

# Variation in behavioral and hormonal responses of adult male gray-cheeked mangabeys (*Lophocebus albigena*) to crowned eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda

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**Abstract** Intensive study of arboreal forest-dwelling primates and their predators in Africa is increasingly revealing that crowned eagles (*Stephanoaetus coronatus*) are major predators of primates. Gray-cheeked mangabeys (*Lophocebus albigena*) are overrepresented in the diets of crowned eagles in Kibale National Park, Uganda, and adult male mangabeys are represented more than females. We focused on the behavior of adult male gray-cheeked mangabeys living in social groups in Kibale National Park (1) to clarify the interactions between mangabeys and eagles that might put adult males at greater risk and (2) to better understand individual variation in behavioral responses to predators. Adult male mangabeys in five groups responded to observer-confirmed presence of crowned eagles 88 times over a 13-month period. While all males gave alarm calls, only the highest-ranking male in each of four groups chased eagles. These males had elevated levels of fecal cortisol metabolites in the days immediately after they engaged in active defense, suggesting that they perceived such

behavior as risky. In the one group where male ranks were unstable and there were no infants, no male was observed to chase eagles. We suggest that males pursue the dangerous tactic of chasing eagles only when they are likely to have offspring in the group. Males in larger groups also spent less time alarm calling to crowned eagles (from first to last call in a group), and our observations confirmed that the duration of their alarm calls was related to eagle presence. Thus, eagles spent less time around larger mangabey groups. Alarm calling by adult male mangabeys may signal to this ambush predator that it has been detected and should move on.

**Keywords** Predator–prey strategies · Alarm call · Active defense · Fecal cortisol

## Introduction

It has long been assumed that animals living in open habitats (e.g., savannahs) are more vulnerable to predation than animals living in more closed habitats (e.g., forests) because there are more predators or fewer refuges in open habitats (Dunbar 1988). This assumption is now being challenged for neotropical birds (Thiollay and Jullien 1998), ground squirrels (Hik et al. 2001), and primates (Isbell 1994). While primates living in more open habitats may be sympatric with a greater number of predator species, they also co-occur with a greater number of nonprimate prey species, which results in a dilution of predator effort on primates (Hayward and Kerley 2005; Hayward et al. 2006). Moreover, as arboreal forest-dwelling primates are more intensively studied, it is becoming more obvious that predation is also a significant cause of mortality for them (Olupot and Waser 2001a; Shultz et al. 2004; McGraw et al. 2006).

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The crowned eagle (*Stephanoaetus coronatus*) is a large raptor that occurs in sub-Saharan Africa and preys mainly on medium-sized animals (Daneel 1979; Skorupa 1989; Struhsaker and Leakey 1990; Mitani et al. 2001; Shultz et al. 2004; McGraw et al. 2006). Crowned eagles use several tactics to kill their prey: (1) ambushing their prey from within the canopy, (2) attacking suddenly from the air, and (3) hunting in pairs, with one eagle swooping past and serving as a distraction while the other flies in to make the kill (Daneel 1979; Leland and Struhsaker 1993; Cordeiro 2003; McGraw et al. 2006). Crowned eagles are a major predator of forest-dwelling primates in Africa. Primates are also a major food source for crowned eagles. For example, primates comprised approximately 58% of the diet of crowned eagles in Taï Forest, Côte d'Ivoire, and 82–89% of the diet of crowned eagles in Kibale National Park, Uganda (Skorupa 1989; Struhsaker and Leakey 1990; Mitani et al. 2001; McGraw et al. 2006).

Skeletal remains below nests in Kibale indicate that crowned eagles disproportionately kill more adult males than adult females (Skorupa 1989; Struhsaker and Leakey 1990; Mitani et al. 2001). Struhsaker and Leakey (1990) suggested that the overrepresentation of adult male primates in the diet of crowned eagles may be a result of the behavior of male primates. In some species, only adult males often travel separately from social groups, only adult males take aggressive action against eagles, and only adult males have loud calls that may attract the attention of eagles. In Kibale, adult male gray-cheeked mangabeys (*Lophocebus albigena*) are particularly vulnerable to eagle attacks (based on remains in eagle nests; Struhsaker and Leakey 1990; Mitani et al. 2001), and they engage in all these behaviors.

Gray-cheeked mangabeys live in multimale, multifemale social groups of five to 25 individuals (Olupot and Waser 2001a). Females remain in their natal groups throughout life, whereas males disperse (Olupot and Waser 2001a, b). Dispersing males may be solitary for a period of time or may join a group and become part of the male dominance hierarchy (Olupot and Waser 2001a; Arlet et al. 2008). Adult male gray-cheeked mangabeys have been observed to chase crowned eagles but, unlike male red colobus (*Procolobus badius*) which join in defensive response to eagles, they always act alone despite the presence of potential allies in the group (Struhsaker and Leakey 1990). Finally, adult male gray-cheeked mangabeys in groups frequently give loud calls (whoop-gobbles) and alarm calls (staccato barks). Males living alone, however, rarely produce whoop-gobbles and do not produce alarm calls (Olupot and Waser 2001a), suggesting that such vocalizations indeed attract attention and that males perceive themselves to be at greater risk when they are outside of groups.

