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Multiple resource values and fighting ability measures influence intergroup conflict in guerezas (*Colobus guereza*)

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Intergroup conflict occurs in many social species and involves potentially complex motivations and interactions. To understand its complexity in wild animals more fully, a comprehensive investigative approach is needed, in which the multiple resource values and measures of fighting ability that potentially influence intergroup contests are simultaneously considered and controlled for. This study uses long-term data on eight neighbouring groups of folivorous black and white colobus monkeys, *Colobus guereza* ('guerezas') in Kibale National Park, Uganda, to investigate the factors influencing intergroup conflict. Adult males were the main participants in intergroup aggression. Of the three resource values investigated, food value had the most unambiguous positive effect on the tendency for males to initiate high-level intergroup aggression and for groups to win. Mate value positively influenced male initiation of high-level intergroup aggression, but not more so for the group that contained high-value mates. The presence of young infants had no obvious effects. Unlike in many other species, males were more likely to initiate intergroup aggression if their groups were smaller and contained fewer adult males than opposing groups. Groups with fewer but larger adult males, and to some extent, smaller groups, were more likely to win encounters. Moreover, the relative number of adult males/group largely affected the degree to which some other factors influenced male initiation of aggression and contest outcome. These findings reveal that a complex interplay between multiple resource values and multiple fighting ability measures can simultaneously influence initiation of and success in intergroup conflict.

Many animals that live in social groups have aggressive encounters with neighbouring groups, with long-term consequences for individual fitness (Williams et al. 2004; Mosser & Packer 2009). As with contests between individual animals, both relative fighting ability and the consequences of winning or losing are expected to influence escalation of fights and encounter outcomes (Maynard Smith & Parker 1976). However, intergroup contests are potentially more complex than those between individuals, with group members having different motivations and levels of participation, and interactions occurring both within and between groups (Heinsohn & Packer 1995; Nunn & Deaner 2004; Majolo et al. 2005). Although clearly multiple types of payoffs (e.g. mates and food) and multiple measures of fighting ability (e.g. body size and group size) may simultaneously influence escalation of fights and outcomes of intergroup contests in wild animals, these are rarely considered together in the same study (exceptions include simulated contests from playback studies; e.g. Spong & Creel 2004). Thus, the full complexity of intergroup conflict may not be well understood.

Subjective resource values are expected to greatly influence the costliness, duration and outcome of fights (Enquist & Leimar 1987). Multiple resource values are potentially at stake in intergroup contests, with males often defending fertile females and females typically defending food using intergroup aggression (Cheney 1987; Fashing 2001a). Males may also defend food against other groups (reviewed in Fashing 2001a), either to attract mates (Emlen & Oring 1977), to increase the reproductive outputs of the females with which they already associate (Williams et al. 2004), and/or to enhance infant survival. Males may also play important roles in infant defence (van Schaik & Kappeler 1997; van Schaik 2000), particularly in species for which between-group infanticide occurs (reviewed in van Schaik 2000), and may alter their behaviour towards other groups when their own groups contain young infants (Kitchen 2004).

Several measures of fighting ability, or resource holding potential, also potentially influence intergroup aggression. Group size is one of the most important predictors of group fighting ability, and it influences intergroup aggression in numerous species (*Alouatta pigra*: Kitchen 2004; *Azteca trigona*: Adams 1990; *Chlorocebus aethiops*: Cheney & Seyfarth 1987; *Formica xerophila*: Tanner 2006; *Pan troglodytes*: reviewed in Wilson & Wrangham 2003; *Panthera leo*: reviewed in Grinnell 2002; *Papio cynocephalus*:

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Cowlishaw 1995; Kitchen et al. 2004). Not all individuals in a group may participate in intergroup aggression, however. In species for which there is an age and sex bias in participation, the number of individuals belonging to the class of individuals that most often participates influences whether the group engages and is successful in intergroup aggression (Cheney & Seyfarth 1987; Wilson & Wrangham 2003; Kitchen 2004). When few individuals per group participate, or when between-group contests involve series of one-on-one duels, individual fighting ability measures, such as body and weaponry size, could also be of great importance (Franks & Partridge 1993).

Studies of intergroup conflict have focused primarily on primates (reviewed in Fashing 2001a), carnivorous mammals (e.g. *Crocuta crocuta*: Boydston et al. 2001; *Panthera leo*: Heinsohn & Packer 1995) and ants (e.g. *Azteca trigona*: Adams 1990; *Atta laevigata*: Whitehouse & Jaffe 1996; *Formica xerophila*: Tanner 2006), and have typically investigated either its functions (i.e. defence of the resource at stake) or measures of fighting ability that influence it (see above). However, both resource value(s) and opponent fighting abilities are thought to concurrently influence animal contests (Parker 1974; Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Enquist & Leimar 1987). Experimental studies of animal contests typically take both into account in their study designs to isolate the effects of each (e.g. Gherardi 2006; Humphries et al. 2006; Tanner 2006; Goubault et al. 2007). Ideally, studies of naturally occurring intergroup contests in wild animals should also simultaneously investigate and control for both resource value and fighting ability (Harris 2007; Crofoot et al. 2008). For example, a group may benefit greatly from defending an important resource, but the costs of doing so against a much larger group could deter it from fighting. The full complexity of intergroup contests, however, is likely to remain poorly understood unless all potentially important resource values and measures of fighting ability are simultaneously considered and controlled for. Such research is hampered by the need for large sample sizes, which are often difficult to obtain in studies of contests among wild animal groups.

