Male resource defence during intergroup aggression among tufted capuchin monkeys

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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 engage in food or mate defense. Yet resource defense as a male mating strategy has been demonstrated primarily in uni-male social systems, while males in multi-male 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 behaviors more consistent with direct mate defense 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 – often associated with infanticide and sexual coercion in non-human primates – has promoted cooperation between the sexes.

Key words: mate defense, reproductive strategies, resource defense, collective action, large-scale field experiments

1 **Introduction**

2 Among group-living species, neighbouring social groups frequently compete for access to
3 resources, and these encounters between groups can be highly aggressive (Cheney 1987; Packer
4 et al. 1990), even in the absence of strict territoriality. Interactions with extragroup individuals
5 can involve chases, threat displays and occasionally lethal attacks (Cheney 1987; Packer et al.
6 1990; Watts et al. 2006). These interactions not only involve direct risks to participating
7 individuals, but can also exhaust energy reserves and directly interfere with opportunities to
8 rebuild these reserves (Peres 1989). Thus individuals are expected to assess the relative costs and
9 benefits of the contest prior to engagement (Maynard Smith and Price 1973; Maynard Smith and
10 Parker 1976), electing to participate only when successful group defence would result in a net
11 benefit to the individual's reproductive success.

12 Due to sex differences in potential reproductive rates and parental investment, however, the
13 relative benefits provided separately by food and mates differ between males and females
14 (Trivers 1972; Clutton-Brock and Vincent 1991). Thus group members may exhibit concordant
15 (Heinsohn and Packer 1995), divergent (Kitchen 2004; Kitchen et al. 2004; Kitchen 2006) or
16 even opposing behavioural strategies (Kinnaird 1992; Cowlshaw 1995), depending on the
17 context of the encounter. In general, female participation is more likely in defence of food
18 resources, whereas males are expected to compete primarily over mating opportunities (Trivers
19 1972). During intergroup encounters, male aggressive behaviour – whether directed at
20 extragroup males or resident females – often serves directly to defend short- or long-term access
21 to fertile females by preventing extragroup copulations (Cheney and Seyfarth 1977; Palombit
22 1994) and takeovers (Grinnell et al. 1995; Fedigan and Jack 2004). Among species that live in
23 multi-male 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 success of several individuals. Thus multiple males may cooperate in defence of sexually receptive females (Cowlishaw 1995; Grinnell et al. 1995; Perry 1996) or discouraging potential male immigrants (Cheney and 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 (Nunn 2000; Harris 2010).

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 (Emlen and Oring 1977; Carranza et al. 1996). Similarly, among species with multi-male 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 (Trivers 1972; Hill et al. 2000; Borries et al. 2001; Williams 2004; Mosser and Packer 2009) and increase infant and juvenile survival (Rubenstein 1986; Cheney and Seyfarth 1987; Beaupre et al. 2005; King et al. 2005; Eide et al. 2012; Nichols et al. 2012; Johnson et al. 2013; LaMontagne et al. 2013; McIntosh et al. 2013), 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 multi-male 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., Kinnaird 1992; Mosser and Packer 2009; Brown 2013).

Among tufted (cf. black-capped) capuchin monkeys (*Sapajus* [*Cebus apella*] *nigrinus*) at Iguazú National Park, Argentina, relative male group size is the critical factor in determining the outcome of aggressive encounters (Scarry and Tujague 2012; Scarry 2013), promoting increased home range exclusivity (Scarry and 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 are pursuing 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 male aggression would be directed primarily towards potential immigrant males, independently of whether sexually receptive females were present. In contrast to previous studies of non-human primates (e.g., Korstjens et al. 2005; Harris 2006; Wich and Sterck 2007; Harris 2010), 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 and Janson 2001a). Nevertheless this limitation is unlikely to have affected the results. Although multiple

infanticides by resident individuals have been documented (Ramírez-Llorens et al. 2008; Janson et al. 2012; B. Tiddi and C.J. Scarry unpub. data), 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 and 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 and Jungers 1997) and canine tooth size (Plavcan and van Schaik 1992), with females being significantly smaller than males (σ^7 : ϕ canine length ratio = 1.41-1.42: Plavcan and van Schaik 1992; body mass ratio = 1.45: Smith and 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 et al. 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, semi-deciduous 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 and 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 (Terborgh 1983; Janson 1985; Brown and Zunino 1990) broadly distributed throughout South America (Fragaszy et al. 2004; Lynch Alfaro et al. 2012). At Iguazú, capuchin monkeys live in multi-male, multi-female groups that range in size from 5-44 individuals (Janson et al. 2012). Interactions between neighbouring groups are uniformly aggressive (Di Bitetti 2001b), varying primarily in the degree of escalation (Scarry and 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 towards extragroup individuals (Di Bitetti

2001b; Scarry 2013). During intergroup encounters, males occasionally transfer (C.J. Scarry, unpub. data), whereas females remain in their natal groups (Di Bitetti 1997; Janson et al. 2012).

