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Male monkeys fight in between-group conflicts as protective parents and reluctant recruits

T. Jean M. Arseneau [a, b, *], Anouk-Lisa Taucher [a, b], Carel P. van Schaik [a], Erik P. Willems [a, b]

[a] Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland
[b] Inkawu Vervet Project, Mawana Game Reserve, KwaZulu-Natal, South Africa

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In many social species, group members cooperate to defend a communal home range. Fighting in between-group conflicts carries an opportunity cost, a risk of injury or death, and the possibility of exploitation by free-riding group members. As a result, it is rare that all group members fight in a given between-group conflict, and individual participation in range defence is often highly variable. Thus, to understand the patterns of behaviour observed at the group level, we must first understand the causes of within- and between-individual variability. Although sex differences have been well studied, our understanding of the relative importance of the various mechanisms promoting between-group aggression within a sex is limited. We observed the participation of 22 male vervet monkeys, *Chlorocebus aethiops pygerythrus*, in 126 between-group conflicts, and then partitioned aggressive acts according to the context in which they occurred. Using this approach, we found evidence that two mechanisms drive male between-group aggression and, therefore, that individual variability is in part driven by the multiple selective benefits of participation. First, males that were likely to have sired offspring tended to exhibit defensive aggression and were more active when infants were present in the group, suggesting they fight to defend probable offspring. Second, males were more likely to support females in initiating between-group aggression just prior to, and during, the mating season. Female vervet monkeys are able to exert female choice, and males that frequently supported female instigators tended to enjoy the highest mating success. These results indicate that males probably use between-group aggression to improve their reputation with choosy females and subsequently maximize their mating success. Our findings indicate that a greater understanding of the evolutionary mechanisms promoting cooperative home range defence can be gained if we consider the context in which acts of between-group aggression occur.

In a diverse array of social species, group members cooperate during between-group (BG) conflicts to defend access to space, mating opportunities, offspring or limiting resources such as food, water and shelter (Boydston, Morelli, & Holekamp, 2001; Hölldobler, 1981; Manson et al., 1991; Mares, Young, & Clutton-Brock, 2012; Mosser & Packer, 2009; Wrangham, 1980). Fighting in BG conflicts is costly because participation carries an opportunity cost, a risk of injury or death, and a risk of being exploited by free-riding group members (Nunn & Lewis, 2001). Home range defence creates a public good, where all group members benefit from the access to defended resources regardless of whether they contributed to range defence or not. Because individuals that do not participate in home range defence gain the greatest net benefits, selection favours a cheating strategy, and home range defence suffers from a collective action problem (Nunn & Lewis, 2001; Olson, 1965; Willems, Hellriegel, & van Schaik, 2013). This problem is avoided when group members are highly related and therefore can gain indirect fitness benefits from cooperating with group members (Nunn & Lewis, 2001), as in cooperative breeders and eusocial insects. However, even in species in which participation in BG conflicts appears to be collective, individual participation is often highly variable and it is rare that all group members are active (Bonanni, Valsecchi, & Natoli, 2010; Boydston et al., 2001; Carlson, 1986; Heinsohn & Packer, 1995; Kitchen, 2006; Nunn & Deaner, 2004; Zhao & Tan, 2011). Thus, it is often the case that BG aggression is not truly a collective action involving all members of a social group, but is rather a 'joint action' by a subset of individuals (Willems & van Schaik, 2015). When action is joint, we should not

* Correspondence: T. J. M. Arseneau, Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, Zurich 8057, Switzerland.
E-mail address: thelmajeanmarie.arseneau@uzh.ch (T. JeanM. Arseneau).

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regard social groups as monolithic units, but instead as complex systems composed of selfish entities (Arrow, McGrath, & Berdahl, 2000). The patterns of cooperative behaviour observed at the group level are an emergent property, which arise because of the individual benefits gained through participation and the social incentives exchanged among group members.

Individual benefits are gained in the process of producing the public good; conversely, social incentives are benefits that are bestowed on cooperative individuals by their fellow group members (Fig. 1). Cooperative individuals may gain individual benefits when they have priority of access to the public good or when group members are close kin. In the context of BG conflicts, high-ranking individuals may gain asymmetric benefits and therefore be more likely to participate than other group members (S. A. Altmann, 1962). Participants may gain inclusive fitness benefits via kin selection (Hamilton, 1964), or BG aggression may serve to protect close relatives. Social incentives can be used to directly coerce group members into cooperating, or cooperative individuals may benefit indirectly by improving their reputation with group members (Alexander, 1987; Glowacki & Wrangham, 2013; Zahavi, 1975). Two potential reputation mechanisms are social prestige and image score, and BG aggression may be used to build reputation with potential coalition partners or potential mates. For the latter to be feasible, females must be able to exert female choice such that males compete with each other to impress choosy females; this may be the case in multimale groups, or when females are able to transfer between groups in order to access preferred males. In the case of social prestige, participation in BG conflicts functions as an honest and costly signal of genetic quality (Zahavi, 1975). Alternatively, reputation based on image score assumes only that participation in BG conflicts makes the participant a more valued group member (Alexander, 1987; Nowak & Sigmund, 2005). Determining the relative importance of these various individual benefits and social incentives in driving participation in BG conflicts will provide new insights into a major question in behavioural ecology: given the selective benefits of cheating, how could cooperation evolve, and how is it maintained?

