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Male and female strategies during intergroup encounters in guerezas (*Colobus guereza*): evidence for resource defense mediated through males and a comparison with other primates

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Abstract Although socioecological theory predicts that differences in male and female parental investment will be reflected in their behavior during intergroup encounters, the strategies actually pursued by adults of each sex during intergroup encounters remain poorly known for most primate species. Over an 11-month period, I examined the functions of adult male and female participation in intergroup aggression in five groups of eastern black-and-white colobus monkeys, or guerezas (*Colobus guereza*), in the Kakamega Forest, Kenya. Guerezas are large-bodied arboreal African colobine monkeys that usually live in one-male multifemale groups, though multimale multifemale groups are not uncommon. During 174 study days, I observed 136 encounters, most of which were aggressive in nature. I evaluated the hypotheses that through intergroup aggression (1) males were directly defending mates, (2) males were indirectly defending mates by directly defending food resources, (3) males were attempting to attract mates via infanticide, and/or (4) females were defending food resources. I found strong evidence consistent with both the direct male mate defense and indirect male mate defense via resource defense hypotheses, but no evidence consistent with the male mate attraction via infanticide hypothesis. There was little evidence in favor of the female resource defense hypothesis beyond the fact that females occasionally participated in intergroup aggression in four of the five study groups. A review of the most intensive studies of primate intergroup encounters suggests that direct male mate defense may occur in almost all primate species, while female resource defense appears to be most common in species with high levels of female phi-

loptry. The indirect male mate defense via resource defense strategy has rarely been evaluated and may be a more common male strategy than is currently believed. I present a hypothesis that predicts when male primates are expected to defend resources for females in their group.

Keywords Intergroup encounters · Aggression · Resource defense · Mate defense · Hired guns · Infanticide

Introduction

Interactions between non-human primate groups range in character from peaceful interminglings (Terborgh 1983; Bocian 1997) to aggressive chases (Struhsaker 1975; Goldizen 1987) to contact aggression resulting in serious injuries or death (Manson and Wrangham 1991; Palombit 1993). Some level of intergroup aggression occurs during intergroup encounters in most primates whether or not they actually defend a home range.

Several hypotheses exist to explain why intergroup aggression occurs in primates (Fig. 1). One explanation is that intergroup aggression is related to female food resource defense (Wrangham 1980). Because female reproductive fitness is believed to be most limited by access to food (Trivers 1972), adult females in female-bonded primate species are expected to cooperatively defend access to food sources in their home ranges against females in other groups (Wrangham 1980).

A second explanation for intergroup aggression is that it is related to male mate defense since male fitness is believed to be determined primarily by reproductive access to females (Trivers 1972). Male mate defense during intergroup encounters can be achieved either directly or indirectly. A male accomplishes direct mate defense during intergroup encounters by driving away extragroup male competitors or by herding the females within his own group away from males in other groups. Through these actions, males attempt to prevent estrous females

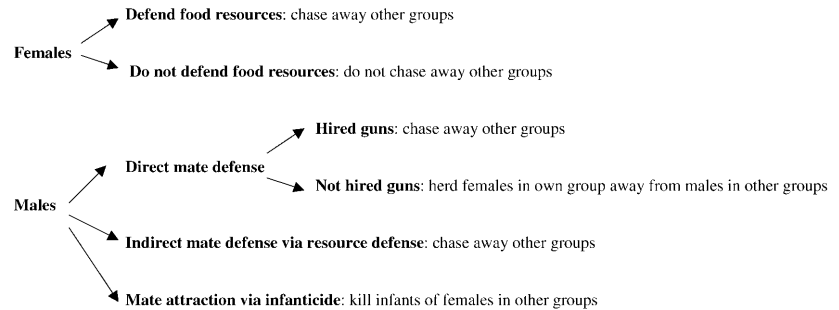
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Fig. 1 Strategies adopted by adult primates during intergroup encounters



in their group from engaging in extragroup copulations (Reichard and Sommer 1997; Steenbeek 1999) or transferring to other groups (Stanford 1991; Sicotte 1993; Sterck 1995; Steenbeek 1999).

Direct mate defense in which a male drives away potential reproductive competitors from locations within his group's home range might effectively serve to protect food resources in those locations as well. This scenario, in which adult females and other group members benefit from resource defense through intergroup aggression related to mate defense by an adult male in their group, is known as the 'hired gun' strategy (Rubenstein 1986; Wrangham and Rubenstein 1986).

Alternatively, a male can engage in indirect mate defense by directly defending food resources for a group in return for receiving primary reproductive access to females in that group. A male can adopt this strategy either by defending a home range to which he attempts to attract females (resource defense polygyny as proposed by Emlen and Oring 1977), or by taking over a group of females and defending resources in their home range.

In addition, adult males of some species may attempt to kill infants in other groups during intergroup encounters as a means of 'attracting' females in these other groups (van Schaik 1996; Steenbeek 1999). By exposing the inability of an adult male to defend his group's infants, an infanticidal male from another group may induce the mother of the infant he kills to transfer out of her original group and into his group (Watts 1989; Steenbeek 1999). A male might also benefit from killing an infant if doing so induces the infant's mother to resume her reproductive cycle and mate with him sooner than would have otherwise occurred (Blaffer Hrdy 1977) or by eliminating a potential competitor for food for the male and his relatives (Struhsaker and Leland 1987). Therefore, infanticide can be viewed primarily as a means to improve reproductive access to females (mate attraction), though it can also serve to eliminate competitors for food (resource defense).