Animals facing a predator are undoubtedly in a stressful situation. Recent developments are now enabling noninvasive estimates of degree of stress through fecal metabolites of cortisol. Cortisol is a glucocorticoid, a steroidal hormone released from the adrenal cortex in times of stress (Harper and Austad 2000). Glucocorticoids are responsible for the mobilization of energy stores (Munck et al. 1984) and therefore are helpful in making quick responses, as would be needed during predation attempts. In European rabbits (*Oryctolagus cuniculus*), levels of fecal glucocorticoid metabolites increased when they were exposed to the odor of foxes (*Vulpes vulpes*), and levels increased more in males than in females (Monclús et al. 2006). Similarly, fecal glucocorticoid levels increased in female chacma baboons (*Papio hamadryas ursinus*) in the month following attacks on their groups by lions (*Panthera leo*) or leopards (*Panthera pardus*; Engh et al. 2006). Given that adult male gray-cheeked mangabeys are highly vulnerable to eagle predation, we also expect them to become more stressed when crowned eagles appear, and this stress should be reflected in higher levels of fecal cortisol metabolites.

Although adult male gray-cheeked mangabeys may behave in ways that increase their risk of predation, they may also behave in ways that are commonly thought to lower the risk of predation, including engaging in vigilance and alarm calling and joining larger groups (Cheney and Wrangham 1987; Scheel 1993; Isbell 1994; Lima 1995). These three behaviors need not be independent. For example, vigilance may increase in larger groups (Isbell and Young 1993; Shultz and Noe 2002; Shultz et al. 2004), and greater vigilance may lead to earlier detection of predators (van Schaik et al. 1983) and therefore earlier alarm calling. One function of alarm calls in primates may be to inform sit-and-wait, or ambush, predators that they have been detected and that they should move on (Zuberbühler et al. 1999); the sooner alarm calling begins, the sooner the predator may leave. Here, we focus on the behavior of adult male gray-cheeked mangabeys living in social groups to clarify the interactions between mangabeys and eagles and to better understand individual variation in behavioral and physiological responses to predators.

## Study site and methods

### Behavioral observations

The study was conducted for 13 months from December 2005 through December 2006 in Kibale National Park (0°13'–0°41' N and 30°19'–30°32' E), near the Makerere University Biological Field Station at Kanyawara. Kibale (795 km<sup>2</sup>) is a moist, evergreen, medium altitude forest with a mosaic of swamp, grassland, thicket, and colonizing

forest (Struhsaker 1975; Chapman and Lambert 2000). Arlet and assistants observed five groups during 241 all-day (0700–1700 hours) follows (3–6 days/ 5 weeks/group): Lower Camp II (LC2), Mikana (MK), CC (CC), Butanzi (BT1), and Lower Camp (LC) (Arlet 2002; Arlet et al. 2007). All these groups have been studied by various researchers since at least 1996 (e.g., Arlet 2002; Olupot and Waser 2001b; Janmaat et al. 2006; Chancellor and Isbell 2008) and are well habituated. Group sizes are listed in Table 1.

During all-day follows, we conducted 819 focal samples on 24 adult males. The sampling order in each group was opportunistically determined by first sighting of males that had not yet been sampled during a particular round (usually a day). Focal animals were observed for 1-h focal samples in the larger groups and 2-h focal samples in the smaller groups (total 1,655.5 h, 11.5–202.5 h/male). All adult males in these study groups were individually recognized by radio or uniquely colored collars from a previous study (Olupot 1999) or by relative size and distinguishing features (e.g., tail shape, scars, and fractures). Relative position in the male dominance hierarchy was determined on the basis of observed chases, fights, and supplants during focal samples, with winners designated higher ranking than losers. Dominance matrices were constructed for each group, with rank order determined by minimizing the number of reversals against the hierarchy (i.e., interactions below the diagonal; Fig. 1).

During the all-day follows, we recorded whenever we observed an adult male producing an alarm call (staccato bark) during his focal sample. Alarm calls are acoustically different from loud calls (whoop-gobbles) and grunts. When we saw and heard the male giving an alarm call, we recorded the time, the animal's location in the forest, if the alarm call was precipitated by alarm calls of birds or other primates, and if a crowned eagle or any other obvious stimulus was observed nearby. Alarm calls that were given within 5 min of each other by the same male were considered one data point. We also recorded male responses to eagles in one of three mutually exclusive categories: (1) alarm calling and remaining still, (2) alarm calling and running toward the eagle, or (3) running toward the

eagle without alarm calling. The latter two behaviors were considered active defense. When alarm calls were produced in the presence of a crowned eagle, we calculated the duration of time in which the group attended to it, as determined from the first to the last alarm call of the focal male.

