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Factors influencing individual participation during intergroup interactions in mountain gorillas

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In group-living species, encounters with extragroup rivals can be one of the riskiest actions in which individuals participate. Different group members often have different incentives to participate during intergroup interactions, and individuals with fewer payoffs of competition, including those of the smaller sex and/or lower rank, may 'free-ride' to avoid the costs of conflict. However, there is little evidence for how different types of intergroup interactions (e.g. interactions that do not involve conflict) can influence the participation of individuals. We examined the ecological, demographic and social predictors of individual participation in interactions between 14 fully habituated mountain gorilla groups in Volcanoes National Park, Rwanda from 2003 to 2015. The probability of an individual participating decreased with group size but remained relatively high in aggressive interactions and in multimale groups, illustrating the potential for 'load lightening' among group members. Males with fewer mating opportunities participated less often than males with more mating opportunities; however, male participation was significantly higher than female participation across all types of intergroup interactions. Females were more likely to be involved in aggressive interactions with solitary males, possibly to avoid the potential cost of infanticide if a resident male is killed or injured. Both sexes demonstrated more affiliative behaviours towards familiar groups, indicating a benefit of maintaining social relationships with familiar groups. Individuals show considerable variation in behaviour during intergroup interactions, and our results suggest that this variation is primarily driven by intergroup familiarity and individual reproductive benefits, both of which may have long-term consequences for individual fitness.

In group-living species, individuals regularly engage in collective intergroup aggression with conspecifics for access to fitness-limiting resources, sometimes with lethal consequences (Cheney & Seyfarth, 1987; Gros-Louis, Perry, & Manson, 2003; Mech, 1994; Radford & Fawcett, 2014; Rosenbaum, Vecellio, & Stoinski, 2016b; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006; Wrangham, 1999). Group defence can benefit all group members, but defensive actions against rivals are often performed by only a subset of group members (Elgar, 1989; Markham, Alberts, & Altmann, 2012; Nunn, 2000). Variation among individuals in their contributions to group defence can depend on different costs of effort (e.g. body size and condition) and variation in the expected gains from defeating the opponent (e.g. reproductive access, Gavrilets, 2015; Kitchen & Beehner, 2007; von Rueden, Gavrilets, & Glowacki, 2015; Willems, Arseneau, Schleuning, & van Schaik, 2015). However, intergroup interactions can be highly variable, and do not always involve aggressive competition between opponents. Thus, the patterns characterizing participation in a range of intergroup interactions remain poorly understood, perhaps because they reflect a complex integration of individual and group level strategies.

In mammals, aggression involving extragroup males is expected when reproductive access to females can be gained or defended, and female aggression is expected when access to food resources are at stake (Fashing, 2001; Trivers, 1972; Wrangham, 1980). However, variation in individual behaviour during intergroup interactions can also exist within each sex. Females may be less likely to participate in intergroup aggression if they have a dependent

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infant to avoid the risk of infanticide (Arseneau-Robar, Taucher, Schnider, van Schaik, & Willems, 2017). In addition, low-ranking males often have fewer opportunities to mate and an inferior body condition to their higher-ranking counterparts, and as a result are less frequent participants in group defence (Arseneau-Robar et al., 2017; Caillaud, Levrero, Gatti, Menard, & Raymond, 2008; Cooper, Aureli, & Singh, 2004; Langergraber, Watts, Vigilant, & Mitani, 2017; Mares, Young, Levesque, Harrison, & Clutton-Brock, 2011; Robbins, 1999). Moreover, in many sexually dimorphic species, participation in intergroup conflict by the larger sex can often suppress participation by the smaller sex (Willems, Hellriegel, & van Schaik, 2013). By investigating the factors that influence individuals to participate during intergroup interactions, we can better understand the causes of variation in intergroup interactions.

When group members have different costs and benefits of intergroup interactions, individuals may 'free-ride' and reap the benefits of group defence without actively incurring the costs of intergroup aggression (Nunn, 2000; van Schaik, 1996). Empirical evidence finds that participation by all group members in large groups is unlikely, because the large division of resources can result in a decrease in individual effort, and potentially compromise aggregate group effort resulting in a collective action problem (Gavrilets, 2015; Willems et al., 2013). Aggressive intergroup interactions therefore illustrate a typical example of the collective action problem, whereby the interests of different group members are not aligned (Olson, 1965), and the individuals participating in an interaction are often those with the largest benefits of competition. However, a reduction in individual effort does not necessarily result in ineffective collective action, as individuals in large groups may be more likely to participate when there are long-term payoffs of remaining within a competitive social group (i.e. via 'group augmentation,' Langergraber et al., 2017). Moreover, participants in large groups may be driven to maximize the group's aggregate effort in order to increase the survival or female fecundity of group members at lower cost to individuals than in smaller groups (i.e. via 'load lightening,' Meade, Nam, Beckerman, & Hatchwell, 2010).

