



Male resource defence during intergroup aggression among tufted capuchin monkeys



Clara J. Scarry ^{a, b, c, *}

^a Department of Anthropology, Miami University, Oxford, OH, U.S.A.

^b Department of Anthropology, University of Texas at Austin, Austin, TX, U.S.A.

^c Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY, U.S.A.

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In group-living species, conflicts between groups frequently involve multiple individuals participating in aggression towards the opposing group. Although defence is a collective action, individuals differ in their motivations. For males, the spatiotemporal distribution of resources should determine whether they defend food or mates. Although resource defence as a male mating strategy has been demonstrated primarily in unimale social systems, males in multimale groups generally directly defend access to females. I examined the factors affecting individual assessment of the costs and benefits of participation in aggressive intergroup encounters among tufted capuchin monkeys, *Sapajus (Cebus apella) nigritus*, at Iguazú National Park, Argentina. Through provisioning and playback experiments I show that male aggression during intergroup encounters in tufted capuchin monkeys is directly related to the presence of a high-quality food resource, whereas behaviours more consistent with direct mate defence were not apparent. Although males and females demonstrated concordant strategies, male responses were stronger than those of females, but no differences were observed between dominant and subordinate males in the presence of a defendable food resource. Resident females may be manipulating male–male competition within groups, using males as ‘hired guns’ to increase access to food resources, thereby increasing infant survivorship and decreasing interbirth intervals. In this population, intersexual conflict, which is often associated with infanticide and sexual coercion in nonhuman primates, has promoted cooperation between the sexes.

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Among group-living species, neighbouring social groups frequently compete for access to resources, and these encounters between groups can be highly aggressive (Cheney, 1987; Packer, Scheel, & Pusey, 1990), even in the absence of strict territoriality. Interactions with extragroup individuals can involve chases, threat displays and occasionally lethal attacks (Cheney, 1987; Packer et al., 1990; Watts, Muller, Amsler, Mbabazi, & Mitani, 2006). These interactions not only involve direct risks to participating individuals, but can also exhaust energy reserves and directly interfere with opportunities to rebuild these reserves (Peres, 1989). Thus, individuals are expected to assess the relative costs and benefits of the contest prior to engagement (Maynard Smith & Parker, 1976; Maynard Smith & Price, 1973), electing to participate only when successful group defence would result in a net benefit to the individual's reproductive success.

Because of sex differences in potential reproductive rates and parental investment, however, the relative benefits provided separately by food and mates differ between males and females (Clutton-Brock & Vincent, 1991; Trivers, 1972). Thus, group members may exhibit concordant (Heinsohn & Packer, 1995), divergent (Kitchen, 2004, 2006; Kitchen, Horwich, & James, 2004) or even opposing behavioural strategies (Cowlshaw, 1995; Kinnaird, 1992), depending on the context of the encounter. In general, female participation is more likely in defence of food resources, whereas males are expected to compete primarily over mating opportunities (Trivers, 1972). During intergroup encounters, male aggressive behaviour, whether directed at extragroup males or resident females, often serves directly to defend short- or long-term access to fertile females by preventing extragroup copulations (Cheney & Seyfarth, 1977; Palombit, 1994) and take-overs (Fedigan & Jack, 2004; Grinnell, Packer, & Pusey, 1995). Among species that live in multimale groups, if mating is not monopolized by a single dominant male (e.g. Janson, 1984), then reproductive opportunities lost to extragroup males potentially affect the lifetime reproductive

* Correspondence: C. J. Scarry, Department of Anthropology, 2201 Speedway C3200, University of Texas at Austin, Austin, TX 78712, U.S.A.

E-mail addresses: cscarry@gmail.com, cscarry@ic.sunysb.edu.

success of several individuals. Thus, multiple males may cooperate in defence of sexually receptive females (Cowlshaw, 1995; Grinnell et al., 1995; Perry, 1996) or in discouraging potential male immigrants (Cheney & Seyfarth, 1977). To avoid incurring the costs of participation, however, males may be tempted to free-ride upon the defensive actions of other group members, which can lead to a collective action problem (Harris, 2010; Nunn, 2000).

While the benefits of increased access to food resources generally are expected to affect male reproductive success only indirectly (Trivers, 1972), among birds and harem-living mammals, resource defence commonly serves as a male tactic to influence female mate choice (Carranza, Fernandez Llarío, & Gomendio, 1996; Emlen & Oring, 1977). Similarly, among species with multimale groups, resource defence has been proposed as a potential male strategy to gain female agonistic support during intrasexual conflict over group membership or within-group dominance (Wrangham, 1980). Because increased access to food resources can shorten female interbirth intervals (Borries, Koenig, & Winkler, 2001; Hill, Lycett, & Dunbar, 2000; Mosser & Packer, 2009; Trivers, 1972; Williams, Oehlert, Carlis, & Pusey, 2004) and increase infant and juvenile survival (Beauplé, Barbraud, Chambellant, & Guinet, 2005; Cheney & Seyfarth, 1987; Eide, Stien, Prestrud, Yoccoz, & Fuglei, 2012; Johnson, Coe, & Green, 2013; King et al., 2005; LaMontagne et al., 2013; McIntosh et al., 2013; Nichols et al., 2012; Rubenstein, 1986), male group-mates with mating access should also experience reproductive benefits of defending access to high-quality home ranges or food resources. Nevertheless, male participation in defence of food resources appears relatively uncommon within multimale groups (but see Janson, 1986; Williams et al., 2004; Crofoot, 2007; Brown, 2013), and behaviours more consistent with direct mate defence generally co-occur during aggressive encounters (e.g. Brown, 2013; Kinnaid, 1992; Mosser & Packer, 2009).