Although female capuchin monkeys lack any external physiological signals of ovulation (e.g., sexual swellings: Dixson 1983), sexual behaviours by females provide a reliable indicator of the periovulatory period (Carosi et al. 1999). These overt behavioural cues include eyebrow raising accompanied by continuous stereotyped vocalizations (estrous calls: Di Bitetti 2001a), “touch-and-go” contact with a male consort, and head cocking (Janson 1984; Carosi et al. 1999) and occur frequently throughout the day (Janson 1984). Extragroup males may be able to use these honest signals to rapidly identify and target resident females that are likely to conceive. Critically, in spite of high mating skew (Janson 1984; Janson 1998a) – a probable indicator of high reproductive skew because dominant males monopolize matings on the days when ovulation is most likely to occur (Tiddi et al. 2013; Tiddi, Wheeler & Heistermann in prep), females generally mate with multiple males during their receptive period (Janson 1984; Lynch Alfaro 2005). Promiscuous mating by resident females creates a non-zero chance of paternity for most males, while the staggered occurrence of female receptivity creates natural variation in the risk of extragroup copulations, even within the mating season.

EXPERIMENTAL DESIGN AND DATA COLLECTION

Within this population, intergroup encounters are associated with long-distance chases (≤ 500 m: Di Bitetti 2001b; C.J. Scarry, unpub. data) that make it difficult to correlate the intensity of aggressive response with resource presence – the method with which previous studies have tested the function of intergroup aggression (Kinnaird 1992; Crofoot 2007; Harris 2010; Brown 2013) – because it is very likely that some food resources would be present in the neighbourhood

of any encounter. Therefore, I conducted playback experiments in combination with artificial manipulation of the resource base (Janson 1998b) to separate the effects of the presence of sexually receptive females and available energy on the intensity of aggressive response by resident males, while introducing minimal spatial and seasonal variation. I assessed individual response following the playback using three measures: 1) whether the focal individual began to approach the speaker; 2) individual acceleration following the presentation of the playback stimulus; and 3) whether the focal individual responded to the playback stimulus with intergroup encounter whistle vocalizations. If the experimental treatment increased the payoff to the winner, then individuals should have been willing to invest more in intergroup aggression (Parker 1974), being either more likely to participate or increasing the strength of their responses.

For each trial ($N = 36$), I considered three factors that could influence responses by the focal males, including: 1) potential mating opportunities within the group, 2) monopolisable food resources in the vicinity, and 3) the rank of the calling male. Potentially contestable resource types – mating opportunities and food – were considered as being either high or low in availability. Low values (i.e., control conditions) for each resource type included days on which no sexually receptive female was present within the focal group ($N = 8$ of 36 trials) and natural levels of food availability ($N = 25$ of 36 trials). Although reproduction is seasonal with the majority of conceptive matings occurring during the austral winter (Di Bitetti and Janson 2001a), female reproductive synchrony is limited (B. Tiddi, personal communication). Therefore, if one or more female was exhibiting receptive sexual behaviour, I considered that the trial included a high availability of mating opportunities. To provide groups with a high-value food resource (pieces of banana approx. 2.5 cm in length), I used provisioning platforms to temporarily increase individual energy gain at a location relative to environmental availability. All

provisioning sites were located within the area of home range overlap (Fig. 1), following established protocols that have been described previously (Janson and Di Bitetti 1997). The total number of bananas provided depended on the number of individuals in the group (range: 30 - 60 pieces), so that *per capita* availability at the site was consistent across groups (~175 kJ/individual) and roughly comparable with large, naturally-occurring fruit patches used by capuchins in other seasons (C.H. Janson, C.J. Scarry, and M.P. Tujague, unpub. data). Finally, potential immigrants, which could increase the future costs of within-group competition over mates, might elicit higher levels of aggression from resident males. Dominant males do not generally surrender a top breeding position in their current group to transfer to another group (Janson et al. 2012), whereas subordinate males have occasionally been observed transferring directly between groups during intergroup encounters (C.J. Scarry, *pers. obs.*). Thus I also explored the possibility that the rank of the calling individual affected responses by focal males.