Although the causes of variation in individual participation during intergroup conflict have been described in a number of primate studies (e.g. reviewed in Kitchen & Beehner, 2007), the dynamics of individual participation under different types of intergroup interaction are not well understood. Groups are thought to fight in order to learn more about each other (i.e. in terms of relative size and mating opportunities), and more frequent interactions with extragroup conspecifics may therefore reduce intergroup aggression (Maynard Smith, 1974). The 'dear enemy' effect implies that interactions between unfamiliar groups cost more than interactions between familiar groups (Getty, 1987; Temeles, 1994), and familiar groups may even intermingle and interact affiliatively (French, Schaffner, Shepherd, & Miller, 1995; Furuichi, 2011; Reichard & Sommer, 1997; Siracusa et al., 2017; Wich & Sterck, 2007). Moreover, related extragroup males may be more tolerant towards each other than unrelated males (Bradley, Doran-Sheehy, Lukas, Boesch, & Vigilant, 2004; Doran-Sheehy, Greer, Mongo, & Schwindt, 2004; Greenway, 2015), which suggests that kin-selected behaviours may account for some variation in behaviour during intergroup interactions. Relatively few empirical studies have addressed the factors influencing affiliative behaviours during intergroup interactions, despite the regular occurrence of peaceful interactions in some species/populations (e.g. Bradley et al., 2004; Cheney, 1987; Furuichi, 2011).

To better understand the variation in costs and benefits of participation for individuals during intergroup interactions, we investigated the factors influencing participation during different types of intergroup interactions in mountain gorillas, *Gorilla beringei beringei*. Mountain gorillas live in groups of from two to more than 40 adults (Gray et al., 2013; Robbins, 1995), and for several reasons are an interesting species to test factors influencing individual participation. First, males are larger and dominant over females (Fleagle, 1988; Plavcan, 2012) and tend to be the main participants in intergroup aggression (Harcourt, 1978; Robbins & Sawyer, 2007; Rosenbaum, Vecellio, et al., 2016). Females may use intergroup interactions to transfer between groups, and interactions with other groups therefore have direct implications for male mating opportunities (Sicotte, 1993; Watts, 1998). However, a recent study by Rosenbaum, Hirwa, Silk, Stoinski, and Ebensperger (2016) reported several lethal attacks on intruder males between 2004 and 2013 that involved aggressive participation by every group member, including females. Thus, participation by individuals during intergroup conflict in mountain gorillas must have significant benefits beyond those pertaining to adult males; however, no research has explicitly determined these benefits of participation.

Second, the social structure of mountain gorilla groups is highly variable. Approximately 40% of mountain gorilla groups contain multiple adult males, in which case the highest-ranking silverback male has primary access to mating opportunities (Bradley et al., 2005; Stoinski et al., 2009), but individuals can live in either multimale/multifemale or single-male/multifemale groups (Gray et al., 2013, see also Table 1). A study on the mountain gorilla population in Bwindi, Uganda found that the highest-ranking silverback was less likely to participate in an intergroup interaction when secondary males were present (Robbins & Sawyer, 2007). If co-residing males are related, individuals may benefit from forming coalitions

Table 1
Composition of the 14 study groups across the study period (including adults only) from 1 Jan 2003 to 30 June 2015

	Group identity	Existence during study period	Fissioned from	Range no. of males	Range no. of females	Range in group size
1	Shinda	2003–2008	Group 5	5–8	7–11	12–17
2	Beetsme	2003–2007	Group 4	3–8	6–10	9–18
3	Pablo	2003–2015	Group 5	3–8	7–20	10–26
4	Titus	2007–2015	Beetsme	1–4	1–4	2–7
5	Bwenge	2007–2015	Beetsme	1	1–7	2–8
6	Kuryama	2007–2015	Beetsme	2–3	2–5	4–8
7	Ugenda	2008–2015	Shinda	2–3	1–7	3–10
8	Ntambara	2008–2015	Shinda	1–3	3–7	4–10
9	Inshuti	2007–2015	Shinda	1	1–4	2–5
10	Isabukuru	2007–2015	Pablo	1–2	2–8	3–10
11	Urugamba	2010–2015	Ugenda	1	2	3
12	Musilikale	2013–2015	Pablo	2–3	1–4	3–7
13	Gushimira	2013–2015	Solitary male	1	1–7	2–8
14	Mafunzo	2014–2015	Solitary male	1	2–3	3–4