#### Fecal cortisol extraction

Fecal samples were collected from adult males during focal samples from December 2005–July 2006. On the first observation day of each period, fecal samples were not collected because we did not know what kinds of experiences males had during previous days when they were not under observation. After that day, when a focal individual defecated, the time was noted and the sample was immediately collected, placed in a sterile scintillation vial, and stored on ice in a cooler. At the end of the day, all samples were placed in a  $-20^{\circ}\text{C}$  freezer until hormone solubilization (Strier and Ziegler 1997; Whitten et al. 1999). We collected 328 fecal samples from 17 adult males.

Hormones were solubilized at the field station using the protocol employed for red colobus (Chapman et al. 2006). A fecal sample was removed from the freezer, thawed, and homogenized using a spatula. Then, 0.50 g was solubilized using a pH 5.0 citrate buffer/95% ethanol solution (10 ml, 1:1) that was mixed for 21–27 h. After mixing, samples were spun in a centrifuge for 30 min at 3,200 rounds per min to separate the supernatant containing the hormones from the fecal pellet, and then 2 ml of the supernatant was passed through a solid phase extraction cartridge (Alltech maxi-clean filter) for storage and transport to the USA (Strier and Ziegler 2005).

The samples were then sent to the Wisconsin National Primate Research Center's (WNRPC) Assay Services, where cortisol was validated and samples analyzed. An assay comparing serial dilutions of pooled mangabey samples to cortisol standards found no significant difference between the slopes ( $t=-1.62$ ,  $df=25$ ,  $p>0.05$ ). Accuracy was determined by adding values from pooled mangabey samples to the standard curve points. The mean accuracy over eight pooled samples was 108.71% with standard deviation 2.91%. The interassay coefficients of variation were 13.6 and 12.8 for the low and high pools, respectively, and the intra-assay coefficients of variation for the same pools were 3.9 and 2.1, respectively.

At the WNRPC, cortisol was extracted from the filters. The cartridges were washed with 1 ml of 20% methanol and the columns were eluted with 2 ml methanol. This methanol was dried, resuspended in 1 ml ethanol, and 50  $\mu\text{l}$  was taken for the enzyme immunoassay (EIA). The WNRPC lab used the antibody R4866, which was developed by Munro and Stabenfeldt (1984) and was well characterized. The antibody cross-reacts 60% with corti-

**Table 1** Gray-cheeked mangabey study groups, group sizes, and numbers of observation days in relation to eagle presence

Group (n)	No. of all-day follows	No. of all-day follows with eagle present	% All-day follows with eagle present
LC2 (9)	52	5	9.6
MK (15)	53	5	9.4
CC (16)	31	7	22.6
BT1 (18)	43	10	23.3
LC (22)	62	6	9.7

**Fig. 1** Male dominance matrices for five groups of mangabeys. All have identifiable highest-ranking males except for LC, which had an unstable hierarchy at the time of fecal collection. The high number of reversals in BT1 suggests that its highest-ranking male was being challenged during the time of fecal collection. He fell in rank about 4 months after the fecal data were collected

		LOSER									
WINNER	<i>GROUP: LC2</i>	<b>IB</b>	<b>NY</b>								
	<b>IB</b>	XX	16								
	<b>NY</b>	5	XX								
	<i>GROUP: CC</i>	<b>KR</b>	<b>MF</b>	<b>GR</b>	<b>KJ</b>						
	<b>KR</b>	XX	9	5	6						
	<b>MF</b>	3	XX	8	4						
	<b>GR</b>	1	4	XX	8						
	<b>KJ</b>	0	1	5	XX						
	<i>GROUP: MK</i>	<b>KY</b>	<b>KC</b>	<b>SH</b>	<b>KAK</b>						
	<b>KY</b>	XX	13	4	6						
	<b>KC</b>	6	XX	5	5						
	<b>SH</b>	0	1	XX	3						
	<b>KAK</b>	0	0	1	XX						
	<i>GROUP: BT1</i>	<b>PL</b>	<b>LM</b>	<b>BG2</b>	<b>KK</b>	<b>BT</b>					
	<b>PL</b>	XX	10	8	5	6					
	<b>LM</b>	6	XX	7	4	3					
	<b>BG2</b>	1	3	XX	5	4					
	<b>KK</b>	0	0	2	XX	5					
	<b>BT</b>	0	0	1	3	XX					
	<i>GROUP: LC</i>	<b>MG</b>	<b>YM</b>	<b>R</b>	<b>HL</b>	<b>BG2</b>	<b>NK</b>	<b>MS</b>	<b>FR</b>	<b>MK</b>	
<b>MG</b>	XX	7	7	6	5	3	4	2	3		
<b>YM</b>	6	XX	6	4	4	5	6	3	2		
<b>R</b>	5	5	XX	5	4	7	5	3	2		
<b>HL</b>	5	4	5	XX	4	6	3	5	2		
<b>BG2</b>	5	2	2	2	XX	6	7	4	3		
<b>NK</b>	1	0	5	3	2	XX	6	6	4		
<b>MS</b>	2	4	3	3	4	5	XX	3	2		
<b>FR</b>	0	0	2	2	4	4	2	XX	6		
<b>MK</b>	0	0	1	0	2	3	0	4	XX		

