



Intra- and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys



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ARTICLE INFO

Article history:

Received 27 May 2016

Initial acceptance 24 June 2016

Final acceptance 6 October 2016

MS. number: 16-00474R

Keywords:

collective action
group level cooperation
intergroup competition
intergroup conflict
intergroup dominance
perceived risk
primate
priority of access
resource defence
risk aversion

In social species, fighting in intergroup conflicts is one of the riskiest cooperative activities group members engage in, particularly for individuals of the smaller sex. In a number of species, female group members are significantly smaller than males, so the costs associated with intergroup aggression outweigh the potential benefits and females avoid participating. Studies conducted on species in which females are active participants have consistently found that they fight to defend access to food resources and that high-ranking females tend to be more active than low-rankers. However, additional factors may modulate the costs and benefits of participation, creating differences between individuals and variability within individuals over time. In this study, we investigated costs and benefits that potentially affect female vervet monkey, *Chlorocebus aethiops pygerythrus*, participation in intergroup conflicts. We observed the participation of 35 females in three groups, during 115 intergroup conflicts. Our findings suggest that female vervet monkeys defend access to valuable food resources, as well as to areas that are intensely used in the long term; however, rank also influenced female participation indicating that the potential benefits gained from resource defence vary with one's priority of access to these resources. We found that females were more likely to participate aggressively when they did not have an infant, and when they received more male support throughout the intergroup conflict, suggesting these factors influence the perceived risk, or costs, of intergroup aggression. Because we observed considerable temporal variability in both the proportion of female group members with infants and the number and identity of male group members (i.e. amount of male support provided), the relative fighting ability of neighbouring groups will inevitably fluctuate. Thus, our findings may help explain the lack of stable intergroup dominance relationships observed in many studies of intergroup conflict.

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Intergroup conflicts are one of the riskiest cooperative acts in which social groups engage as they can potentially result in the injury or even death of participants (Cant, Otali, & Mwanguhya, 2002; Cheney & Seyfarth, 1987; Fashing, 2001; Goodall, 1986; Hölldobler & Lumsden, 1980; Mech, 1994; Mills, 1983; Mosser & Packer, 2009). Even when the risk of injury is relatively low, intergroup conflicts can last for long periods and involve vigorous activities such as long chases (Sillero-Zubiri & Macdonald, 1998; Sorato, Gullett, Creasey, Griffith, & Russell, 2015; Wich & Sterck, 2007) and impose significant opportunity costs on participants (Mares, Young, & Clutton-Brock, 2012). Individual group members must each weigh these costs against potential benefits and decide whether to participate or defect from cooperative intergroup

aggression. Because male fitness is primarily limited by access to receptive females (Trivers, 1972), it is thought that males mainly participate in intergroup conflicts to defend access to mates (Cooper, Aureli, & Singh, 2004; Fashing, 2001; Kitchen & Cheney, 2004; Koch, Signer, Kappeler, & Fichtel, 2016; Majolo, Ventura, & Koyama, 2005; Payne, Lawes, & Henzi, 2003; Zhao & Tan, 2010). Conversely, female fitness is most limited by access to the resources required to produce and raise offspring (Trivers, 1972) and, therefore, females are thought to participate in intergroup conflicts to defend access to resources such as territory, food, shelter and/or water (Boydston, Morelli, & Holekamp, 2001; Kinnaird, 1992; Nunn & Deaner, 2004; Zhao & Tan, 2010). A number of other factors probably modify these basic costs and benefits; however, few studies have specifically investigated how females decide whether to defect or participate in intergroup conflicts (Reviewed in Kitchen & Beehner, 2007). In a number of social species, females are significantly smaller than males, making the risk of being injured

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during intergroup conflicts so great that they may not participate at all (Willems, Hellriegel, & van Schaik, 2013). Female motivations for intergroup aggression are thus often not expressed and cannot be studied. Even in species in which females do participate in intergroup conflicts, they are often less active than males (reviewed in Cheney, 1987; Koch et al., 2016), making it difficult to obtain the data necessary to effectively examine the factors that influence intra- and interindividual variability in participation.

Although there is a risk of injury when two groups fight over contested resources, the level of risk may differ between groups and between individual group members, and may depend on the behaviour of both fellow and opposing group members. An individual's reproductive status, age, size and fighting ability relative to the participants from the opposing group can all affect how risky an intergroup conflict is perceived to be (Kitchen & Beehner, 2007). For females, the level of sexual dimorphism and their reproductive status are likely to have a significant influence on risk perception. In species in which sexual dimorphism exists, but is moderate enough that females are willing to participate in intergroup conflicts, females may perceive the risk of injury to be higher if males from the opposing group are likely to participate aggressively. Mothers have invested significant time and resources into each of their offspring, and infants are particularly vulnerable group members (Arseneau, Taucher, Van Schaik, & Willems, 2015; Cheney & Seyfarth, 1987; Hrdy, 1974; Packer & Pusey, 1983); thus, mothers could be expected to be risk averse during intergroup conflicts (van Schaik, 1996).