Attempts at evaluating the validity of the female resource defense, male mate defense, hired gun, male resource defense, and male mate attraction via infanticide hypotheses have been hindered by the fact that the different hypotheses are not necessarily mutually exclusive. Female resource defense can take place simultaneously with male mate defense (Kinnaird 1992) and, as dis-

cussed earlier, some males become hired guns through their mate defense (Rubenstein 1986).

The functions of intergroup aggression have been intensively studied for only a few primate species (e.g., Stanford 1991; Kinnaird 1992; Cowlshaw 1995) and have been examined to lesser extents for a number of other species (e.g., Manson and Wrangham 1991; van Schaik et al. 1992; Jolly et al. 1993). A lack of quantitative data on the patterns of intergroup encounters and how they vary with ecological and social variables greatly hinders efforts to determine the function(s) of intergroup aggression for most primate species. Few studies have provided quantitative data on the patterns of intergroup encounters (e.g., Stanford 1991; Cowlshaw 1995; Perry 1996; Reichard and Sommer 1997) and even fewer have examined these patterns quantitatively with respect to ecological variables (Peres 1989; Kinnaird 1992; Garber et al. 1993; Steenbeek 1999). Even the most quantitative studies to date have not completely evaluated each of the hypothesized functions for intergroup aggression.

The subfamily of Old World primates known as the colobine monkeys is a good taxonomic group on which to focus studies of intergroup aggression. Not only have intergroup encounters been found to occur relatively frequently at a number of colobine monkey study sites (Struhsaker 1975; Oates 1977b; Stanford 1991), but the small group sizes and spatial cohesion characteristic of many colobine species (Oates 1977b; Stanford 1991) also make it possible to monitor most or even all group members during intergroup encounters at sites where observational conditions are good. Descriptions of the basic patterns of interactions between groups are available for a number of colobine species (e.g., *Procolobus badius*: Struhsaker 1975; *Colobus guereza*: Oates 1977a, 1977b; *Trachypithecus pileatus*: Stanford 1991; *Colobus satanas*: Fleury and Gautier-Hion 1999; *Presbytis thomasi*: Steenbeek 1999), though the functions of intergroup aggression have been investigated for only a few (*T. pileatus*: Stanford 1991; *P. thomasi*: Steenbeek 1999).

I conducted an 11-month study of the functions of intergroup aggression in eastern black-and-white colobus monkeys, or guerezas, (*C. guereza*) in the Kakamega Forest, Kenya. I attempted to test three hypotheses for the functions of male intergroup aggression in guerezas: (1) males were defending reproductive access to females (male mate defense hypothesis), (2) males were defend-

ing access to food resources for females and their offspring in return for priority of reproductive access to the females (male resource defense hypothesis), and (3) males were attempting to attract mates via infanticide (male mate attraction via infanticide hypothesis). I also tested one hypothesis for the function of female intergroup aggression in guerezas: that females were defending access to food resources (female resource defense hypothesis).

If *male mate defense* occurs during intergroup aggression, I predicted that:

1. males should participate in intergroup aggression;
2. males should react more aggressively toward bachelor males than toward males in other bisexual groups, since bachelor males have less access to estrous females than males in bisexual groups;
3. males should react more aggressively to extragroup males when females in their group are in estrous than when they are not.

If *male resource defense* occurs during intergroup aggression, I predicted that:

1. males should participate in intergroup aggression;
2. levels of male aggression during intergroup encounters should be related to the amount of time group members recently spent feeding in the quadrat, or grid cell, where an encounter occurs;
3. males should be aggressive during intergroup encounters even when no females in their group are in estrus;
4. males should be aggressive toward intruders regardless of age/sex class;
5. males should engage in most, if not all, copulations involving females in their groups.

If *male mate attraction via infanticide* occurs during intergroup aggression, I predicted that:

1. males should be observed killing or attempting to kill infants in other groups during intergroup encounters;
2. females should 'hang back' during encounters when they have infants at an age when they are at risk of infanticide;
3. females should mate with and/or transfer to the groups of males that kill their infants.

If *female resource defense* occurs during intergroup aggression, I predicted that:

1. females should participate in intergroup aggression;
2. levels of female aggression during intergroup encounters should be related to the amount of time group members recently spent feeding in the encounter quadrat.

To test these predictions, data were collected on the behavior of individual adult males and females during intergroup encounters, the geographic locations of intergroup encounters, the geographic locations of feeding records, and the patterns of mating activity within the study population.

Methods

Study area

I conducted my study of guerezas at Isecheno study site in the Kakamega Forest, western Kenya (0°19' N, 34°52' E; elevation 1,580 m; Cords 1987b; von Hippel 1996). Isecheno is situated in the largest block (86 km²) of forest remaining at Kakamega (Brooks et al. 1999). Preliminary research was conducted in July 1993, November–December 1995, and November 1996–March 1997, while intensive investigation of male and female strategies during intergroup encounters was carried out from April 1997 to February 1998. Over the course of the study, I collected more than 3,000 h of observation on guerezas at Isecheno.