I simulated intergroup encounters by reproducing between-group aggression whistle series (Di Bitetti 2001a) given by individually-identified adult and subadult males in neighbouring groups (preceded by recordings of ambient noise), using a portable speaker (SME-AFS, Saul Mineroff, New York, USA) connected to an iPod mp4-player. These calls are produced by vanguard individuals upon detection of a neighbouring group and are typically short in duration (~4 sec), serving to rally lagging group members (Di Bitetti 2001a). Subsequent behaviour by the caller is dependent upon the receivers' responses (e.g., vocal interchange, retreat, or approach: C.J. Scarry, unpub. data), so I presented only the initial vocal stimulus. I recorded all calls during naturally-occurring intergroup encounters, using a solid-state audio recorder (PMD670 or

182 PMD660, Marantz, New Jersey, USA) with a shotgun microphone (ME 67 or ME 66,
183 Sennheiser, Wedemark, Germany) at a sampling rate of 44.1 kHz.

184 Because the location of an encounter relative to the home range centre can affect the
185 behavioural responses of group members (Wich et al. 2002; Crofoot and Gilby 2012), all
186 playbacks were conducted in the vicinity of the provisioning sites (≤ 50 m), whether or not active
187 provisioning was occurring. Each field season consisted of both provisioning and control
188 periods, limiting the effects of seasonal or interannual variation in fruit availability in the
189 surrounding area. Although the order of presentation of the two food contexts varied across the
190 three groups, all groups became accustomed to the resource distribution before playback
191 presentations began. The whistle series family of calls has individually-distinct acoustic
192 properties (Di Bitetti 2001a), and anecdotal results of playback experiments ($N = 3$) suggest that
193 individuals can hierarchically classify extra-group individuals on the basis of their calls (C.
194 Scarry, unpub. data); in response to the presentation of a recorded vocalisation in areas where the
195 caller would not normally be encountered (cf. Cheney and Seyfarth 1982), group members
196 rapidly approached the speaker in the absence of either a defensible food resource or a sexually
197 receptive female. Thus to ensure that individual responses did not reflect a violation of
198 expectation (Cheney and Seyfarth 1982), I presented only vocalizations from groups that had
199 been previously encountered in the area. To avoid habituation to the playback recordings, at least
200 two days passed between consecutive experiments with a single group, and experiments were not
201 conducted on days on which natural encounters had already occurred.

202 To limit the effects of satiation on the aggressive response of individuals (Janson and Vogel
203 2006), I conducted experiments early in the day – when the group typically is focused on fruit
204 feeding (Terborgh 1983). For all trials, the speaker was positioned less than 150 meters from the

205 edge of the group, which falls within the natural detection distance of neighbouring groups (C.J.
206 Scarry, unpub. data). Whenever possible, my assistants and I collected data on the behavioural
207 responses of multiple individuals, preferentially selecting one adult male and one adult female
208 per trial. One minute prior to the stimulus presentation, we established baseline measures for the
209 focal individuals by recording general behaviour and current velocity (defined as the summed
210 horizontal and vertical displacement within one minute, measured in 10-m intervals). I was then
211 able to compare these data to matched samples recorded one minute following the playback to
212 determine the strength of the individual's response. In addition, we recorded whether or not the
213 focal individual began to approach the speaker or produce between-group aggressive whistles
214 within one minute of the stimulus playback (similar to the latency to movement measure used in
215 other studies). I only considered immediate responses – and not arrival to the speaker or delayed
216 approaches – because the placement of playback speaker at the provisioning site made it
217 impossible to tell whether these more delayed behaviours were an indication of interest in the
218 neighbouring group or simply a response to the expectation of the food resource present.
219 Moreover, because focal individuals were sometimes within the critical radius at which
220 capuchins begin rapid directed movements towards known food sources (Janson 1998b, Tujague
221 et al. *in press*), during provisioning periods, I only included cases in which the focal animal
222 altered its general behaviour to begin travelling to avoid artificially inflating the importance of
223 the high-quality resource on approach behaviour. As such, the apparent effect of the presence of
224 a defensible food resource is likely to be a conservative estimate. This restriction was not
225 necessary for the analysis of individual acceleration because change in velocity – and not the
226 approach speed *per se* – was measured, which controlled for the directed movement towards the

provisioning platforms. Because both the location and the season were held constant, any difference in individual response can be attributed to the experimental treatment.