sone (a metabolite of cortisol), 2.5% with corticosterone, and less than 1% for other steroids (Ziegler et al. 1995). These analyses provided data on the metabolites of cortisol found in the supernatant, validated the EIA, and resulted in a measure of the amount of cortisol metabolites in each sample in nanograms per gram of dry feces. The dry weight of each sample was calculated in the field by drying to constant weight and calculating the percent water (Ziegler et al. 1995; Chapman et al. 2006).

#### Statistical analyses

Only those alarm calls that were associated with the presence of eagles, as confirmed by observers, were used in analyses. Rates of alarm calls were estimated using a Poisson distribution. The Poisson distribution gives a basic model for the number of alarm calls, under which the rate,

$r$ , for a male is estimated by the total number of calls by that male divided by the number of focal hours for that male, and the standard error (SE) is the square root of his alarm calls divided by his focal hours. For fecal cortisol responses to eagles, we compared cortisol metabolite levels from fecal samples of individual males based on the timing of fecal elimination relative to presence or absence of eagles. Forty-nine fecal samples were collected between 24.5–30.5 h after an eagle appeared (mean=27 h±0.16 SE) and thus were within the 22.7–38-h window of passage time for gray-cheeked mangabeys based on digestive transit time and mean retention time (Lambert 1998).

Mixed model analysis of the natural logarithm of cortisol levels was used to compare cortisol levels in the presence and absence of eagles within and among males. The model had fixed effects for presence of an eagle on the previous day, male identity as a defender, and the interaction

between these effects, along with random effects for males. We carried out a regression to test whether differences in group size were associated with differences in duration of eagle presence as determined by our observations and the duration of alarm calling by adult males. Analyses were performed using Statgraphics 5.0 and SPSS 16.0, and alpha was set at 0.05.