Study species

Guerezas are large colobine monkeys that inhabit the forests of equatorial Africa. They typically live in one-male groups that also include several adult females and their dependent offspring, though multimale groups are not uncommon (Oates 1977b; Fashing 1999). Adult males not belonging to bisexual groups appear to most often travel alone or in pairs, though larger all-male bands are observed occasionally as well (personal observation).

Guerezas have often been reported to be among the most folivorous of primates (Oates 1977a; Bocian 1997), though both leaves and fruit make substantial contributions to their diet at Kakamega (Fashing, in press b). Guereza population density, home range size, and amount of home range overlap vary widely between study sites (Oates 1977a; Dunbar 1987; Bocian 1997). The population density of 150 individuals/km² at Kakamega (Fashing and Cords 2000) represents a relatively high value for guerezas at a large (≥50 km²) rainforest site (Oates 1974; Suzuki 1979; Bocian 1997). However, the mean home range size (18 ha; $n=2$ groups; Fashing, in press a), mean home range overlap (67%; $n=5$ groups; Fashing, in press a), and presence of site-specific home range defense at Kakamega (Fashing 1999) are typical for guerezas in large rainforests (Oates 1977a). Populations of guerezas do not appear to be characterized by seasonality of births (Oates 1977b; P.J. Fashing, unpublished data). Males are known to transfer between groups (Oates 1977b), and there is circumstantial evidence that females may transfer between groups as well (personal observation). Changes in adult male membership in bisexual groups appear to occur via takeovers (Oates 1977b).

Study groups

Five groups of guerezas were studied from April 1997 to February 1998 and the sizes and compositions of those groups during that period are provided in Table 1. Animals that had reached full size and that appeared to have reached reproductive maturity were classified as adults. Subadult males were at least equal in body size to adult females, but smaller than adult males in body size, testicle size, or both. Juveniles were not yet adult or subadult size and were no longer being carried by their mothers. Infants were small in size and still being carried by their mothers.

Data collection

Intergroup encounter data were collected on 55 days for O group, 54 days for T group, 22 days for GC group, 22 days for BS group, and 21 days for ML group. Each study day represented an all-day follow and all occurrences of intergroup encounters were noted.

Intergroup encounters were defined as those occasions when two groups were within 50 m of each other (Oates 1977b; Stanford 1991). Encounters rarely involved more than two groups, but when they did, the focal group (the group on which the all-day follow was being conducted) was considered to be having encounters with each of the other groups present. Encounters were con-

Table 1 Group size and composition in the five study groups from April 1997 to February 1998

Group	Group size		Adult males		Adult females		Subadult males		Juveniles		Infants	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
T	11	10-13	1	1-2 ^a	5	5	0	0	3	3	2	0-4
O	7	7-8	1	1	3	3	0	0	0	0-1	3	1-3
GC	10	10	1	1	3	3	0	0	4	4	2	2
ML	15	13-16	2	2-3	4	3-4	1	1	4	4-5	4	3-4
BS	21	19-23	5	3-6	4	4	3	1-3	8	6-9	1	0-2

^a A second adult male was present intermittently in T group on 5 days early in the study. Data from intergroup encounters on these days have been excluded from the dataset

sidered to have ended when no members of either group were still within 50 m of each other. On 21 occasions (15% of all encounters), groups that encountered one another earlier in the day returned to within 50 m of each other at some point later in the day. These re-encounters were considered to be another phase of the earlier encounter rather than a new encounter, since in many cases groups remained within sight of each other during the period between re-encounters. Because it would generally be inappropriate to analyze second and third phases of encounters as though they were independent of the first phase of an encounter, only behavior during the first phase of each encounter is analyzed for this paper.

All intergroup encounter data were collected ad libitum (Altmann 1974). For each intergroup encounter, I attempted to determine: (1) the time it began, (2) the time it ended, (3) the identity of the group encountered, (4) the locations of both groups throughout the encounter, (5) the behavior of all individuals in each group, and (6) the result of the encounter: win, loss, or draw.

'Wins' occurred when the focal group displaced its opponent either through a chase or an approach. 'Losses' occurred when the focal group was displaced by its opponent either through a chase or an approach. 'Draws' occurred when neither the focal group nor its opponent were clearly displaced by the other group.

Individuals in the focal group were assigned aggression scores of 'intense,' 'weak,' or 'none.' An 'intense' score was given to individuals that chased (common) and/or physically attacked (rare) monkeys in the other group. A 'weak' score was given to individuals engaging in relatively low risk threats such as 'tongue clicks' (Oates 1977b), 'legs-out' displays (Oates 1977b), or leaping displays. A score of 'none' was given to individuals not observed participating in aggression directed toward the other group.

During each intergroup encounter, the locations of both the study group and the group(s) they encountered were plotted on a map of the study site. Dietary data were collected for two (T and O) of the five study groups as well. Data on plant parts and species consumed were collected via scan samples at 15-min intervals on up to the first six adults and juveniles and all infants visible at the time of the scan [see Fashing (in press b) for further details]. The geographic location of each feeding record was also recorded and plotted on a map of the study site.

Data analysis

A transparent map of 50×50 m grid cells, or quadrats, was laid over the maps of feeding locations to determine the percentage of the total monthly feeding records that were obtained from each quadrat in each study group's home range. An identical transparent map of 50×50 m grid cells was also laid over maps of the locations of intergroup encounters to determine how the outcomes of intergroup encounters were related to dietary patterns.