This study uses long-term data on eight neighbouring groups of black and white colobus monkeys, *Colobus guereza* ('guerezas') in Kibale National Park, Uganda, to investigate the hypothesis that multiple resource values and measures of fighting ability simultaneously influence intergroup aggression and contest outcomes. Because males are the main participants in intergroup aggression in guerezas (Oates 1977; Fashing 2001a), I focus on their behaviours.

The Kibale guereza study population is ideal for this type of investigation because intergroup interactions occur frequently and are typically very visible, and there is reason to believe that contests between males from different groups may involve multiple resource values and measures of fighting ability. The resource values I consider are food, mates and infants. The factors influencing intergroup encounter outcomes in guerezas are not well understood, but previous studies of guerezas (Fashing 2001a; Harris 2006) and other colobine monkeys (reviewed in Fashing 2007) have provided evidence that male participation in intergroup aggression is related to food. Although female guerezas are typically philopatric (Harris et al. 2009), males might also defend periovulatory females against other groups to prevent between-group copulations (documented once in Kenya: Fashing 2001a; one case confirmed for the Kibale study population using genetic paternity analysis: T. R. Harris, unpublished data). Because infanticide has also been observed during an intergroup encounter in this study population (Harris & Monfort 2003), males might also defend infants during between-group contests.

The role of fighting ability in guereza intergroup contests has received little attention, but potentially important measures investigated here are relative male body size, relative number of males/group and relative group size. Although relative group size greatly influences intergroup contests in other species and female guerezas sometimes participate in intergroup aggression (Fashing 2001a), the most intense interactions between guereza groups often involve one to three males from each group, making the number of males/group and male body size potentially influential.

METHODS

Study Subjects and Site

Guerezas are medium-sized arboreal primates, found throughout east and central Africa (Oates et al. 1994). My assistants and I studied eight guereza groups with overlapping home ranges (Harris & Chapman 2007) at the Kanyawara research site in Kibale National Park, Uganda, during July 2002–November 2003 and June 2005–June 2006 (six groups for ~3 months each in 2002–2003, and four groups, including two previously studied groups, for ~5 months each in 2005–2006). We often split up into teams, following and collecting data on two groups at a time, and typically followed groups from 0800 hours to dusk. Each assistant observed a particular study group for its entire study period, and I often rotated between the two groups that were being followed at any given time. Two assistants were employed full-time during both study periods and five others collected data for shorter time periods. I personally trained and supervised all assistants and checked their data sheets against one another when an encounter involved two study groups to ensure interobserver reliability.

Study groups were small, ranging from 4 to 11 individuals (Table 1), and fully habituated. We used Fashing's (2001b) descriptions to make age/sex classifications. Field assistants monitored study group compositions in the interim between the two main study periods so that they remained identifiable across years. Adults and usually other individuals within groups were individually recognizable by all observers using facial markings, tail shape, body size and sex differences in coat coloration near the genital region.

Intergroup Encounter Data

During each group's study period, we collected data on all intergroup encounters involving the focal group. I defined intergroup encounters as occurring when two or more guereza groups were within 50 m (sensu Oates 1977; Fashing 2001a). When two groups encountered one another multiple times in a day, I used only the first encounter in analyses (sensu Fashing 2001a). If we followed two groups on a given day and the two groups encountered one another, I randomly chose one of the groups to be the 'focal group' and counted the encounter only once.

For every encounter, we recorded the identities of the groups, if known; otherwise, we recorded group compositions and identifiable characteristics. We also noted the colour of infants in each group (white infants are generally <8 weeks old; grey infants = 8–12 weeks old; black and white infants >12 weeks old but are still carried by their mothers; Oates 1977). UTM coordinates of encounter locations were taken using a Garmin eTrex Vista GPS unit. If groups were close (<15 m apart), I used the initial location where the two groups met; otherwise, I used the location of the approached group.

We also recorded the highest aggression level that occurred (none = no aggression; mild = visual or vocal threats; high = chasing or lunging), the individuals that initiated and participated in high-level aggression, and whether either group won (i.e. displaced the other group (cf. Fashing 2001a), or caused the other group to move from a stationary position or to change direction of