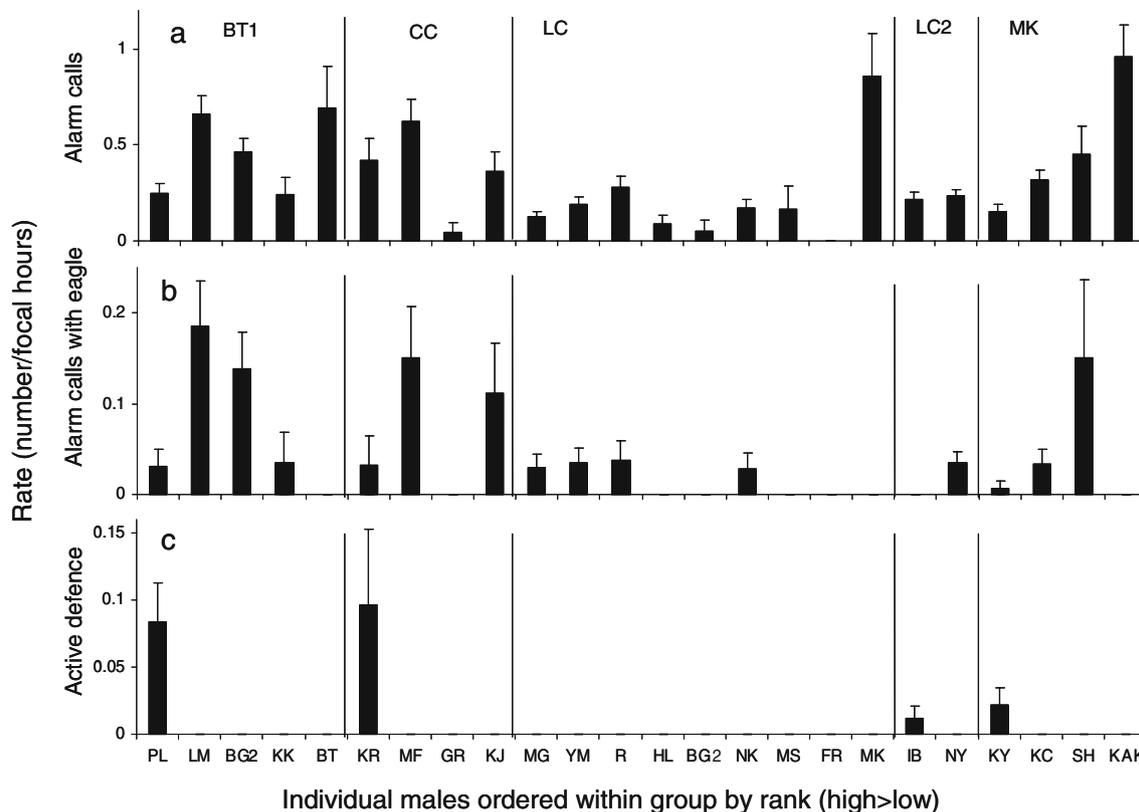
## Results

We observed 21–257 agonistic interactions per group (Fig. 1). The percentage of reversals against the hierarchy ranged from 18.2–25.9% for four groups, and it was obvious that one male was the most dominant male in each of these four groups, though in BT1, the beta male was beginning to challenge the alpha male. In the fifth group (LC), in which there were nine males, there was no clearly dominant male and 37.7% of agonistic interactions were reversals. Among the four males at the top of the hierarchy in LC, reversals accounted for 30 out of 65 (46.1%) interactions (Fig. 1).

We recorded 478 alarm calls from 23 of 24 (95.8%) adult males of different ranks (Fig. 2a). Estimates of the rates of alarm calls and standard errors show clear overlap among

males. The majority of alarm calls (347; 72.6%) were given to unidentified stimuli. Of the 131 alarm calls given to or after identified stimuli, 24 (18.3%) occurred after other primate species gave alarm calls, 12 (9.2%) occurred after great blue turacos (*Corythaeola cristata*) and black-and-white casqued hornbills (*Bycanistes subcylindricus*) gave calls, and seven (5.3%) occurred when baboons (*Papio hamadryas anubis*) and chimpanzees (*Pan troglodytes*) were present. Chimpanzees are known predators of mangabeys (Watts and Mitani 2002). We did not observe a crowned eagle nearby for any of these calls. Eighty-eight of the 131 alarm calls (67.2%) occurred when a crowned eagle was clearly present, and they were present on 33 of 241 days (7.3%). Groups varied in the percentage of days eagles were confirmed as present (Table 1).

Of the 88 alarm calls given in the presence of eagles, 15 of 24 (62.5%) adult males were involved (Fig. 2b). The most common behavioral response in addition to alarm calling was sitting still (72 responses; 81.8%). Sixteen responses (18.2%) involved alarm calling with active defense and these were limited to four adult males (16.7%). All males involved in active defense were the highest-ranking males within their groups (Fig. 2c). No male from LC responded with active defense.



**Fig. 2** **a** Rate of alarm calls ( $n=478$ ) per focal hour of observation for each adult male, **b** alarm call rate when eagle presence was confirmed by observers (total 72), and **c** rate at which males engaged in active

defense (total 16). The error bars depict  $\pm 1$  standard error of the rate. Note that because ranks in LC were unstable, they do not necessarily reflect rank order

Mixed model analysis of the natural logarithm of cortisol levels showed that there is a significant interaction between male identity as a defender (defender) and observation of an eagle near the group (eagle; Table 2). On average, male defender status did not affect cortisol levels in the absence of eagles (in the absence of eagles, defender males had approximately 0.93 times lower cortisol levels than non-defender males, with approximate 95% confidence interval (CI) 0.23, 3.75). However, those males that were involved in active defense against eagles had 2.25 times higher cortisol levels the day after an eagle was observed than on other days, with 95% CI 1.48, 3.42. Males that were not involved in active defense against eagles did not show such a response, as they had 0.76 times lower cortisol levels the day after an eagle was observed than on other days, with 95% CI 0.47, 1.22. On average, males that defended against eagles had approximately 2.75 times higher cortisol levels than other males the day after an eagle was observed, with approximate 95% CI 0.70, 10.86. The first and last CIs are relatively wide because they necessarily account for male-to-male variation (the variance of the male-specific random effects for log-cortisol was estimated as 0.19). This pattern was consistent among the four groups in which males were involved in active defense (Table 3).

As total group size increased, focal adult males in groups spent less time alarm calling when an eagle was present (regression:  $F=84.14$ ,  $R^2=0.96$ ;  $p=0.002$ ; Fig. 3). The time spent alarm calling by focal adult males was also negatively correlated with greater numbers of adults only ( $R^2=0.78$ ,  $p=0.04$ ).

## Discussion

Though eagles are sometimes killed by mangabeys (Jones et al. 2006), crowned eagles in Kibale appear to have the upper hand and prey disproportionately on male gray-cheeked mangabeys (Skorupa 1989; Struhsaker and Leakey 1990; Mitani et al. 2001). Our results suggest that their greater predation rate is partly because only one adult male

per mangabey group chases eagles. As Struhsaker and Leakey (1990) suggested, chasing eagles is risky because it puts males within closer range of the eagle. During this study, we did not witness successful attacks by eagles on males that were engaged in active defense. In 1999, however, Arlet and her field assistant observed a radio-collared male being attacked and grabbed by a crowned eagle after he chased it; the male's body was located with telemetry shortly afterwards. At the end of the present study, another "defending male" disappeared and it is possible that he was killed by an eagle.