In social species, competitive ability is typically thought to be a product of group size (Cheney, 1987; Mosser & Packer, 2009; Williams, Oehlert, Carlis, & Pusey, 2004) and, therefore, individuals in numerically inferior groups may be at a greater risk of injury (Hölldobler, 1981; Mosser & Packer, 2009; Sillero-Zubiri & Macdonald, 1998). However, whenever cooperative intergroup aggression is not a collective but a joint action by a subset of group members only (Willems, Arseneau, Schleuning, & van Schaik, 2015), the relative number of active participants, rather than relative total group size, may determine the outcome of intergroup conflicts (Zhao & Tan, 2010) and the perceived risk of intergroup aggression. Furthermore, the identity of active group members may also influence individual decisions, with larger or more experienced fighters being more valued allies (Cassidy, MacNulty, Stahler, Smith, & Mech, 2015). For example, it is possible that for females, having support from larger male group members may mitigate the perceived risk of participation in intergroup conflicts. Individuals may thus make instantaneous participation decisions based on the current activity of group members.

Females are predicted to fight in intergroup conflicts for access to limiting resources when these are patchily distributed so as to be defensible (van Schaik, 1989; Sterck, Watts, & van Schaik, 1997; Wrangham, 1980). However, when females reside in a stable home range, areas that consistently produce defensible resource may also be valuable and females may defend these spaces, even when current resource availability is low. How females value space and food is likely to vary from species to species, depending on their diets, their local habitat and the intensity of intergroup competition. The benefits gained from defending contested resources may also vary between individual group members, with high-ranking females, who have priority of access, experiencing the greatest incentive to participate in intergroup conflicts (Nunn & Deaner, 2004; Payne et al., 2003; van Schaik, 1989).

In this study, we investigated the costs and benefits of female intergroup aggression in vervet monkeys, *Chlorocebus aethiops pygerythrus*. Vervet monkeys live in multimale, multifemale groups and, although females are smaller than males, the level of sexual dimorphism is modest enough that females are willing to participate aggressively during intergroup conflicts (Cheney,

1981). Females fight with and without male support, and can even physically attack members of opposing groups (Cheney & Seyfarth, 1987). Although females direct intergroup aggression towards both males and females (Cheney, 1981), their tendency to form a coalition when attacking males during intragroup conflicts (Arseneau-Robar et al., 2016) suggests that targeting males carries a relatively high risk of injury if the male retaliates. Therefore, the support of group members, in particular larger male group members, may mitigate the perceived risk of participation in intergroup conflicts. Vervet monkeys are a particularly suitable species for investigating intra- and interindividual variability in participation, as usually only a handful of group members are active in a given intergroup conflict, individual participation is highly variable and larger groups are not guaranteed to win (Arseneau et al., 2015; Willems et al., 2015). As a result, individual decisions to defect or participate may have real consequences for the outcome of intergroup conflicts, subsequent resource access and potentially the fitness of group members (Cheney & Seyfarth, 1987; Lee & Hauser, 1998).

The goal of this study was to examine the factors that influence female participation in intergroup conflicts, and thereby gain a better understanding of the costs and benefits of participation versus defection from cooperative intergroup aggression. We considered three factors that could potentially modulate the risk of injury, and thus the costs, associated with intergroup aggression: female reproductive status, relative group size and the amount of male support. We hypothesized that females with vulnerable infants would be more averse to the risks posed by intergroup conflicts and, therefore, we expected that these mothers would avoid participating in intergroup aggression. We also expected that having support from male group members would mitigate the perceived risk of injury and, therefore, that females would be more likely to participate when they had greater support from their larger male group members. Because individual participation is highly variable and only a handful of group members typically participate in a given intergroup conflict, we did not expect relative total group size to have a strong effect on the perceived risk of intergroup conflicts, and therefore we predicted this variable would have a minimal impact on the likelihood of females exhibiting intergroup aggression. Given the prevalence of evidence for female food defence in the literature (reviewed in Kitchen & Beehner, 2007), we predicted that females would be more likely to participate in intergroup conflicts that occurred in the season when, and in areas of their home range where, food availability was greatest. However, because females are the philopatric sex, it is also possible that the long-term value of the intergroup conflict location (i.e. areas that are consistently used at a high intensity) could influence female participation. We further predicted that high-ranking females, who have priority of access to food resources and therefore receive a disproportionate amount of the benefits of cooperative intergroup aggression, would be more likely to participate in intergroup conflicts.

METHODS

Study Site, Subjects and Data Collection

Data were collected on three habituated groups of vervet monkeys at the Mawana Game Reserve (28°00'S, 31°12'E), KwaZulu-Natal, South Africa, between January 2012 and February 2014. Three seasons are important in this species/population: the birth season, the summer season and the mating season (Arseneau et al., 2015). The birth season was indexed by the number of dependent infants (less than 3 months old) in the group; the first birth typically occurred in early October and the number of infants in the group peaked in late November to early December. Seasonal

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