In addition to the data collected during the experimental trials, I recorded female sexual behaviour (e.g., proceptive behaviours associated with the periovulatory period [Carosi et al. 1999], copulations and the male target of female solicitations) daily to categorize the reproductive context for each experiment. To determine within-group dominance relationships among males, I also recorded the outcome of intragroup dyadic aggression *ad libitum* (Altmann 1974), identifying two dominance classes – dominant ($N = 3$ individuals) and subordinate males ($N = 8$ individuals) – based on whether or not the individual received aggression from same-sex individuals. These categories correspond to distinct socio-spatial subgroups which differ in their access to both food resources (Di Bitetti and Janson 2001b) and mates (Janson 1984).

All data were collected in accordance with Guidelines for Use of Animals in Research outlined by the ASAB/ABS. This study was conducted with the permission of the Argentine Administration of National Parks and in accordance with Stony Brook University's Institutional Animal Care and Use Committee guidelines (protocol numbers 2007-1580, 2008-1580, 2009-1560 and 2010-1560).

STATISTICAL ANALYSES

I fitted generalized linear mixed-effects models (GLMM) in R (R Development Core Team 2010) using the lme4 package (Bates and Maechler 2011) to identify factors that influence the probability of individual approach ($N = 57$), change in individual velocity ($N = 42$), and the probability of vocal response ($N = 54$). I calculated individual acceleration as the difference in velocity post- and pre-stimulus presentation, before log-transforming the raw values to conform to the assumption of a normal distribution of residuals. Because the response variables (e.g.,

approach/non-approach) were binomially-distributed, I used a logit-link function for the analyses of individual approach and vocal behaviours. I ran three sequential analyses, beginning with the identification of the contexts promoting male aggression during intergroup encounters. Fixed effects for these model included the presence of a defensible food resource, the presence of a receptive female, and the relative rank of the caller. Given the relatively small sample size of trials with sexually receptive females present, I also ran simulation-based power analyses in R, using scripts from Johnson et al. (2015), for the models containing only the presence of a receptive female as a fixed effect. Once the nature of the defensible resource was identified, I examined the effects of male rank on individual participation and then addressed sex differences in participation. Focal animal identity and focal group identity were included in all models as crossed random effects. To control for both the potential for reduced marginal benefits of participation by males in large groups and the increased risks of engagement for males in small groups, male group size as a fixed effect in all global models.

I used an information theoretic approach to incorporate the uncertainty inherent in selecting a single best fit model, fitting a global model that included all predictor variables and biologically relevant interactions and all subset models (Symonds and Moussalli 2011) for each of the response variables. I calculated the Akaike Information Criterion corrected for small sample size (AICc: Burnham and Anderson 2002) for each model using the MuMIn package (Bartoń 2012), and used the Akaike weights of models (w_i : Burnham and Anderson 2002) to calculate variable weights ($\omega_+(j)$) for all main effects and identify the 95% confidence set of models (see Supporting Information Table 1). From this subset of models, I calculated unconditional parameter estimates ($\hat{\theta}$) and standard errors ($\widehat{se}(\hat{\theta})$) (Burnham and Anderson 2002; Burnham et al. 2011; Symonds and Moussalli 2011), using the zero method of model averaging (Burnham

and Anderson 2002; Nakagawa and Freckleton 2011). For models to explain variation in individual approach behaviour, I was unable to obtain reliable estimates of the conditional standard error for most models due to the overriding effect of a single predictor variable (Hauck and Donner 1977); thus unconditional standard errors were not calculated.