That single males are at greater risk than multiple males is suggested by the fact that adult male red colobus are not killed more than expected (Mitani et al. 2001). Like mangabeys, red colobus live in multimale, multifemale groups and they also chase crowned eagles. In contrast to mangabeys, male red colobus often coordinate their actions together to chase the eagles (Leland and Struhsaker 1993). Why do male mangabeys not cooperate in defense when there appears to be a distinct advantage in doing so? Differential cooperation in these two species is consistent with expectations from kin selection theory: Male red colobus are typically philopatric and are likely to be closely related whereas male mangabeys disperse from their natal groups and are likely to be unrelated to males in their new groups (Struhsaker 1975; Olupot and Waser 2001a).

In addition, our results revealed that only the highest-ranking male in each group engages in active defense against eagles. The males themselves apparently perceive this behavior as dangerous because levels of fecal cortisol metabolites were significantly higher in males that chased eagles than in nondefending males only on the days immediately following eagle visitations. An earlier study found that the highest-ranking males had the greatest mating success (Arlet et al. 2007). We suggest therefore that the rank-related difference in active defense may exist because the highest-ranking males are more likely to have offspring in their groups. This is also supported by the exceptional behavior of males in LC. In contrast to the other groups, no males in LC engaged in active defense, and the dominance hierarchy in LC was unstable, with no obvious alpha male (Fig. 1). Moreover, despite periods with multiple estrous females and observed matings, there were no infants in this group. With no offspring to protect, the risk of actively approaching eagles may be too high relative to the payoff.

If adult males are the ones most often eaten by eagles, why do we suggest that infants are the initial targets of eagle attacks? Eagles likely go for the easiest individuals in a group to kill. All else being equal, smaller monkeys, i.e., infants, may be preferred prey because they are least likely to inflict damage on eagles. When an eagle attacks, however, immatures and adult females typically drop down in the canopy and actively avoid the eagle while the highest-ranking male in a

**Table 2** Type III tests of fixed effects for mixed model analysis of the natural logarithm of cortisol levels in male gray cheeked mangabeys

Source	Num df	Denom df	F	p value
Intercept	1	15.75	918.95	<0.001
Eagle	1	314.71	4.85	0.028
Defender	1	15.75	2.89	0.109
Eagle × defender	1	314.71	20.03	<0.001

The model has fixed effects for presence of an eagle on the previous day (eagle), male identity as a defender (defender), and the interaction eagle × defender, along with random effects for males. Four out of 18 males were observed to defend their group against eagles

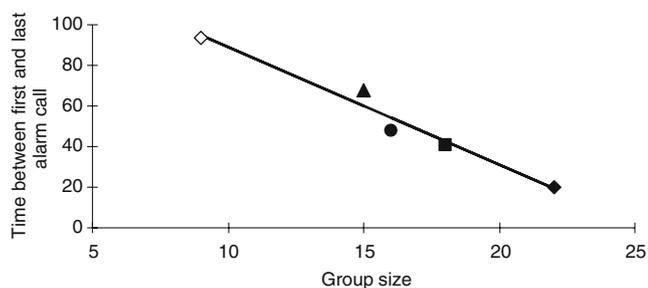
**Table 3** Fecal cortisol levels of adult male gray-cheeked mangabeys

Male	Group	Eagle absent cortisol (ng/g)		Eagle present cortisol (ng/g)	
		Defending male	Other males	Defending male	Other males
PL	BT1	107.6 (10)	70.9 (53)	250.0 (8)	39.9 (16)
KR	CC	57.8 (4)	60.6 (11)	93.0 (3)	118.2 (5)
IB	LC2	44.4 (23)	43.1 (22)	84.8 (2)	14.5 (3)
KY	MK	71.7 (13)	48.3 (20)	91.9 (3)	47.4 (9)

Comparisons were of (1) cortisol levels of individuals on the days after they participated in active defense against eagles vs. those in the days when eagles were absent and (2) cortisol levels of males engaged in active defense vs. those of males not engaged in active defense. Males in LC could not be compared because no males engaged in active defense. Sample sizes are in parentheses

group actively approaches it, resulting in eagle attacks on males that are more opportunistic.

Our results also showed that the duration of alarm calling by adult males is shorter in larger groups. These results, coupled with our own confirmation of crowned eagle presence, suggest that alarm calling stops when crowned eagles fly away from groups. Thus, it appears that crowned eagles spend less time around larger groups. One of the most consistently reported benefits for animals of living in larger groups is a per capita decrease in vigilance while overall vigilance either remains the same or increases (Pulliam 1973; Powell 1974; Barnard 1980; Bertram 1980; Elgar 1989; Lima 1995; Roberts 1995; but see Treves 2000). This effect has also been reported in some primates (wedge-capped capuchins, *Cebus olivaceus*, and vervets, *Cercopithecus aethiops*; de Ruiter 1986; Isbell and Young 1993). Among birds, larger groups often detect predators earlier than smaller groups (Powell 1974; Siegfried and Underhill 1975; Kenward 1978; Lazarus 1979; Cresswell 1994). This group size effect has also been reported for primates. Larger groups of long-tailed macaques (*Macaca fascicularis*) detect humans earlier than smaller groups (van Schaik et al. 1983). It is conceivable, then, that larger groups of mangabeys spend more time in vigilance or detect predators more quickly than smaller groups, but further research needs to be conducted to confirm this.



