Dynamics of Intergroup Relationships in Primates: Introduction to the Special Issue

Sarie Van Belle¹ · Cyril C. Grueter^{2,3} · Takeshi Furuichi⁴

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Intergroup relationships vary greatly among primate species from peaceful intermingling in some species, to the consistent defense of territorial borders in others, to ritualized signaling of resource-holding potential, aggressive stand-offs, or even lethal attacks. They form an integrative part of primate social systems and affect and are affected by male and female reproductive strategies, population density and patterns of intergroup spacing, intergroup communication systems, and dispersal regimes. This special issue is the result of a symposium entitled “Dynamics of Intergroup Relationships in Primates” that we organized during the 27th Congress of the International Primatological Society in Nairobi, Kenya in 2018. The symposium and this special issue aim to explore a broad range of perspectives on intergroup dynamics, including intergroup spacing mechanisms and territoriality, social, and ecological drivers of intergroup conflicts, individual participation in collective group defense, consequences of intergroup interactions on social dynamics, and dispersal patterns. By exploring this across the primate order, this special issue highlights the complexity and diversity of the relationships among social groups and contributes to our comprehension of the relative influences of social, ecological, and genetic factors shaping primate sociality.

Intergroup interactions in primates are behaviorally diverse and span the whole gamut from affiliative or neutral to hostile and even lethal (e.g., Grueter and White 2014; Mirville *et al.* 2018; Perry 1996; Sommer and Reichard 1997; Wilson *et al.* 2014). Intergroup conflict is a complex phenomenon involving an interaction between competitive ability, which is affected by group size, and the value of the resources at stake (e.g., mates, territories, or food). Relatedness and familiarity between groups can

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✉ Sarie Van Belle
sarievanbelle@gmail.com

¹ Department of Anthropology, University of Texas at Austin, Austin, TX, USA

² School of Human Sciences, the University of Western Australia, Perth, Australia

³ Centre for Evolutionary Biology, School of Biological Sciences, the University of Western Australia, Perth, Australia

⁴ Primate Research Institute, Kyoto University, Inuyama, Aichi, Japan

mediate aggression. All these factors concurrently influence the likelihood, escalation potential, and outcome of intergroup disputes (Cheney 1987; Kitchen and Beehner 2007). Three contributions to this special issue examine variation in the nature of intergroup encounters and their socioecological underpinnings. Cooksey *et al.* (2020) analyze data from three groups of western lowland gorillas (*Gorilla gorilla gorilla*). Their main findings are that the likelihood of intergroup interactions decreased with an increasing number of supporting males in the group and that the outcome of these interactions varied in relation to whether the opponent was another group or a solitary male. Their study confirms that mate defense is instrumental in influencing the nature of intergroup encounters in gorillas. Furuichi (2020) reviews the great ape literature and describes variation in intergroup relationships at different levels (between species, between populations, and within populations) and discusses—among other aspects—the roles males and females play in causing this variation. He emphasizes the importance of peaceful and tolerant encounters, which have not received the academic attention they deserve (*cf.* Pisor and Surbeck 2019). Hashimoto *et al.* (2020) follow on from that review and present anecdotal evidence of tolerant intergroup encounters involving female chimpanzees (*Pan troglodytes schweinfurthii*). They also review reports across subspecies and field sites on chimpanzee encounters involving females and show that those involving a party of one or few females and their offspring were more likely to be peaceful than encounters between mixed-sex or male-only parties of neighboring groups and may provide nulliparous females with opportunities to evaluate other groups for future dispersal. Research into the socioecological drivers underlying intergroup enmity and amity in primates has important implications for an understanding of the evolution of supragroup organization in humans.

The outcome of intergroup encounters can have important effects on space use. Losing intergroup encounters may result in subsequent further or faster travels or in temporal or permanent loss of access to areas surrounding the encounter location (Crofoot 2013; Markham *et al.* 2012). Such costs, in addition to the risk of physical injuries during intergroup encounters, might lead groups to underuse areas in their home range that overlap with neighboring groups as a strategy to avoid encounters (Wrangham *et al.* 2007). Other strategies may include confronting rivals when the expected benefits of winning the contest outweigh the costs of losing. Thus, prior to intergroup encounters, groups may use vocal or olfactory cues to obtain information about the current or recent location of neighboring groups and use such information to decide to approach, retreat, or ignore neighbors. Such intergroup spacing mechanisms can result in long-term stable home ranges among adjacent groups. In this special issue, four contributions examine the impact of intergroup relationships on long-term spatial use, as well as movement patterns prior to intergroup encounters. Bonadonna *et al.* (2020) analyze home range and core area stability of three contiguous groups of indris (*Indri indri*). Over the 5-year study, home ranges were mostly stable, yet shifts in the home range location of one group caused corresponding shifts in a neighboring group in order to maintain spatial exclusivity of their defended territories. Tórrez-Herrera *et al.* (2020) examine whether white-faced capuchins (*Cebus capucinus*) alter their behaviors at the periphery of their home ranges, areas that are underused potentially because of the costs and risks associated with intergroup encounters. They found that capuchins did not adjust their foraging behavior as predicted. Instead, they visited *Attalea butyracea* trees at the periphery of their ranges for longer, ate more fruits, and