Results

The presence of a defensible fruit resource dramatically increased the probability that focal male approached the speaker (Fig. 2; $\hat{\theta}_{Fruit} = 21.72$, Relative risk [RR] = 2.99, $\omega_+(Fruit) = 1.00$, N = 28). Following the presentation of the playback stimulus, focal males approached the speaker on 19 occasions. These approaches included all 14 focal follows that occurred while the group was being actively provisioned at the platform site, whereas the focal male approached the speaker during only 5 of the 13 follows (38%) that occurred in the absence of direct provisioning. Although standard errors could not be calculated for models of approach behaviour (Hauck and Donner 1977), the presence of this variable in all models within the 95% confidence set provides a good indicator of the robusticity of the effect (Symonds and Moussalli 2011). Additionally, males accelerated more following the presentation of the playback stimulus during periods of active provisioning (Figs. 2 and 3; $\hat{\theta}_{Fruit} = 1.04 \pm 0.18 \log_{10}[\text{m/min}]$, $\omega_+(Fruit) = 1.00$, N = 21 trials), including individuals that were already approaching the food resource. During provisioning periods, males increased their travel speed by nearly an order of magnitude after hearing the vocalisation ($\overline{\Delta v}_{\text{Present}} = 24.28 \pm 13.84 \text{ m/min}$ ($\pm \text{s.e.}$), N = 14) relative to simulated encounters occurring when resource levels were at their natural low ($\overline{\Delta v}_{\text{Absent}} = 2.50 \pm 8.60 \text{ m/min}$, N = 10).

In contrast to other species in which males participate in defending food resources (e.g., Kinnaird 1992; Mosser and Packer 2009), behavioural responses by focal males were not simultaneously affected by the reproductive status of resident females. Neither the probability that a male approached the speaker (Fig. 2; $\hat{\theta}_{Female} = -0.10 \pm 0.60$, $RR = 0.94$, $\omega_+(Female) = 0.19$, $N = 28$, $Power = 0.55$) nor the rate of approach differed in the presence of a sexually-receptive female (Figs. 2 and 3; $\hat{\theta}_{Female} = -0.04 \pm 0.12 \log_{10}[m/min]$, $\omega_+(Female) = 0.13$, $Power = 0.67$, $N = 21$; $\overline{\Delta v}_{Present} = 7.00 \pm 16.01 \text{ m/min}$ vs. $\overline{\Delta v}_{Absent} = 6.25 \pm 15.84 \text{ m/min}$). *Post hoc* analysis revealed that the effect of a sexually receptive female on individual response to the simulated presence of an extragroup male was similar for both males and non-receptive females (GLMM: $\hat{\theta}_{Female*Sex} = -0.03 \pm 0.17 \log_{10}[m/min]$, $\omega_+(Female * Sex) = 0.04$, $N = 41$), after controlling for the presence or absence of fruit resources, and males were never observed to herd resident females away from extragroup males or otherwise discourage their participation during either the playback experiments or naturally-occurring intergroup encounters. Similarly, although the potential long-term consequences of interactions with neighbouring groups vary with the rank of the extragroup male, approaches to the speaker were no more likely following recordings from subordinate males in neighbouring groups than those from dominant males (Fig. 2; $\hat{\theta}_{Male} = 0.08 \pm 0.55$, $RR = 1.05$, $\omega_+(Caller) = 0.19$, $N = 28$), and no differences in acceleration were discernible in relation to the rank of the calling male ($\omega_+(Caller) = 0.08$, $N = 21$).

The context of the simulated encounter had no effect on the probability that the focal male responded to the playback stimulus with intergroup encounter whistle calls ($\hat{\theta}_{Fruit} = 0.24 \pm 0.62$, $\omega_+(Fruit) = 0.28$; $\hat{\theta}_{Female} = -0.33 \pm 0.86$, $\omega_+(Female) = 0.42$; $\hat{\theta}_{Male} = 0.76 \pm 1.22$, $\omega_+(Male) = 0.59$, $N = 27$).

Effects of male rank

Contrary to predictions based on the expected within-group payoff structure driven by the strong effects of within-group contest competition, dominant and subordinate males exhibited no differences in their willingness to approach the playback speaker (Figs. 2 and 4; $\hat{\theta}_{Subordinate} = 0.76 \pm 1.33$, RR = 1.55, $\omega_+(Subordinate) = 0.32$, N = 31) or in the intensity of their response, as measured by their acceleration upon hearing the playback vocalization (Fig. 2; $\omega_+(Subordinate) = 0.09$, N = 23). The pattern remains unchanged when only trials conducted during active provisioning are considered ($\omega_+(Subordinate) = 0.04$, N = 14). Subordinate males, however, were more than five times less likely to issue aggressive intergroup encounter vocalizations ($\hat{P}(Vocalize|Subordinate) = 0.11$) following the playback than were dominant males (Fig. 5; $\hat{P}(Vocalize|Dominant) = 0.61$; $\hat{\theta}_{Subordinate} = -2.50 \pm 1.00$, RR = 0.19, $\omega_+(Subordinate) = 0.94$, N = 30).