**Fig. 3** Time spent by eagles close to the group (measured in minutes from the first alarm call to the last one for the focal male) is negatively related to group size. In this figure, each point represents one group. Symbol of the groups: closed square BT1, closed circle CC, closed diamond LC, open diamond LC2, closed triangle MK

Alarm calls by mangabeys may indicate to the eagles that they have been detected, thus spoiling the element of surprise, a necessary condition for their hunting success (Mitani et al. 2001; Shultz and Noe 2002; Shultz et al. 2004), so that the eagles move on. This function of alarm calling has also been documented for a community of primates in relation to leopards, another ambush predator, but not to chimpanzees, which do not hunt by stealth (Zuberbühler et al. 1999). Interestingly, male mangabeys living away from groups do not give alarm calls, even under circumstances that elicit alarm calls from males in groups, and they spend more time scanning than group-living males (Olupot and Waser 2001a). Solitary male mangabeys appear to be at even greater risk of eagle predation than males in groups (Olupot and Waser 2001a), and their behavioral adjustments are consistent with the idea that they perceive themselves to be in greater danger when they are alone. Future research might examine cortisol levels of males living away from groups to test this hypothesis.

Our results show that (1) social behavior of males varies among groups and relates to group defense, (2) only the highest-ranking males are involved in active defense against eagles and they perceive this as a stressful event, (3) lower-ranking males give alarm calls but never engage in active defense and do not experience the presence of eagles as stressful, and (4) eagles spend less time near larger groups. Individual-based observation and noninvasive hormonal analyses, as we employed in this study, hold much promise for gaining new insights into patterns in stress and mortality in other wild social animals that will improve our understanding of life-history trajectories and population-level processes.