A number of analyses described in the Results section refer to the 'encounter quadrat.' Because the location of the group that is displaced is probably more biologically relevant to what is being contested than the location of the winning group, 'encounter quadrat' refers to the quadrat occupied at the start of the encounter by the group that eventually lost.

Most statistical analyses performed in this paper were conducted on each study group separately. However, in cases where analyses were conducted on data from the five study groups combined, all groups exhibited similar trends when analyses were conducted on each group individually. All statistical tests used were non-parametric and two-tailed (Siegel and Castellan 1988).

Results

In this section, I use data gathered during my study to evaluate the predictions of each hypothesis for the functions of intergroup aggression in adult male and female guerezas. I begin by examining the strategies pursued by males and then consider the strategies pursued by females.

Male strategies

Direct mate defense

Prediction 1: adult males should participate in intergroup aggression. Adult males in the study groups were aggressive during 50–82% of intergroup encounters (Table 2). This aggression reached the 'intense' level (chases or physical attacks) in 18–42% of the intergroup encounters involving four (T, O, GC, ML) of the five study groups. Therefore, consistent with prediction 1, adult males exhibited at least some aggression in most encounters and 'intense' aggression in many encounters.

Prediction 2: adult males should be more aggressive toward bachelor adult males living alone or in all-male bands than toward adult males in other bisexual groups. Because encounters with bachelor males were rare ($n=6$), data were pooled for the five study groups to compare reactions toward bachelor males with reactions toward bisexual groups. Consistent with the mate defense hypothesis, study group adult males were significantly more likely to be 'intensely' aggressive toward bachelor males than toward bisexual groups (Fig. 2; Fisher's exact test: $P=0.007$).

Prediction 3: adult males should react more aggressively to extragroup males when females in their group are in estrous than when they are not. Unfortunately, since fe-

Table 2 Rates of participation in intergroup aggression for adult males and females in the five study groups. The value in parentheses is the number of encounters for which level of aggression could be measured (IE=intergroup encounters)

Group	Percentage of total IE in which at least one individual was aggressive		Percentage of total IE in which at least one individual was 'intensely' aggressive	
	Adult male(s)	Adult females	Adult male(s)	Adult females
T	64 (33)	7 (33)	18 (34)	0 (34)
O	77 (53)	26 (51)	42 (53)	14 (51)
GC	67 (18)	33 (18)	22 (18)	11 (18)
ML	82 (11)	10 (10)	36 (11)	0 (10)
BS	50 (10)	0 (10)	0 (10)	0 (10)

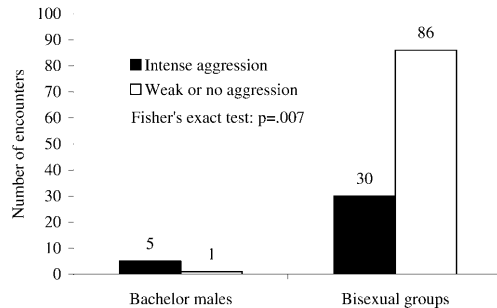


Fig. 2 Comparison of study group male reactions to bachelor males and bisexual groups

male guerezas do not develop estrous swellings, estrous could only be detected when females were observed copulating or soliciting copulations. Furthermore, despite the fact that at least six adult females in T and O groups conceived infants during my study, I observed copulations involving no more than three of these females. Therefore, since I failed to detect several of the periods during which females in my study groups were in estrous, prediction 3 cannot be properly evaluated.

Anecdotal evidence. Several lines of anecdotal evidence are consistent with the male mate defense hypothesis. One comes from an intergroup encounter that took place on the morning of 3 January 1997 between the focal group, T, and R group. Early in the encounter, I observed an adult female in T group, TF, being mounted by an adult male in R group, RM. Shortly after this mount ended, an adult male in T group, TM, came running over and prevented TF from reapproaching RM. Over the next hour, TM prevented TF from approaching RM on at least two more occasions and chased away RM on at least one occasion. This observation of mate guarding by TM during an intergroup encounter is consistent with the mate defense hypothesis for intergroup aggression.

Also consistent with the male mate defense hypothesis is the observation that adult males often leaped flamboyantly in the direction of infants and/or adult females in their own groups during intergroup encounters. Most often, these 'flashy leaps' frightened infants, causing them to squeal, but on some occasions, adult females also cowered in response to male leaps. While 'true' herding behavior (e.g., Stanford 1991; Steenbeek 1999) was not observed, flashy leaps may have repre-

sented a more subtle form of intimidation of the adult females within a male's group during intergroup encounters.

Indirect mate defense via resource defense

Prediction 1: adult males should participate in intergroup aggression. As demonstrated above, males regularly participated in intergroup aggression.