Sex differences in approach behaviour

During naturally occurring periods of resource scarcity, when a contestable food resource was not present, females were less likely to approach the speaker ($\hat{P}(Approach|\varnothing) = 0.00$) than males (Fig. 4; $\hat{P}(Approach|\sigma) = 0.46$; $\hat{\theta}_{Male} = 37.11$, $\omega_+(Male) = 0.89$, N = 24). Although participation by both sexes increased during provisioning periods, females were less likely to approach the speaker than the larger-bodied males (Fig. 4; $\hat{\theta}_{Male} = 4.99$, RR = 1.14, $\omega_+(Male) = 0.28$, N = 33), although this difference was less pronounced ($\hat{P}(Approach|\varnothing) = 0.87$ vs. $\hat{P}(Approach|\sigma) = 1.00$). Among participating individuals, however, intersexual differences in approach velocity were not present ($\hat{\theta}_{Male} = 0.21 \pm 0.25 \log_{10}[\text{m/min}]$,

$\omega_+(Male) = 0.53$, $N = 23$; $\overline{\Delta v}_{\sigma} = 24.28 \pm 13.85$ m/min, $N = 14$; $\overline{\Delta v}_{\varphi} = 13.89 \pm 13.41$ m/min, $N = 9$).

Discussion

PROXIMATE DRIVERS OF MALE AGGRESSION

In some species, responses towards extragroup individuals during intergroup encounters are influenced by multiple resource types (e.g., food resources, mates, infants). Consequently, context-dependent variation in the identity and level of engagement by participating individuals can occur because individual assessments of the cost-benefit tradeoff of defending a particular resource vary (e.g., black-and-white colobus monkeys, *Colobus guereza*: Harris 2010; reviewed in Kitchen and Beehner 2007). In contrast, the current results suggest that among tufted capuchin monkeys aggressive behaviour by both males and females during intergroup encounters serves solely or primarily as a tactic to defend access to high-quality food resources. During provisioning periods, group members responded to the simulated presence of a neighbouring group by increasing travel speed and approaching the speaker. Notably, in spite of more direct links between increased access to food and reproductive success among females (Trivers 1972), focal males always approached the speaker, whereas females occasionally defected from the collective response (i.e., refrained from approaching the ‘neighbouring group’).

Because the current analysis examined only initial responses, the possibility that individuals may discontinue participation mid-encounter or otherwise provide unequal contribution to the collective effort remains open (see for example Kitchen 2004; Kitchen et al. 2004). Nevertheless, aggressive behaviour by capuchin males during intergroup encounters does not appear consistent with simultaneous defence of immediate mating opportunities. Instead, the intensity and

probability of response by the focal male varied independently of resident female sexual behaviour. Moreover, although receptive females occasionally approach extragroup males during naturally-occurring intergroup chases (C. Scarry, pers. obs.) or following encounters (B. Tiddi, personal communication), focal males were never observed to direct aggression at resident females or otherwise attempt to herd them away from extragroup males (*vs.* Cheney and Seyfarth 1977; Kinnaird 1992; Sicotte 1993; Palombit 1994; Cowlshaw 1995; Agoramoorthy and Hsu 2000). Among tufted capuchin monkeys, strong female preference for males that provide direct benefits (i.e., access to monopolisable resources: Janson 1984) may reduce the need for males to use aggressive behaviour to prevent extragroup copulations.

THE ROLE OF MALES AS “HIRED GUNS”

The overriding importance of high-quality food resources in promoting aggression by tufted capuchin males appears unusual among group-living mammals. Critically, these aggressive responses in defence of high-quality food resources were not restricted to dominant males (*vs.* Peruvian tufted capuchin monkeys, *S. macrocephalus*: Janson 1986); rather, rank-related differences in patterns of participation were not apparent among males during provisioning periods. To date, evidence of resource defence as the sole male strategy has been limited to species with uni-male or harem groups (Emlen and Oring 1977; Rubenstein 1986; Carranza et al. 1996; Linklater et al. 1999; but see Mitani et al. 2010 for a discussion of resource defense polygyny in chimpanzees, *Pan troglodytes*). Yet these results add to a growing body of evidence that suggests dominant and subordinate capuchin males are serving as “hired guns” within this population (cf. Rubenstein 1986), such that resident females derive both short- and long-term foraging benefits from the presence of additional males within the group (cf. Wrangham 1980).

