis 1983; Deputte 1991). In this study, individual females could be recognized individually only during the period with sexual swelling and not across the cycles.

### Observation Methods

From Jan. 2001 to Jun. 2001, two observers collected behavioural observations for 8–9 h/d, for six consecutive days per week, for a total of 2036 h. To measure the rate of movement of males between groups, we censused the focal group every day during each observation period. Dominance interactions among males were recorded on the basis of approach–retreat interactions following De Waal (1987), that were scored for all nearby males during focal follows of oestrous females. Dominance relationships are ordinal within a group and, therefore, we simplified this classification to compare males across groups: the highest ranking male was classified as high ranking and others as low ranking. In two groups, the ranks of the two highest ranking males could not be distinguished and both males were classified as high ranking. Mate guarding was defined as staying within 3 m of the focal female and following her wherever she moved, and chasing approaching males. We recorded one loud call as a bout of whoop-gobbles given by a single male. Mating was defined as a mount involving intromission (Wallis 1983) and mating success of a male was measured as the number of observed matings.

We predominantly followed females with sexual swellings. Focal females were classified as ‘adult female’ – without sexual swelling, or female with sexual swelling – ‘inflating female’, ‘peak female’ and ‘deflating female’. The behaviours of focal females were recorded all day, divided into 30-min sampling blocks with no more than 5 min between blocks. During these all-day follows we recorded female behaviour. During focal sampling of females with sexual swellings, we recorded all occurrences of interactions with males and other group members within 10 m of the focal female. Individuals can be lost during follows in the forest environment, but the sexual swellings provided a strong visual signal so that individuals were not lost frequently and found quickly, and we observed several sneaky matings (Arlet et al. 2007).

### Data Analysis

To compare the behaviour of high-ranking, low-ranking and transient males, the number of mate-guarding observations, loud calls, aggression towards females and juveniles, and matings, were used as

dependent variables in Poisson Regression Models (McCullagh & Nedler 1989), with natural logarithm of observation days as covariable, and male status (high-ranking/low-ranking/transient) as categorical factor. The tendency for transient males to have fewer days of observation is a structural feature of these data. Generally speaking, a male's identity as transient is a surrogate for fewer days of observation. This association between the variables for male status and days of observation is likely responsible for the lack of significance of days of observation as a predictor of dependent count variables. Basic principles would ordinarily suggest that number of days of observation would be a predictor of the number of mate-guarding observations, and aggression towards females and juveniles. Model results of Poisson Regression are presented in tables, with 95% confidence intervals (CIs) given for each parameter of the model. An effect is called significant at level 0.05 if the CI does not contain zero. Estimates for effects because of male status are comparisons between high- and low-ranking males with transient males (the effect for transient males is always the baseline).

To simultaneously explore multiple factors and their interactions we used an Analysis of Multi-Factor Regression (GLM) approach on the number of events (such as matings) per the number of days an interaction could have occurred, thus using a single data point for each male. Analysis of variance (ANOVA) was used to compare rates of aggression and the frequency of loud calls. The analyses were performed using STATGRAPHICS 5.0.

## Results

### Male Migrations

The average sex ratio of a group at the time a male joined was significantly less male biased ( $n = 12$

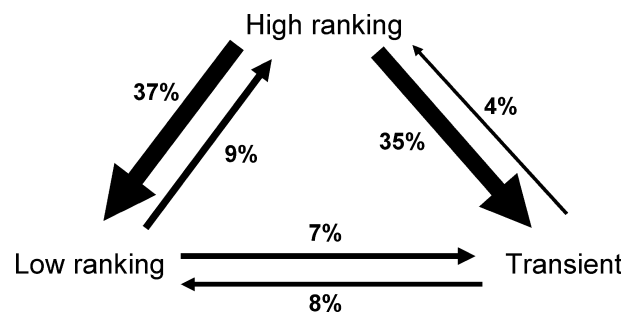
events, average 0.59 with 95% CI 0.49–0.69), than when males left ( $n = 16$  events, average 0.79 with 95% CI 0.74–0.84).

### General Patterns in Male Behaviour

Mating success, loud calls, mate-guarding observations and aggression towards females and males were correlated with each other (Table 2) and related to male rank. High-ranking males were more often involved in mate guarding, mated more, gave more loud calls, and were more aggressive towards adult females and males. Only transient males were frequently aggressive towards juveniles.

### Interactions Among Males

We recorded 37 aggressive encounters among high-ranking, low-ranking and transient males when oestrous females were present. High-ranking males were the most aggressive towards other males (ANOVA single factor,  $p = 0.017$ ,  $df = 1$ ,  $F = 6.37$ ) and displayed with similar frequency towards low-ranking and transient males (Fig. 1).