Prediction 2: levels of adult male aggression during intergroup encounters should be related to the amount of time group members recently spent feeding in the encounter quadrat. This prediction was evaluated with data from T and O groups, the only groups for which both feeding and intergroup encounter data were gathered. As predicted by the male resource defense hypothesis, male aggression level during intergroup encounters differed with the percentage of *monthly* feeding time the male's group spent feeding in an encounter quadrat. In each group, the percentage of *monthly* feeding time was significantly higher in encounter quadrats characterized by 'intense' adult male aggression (T group: mean=8.9% of monthly feeding time; O group: mean=3.3% of monthly feeding time) than in encounter quadrats characterized by 'weak' or 'no' male aggression (T group: mean=2.2% of monthly feeding time; O group: mean=1.5% of monthly feeding time) (T group: $U=25.0$, $n_1=6$, $n_2=23$, $P=0.012$; O group: $U=148.0$, $n_1=19$, $n_2=26$, $P=0.015$). Therefore, adult males were most often 'intensely' aggressive when encounters occurred in quadrats in which their group fed frequently, suggesting that males were engaging in resource defense during intergroup aggression.

Prediction 3: adult males should be aggressive during intergroup encounters even when no adult females in their group are in estrous. This prediction could not be evaluated conclusively since, as noted earlier, monitoring temporal changes in the reproductive status of female guerezas was difficult. However, the fact that T and O group males engaged in aggression toward other groups during 91% (20/22) of the 5-day samples in the study suggests that, unless females were in estrous during nearly all of the 5-day samples, males were probably aggressive toward other groups even during those samples when females in their group were not in estrous.

Prediction 4: adult males should be aggressive toward intruders regardless of their age/sex class. Identifying the targets of male aggression during encounters was often difficult because of the limited spatial dispersion between members within guereza groups and the fact that when chased, group members generally all fled at once. In encounters characterized by 'weak' aggression, adult males generally appeared to direct their threats toward adult males in opposing groups. In encounters characterized by 'intense' aggression, an adult male normally led the chase, or conducted the chase all by himself, but appeared to direct his aggression toward the animal bringing up the rear of the group being displaced. Though the animal in the rear of the fleeing group was sometimes an adult male, this was not always the case. For example, at the beginning of an encounter on 1 April 1997, a T group adult male clearly chased away an S group large juvenile female that remained behind to feed on *Zanthoxylum gillettii* leaves for several seconds after the remainder of her group fled. Therefore, adult males did not direct their aggression exclusively toward other adult males, a finding consistent with prediction 4.

Prediction 5: adult males should engage in most, if not all, copulations involving females in their groups. Each of the four copulations recorded in O group occurred between an O group female and the O group male, OM. These copulations took place over an 8-month period and involved all three adult females (DF twice, SF once, VF once), suggesting that all three females in O group chose to mate with their group male when in estrous. Of the three copulations recorded in T group, two occurred between a female in T group and a T group male (the anecdote discussed earlier describes the one exception). Therefore, consistent with the male resource defense hypothesis, T and O group females chose to mate with their group males during almost all of the copulations recorded during the study.

Mate attraction via infanticide

Prediction 1: adult males should be observed killing or attempting to kill infants during intergroup encounters. I found no evidence that males attempt to commit infanticide during intergroup encounters. Males sometimes single-handedly chased other groups away, but physical attacks on members of other groups were rare and I never observed male aggression directed specifically at infants in opposing groups.

Prediction 2: adult females should 'hang back' during encounters when they have infants at an age when they are at risk of infanticide. Van Schaik (1996, p. 24) predicted that if infanticide risk affects patterns of intergroup relationships, females with infants should 'hang back' during encounters to minimize the chances that their infants will be attacked. The interbirth interval for guerezas at Kakamega is estimated at approximately

16 months (P.J. Fashing, unpublished data) and the gestation period for captive guerezas has been estimated at approximately 6 months (Rowell and Richards 1979). Based on these reproductive parameters, if their strategy is to decrease the period of postpartum reproductive suppression in females, then adult males should attempt to kill only those infants less than 10 months old. Therefore, if infanticide risk plays a role in intergroup relationships, females should participate less often in chases of other groups when their infants are less than 10 months old than when their infants are older or when they have no infants. O group was the only group with sufficient data on the strategies of individual adult females to test this hypothesis. Based on 11 months of data, O group adult females did not participate in chases at significantly lower rates when they had infants under 10 months old than when they had older or no infants (Fisher's exact test: $P=0.221$).

Prediction 3: adult females should mate with and/or transfer to the groups of adult males that kill their infants. Since males were never observed killing or attempting to kill infants, there is no evidence in favor of prediction 3.

Female strategies

Female resource defense

Prediction 1: adult females should participate in intergroup aggression Adult females participated in intergroup aggression in four of the five study groups. Females exhibited at least some aggression in 0–33% of intergroup encounters and 'intense' aggression in 0–14% of intergroup encounters (Table 2). However, female rates of participation in intergroup aggression were significantly lower than those of males in four groups (Table 2; Fisher's Exact test: T group, $P<0.0001$; O group, $P<0.0001$; ML group, $P=0.0005$; BS group, $P=0.033$) and nearly significantly lower in the fifth group (GC group, $P=0.094$). Therefore, while females sometimes participated in intergroup aggression, their participation was not as regular a feature of intergroup encounters as that of adult males.