Among tufted (cf. black-capped) capuchin monkeys, *Sapajus (Cebus apella) nigritus*, at Iguazú National Park, Argentina, relative male group size is the critical factor in determining the outcome of aggressive encounters (Scarry & Tujague, 2012; Scarry, 2013), promoting increased home range exclusivity (Scarry & Tujague, 2012) and per capita resource availability (Scarry, 2013). Home range exclusivity, however, may emerge in the absence of active resource defence by resident males. Thus, in the current study, I examined the behavioural responses of male tufted capuchin monkeys during simulated intergroup encounters to identify the proximate trigger of male aggression. If capuchin males pursue a resource defence strategy, then I predicted that the presence of a neighbouring group in the vicinity of a high-quality food resource would elicit an aggressive response by resident males. Alternatively, if intergroup differences in home range quality emerge as a by-product of male mate defence, then males should respond to potential threats to current or future reproductive opportunities independently of the proximity to food resources. To prevent extragroup copulations (i.e. short-term mate defence), I predicted males would respond aggressively only when sexually receptive females were present within the group. In contrast, if male aggression functions primarily to limit future competition for mates by discouraging male transfers (i.e. long-term mate defence), then I predicted that male aggression would be directed primarily towards potential immigrant males, independently of whether sexually receptive females were present. In contrast to previous studies of nonhuman primates (e.g. Harris, 2006; Harris, 2010; Korstjens, Nijssen, & Noë, 2005; Wich & Sterck, 2007), I did not consider infant defence or infanticidal attacks as a potential explanation for aggression towards neighbouring groups, due in part to logistic constraints; no dependent infants were present during the study period as a result of strong birth seasonality (Di Bitetti & Janson, 2001a). Nevertheless this limitation is unlikely to

have affected the results. Although multiple infanticides by resident individuals have been documented (Janson, Baldovino, & Di Bitetti, 2012; Ramírez-Llorens, Di Bitetti, Baldovino, & Janson, 2008), no evidence for infanticide by extragroup males or recent immigrant males has been observed in this population to date.

I further tested the hypothesis that, for a given resource type, individuals differ in their assessment of the relative costs and benefits of participation. If resources (i.e. food or potential mates) provide disparate benefits to group members, individual differences in participation should emerge depending on within-group division of resource or the nature of the resource(s) at stake. Within-group dominance relations directly affect individual access to both food resources (Janson, 1985) and mates (Janson, 1984; Tiddi, Wheeler, & Heistermann, 2013); therefore, the payoffs for participation on individual investment are expected to be lower for subordinate males, and I predicted they would invest less in aggressive defence than dominants (i.e. be more likely to defect or participate primarily as laggards; cf. Heinsohn & Packer, 1995). Because both sexes participate during aggressive intergroup encounters (Di Bitetti, 2001b; Scarry, 2013), I also explored the degree of concordance in individual strategies between males and females. Tufted capuchin monkeys display sexual dimorphism in both body mass (Smith & Jungers, 1997) and canine tooth size (Plavcan & van Schaik, 1992), with females being significantly smaller than males ($\delta:\text{♀}$ canine length ratio = 1.41–1.42; Plavcan & van Schaik, 1992; body mass ratio = 1.45; Smith & Jungers, 1997). If females and males actively defend the same resource type (e.g. high-quality food sources), then the perceived costs of participation may be greater for females due to their increased risk of injury (e.g. Kitchen, 2006), especially for females with dependent infants (McComb, Pusey, Packer, & Grinnell, 1993); thus I predicted that females would be more likely to defect for all resource types. Furthermore, while either or both sexes could participate in encounters over access to food resources, access to reproductive females is a resource that is uniquely beneficial to males, and I would not expect that female participation is affected by the presence of other sexually receptive females.

METHODS

Study Site and Subjects

Iguazú National Park is a 60 000 ha preserve of subtropical, semideciduous forest in northeastern Argentina (for a detailed site description see Janson et al., 2012). Located near the southern limit of the Atlantic forest, the site exhibits marked seasonality in temperature with corresponding variation in the availability of fleshy fruits and arthropods (Brown & Zunino, 1990) that reaches an annual low during the austral winter (June–August; Di Bitetti, 1997). During this naturally occurring nadir in food availability, I conducted experiments with three fully habituated groups of tufted capuchin monkeys (Macuco: 27 individuals, including 5 males; Rita: 11 individuals, including 2 males; Silver: 24 individuals, including 4 males) between 2009 and 2010.

Tufted capuchin monkeys (genus *Sapajus*) are small-bodied, omnivorous primates (Brown & Zunino, 1990; Janson, 1985; Terborgh, 1983) broadly distributed throughout South America (Fragaszy, Visalberghi, & Fedigan, 2004; Lynch Alfaro et al., 2012). At Iguazú, capuchin monkeys live in multimale, multifemale groups that range in size from 5 to 44 individuals (Janson et al., 2012). Interactions between neighbouring groups are uniformly aggressive (Di Bitetti, 2001b), varying primarily in the degree of escalation (Scarry & Tujague, 2012). The outcomes of these encounters are determined by the asymmetry in male group size (Scarry, 2013), although both sexes participate in directing aggressive behaviours

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