**Fig. 1:** Frequency of aggression between high ranking, low-ranking and transient males. Shaded area of arrow is proportional to the number of aggressive interactions per day. The percentages in the figure add to 100%.

	Matings	Loud calls	Mate guarding	Aggr. toward		
				Females	Juveniles	Males
Matings	1.00					
Loud calls	0.46 (0.009)	1.00				
Mate guarding	0.69 (<0.001)	0.35 (0.038)	1.00			
Agg. females	0.36 (0.036)	0.33 (0.049)	0.33 (0.048)	1.00		
Agg. juveniles	-0.032 (0.44)	-0.20 (0.16)	-0.21 (0.149)	-0.057 (0.319)	1.00	
Agg. males	0.48 (0.007)	0.49 (0.006)	0.41 (0.018)	0.52 (0.003)	-0.109 (0.30)	1.00

Five of the six male behaviours included are significantly correlated with each other and can be viewed as correlates of male rank. Only aggression towards juveniles was not correlated with other behaviours because only transient males were often observed to be aggressive towards juveniles (5 of 10 transient males).

**Table 2:** Correlation matrix on rate of behaviour (no. behaviour/no. days of observation in relevant context) with p-values of one-tailed tests

**Mate Guarding**

Particular males spent 2–3 d in the proximity to females at the peak of sexual swelling, by following them (or females followed males) and chasing away approaching males. There were significant differences in number of mate-guarding observations among male classes for a given number of days of observation (Poisson Regression; Table 3). High-ranking males guarded oestrous females 13.6 times more often than transient males (at  $e^{2.61} = 13.6$  times). Low-ranking males guarded oestrous females about four times more than transient males (at  $e^{1.35} = 3.9$  times). Note that other males can not guard females that are guarded by higher ranking males. The number and duration of mate-guarding periods performed by high-ranking males was positively correlated with the number of other males who attempted to approach the female with sexual swelling at that time (Regression;  $F = 80.94$ ,  $df = 1$ ,  $R^2 = 0.96$ ,  $p = 0.003$ ).

**Aggression Towards Females**

All male classes were aggressive towards females, but only resident males were aggressive towards oestrous females. We recorded five open attacks on peak and deflating females (these included focal animals), and 11 towards non-oestrous females (all occurrence scans). There were significant differences between the three male categories in the frequency of these aggressive displays for a given number of days of observation (Poisson Regression: Table 4, Fig. 2). High-ranking males were about five times more aggressive towards females than transient males (Poisson Regression:  $e^{1.56} = 4.76$  times). Low-ranking males behaved almost three times more aggressively towards females than transient males (Poisson Regression:  $e^{1.06} = 2.89$  times).

**Table 3:** Estimates for the main effects in the model for number of observations of guarding of oestrous females among high-ranking, low-ranking, and transient males of grey-cheeked mangabeys in Kibale National Park, Uganda (Poisson Regression; model p-value  $<10^{-4}$ , residual deviance 30.82 on 22 df)

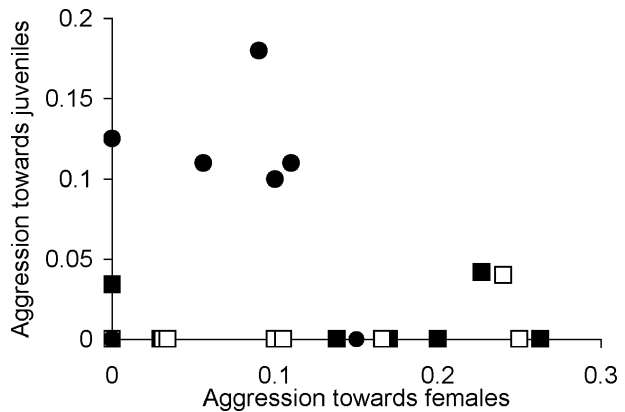
Parameter	Estimate	SE	Confidence interval
Intercept	-1.07	1.11	-3.25 to 1.10
Log (d)	0.065	0.42	-0.75 to 0.88
High-ranking male	2.61	0.6	1.44 to 3.80
Low-ranking male	1.35	0.65	0.07 to 2.63

The effect for transient males is fixed at zero.