Prediction 2: levels of adult female aggression during intergroup encounters should be related to the amount of time group members recently spent feeding in the encounter quadrat. An analysis of 'intense' female aggression and its relationship to time spent feeding in encounter quadrats could not be conducted for T group since females in this group were never intensely aggressive. In O group, where females occasionally exhibited 'intense' intergroup aggression, the percentage of monthly feeding time was *not* significantly higher in encounter quadrats characterized by 'intense' adult female aggression (mean=0.9% of monthly feeding time) than in encounter quadrats characterized by 'weak' or 'no' female aggres-

sion (mean=2.5% of monthly feeding time) ($U=84.0$, $n_1=5$, $n_2=38$, $P=0.654$). Furthermore, the percentage of *yearly* feeding time in O group was also *not* significantly higher in encounter quadrats characterized by 'intense' adult female aggression (mean=0.9% of yearly feeding time) than in encounter quadrats characterized by 'weak' or 'no' female aggression (mean=1.9% of yearly feeding time) ($U=92.5$, $n_1=5$, $n_2=38$, $P=0.924$).

Since females so rarely engaged in 'intense' intergroup aggression, I also reran the Mann-Whitney U -tests conducted above with 'any' ('intense' or 'weak') female aggression and 'no' female aggression as the two-group variables. This time I also found that in both groups, the percentage of *monthly* feeding time was *not* significantly higher in encounter quadrats characterized by 'any' adult female aggression (T group, mean=9.6% of monthly feeding time; O group, mean=4.1% of monthly feeding time) than in encounter quadrats characterized by 'no' female aggression (T group, mean=2.5% of monthly feeding time; O group, mean=1.8% of monthly feeding time) (T group, $U=26.5$, $n_1=3$, $n_2=28$, $P=0.265$; O group, $U=125.0$, $n_1=11$, $n_2=32$, $P=0.127$). Furthermore, the percentage of *yearly* feeding time was also *not* significantly higher in encounter quadrats characterized by 'any' adult female aggression (T group, mean=2.5% of yearly feeding time; O group, mean=2.0% of yearly feeding time) than in encounter quadrats characterized by 'no' female aggression (T group, mean=1.5% of yearly feeding time; O group, mean=1.7% of yearly feeding time) (T group, $U=15.0$, $n_1=3$, $n_2=28$, $P=0.070$; O group, $U=150.5$, $n_1=11$, $n_2=32$, $P=0.477$).

Therefore, in none of the tests conducted was level of female aggression significantly related to the amount of time group members spent feeding in encounter quadrats.

Discussion

Male and female guereza strategies during intergroup encounters

Data from guerezas at Kakamega are strongly consistent with the hypothesis that during intergroup encounters males engage in direct mate defense. The data are also equally, if not more, consistent with the hypothesis that males engage in indirect mate defense via resource defense. However, the male resource defense hypothesis was tested for only two groups, both featuring only one adult male, and even in these groups, male reproductive success could only be inferred from mating success (an approach that has been validated from long-term data for at least one primate population: Altmann et al. 1996). Because males in these groups appear to be defending resources directly, any 'hired gun' role played by males, in which females receive resource defense indirectly via direct male mate defense (Rubenstein 1986), is probably of limited significance. The possibility that not all groups have resource-defending males must also be con-

sidered, especially for BS group in which the three to six males engaged in no aggression during a large percentage of encounters and never engaged in 'intense' aggression. Finally, there was no support for the hypothesis that males attempt to attract mates via infanticide.

Female guerezas were significantly less often involved in intergroup aggression than males and appeared to rely on males to engage in most of the resource defense. The occasional participation of females in intergroup aggression is difficult to explain, however, without invoking the resource defense hypothesis (Wrangham 1980; Cheney 1992). Therefore, although levels of female aggression could not be directly linked to locations of dietary importance in their range the way they could for males, females in some groups apparently did engage in resource defense, albeit at low rates.

Intergroup aggression in other primate taxa

How do the strategies adopted by male and female guerezas during intergroup encounters at Kakamega compare to those of adults in other primate species for which the functions of intergroup aggression have been intensively studied? A summary of male and female strategies during intergroup encounters in 29 primate species is presented in Table 3. The methods and durations of the studies summarized in the table vary considerably, as does the quality of the evidence for or against the various hypothesized functions of intergroup aggression. Therefore, for this table, I defined consistent criteria for what I would consider strong evidence for each hypothesis. Evidence of frequent male mate guarding, herding of females, or chasing away of rival males in other groups was considered strong evidence in favor of the direct male mate defense hypothesis. Evidence that males defended access to food during intergroup aggression and achieved nearly all of the copulations involving females in their groups was considered strong evidence in favor of the indirect mate defense via resource defense hypothesis. Evidence that males committed infanticide during intergroup encounters and that at least one female whose infant was killed later transferred to an infanticidal male's group was considered strong evidence in favor of the male mate attraction via infanticide hypothesis. Finally, regular female participation in intergroup aggression was considered to be strong evidence in favor of the female resource defense hypothesis.

Long-term quantitative data on the strategies adopted by adults of each sex during intergroup encounters are available for only 9 of the species for which the functions of intergroup aggression are summarized here. For the other 20 species, valuable data on interactions between groups are available, but the strategies of adult males and females during intergroup encounters have been examined less thoroughly.