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## References

- Arlet ME (2002) Social strategies in grey-cheeked mangabeys in Kibale National Park, Uganda. Ph.D. thesis, Jagiellonian University, Poland
- Arlet ME, Molleman F, Chapman CA (2007) Indications for female mate choice in grey-cheeked mangabeys *Lophocebus albigena johnstoni* in Kibale National Park, Uganda. *Acta Ethol* 10:89–85
- Arlet ME, Molleman F, Chapman CA (2008) Mating tactics in male grey-cheeked mangabeys (*Lophocebus albigena johnstoni*). *Ethology* 114:851
- Barnard CJ (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim Behav* 28:295–309
- Bertram BCR (1980) Vigilance and group size in ostriches. *Anim Behav* 28:278–286
- Chancellor RL, Isbell LA (2008) Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*) in Kibale National Park, Uganda. *Behav Ecol* (in press). doi: 10.1093/beheco.am117
- Chapman CA, Lambert JE (2000) Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *Am J Primatol* 50:169–186
- Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TL (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *Am J Phys Anthropol* 131:525–534
- Cheney DL, Wrangham RW (1987) Predation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 227–239
- Cordeiro NJ (2003) Two unsuccessful attacks by crowned eagles (*Stephanoaetus coronatus*) on white-throated monkeys (*Cercopithecus mitis*). *Afr J Ecol* 41:190–191
- Cresswell W (1994) Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Anim Behav* 47:433–442
- Daneel ABC (1979) Prey size and hunting methods of the crowned eagle. *Ostrich* 50:120–121
- de Ruiter J (1986) The influence of group size on predator scanning and foraging behaviour of wedge-capped capuchin monkeys (*Cebus olivaceus*). *Behaviour* 98:240–258
- Dunbar RIM (1988) *Primate social systems*. Cornell University Press, Ithaca
- Elgar MA (1989) Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol Rev* 64: 13–33
- Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006) Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc R Soc Lond B* 273:707–712
- Harper JM, Austad SN (2000) Fecal glucocorticoids: a non-invasive method of measuring adrenal activity in wild and captive rodents. *Physiol Biochem Zool* 73:12–22
- Hayward MW, Kerley GIH (2005) Prey preferences of the lion (*Panthera leo*). *J Zool Lond* 267:309–322
- Hayward MW, Henschel P, O'Brien J, Hofmeyr M, Balme G, Kerley GIH (2006) Prey preferences of the leopard (*Panthera pardus*). *J Zool Lond* 270:298–313
- Hik DS, McColl CJ, Boonstra R (2001) Why are arctic ground squirrels more stressed in the boreal forest than in alpine meadows? *Ecoscience* 8:275–288
- Isbell LA (1994) Predation on primates: ecological patterns and evolutionary consequences. *Evol Anthropol* 3:61–71
- Isbell LA, Young TP (1993) Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. *Behav Ecol Sociobiol* 32:377–385
- Janmaat KRL, Byrne RW, Zuberbuhler K (2006) Primates take weather into account when searching for fruits. *Curr Biol* 16: 1232–1237
- Jones T, Laurent S, Mselewa F, Mtuli A (2006) Sanje mangabey *Cercocebus sanjei* kills an African crowned eagle *Stephanoaetus coronatus*. *Folia Primatol* 77:359–363
- Kenward RE (1978) Hawks and doves: attack success and selection in goshawk flights at wood-pigeons. *J Anim Ecol* 47:449–460
- Lambert J (1998) Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evol Anthropol* 7:8–20
- Lazarus J (1979) The early warning function of flocking in birds: an experimental study with captive quelea. *Anim Behav* 27:855–865
- Leland L, Struhsaker TT (1993) Teamwork tactics. *Nat Hist* 102 (4):42–48
- Lima SL (1995) Back to the basics of anti-predatory vigilance: the group size effect. *Anim Behav* 49:11–20
- McGraw SW, Cooke C, Shultz S (2006) Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: implications for primate predation and early hominid taphonomy in South Africa. *Am J Phys Anthropol* 131:151–165
- Mitani JC, Sanders WJ, Lwanga JS, Windfelder TL (2001) Predatory behavior of crowned hawk-eagles (*Stephanoaetus coronatus*) in Kibale National Park, Uganda. *Behav Ecol Sociobiol* 49: 187–195
- Monclús R, Rödel HG, Palme R, Von Holst D, de Miguel J (2006) Non-invasive measurement of the physiological stress response of wild rabbits to the odour of a predator. *Chemoecol* 16:25–29
- Munck A, Guyre P, Holbrook N (1984) Physiological functions of glucocorticoids during stress and their relation to pharmacological actions. *Endocrine Rev* 5:25–47
- Munro C, Stabenfeldt G (1984) Development of cortisol enzyme immunoassay in plasma. *Clin Chem* 31:985 (Abstract)
- Olupot W (1999) *Mangabey dispersal and conservation in Kibale Forest National Park, Uganda*. Dissertation, Purdue University, USA
- Olupot W, Waser PM (2001a) Activity patterns, habitat use and mortality risks of mangabey males living outside social groups. *Anim Behav* 61:1227–1235
- Olupot W, Waser PM (2001b) Correlates of intergroup transfer in male grey-cheeked mangabeys. *Int J Primatol* 22:169–187
- Powell GVN (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim Behav* 22:501–505
- Pulliam HR (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- Roberts G (1995) Why individual vigilance declines as group size increases. *Anim Behav* 51:1077–1086
- Scheel D (1993) Profitability, encounter rates, and prey choice of African lions. *Behav Ecol* 4:90–97
- Shultz S, Noe R (2002) The consequences of crowned eagle central-place foraging on predation risk in monkeys. *Proc R Soc Lond B* 269:1797–1802

- Shultz S, Noe R, McGraw SW, Dunbar RIM (2004) A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition. *Proc R Soc Lond B* 271:725–732
- Siegfried WR, Underhill LG (1975) Flocking as an anti-predator strategy in doves. *Anim Behav* 23:504–508
- Skorupa JP (1989) Crowned eagles *Stephanoaetus coronatus* in rainforest: observations on breeding chronology and diet at a nest in Uganda. *Ibis* 131:294–298
- Strier KB, Ziegler TE (1997) Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *Am J Primatol* 42:299–310
- Strier KB, Ziegler TE (2005) Advances in field-based studies of primate behavioral endocrinology. *Am J Primatol* 67:1–4
- Struhsaker TT (1975) The red colobus monkey. University of Chicago Press, Chicago
- Struhsaker TT, Leakey M (1990) Prey selectivity by crowned hawk-eagles on monkeys in the Kibale Forest, Uganda. *Behav Ecol Sociobiol* 26:435–443
- Thiollay JM, Jullien M (1998) Flocking behavior of foraging birds in a neotropical rain forest and the antipredator defence hypothesis. *Ibis* 140:382–394
- Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722
- van Schaik CP, van Noordwijk MA, DeBoer RJ, Den Tonkelaar I (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques. *Behav Ecol Sociobiol* 13:173–181
- Watts DP, Mitani JC (2002) Hunting and meat sharing by chimpanzees at Ngogo, Kibale National Park, Uganda. *Int J Primatol* 23:1–29
- Whitten PL, Brockman DK, Stavisky RC (1999) Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Am J Phys Anthropol* 107:1–23
- Ziegler TE, Scheffler G, Snowdon CT (1995) The relationship of cortisol levels to social environment and reproductive functioning in female cotton-top tamarins, *Saguinus oedipus*. *Horm Behav* 29:407–424
- Zuberbühler K, Jenny D, Bshary R (1999) The predator deterrence function of primate alarm calls. *Ethology* 105:477–490