depleted these trees more fully than trees in the central area of the home range, suggesting that foraging benefits outweighed the potential costs and perceived risks of intergroup encounters. Van Belle and Estrada (2020) found that black howler monkey (*Alouatta pigra*) groups encountered neighboring groups more often than would be expected by chance, and that they were more likely to move toward recent calls of nearby but out-of-sight neighboring groups, particularly when fruits were scarce, suggesting that they were more willing to confront their opponents when important resources were limited. Similarly, Brown (2020) studies the movement responses of individual gray-cheeked mangabeys (*Lophocebus albigena*) to natural or simulated loud calls of out-of-sight neighboring groups. Males approached more frequently than females, yet all individuals tended to retreat when the neighbors were close by (<500 m).

The initiation of an intergroup contest, the level of aggression during the contest, and the contest outcome is mediated by asymmetries between rival groups in their fighting abilities (i.e., resource-holding potential) and the expected payoffs if they were to win the encounter (Arnott and Elwood 2009; Maynard Smith 1974; Parker 1974). The difference in group size is commonly used as a proxy for asymmetries in groups' competitive abilities, yet the number of participants or the fighting ability of particular group members may be a better predictor of intergroup encounter aggression (Harris 2010; Van Belle and Scarry 2015; Zhao and Tan 2011; for a human example see Grueter *et al.* 2016). Participative behaviors of group members may vary across age, sex, social status, and dominance rank, and according to the expected payoffs of winning the contest (Arseneau-Robar *et al.* 2017; Crofoot *et al.* 2008; Fashing 2001; Van Belle *et al.* 2014). Furthermore, natural selection should favor individuals that refrain from participating in intergroup encounters and therefore incur no costs, yet reap the benefits of the defensive actions by other group members, known as the "collective action problem" (Nunn 2000; Nunn and Lewis 2001). In this special issue, Majolo *et al.* (2020) examine these effects by comparing the findings from 52 studies on 31 primate species. They found that larger groups are more likely to win encounters against smaller groups, but found no effects of age, dominance rank, and sex of individuals on the level of aggressive behaviors individuals displayed. They suggest that the lack of support for the effects of these individual traits may be due to differences in species-specific strategies employed by different group members. Indeed, their analyses show that some species showed positive while others showed negative impacts of sex on frequency of aggressive participation in intergroup encounters. Brown's (2020) study on gray-cheeked mangabeys' movement responses to loud calls of neighboring groups shows that males and females in smaller groups were more likely to move away, while individuals in larger groups both approached and retreated, consistent with the hypothesis that numerical superiority evokes higher group-level resource-holding potential (Kitchen and Beehner 2007). In contrast, Lewis *et al.* (2020) show that, in Verreaux's sifakas (*Propithecus verreauxi*), larger groups were not more likely to supplant smaller groups. Tendencies to participate largely differed by sex, with males being the primary participants, likely representing defense of mating opportunities with resident females. Females more likely participated in encounters during the lactation season when food resources were scarce.

Intergroup conflict (or intergroup competition more generally) can bring about behavioral consequences in group members, which unfold over the short and long