A comparison of the nine intensively studied species yields some insight into the functions of intergroup aggression across taxa. For each of these species there is at

Table 3 Male and female strategies during intergroup encounters in primates. (Only the first nine studies present the results of long-term research focused on evaluating the hypothesized functions of intergroup aggression); + denotes strong evidence for a hypothesis; * denotes evidence for a hypothesis but that the form of de-

fense is occurring at low rates; – denotes strong evidence against a hypothesis; () denotes that evidence for or against a hypothesis is present but not entirely convincing; blank spaces indicate that a hypothesis was not evaluated

Species	Study site	Philopatric sex	Number of encounters	Male Mate defense	Male resource defense	Male mate attraction via infanticide	Female resource defense	Any resource defense	References
<i>Cebus capucinus</i>	Lomas Barbudal, Costa Rica	F	44	(+) ^a			*b	*b	Perry (1996)
<i>Chlorocebus aethiops</i>	Amboseli, Kenya	F	234	+			+ ^b	+ ^b	Cheney (1981); Cheney and Seyfarth (1987); Isbell et al. (1991)
<i>Cercocebus galeritus</i>	Mchelelo, Kenya	F		+			+	+	Kinnaird (1992)
<i>Papio ursinus</i>	Tsaobis, Namibia	F	27	+	(–)		–	(–)	Cowlishaw (1995)
<i>Colobus guereza</i>	Kakamega, Kenya	None?	136	+	+	(–)	*	+	This study
<i>Trachypithecus pileatus</i>	Madhupur, Bangladesh	None	86	+	(–)		–	(–)	Stanford (1991)
<i>Presbytis thomasi</i>	Ketambe, Indonesia	None	594	+		+	–		Steenbeek (1999)
<i>Hylobates lar</i>	Khao Yai, Thailand	None	162	(+) ^c			–		Reichard and Sommer (1997)
<i>Gorilla gorilla</i>	Karisoke, Rwanda	M	58	+	(–)	+	–	(–)	Watts (1989); Sicotte (1993)
<i>Hapalemur griseus</i>	Lac Alaotra, Madagascar	None	18		(+) ^d			(+) ^d	Nievergelt et al. (1998); Mutschler et al. (2000)
<i>Lemur catta</i>	Berenty, Madagascar ^e	F	163		(–)		+ ^b	+	Jolly et al. (1993); Sauther et al. (1999)
<i>Leontopithecus rosalia</i>	Poco d'Antas, Brazil		60				(+) ^b	+	Peres (1989)
<i>Saguinus mystax</i>	Padre Isla, Peru	None	67	(+)				+ ^f	Garber et al. (1993)
<i>S. mystax/S. fuscicollis</i>	Rio Blanco, Peru		32				(+) ^b	+	Garber (1988)
<i>S. mystax/S. fuscicollis</i>	Urucu River, Brazil		39					(+) ^f	Peres (1992)
<i>Cebus olivaceous</i>	Hato Masaguaral, Venezuela	F			(+)			(+)	Robinson (1988)
<i>Macaca fuscata</i>	Yakushima, Japan	F	152	(+)			*b	*	Saito et al. (1998)
<i>Macaca silenus</i>	Varagaliyar, India	F	31	+			(+) ^b	(+) ^b	Kumar and Kurup (1985)
<i>Papio spp.</i> ^g	Africa	F		(+)			(–)	(–)	Cowlishaw (1995)
<i>Cercopithecus diana</i>	Tiwai Island, Sierra Leone	F	3		(–)		+ ^b	+	Hill (1991)

Table 3 (continued)

Species	Study site	Philopatric sex	Number of encounters	Male Mate defense	Male resource defense	Male mate attraction via infanticide	Female resource defense	Any resource defense	References
<i>Cercopithecus mitis</i>	Cape Vidal, South Africa		58					+ ^f	Lawes and Henzi (1995)
<i>Cercopithecus mitis</i>	Kakamega, Kenya	F			(-)		+ ^b	+	Rowell et al. (1991)
<i>Chlorocebus aethiops</i>	Niokolo-Koba, Senegal	F	27		(+)		* ^b	+	Harrison (1983)
<i>Chlorocebus aethiops</i>	Cameroon							(+) ^f	Kavanagh (1981)
Southeast Asian langurs ^b	Southeast Asia	None		(+) ⁱ			-		van Schaik et al. (1992)
<i>Semnopithecus entellus</i>	Jodhpur, India ^c	F					+	+	Borries (1993)
<i>Pan troglodytes</i>	Africa	M		+			-		Manson and Wrangham (1991)

^a Evidence shows males were clearly the most aggressive group members during intergroup encounters, but what males were defending was not directly investigated

^b Female participation in intergroup aggression was assumed to represent resource defense

^c Males were the most active participants in intergroup aggression; direct evidence for mate defense comes from only one incident of mate guarding while there were two instances in which a male failed to prevent the female in his group from mating with a male in another group

^d Provides some evidence that males defend a patch of land and attract one or two females to it

^e Population is provisioned

^f Does not describe or evaluate the strategies of each sex

^g Based on data from populations of four *Papio* species: *P. anubis*, *P. cynocephalus*, *P. hamadryas*, *P. ursinus*

^h Based on data from 12 populations of five species: *Presbytis comata*, *P. melalophos*, *P. rubicunda*, *Trachypithecus cristatus*, *T. obscurus*

ⁱ Provides evidence that males are the only participants in intergroup aggression, though no direct tests of the mate defense hypothesis are provided

least some evidence in support of the direct male mate defense hypothesis. This finding is consistent with the idea that male fitness is most limited by reproductive access to adult females (Trivers 1972; Wrangham 1980), and that males of most, if not all, primate species are likely to directly defend reproductive access to females during at least some intergroup encounters. In contrast, substantial evidence consistent with the hypothesis that adult males are indirectly defending access to mates by defending access to food resources was produced for only one (this study) of the nine intensively studied species. However, as will be discussed in the final section, the male resource defense strategy may be more widespread among primate males than is suggested by Table 1. In two of the nine intensively studied species, there is evidence that males succeed in attracting mates by killing their infants during intergroup encounters (Watts 1989; Steenbeek 1999).