Males are more likely to participate in naturally occurring intergroup encounters during seasons in which groups feed at large fruit trees (C.J. Scarry, unpub. data), and the results of the current playback experiments suggest that the individual assessments underlying this increased willingness to participate may be influenced by the current productivity of high-quality food resources in the vicinity. Yet competitive advantages in intergroup contests over these individual food resources – which are decided on the basis of relative male group size – are also critical in mediating long-term access to both space and food resources (Scarry and Tujague 2012; Scarry 2013).

MALE TRANSFER AND RESPONSES TO POTENTIAL IMMIGRANTS

In contrast to females and dominant males, subordinate males occasionally approached the speaker during periods of natural resource availability; however, these approaches lacked the velocity and degree of agitation observed when high-quality food resources were at stake. Rather than actively defending a resource, subordinate males may be assessing the reproductive opportunities available within neighbouring groups, which could influence transfer decisions (Packer 1979; Cheney 1981; Cheney and Seyfarth 1983; van Noordwijk and van Schaik 1985; Lazaro-Perea 2001). Yet the playbacks of subordinate male vocalisations suggest that resident males do not perceive this reconnaissance behaviour as threatening their long-term reproductive success – due to either an aggressive takeover (Grinnell et al. 1995; Steenbeek 1999; Kitchen 2004) or increased male immigration (Cheney and Seyfarth 1977). In addition to advertising the general presence of another group in the vicinity, calls from subordinate males provide additional information that could be used pinpoint the exact position of a potential immigrant, allowing

resident males to respond more rapidly with targeted aggression; yet the caller's rank had no effect on approach behaviour by resident males.

The undifferentiated response to dominant and subordinate extragroup males likely reflects the fact that male tufted capuchin monkeys do not regularly form coalitions to gain entry into bisexual groups (Janson et al. 2012), as has been observed in other species (Pope 1990; Grinnell et al. 1995; Steenbeek 1999; Kitchen 2004; Perry 2012). In the absence of coalitionary support, immigrant males, which are generally younger and smaller-bodied than resident males, enter low in the hierarchy and typically need several years before being able to successfully challenge the alpha male (Janson et al. 2012). Furthermore, females generally avoid soliciting copulations with subadult males (Janson 1998a); consequently, until these immigrants reach adult body size, they pose little threat to the reproductive success of resident males.

THE MAINTENANCE OF COLLECTIVE RESOURCE DEFENCE

Previous theoretical (van Schaik 1996; Nunn 2000; Willems et al. 2013) and empirical studies (Harris 2010; Crofoot and Gilby 2012) suggest that male collective action is difficult to maintain in the context of food resource defence, due to the more indirect nature of the fitness benefits accrued through access to food relative to additional mating opportunities (Trivers 1972). Diminishing returns on individual investment in resource defence appear to lead to a collective action problem among other species with multi-male groups (Linklater and Cameron 2000; Harris 2010; Crofoot and Gilby 2012). In contrast, collective response by tufted capuchin males promote success in cooperative defence (Scarry and Tujague 2012; Scarry 2013), allowing groups with more males to consistently dominate numerically weaker neighbours (vs. *Cebus capucinus*: Crofoot et al. 2008).