**Table 4:** Estimates for the main effects in the model for number of aggressive displays towards females among high-ranking, low-ranking, and transient males of grey-cheeked mangabeys in Kibale National Park, Uganda (Poisson Regression; model p-value = 0.009, residual deviance 42.33 on 22 df)

Parameter	Estimate	SE	Confidence interval
Intercept	-1.55	1.3	-4.1 to 1.0
Log (d)	0.43	0.5	-0.56 to 1.42
High-ranking male	1.56	0.56	0.45 to 2.66
Low-ranking male	1.06	0.58	0.09 to 2.2

The effect for transient males is fixed at zero.



**Fig. 2:** Plot with for each of 26 males the number of aggressive displays towards females and juveniles per day of observation. Two low-ranking and four transient males did not display aggressively. (■) high-ranking males; (□) low-ranking males; (●) transient males.

**Aggression Towards Juveniles**

There were significant differences between the male categories in the frequency of aggressive displays (chasing and biting) towards juveniles for a given number of days of observation (Poisson Regression: Table 5, Fig. 2). High-ranking males were 7.4 times less aggressive towards juveniles than transient males (Poisson Regression:  $e^{-2} = 0.135$  times). In comparison to transient males, low-ranking males were 14 times less aggressive towards juveniles (Poisson Regression:  $e^{-2.7} = 0.07$  times). Of the 10 transient males, five were aggressive towards juveniles (Fig. 2) and all but one of these were observed to mate, while out of the other five transient males (that were not aggressive towards juveniles) only one was observed to mate.

**Mating Success**

There were significant differences (GLM analysis:  $R^2 = 0.60$ ) in numbers of matings among male

**Table 5:** Estimates for the main effects in the model for number of aggressive displays towards juveniles among high-ranking, low-ranking, and transient males of grey-cheeked mangabeys in Kibale National Park, Uganda (Poisson Regression; model  $p$ -value = 0.022, residual deviance 19.35 on 22 df)

Parameter	Estimate	SE	Confidence interval
Intercept	-3.35	2.4	-8.07 to 1.36
Log (d)	1.26	0.92	-0.54 to 3.07
High-ranking male	-2.0	0.97	-3.91 to -0.1
Low-ranking male	-2.7	1.2	-5.02 to -0.37

The effect for transient males is fixed at zero.

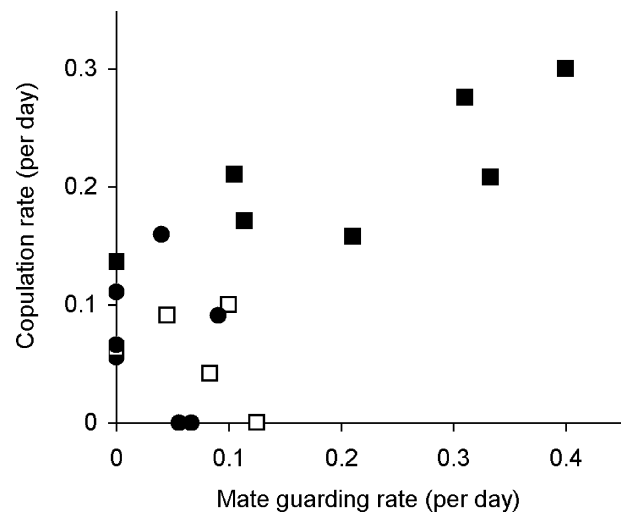
categories ( $p = 0.0002$ ,  $df = 2$ ,  $F = 9.67$ ), and female stage of sexual swelling ( $p = 0.00001$ ,  $df = 2$ ,  $F = 29.53$ ). High-ranking males mated more than other males, and mainly with females at the peak of sexual swelling, while transient males mated mainly with deflating females: interaction between male class and female sexual swelling stage  $p = 0.00001$ ,  $df = 4$ ,  $F = 7.86$  (see Arlet et al. 2007). Involvement in guarding of females at the peak of sexual swelling was correlated positively with mating success (Regression;  $F = 18.01$ ,  $R^2 = 0.51$ ,  $n = 19$  males,  $p = 0.0005$ ). However, there was considerable variation: some males guarded females without any observed matings, while others who were not observed to guard, achieved mating success (Fig. 3).

