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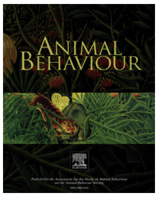

Social and genetic factors mediating male participation in collective group defence in black howler monkeys

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Cooperative group defence can provide benefits both to participants in the collective actions and to free-riding group members. The study of individual strategies used during collective action is thus useful for our understanding the nature and evolution of cooperation in animal societies. Here, we examine social and genetic factors influencing the participation of adult and subadult males in naturally occurring howling bouts of five multimale-multifemale groups of black howler monkeys, *Alouatta pigra*, at Palenque National Park, Mexico during a 28-month study. Among howler monkeys, howling bouts are often used in the context of intergroup spacing as a form of cooperative group defence. For howling bouts in which all resident males were in view at least 80% of the time ($N = 387$ bouts), we calculated the percentage of time that each male participated and the percentage of time that each intragroup male–male dyad participated mutually. Male participation was significantly greater during howling bouts that were part of intergroup encounters compared to spontaneous calls or calls in response to nearby calls when there was no visual contact with rival groups. Adult males initiated and participated during howling bouts significantly more than subadult males. Among adult males, those that had sired offspring in the group initiated and participated significantly more than males without offspring in the group. Kinship and proximity patterns among pairs of males did not influence the percentage of time that those dyads howled mutually. Together, these findings suggest that cooperative group defence in male black howler monkeys evolved principally through mutualism in which participants gain direct fitness benefits.

Group living requires that individuals form predictable social relationships, share common resources and develop cooperative alliances to defend resources against other groups (Nunn, 2000; Sussman & Garber, 2011; van Schaik, 1983). Behaviours associated with group defence, such as fighting, vocalizing and vigilance, performed by a single individual may provide advantages to both the actor and other group members when the benefits cannot be monopolized (Nunn, 2000). Thus, cooperation might be threatened by the presence of ‘free-riders’, which reap the benefits of successful group action but incur no (or limited) costs by not joining in these actions (Nunn, 2000; Nunn & Lewis, 2001). The collective action framework examines group members' motivation to contribute to collective action by analysing cost–benefit trade–offs to individuals based on factors such as sex, age, social status, physical condition, reproductive success and the number and actions of alliance partners (Kitchen & Beehner, 2007; Nunn & Lewis, 2001).

Given that cooperation during intergroup conflicts is commonly observed in group-living animals (e.g. spotted hyaenas, *Crocuta crocuta*: Boydston, Morelli, & Holekamp, 2001; brown jays, *Cyanocorox morio*: Hale, Williams, & Rabenold, 2003; white-faced capuchin monkeys, *Cebus capucinus*: Crofoot & Gilby, 2012; Meunier, Molina-Vila, & Perry, 2012; meerkats, *Suricata suricatta*: Mares, Young, & Clutton-Brock, 2012), collective action problems clearly can be overcome, despite the potential for free-riding individuals (Nunn & Lewis, 2001). This is particularly true when collective benefits are unevenly distributed among group members, with participants benefiting more than nonparticipants. In this regard, higher-ranking individuals, which are likely to accrue the greatest benefits (through their priority of access to contested resources such as food or mates) or to incur the lowest costs (through their better physical condition), are expected to be the most likely

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to provide group defence (Cheney, 1987; Kitchen & Beehner, 2007). Indeed, variation in participation in group defence has been explained by dominance rank (e.g. coyotes, *Canis latrans*: Gese, 2001; chacma baboons, *Papio ursinus*: Kitchen, Cheney, & Seyfarth, 2004; Japanese macaques, *Macaca fuscata*: Majolo, Ventura, & Koyama, 2005) or mating success (e.g. chacma baboons: Kitchen, Cheney, et al., 2004; chimpanzees, *Pan troglodytes*: Watts & Mitani, 2001), as well as by the costs associated with collective action (meerkats: Mares et al., 2012).

The collective action problem might also be resolved when cooperation provides benefits through kinship and gains in inclusive fitness (Nunn, 2000; Nunn & Lewis, 2001). Free riding is expected to be lower and cooperation higher among kin than among nonkin residents (Clutton-Brock, 2002; Hamilton, 1964; Nunn & Lewis, 2001). Among ringtailed lemurs, *Lemur catta*, for example, Nunn and Deaner (2004) found greater variance in female participation in aggressive intergroup encounters for one group whose resident females were less closely related compared to a second study group whose adult females were all direct descendants of the same female present in the group. However, kinship might not always influence patterns of collective actions when all actors, irrespective of kinship, receive an immediate benefit (i.e. mutualism: Dugatkin, 1997). For example, among lions, *Panthera leo*, the amount of time that pairs of males walked in parallel or glanced at one another (two behaviours that monitor the actions of companions) while approaching speakers during playback experiments simulating an intrusion of unfamiliar males was not affected by genetic relatedness (Grinnell, Packer, & Pusey, 1995). Given that a male's reproductive success is strongly correlated with his membership in a coalition that is large enough to defend females, an individual male's defection during group defence could lead to his partner(s) being wounded or killed, thus reducing his own ability to deter future intruders, suggesting that all males benefit from participating in collective group defence (Grinnell et al., 1995).