At present, the mechanism allowing tufted capuchin males to overcome the potential collective action problem remains unclear. Relative to species in which female participation in intergroup aggression is limited or absent (e.g., *Colobus guereza*: Harris 2010), the potential costs of increased intragroup mating competition incurred by participating males are reduced because of the active role taken by resident females during aggressive intergroup encounters. By lagging behind during an encounter, males cannot sneak copulations opportunistically while competitors are occupied elsewhere. Because these coalitions are not mutual endeavours to maintain access to reproductive females and prevent takeovers by extragroup males (cf. byproduct mutualism; vs. lions, *Panthera leo*: Grinnell et al. 1995; primates: Pope 1990; Fedigan and Jack 2004; Port et al. 2010; Port et al. 2011; Port et al. 2012), however, the energy and opportunity costs involved (e.g., lost foraging time) should still favour defection in the absence of counterbalancing benefits for the individual (Harris 2010; Linklater et al. 2013). Resident males that sire infants may derive benefits from cooperative defence of food resources, such as: provisioning offspring, increasing the frequency of mating opportunities (Di Bitetti and Janson 2001a), and solidifying female support, allowing males to retain their rank beyond their physical prime (Janson et al. 2012). Yet – for subordinate males – the potential for immediate direct fitness benefits of participation appear minimal due to high mating skew (Janson 1998a) and long alpha male tenure (Janson et al. 2012). Similarly, the pattern of solitary male dispersal likely reduces indirect fitness benefits, limiting the potential for collective action to be promoted through kin selection (Hamilton 1964; Pope 1990; Packer et al. 1991).

Alternatively, subordinate males may be directly defending access to food resources because they are critical to their own future reproductive success. In this context, benefits to females are simply a by-product of male mating competition, rather than the basis of female mate choice (cf.

Rubenstein 1986). Tufted capuchin males transfer prior to attaining adult body size, and typically wait several years before they are able to successfully challenge the dominant male (Janson et al. 2012). Thus, given the demographic and morphological profile of reproductive males, subordinate males may be allocating available energy to growth and maintenance, instead of reproductive effort (cf. Gadgil and Solbrig 1972). Moreover, while they occupy relatively high positions in within-group dominance hierarchies (Di Bitetti 1997), subordinate males continue to receive high rates of aggression from the dominant male and resident females (Janson 1985), which negatively impacts their daily energy intake (Janson 1985). Through their participation in intergroup encounters over high-quality food resources, subordinate males increase *per capita* food availability for the group (Scarry 2013) and the overall magnitude of within-group competition may be reduced (Janson and van Schaik 1988).

Among other species, such continued exposure to frequent agonism due to within-group contest competition can increase physiological indicators of stress (Abbott et al. 2003; Sapolsky 2005), leading subordinate males to exhibit suboptimal body condition (Setchell et al. 2010) or delayed physical maturation. Thus, although parental investment theory suggests that males should compete primarily over access to mating opportunities (Trivers 1972), intolerance at food resources could also serve as a form of intrasexual competition (Janson 1985), whereby the dominant male is able to prolong his tenure as alpha and increase his lifetime reproductive success (Muniz et al. 2010). To attenuate these effects of intrasexual competition, subordinate males may be trading participation during intergroup encounters for increased tolerance from more central group members (Janson and Di Bitetti 1997) at contestable food resources (cf. grooming for tolerance: Tiddi et al. 2011). If group cohesion is increased near high-quality resources – like the provisioning platforms or large fruit trees, male participation may be elicited

in part through an audience effect (reviewed in Earley 2010; Meunier et al. 2012). Understanding the degree to which females – or other group members – are manipulating this competition, therefore, requires further analyses examining the relationship between co-feeding and male behaviour during intergroup encounters.

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Figure Legends

Figure 1. The location of provisioning sites from which playback experiments were conducted within the home ranges (95% kernel density estimate) for the three groups.

Figure 2. Model-averaged parameter estimates for the models of male approach behavior and acceleration. For approach behavior, the relative risk – the proportional change in the probability of approach – is shown, not the beta coefficients. Values in blue (above) show the results of the initial analysis comparing the effects of potentially contestable resources, and values in red (below) show the results of the analysis of the effects of individual rank.

Figure 3. Individual rate of acceleration ($\Delta v/min$, log-transformed) by focal males under control conditions and in the presence of a contestable resource (fruit resources and sexually receptive

females). All other variables are maintained constant (i.e., playback of dominant male long-distance whistle). Open circles indicate original values of focal male responses under each condition.

Figure 4. Probability of approach by males and females depending on the presence or absence of a defendable fruit resource. Subordinate males (striped) are more likely to approach the speaker in the absence of a high-quality food resource; however, during periods of active provisioning, both dominant (solid) and subordinate males always approached. Reliable estimates of the standard error could not be determined (Hauck and Donner 1977).

Figure 5. Probability of vocalization by dominant and subordinate males following the playback stimulus in the presence or absence of a defendable fruit resource. All other variables are maintained constant (i.e., playback of dominant male long-distance whistle, no sexually receptive females).

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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5