### Loud Calls

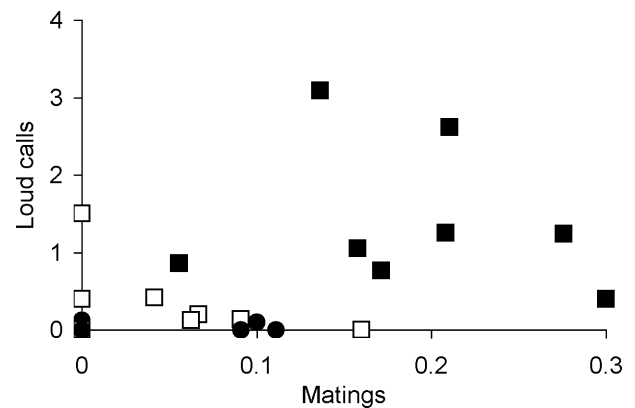
There were significant differences in the number of loud calls (whoop-gobbles) among males (ANOVA:  $p = 0.0002$ ,  $df = 2$ ,  $F = 12.29$ ): 79% of all calls were by high-ranking males, 17% by low-ranking males and 3% by transient males. There was a significant correlation between mating frequency and loud calls (Table 2), as high-ranking males gave loud calls more frequently than other males and also mated more. However, transient males that mated with oestrous females gave few loud calls (Fig. 4). In the smaller groups, high-ranking males were giving less loud calls, even though they mated frequently (regression of the number of loud calls by high-ranking males on the number of males in the group:  $n = 5$  groups,  $R^2 = 0.42$ ,  $F = 4.37$ ,  $p = 0.019$ ).

### Discussion

Male grey-cheeked mangabeys can influence their mating success by strategically moving between groups and subsequently using a wide variety of sexual tactics. Our results corroborate those of Olupot &



**Fig. 3:** Among five groups of grey-cheeked mangabeys in Kibale NP, there was a significant correlation between the frequency of mate guarding and male-mating success ( $p = 0.0005$ ,  $F = 18.01$ ,  $R^2 = 0.51$ ,  $n = 19$ ). However, there was considerable variation, and some males followed females without many (or any) observed copulations, while others who were not observed to follow, but did have mating success. Especially transient males did not follow frequently but had mating success. Inter-group differences in the guarding behaviour of high-ranking males depended on the number of males in the group that mate guarded (Regression,  $p = 0.003$ ,  $df = 1$ ,  $F = 80.94$ ,  $R^2 = 96.42$ ), for example, in Mikana (only two adult males), the high-ranking male never engaged in mate guarding. (■) high-ranking males; (□) low-ranking males; (●) transient males.



**Fig. 4:** Plot of the number of loud calls and matings of males per day of observation. Two low-ranking and five transient males did not mate nor call. (■) high-ranking males; (□) low-ranking males; (●) transient males.

Waser (2001) that males predominantly migrate into groups with more female-biased sex ratios and tend to migrate from groups with many males (Kvarnemo & Ahnesjo 1996). We also showed that these

transient males compete with resident males for matings by actively competing or sneaking opportunistic copulation. The behaviour of these transient males differed from resident males in the high rate of aggression towards juveniles in half of the transient males, and the absence of aggression towards females with sexual swelling. Competition for females by males entering the group has been documented in other primate species (Harcourt 1987; Bercovitch 1991, 1995, 1997; Smith 1992), and roaming is an alternative male reproductive tactic that is widely used throughout the animal kingdom (Yamagiwa 1986; Clutton-Brock 1988; Sandell & Liberg 1992; Karczmarski 1999; Bennett & Owens 2002).

Because paternity data are lacking, this paper focuses on mating success. Therefore, the consequences of these behaviours for reproductive success are obscured for three reasons: (1) matings can have occurred out of sight of observers (some sneaky matings were observed: Arlet et al. 2007); (2) the relationship between sexual swellings and the timing of female fertility is unknown; and (3), the correlation between mating success and paternity is unknown for this species (Altmann et al. 1996; Engelhardt et al. 2006). In addition, an important behavioural pattern that would have been missed because females were not recognized individually outside their period with sexual swelling, is friendships between particular males and females (Smuts 1983).

Males in multi-male systems can obtain reproductive success by (1) preventing other males from mating (male–male competition), (2) coercing females into mating with them (coercion) or (3) presenting themselves as beneficial partners (female mate choice: Cluttonbrock 1995b; Muller 2007; Smuts & Smuts 1993). Male dominance plays an important role in grey-cheeked mangabeys: high-ranking males are responsible for the great majority of matings with peak females, as is often the case in primate species (Cowlshaw & Dunbar 1991; Robbins 1999). These males guard females and are aggressive towards both males and females, including females with sexual swellings. Harassment of females by males may be a form of persuading females to mate (East et al. 2003), or to prevent these females from mating with other males (Cluttonbrock 1995b; Sicotte 2002). However, our data are insufficient to show that high-ranking males are more aggressive towards oestrous females given their greater proximity to them, or that this aggression helps them to obtain matings or prevent them from mating with other males. The tactic of high-ranking males could

be a combination of male–male competition, coercion, and possibly also female mate choice (see below). The guarding of peak females by high-ranking males is an important factor and could affect most of the parameters discussed below: e.g. transient males have less chance to be aggressive towards females with sexual swellings.