term. Some of these consequences include changes in group cohesion and social relationships, which can have significant fitness consequences (Lemoine *et al.* 2020; Majolo *et al.* 2016). The link between intergroup conflict and intragroup affiliation in primates was first explicitly explored by Cheney (1992) but then research on this topic remained dormant until a surge of interest in recent years, which was at least partly motivated by work in the human behavioral sciences (Puurinen and Mappes 2009; Rusch 2014; Sherif *et al.* 1961). The available evidence for an effect of intergroup conflict on intragroup cohesion in primates is mixed (e.g., Grueter 2013; Majolo *et al.* 2016); disagreement in the literature indicates that various modulating factors may be at play such as the social system, conflict characteristics and conflict outcome, and familiarity between opposing groups (for a review see Radford *et al.* 2016). Three articles in this special issue examine this topic: Samuni *et al.* (2020) collected data on two communities of chimpanzees (*Pan troglodytes verus*), and show associations between border patrols and intergroup encounters and several measures of in-group cohesion, i.e., modularity, party size, and intragroup aggression. Yi *et al.* (2020) examine behavioral responses to intergroup aggression in territorial, pair-living Javan gibbons (*Hylobates moloch*) and found changes in activity budgets and sleeping tree locations; contrary to their prediction, pairs groomed less in the hour post-encounter than in the matched-control period. Mirville *et al.* (2020) compare the proximity patterns, activity budgets, and affiliative behavior of mountain gorilla (*Gorilla beringei beringei*) group members before and after aggressive intergroup interactions. Their results show that responses are not that clear-cut but modulated by familiarity, conflict outcome, and sex. These articles enhance our understanding of the interplay between intergroup conflict and intragroup behavioral consequences and will undoubtedly stimulate further empirical research in this space.

Dispersal regimes, particularly transfer between neighboring groups, can influence intergroup relationships, as familiarity and relatedness between groups may mediate aggression (Bradley *et al.* 2004; Cooksey *et al.* 2020). Additionally, intergroup encounters may provide opportunities to individuals of the dispersing sex to gain information about potential dispersal opportunities (Hashimoto *et al.* 2020), or transfer may occur only during intergroup encounters (Furuichi 2020; Sicotte 1993). Two contributions to this issue deal with genetic and behavioral correlates of intergroup transfer of females in a wild bonobo (*Pan paniscus*) population. Ishizuka *et al.* (2020) examine the proportion of transfers of females from their natal group to a neighboring group by both observational and genetic analyses. Their findings indicate that around 60% of females transfer to a neighboring group and settle there to reproduce, suggesting that female bonobos do not disperse far from their natal groups because they usually transfer between groups during peaceful intergroup encounters. Toda and Furuichi (2020) examine aggression from resident females toward immigrant females, and show that the rate of aggression against immigrant females was low and decreased with age in resident females, probably because older females are higher in dominance rank and suffer from little food competition with immigrant females. These tendencies of transfer to neighboring groups during peaceful encounter and social tolerance of resident females to immigrant females may explain the fact that female bonobos leave their natal group at a younger age than do female chimpanzees (Sakamaki *et al.* 2015).

The contributions to this special issue and relevant citations therein demonstrate the complexity of intergroup relationships in primates, and the variation among species,

among populations of the same species, among pairs of groups within a population, and within pairs of groups over time. With this special issue, we emphasize the great variety of aspects associated with intergroup relationships that may be studied. We end with a series of research questions that we deem critical to the study of dynamics of intergroup relationships in primates:

1. What are the immediate, short-term, and long-term benefits or costs of winning or losing intergroup encounters? What demographic, social, physiological, and ecological factors underlie these costs and benefits?
2. What are the selective incentives for tolerant and cooperative interactions between individuals residing in different groups (e.g., reconnaissance before transfer, extragroup mating, and enhanced food procurement)? How does intergroup tolerance vary in relation to characteristics of and relationships between the interactants and socioecological circumstances?
3. How do individuals differ in their post-intergroup conflict behavioral response, and how are differences affected by individual contribution to conflict, opponent identity, and resources at stake?
4. How do group members overcome collective action problems during intergroup defense? Which mechanisms underlie individuals' participation patterns (e.g., kin selection, byproduct mutualism, punishment), and how do these mechanisms differ with social systems?
5. Can measurements of relative group-level resource-holding potential that reflect the number of participants, the amount each participates, or participants' fighting abilities better predict the initiation of intergroup contests, the level of aggression during contest, or contest outcome than does relative group size, a commonly used proxy for group-level competitive ability?
6. Do loud calls that are hypothesized to play a role in intergroup communication mediate movement decisions of listening groups and thus impact intergroup spacing mechanisms?
7. How do intergroup conflicts influence large-scale patterns of space partitioning between groups within a habitat? Do gradual or abrupt shifts in a group's home range cause corresponding shifts in neighboring groups? Does this effect differ between territorial and nonterritorial primate species?

Answering these questions across many primate species will move forward the field of primate behavioral ecology by considering the relationships between neighboring social groups as a core component of the social structure in describing primate species' social systems (*sensu* Kappeler 2019).

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