Similarly, the strength of social relationships and partner competence might be of greater importance than genetic relatedness in understanding collective actions (Chapais, 2006). For example, male chimpanzees frequently join boundary patrols with unrelated or distantly related males with whom they have frequently groomed and jointly hunted (Watts & Mitani, 2001), despite their preference to affiliate and cooperate with their maternal, but not paternal, brothers (Langergraber, Mitani, & Vigilant, 2007; Mitani, 2009). Likewise, in free-ranging packs of dogs, *Canis lupus familiaris*, individuals with a high number of affiliative partners are more likely to participate in intergroup aggression than are socially peripheral group members (Bonanni, Valsecchi, & Natoli, 2010). Individuals might gain increased benefits by cooperating with competent partners (i.e. those who refrain from defecting during group defence). Cooperation in chimpanzees and dogs then might be based on reciprocity (defined as a set of long-term social relationships in which one individual receives an immediate benefit and one individual receives an immediate cost during any single interaction, but over time, costs and benefits are relatively equal; Dugatkin, 1997) as individuals preferentially cooperate with those partners that they received support from in the recent past (Axelrod & Hamilton, 1981).

In the present study, we examine social and genetic factors that promote the contribution of individual resident males in collective group defence, through their participation in naturally occurring loud calls and intergroup encounters, in black howler monkeys, *Alouatta pigra*. Black howler monkeys live in relatively small groups of one to three adult males, one to three adult females, and their offspring (Van Belle & Estrada, 2006). They represent a valuable model from which to investigate the interplay among collective group defence, kinship, social relationships, and asymmetrical benefits among males because resident males may be either kin or nonkin (Van Belle, Estrada, Strier, & Di Fiore, 2012), and one male (the central male) is able to monopolize the majority of group reproductive opportunities despite the absence of a strict agonistic dominance hierarchy (Van Belle, Estrada, & Strier, 2008).

Howler monkeys produce loud calls (i.e. howling) either spontaneously (i.e. without a discernable external stimulus), in response to nearby calling produced by neighbouring groups or extragroup individuals with whom they have no visual contact, or during encounters (i.e. visual contact) with neighbouring groups or extragroup individuals (Van Belle, Estrada, & Garber, 2013; Whitehead, 1987). These calls appear to serve several purposes, but most frequently the defence of major feeding sites (Chiarello, 1995; Hopkins, 2013; Sekulic, 1982a; Van Belle, Estrada, & Garber, 2014; Whitehead, 1987; but see Holzmann, Agostini, & Di Bitetti, 2012). During encounters with lone males or coalitions of two or three extragroup males, however, loud calls also may function to defend resident females and infants by discouraging attempts to take over the group (Sekulic & Chivers, 1986; Van Belle, Estrada, Garber, 2014). Successful group take-overs may result in the eviction of resident males and infanticide (Crockett, 2003; Van Belle et al., 2008; Van Belle, Kulp, Thiessen-Bock, Garcia, & Estrada, 2010).

Despite the fact that all or many group members may benefit from successful group defence, adult males are the primary participants in howling bouts, although adult females, subadults and even juveniles may participate as well (Baldwin & Baldwin, 1976; Chiarello, 1995; Kitchen, 2006; Kitchen, Horwich, & James, 2004). Each male's contribution to group defence is expected to be influenced by the highly skewed mating opportunities among resident black howler males (Van Belle et al., 2008). Resident males seldom engage in agonistic or affiliative interactions with one another, and no agonistic dominance hierarchy can be discerned. Nevertheless, one resident male, referred to as the ‘central’ male, typically spends more time in close proximity to resident females, mate-guards and forms consortships with receptive females, and is chosen as the preferred mate by females, resulting in his almost exclusive access to fertile females, whereas ‘noncentral’ males have few or no mating opportunities (Van Belle, Estrada, Ziegler, & Strier, 2009). During playback experiments simulating the intrusion of unfamiliar males, Kitchen, Horwich, et al. (2004) observed that central males howled more frequently than noncentral males, as would be expected if differential benefits played an important role in male participation. In a study of naturally occurring howling bouts, however, Van Belle et al. (2008) reported that both central and noncentral males participated equally, although central males initiated more howling bouts than noncentral males.

In the study by Kitchen, Horwich, et al. (2004), participation by noncentral males ranged from seldom to frequent, and noncentral males that had longer-term associations (>5 years) with their central male were more likely to call and to approach the speakers than noncentral males that had shorter-term associations (<4 years) with their central male. Based on 10 years of demographic census data, Kitchen, Horwich, et al. (2004) assumed that at least some of these longer-term associations involved related males (father–son), while shorter-term associations presumably represented unrelated males. Although no genetic data were collected, these authors suggested that kinship, as well as the duration and strength of the social relationships among males, collectively influence individual participation in cooperative group defence. In the present study, we examine the interplay between kinship (evaluated using molecular methods) and social relationships and explore how these factors influence male participation in group defence in black howler monkeys.

Male participation in group defence through howling also might be influenced by the social context in which loud calls are produced