In this paper, we focus on identifying the mechanisms driving male participation in BG conflicts in wild vervet monkeys, *Chlorocebus aethiops pygerythrus*. Vervet monkeys live in multimale multifemale groups and members of both sexes are active in BG conflicts. Although females are smaller than males, both sexes can initiate BG aggression and, in rare cases, physically attack members of opposing groups. Vervet monkeys are a highly suitable species for investigating individual variability in BG aggression as usually only a handful of group members are active in a given BG conflict, and participation is highly variable both within and between individuals. Male BG aggression is particularly interesting because males may gain a variety of selective benefits from it (Fashing, 2001). Males are the dispersing sex in vervet monkeys, and, as a result, kinship benefits are more likely through parental care than kin selection (Fig. 1). Although offspring defence has primarily been seen in species that exhibit infanticide (Grinnell, Packer, & Pusey, 1995; Kitchen, 2004), BG conflicts can result in infant mortality in this species (Cheney & Seyfarth, 1987), which indicates that offspring defence could provide fitness benefits to males. Because male fitness is limited by access to receptive females (Trivers, 1972), and male vervet monkeys often try to prevent immigration of other males, mate defence may be an important individual benefit (Cheney, 1981). If so, then males with priority of access to mating opportunities (e.g. high-ranking males) should be more likely to exhibit BG aggression (Cooper, Aureli, & Singh, 2004; Kitchen, 2004). If males, in defending mates, also end up defending food resources as a by-product, they are said to act as 'Hired Guns' (Fashing, 2001; Wrangham & Rubenstein, 1986). Males may also directly defend food resources to increase the reproductive output of their mates (Williams, Oehlert, Carlis, & Pusey, 2004), a potentially beneficial strategy since resource availability has been linked to infant survival in vervet monkeys (Cheney & Seyfarth, 1987; Lee & Hauser, 1998). Alternatively, males may use BG aggression to enhance their reputation with choosy females, and subsequently increase their mating success. Moderate sexual dimorphism, female choice (Struhsaker, 1967) and the presence of multiple males in a group indicate that there is the potential for reputation effects

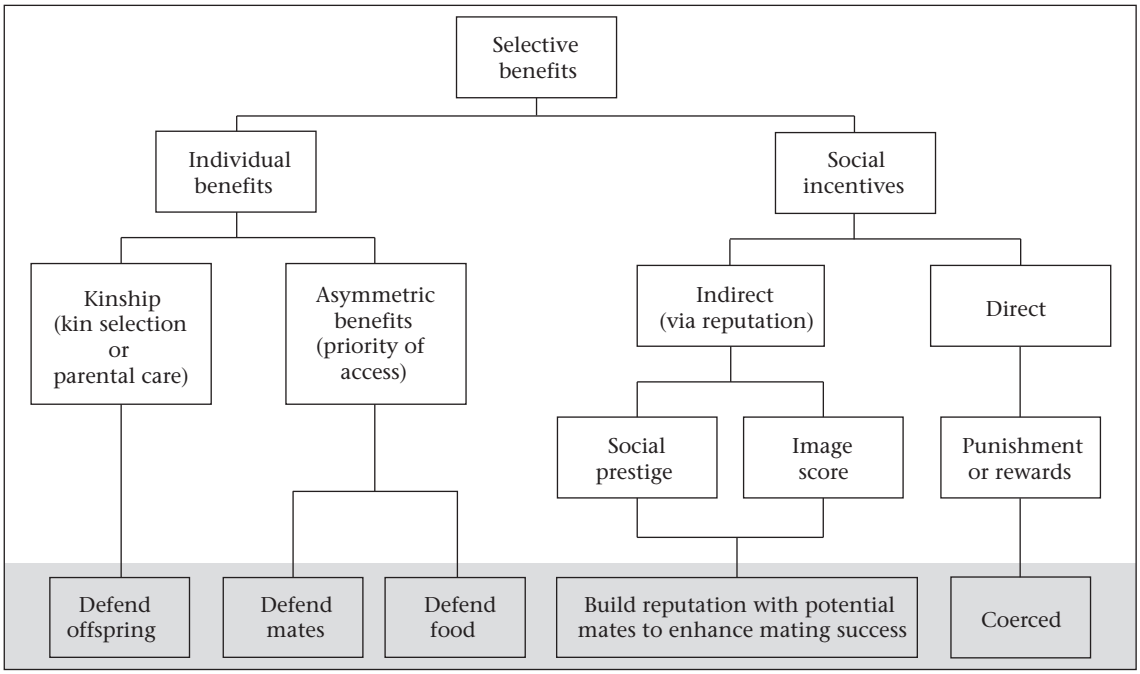

Figure 1. Potential selective benefits of cooperation in a social group (white background) (adapted from Bshary & Bergmüller, 2008; Fashing, 2001; Nunn & Lewis, 2001) and associated reasons for male vervet monkeys' participation in between-group conflicts (grey background).