Most low-ranking resident males have a low-mating success, as they have similar behaviours as high-ranking males, but at a lower frequency. Some transient males mated more than the average low-ranking resident male, but they mated mainly deflating females and may thus have had a low chance on fertilization (Deschner et al. 2004). Interestingly, transient males did not guard peak females often, but had mating success while either avoiding or challenging the high-ranking male. This may be a consequence of female mate choice, as in some of the studied groups of mangabeys, particular females with sexual swellings avoided the high-ranking male, and initiated matings with transient males outside the group (Arlet et al. 2007). This female behaviour may be a counter strategy to male aggression towards juveniles. We did not observe attacks on infants (that are carried by females), but infants tend to disappear when transient males enter the group (M. E. Arlet, unpubl. data; Arlet et al. 2007). Some transient males may intend to become high-ranking residents in the group they move into and may kill infants so that females will become receptive sooner. This aggression toward juveniles may be reduced when mothers have sexual swellings and mate with these males. Females can also reduce future aggression towards juveniles by adopting a promiscuous mating tactic to confuse paternity (Agrell et al. 1998; Nunn 1999; Heistermann et al. 2001; Wolff & Macdonald 2004). Aggression towards juveniles and infanticide could then be an effective tactic for transient males for obtaining matings as observed in many animals (Struhsaker & Leyland 1985; Agrell et al. 1998; Palombit 1999; Jolly et al. 2000; van Noordwijk & van Schaik 2000; Soltis et al. 2000; Buchan 2003; Harris & Monfort 2003). In the closely related baboons infanticide is common (Tarara 1987; Chalyan 1990; Oconnell & Cowlshaw 1994; Mori 1997, 2003; Weingrill 2000; Swedell 2003; Cheney et al. 2004) and it is also known from the more distantly related terrestrial mangabeys (Busse 1983; Gust 1994, 1995; Range 2005). On the other hand, transient males do not seem to coerce females directly as aggression towards females is rare. An alternative explanation for this aggression towards juveniles is that they punish (Cluttonbrock 1995a)

them for disturbing their attempts to sneaky matings by conspicuously following their mothers or vocalizing (M. E. Arlet, unpubl. data).

Possible benefits females may gain from mating particular males are difficult to detect as they include offspring fitness through mating with partners with good genes, compatible genes and inbreeding avoidance, as well as paternal care (Keddy-Hector 1992; Small 1993; Pusey & Wolf 1996; Hosken & Stockley 2003; Simmons 2003; Stockley 2003). In this light, female mate choice for high-ranking males could be interpreted as a choice for good genes that were indicated by the outcome of male–male competition, while female mate choice for transient males (including the transient male that was not observed to be aggressive toward juveniles, but did mate females) could be interpreted as inbreeding avoidance.

Male grey-cheeked mangabeys can produce loud calls (whoop-gobbles). Such calls have been shown to be a multifunctional phenomenon in primates (Wich & Nunn 2002; Oliveira & Ades 2004) that can act as a home range defence signal (Waser 1977b; da Cunha & Byrne 2006), but may also be involved in signalling dominance status or play a role in mate attraction if it is an indicator of male size (Harris et al. 2006). In our study, both resident and transient males gave loud calls, but within all groups high-ranking males were much more likely to produce whoop-gobbles, and number of loud calls was positively correlated with mating success. Similar in baboons (Kitchen et al. 2003), frequency of loud calls in grey-cheeked mangabeys is a predictor of dominance rank within a group. That in the smaller groups, high-ranking males were giving less loud calls, could be due to the lower number of competing males in these groups, as the number of whoop-gobbles produced by the high-ranking male was higher in groups with more males. That transient males did not frequently give loud calls could be a part of a secretive tactic.

Our results corroborate that males migrate to increase mating success (Olupot & Waser 2001). Transient males of grey-cheeked mangabeys actively compete with resident males for access to females with sexual swellings and had slightly higher chances on mating success compared with low-ranking males who stayed within groups. While the tactics of high-ranking males was characterized by mate guarding and aggression towards females, transient males were aggressive towards juveniles but not towards oestrus females and rarely guarded females. We emphasize that a transient male's sexual strategy is probably not fixed, but rather a temporary tactic

to obtain mating success during certain phases of his life. Male mating tactics varied greatly among the five studied groups, probably as a function of the intensity of male–male competition. This description of male behaviours will progress further elucidation of the life history trajectories of male mangabeys and the costs and benefits of mating tactics (Saunders et al. 2005; Pelletier et al. 2006).

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