In four of the nine intensively studied species, females appear to be defending access to food resources (Cheney 1981; Kinnaird 1992; Perry 1996; this study), but in only two of these four species does female resource defense appear to be common (Cheney 1981; Kinnaird 1992). The two well-studied species in which female resource defense appears to be common, and the four less thoroughly studied species for which strong evidence was found in favor of the female resource de-

fense hypothesis (Hill 1991; Rowell et al. 1991; Borries 1993; Jolly et al. 1993) are characterized (or are believed to be characterized) by high levels of female philopatry (i.e., female bonding; Wrangham 1980). This pattern is consistent with Wrangham's (1980) prediction that females in female-bonded species will participate in intergroup aggression.

When should males adopt the resource defense strategy?

My study is the first to evaluate and find strong evidence consistent with the indirect mate defense via resource defense hypothesis for male intergroup aggression in a primate species. Though I expect that male primates of almost all species will adopt the strategy of direct mate defense during intergroup encounters, males of some species may supplement this defense with indirect mate defense via resource defense when it is advantageous to do so. Here, I present a hypothesis that predicts when male primates are expected to adopt the resource defense strategy (Fig. 3). First, food must be limiting and distributed in defensible patches (Wrangham 1980; van Schaik 1989). Second, groups must include relatively small numbers of females and/or females exhibiting estrous asynchrony so that the females are virtually reproductively monopolizable. Third, females are expected to

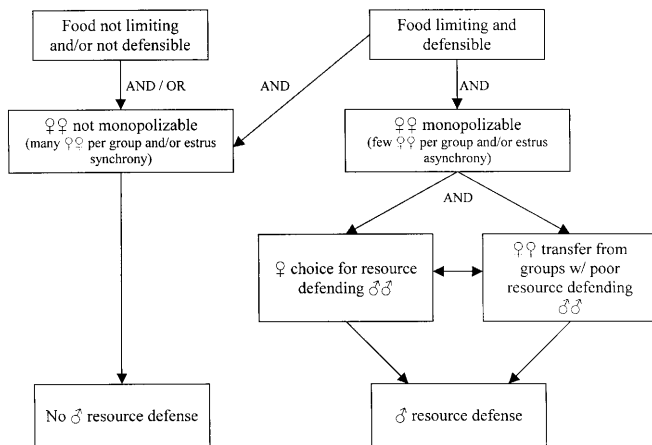


Fig. 3 When should males adopt the resource defense strategy?

choose to mate with males that defend resources, and to transfer to other groups once the male in their group begins to defend resources poorly. I predict that species that both meet the above predictions and include only one adult male per group are the most likely to feature males adopting the resource defense strategy. Species that may meet the above criteria include gibbons (*Hylobates lar*: Reichard and Sommer 1997; Brockelman et al. 1998), tamarins (*Saguinus mystax*: Garber et al. 1993), gentle lemurs (*Haplemur griseus*: Nievergelt et al. 1998; Mutschler et al. 2000), and many colobine monkeys (e.g., *P. thomasi*: Steenbeek 1999; *C. guereza*: this study).

In species characterized by more than one male per group, males might cooperatively defend resources, with each male attaining some reproductive access to the females in their group in return. Some evidence exists to suggest that male vervets (*Chlorocebus aethiops*) in multimale groups in Senegal cooperatively defend resources for their groups during intergroup aggression (Harrison 1983). However, the extent to which these males share reproductive access to females in their groups is not known. Males in multimale groups are only expected to cooperatively defend resources if by doing so, each male in the group is able to achieve greater reproductive success than if he did not. If males cooperate during intergroup aggression but some males attain greater reproductive access to females in the group than others or if some males choose to become freeloaders and benefit from the resource defense of other male group members, a 'collective action problem' (van Schaik 1996; Nunn 2000) may arise. For this reason, males in multimale groups may be less likely to adopt the resource defense strategy than males in one-male groups.

In species in which males do not have priority of reproductive access to females in their groups, males are not expected to defend food resources during intergroup encounters. For example, in some cercopithecine species characterized by groups of many females and one male, including patas monkeys (*Erythrocebus patas*) and at

least two species of guenons (*Cercopithecus ascanius* and *Cercopithecus mitis*), the resident male is joined during the mating season by an influx of non-resident males with whom he must compete for copulations (Cords 1987a, 1988). Not surprisingly, adult males in these species rarely take part in intergroup aggression, leaving the females to engage in range defense for themselves (Cords 1987a; Rowell et al. 1991). Therefore, males are not expected to adopt the resource defense strategy in all primate species, but instead only in those in which males can attain greater reproductive success by defending resources for females than if they do not. Further efforts toward evaluating the male resource defense hypothesis are necessary since the results of my research on guerezas suggest that resource defense represents a viable male strategy that is likely to be more widespread than is currently believed.

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