Individual participation in intergroup contests is mediated by numerical assessment strategies in black howler and tufted capuchin monkeys

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Asymmetries in resource-holding potential between opposing groups frequently determine outcomes of intergroup contests. Since both numerical superiority and high intergroup dominance rank may confer competitive advantages, group members should benefit from assessing the relative strength of rivals prior to engaging in defensive displays. However, differences in individual assessment may emerge when cost–benefit trade-offs differ among group members. We examine the influence of numerical superiority and intergroup dominance relationships on individual participation in intergroup encounters in black howler monkeys (Alouatta pigra) and tufted capuchin monkeys (Sapajus nigritus). Black howlers responded with longer vocal displays during encounters with neighbours with an equal number of resident males, while tufted capuchins increased their participation with increasing relative male group size. Within each species, males and females responded similarly to varying numerical odds, suggesting that despite pay-off asymmetries between males and females, both sexes were similarly influenced by numerical asymmetries in deciding to participate in collective group defence. Whereas the outcome of contests among tufted capuchins was determined by relative male group size, reflected in a pronounced intergroup dominance hierarchy, the absence of dominance relationships among black howler groups may have provoked prolonged vocal displays in order to assess rival groups with matching competitive abilities.

1. Introduction

In many group-living animals, individuals cooperate in defence of home ranges, food resources or mating opportunities. Similar to contests between single individuals, aggressive encounters between groups often involve high costs to participants, including the risk of injury or death [1,2]. Because asymmetries in competitive ability frequently determine the outcome of aggression, selection may favour the evolution of individual strategies to assess the relative strength of rivals and avoid contests with competitively stronger groups or when the potential benefits of access do not outweigh the costs of aggression. Large group size—which increases the number of available coalitional partners—may confer a competitive advantage during contests (2–6, but see [7]). Accordingly, in some species, groups are more likely to initiate an encounter when they outnumber their rivals (table 1), suggesting that individuals may use relative group size to assess competitors. Because sex differences in parental investment can promote discordant strategies of engagement by males and females [38–41], individual assessment may reflect asymmetries in total group size or the number of individuals of a particular age–sex class depending on the context of aggression (e.g. resource, mate or infant defence; table 1). Yet in many species, group members may not numerically assess their neighbours...
when deciding to participate in their group’s defence efforts (table 1), suggesting that additional factors may play a role as well.

In contrast to contests between single competitors, wherein intrinsic properties of the individuals (e.g. body size, weaponry) frequently determine competitive asymmetries, the potential competitive advantage provided by large group size depends on the willingness of group members to participate in collective defence. When contested resources are not monopolizable (i.e. ‘public goods’ such as home ranges), cooperative defence becomes vulnerable to the presence of ‘free-riders’ [42,43]—individuals who reap the benefits of successful group action at little or no cost to themselves. Many behaviours associated with group defence (e.g. vocalizations, lost feeding opportunities, threat displays and physical contests) are only costly to participants; thus, individuals may be tempted to avoid these costs through lagging or limited participation (‘weak free-riders’) or complete

Table 1. Studies reporting the effect of numerical asymmetry (relative group size, relative number of males, females or adults) on intergroup defence strategies of the group or a subgroup of individuals of particular age–sex classes. A, adult; M, males; F, females; +, positive effect; −, negative effect; ×, no effect.

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defection (‘strong free-riders’). Because the marginal value of each participant decreases as coalitionary size increases [44], large group size—rather than providing a competitive advantage—may actually deter individual participation, causing the realized competitive ability to fall below the optimum [42,44].

Even when access to the contested resource provides fitness benefits to multiple group members, the cost–benefit trade-off of intergroup contests frequently differs among individuals due to factors such as sex and rank [45,46]. For example, sexual dimorphism and the presence of dependent offspring can lead to higher costs of participation for females relative to males [2]. Similarly, better body condition and priority of access to contested resources may lower the costs of participation for high-ranking individuals while increasing benefits from contesting access to key resources [18,40,47–49]. If group members adjust their participation accordingly, the maximum collective benefit may still be obtained [42], but sex- and rank-based differences in individual assessment may emerge that affect willingness to participate (e.g. [8–10,32]).

Interindividual differences in participation can also limit the utility of group size as a reliable indicator of competitive ability if similarly sized groups vary in demographic composition or degree of intragroup tolerance and cooperation. Other factors, such as the relative fighting ability of specific individuals (e.g. [50,51]) or perceived ownership (e.g. [12,28]), may instead be better predictors of contest outcomes. In contests with familiar neighbouring groups (versus unfamiliar intruders), if these asymmetries remain consistent across contests (versus state-dependent asymmetries in motivation [52]), stable or site-dependent dominance relationships may form among neighbouring groups [6,7,53,54]. As such, individuals may use additional information gained through prior experience to base their assessment of competing groups, and patterns of individual participation may reflect intergroup dominance relationships instead of numerical superiority per se.

In this study, we examine the influence of numerical superiority and intergroup dominance relationships on individual participation during naturally occurring intergroup encounters (IGEs) in two Neotropical primates—black howler monkeys (Alouatta pigra) and tufted capuchin monkeys (Sapajus nigritus). In both species, males and females participate during aggressive interactions with neighbouring bisexual groups [6,55–58], but observational and experimental studies suggest that sex and/or rank differences in participation may exist [8,9,55,57–59] that are consistent with the pronounced sexual dimorphism [60,61] and mating skew [57,62,63] in each species. It is unclear, however, whether these interindividual differences reflect overall lower levels of participation by females and subordinate males (cf. ‘unconditional laggards’ [25]) or distinct thresholds for participation based on the relative threat posed by another group (cf. ‘conditional laggards’ and ‘conditional cooperators’ [25]).

Intergroup aggression in both species functions primarily to defend long-term access to space, rather than individual food resources or short-term mating opportunities [59,64]. In accordance with the relatively low fitness gains accrued by the winning group, encounters rarely involve physical aggression [56]: S.V.B. 2012, personal observation. Given the concomitant lower risk of injury, interindividual differences in body size and canine tooth size may be less of a deterrent to individual participation than has been observed in other species (e.g. [15])—although these factors are likely to affect both leadership and participation in escalated contests. Individual assessment may depend instead on the energy and opportunity costs of participation, which are likely to be high in both species. Although black howler monkeys generally exhibit an energy minimizing lifestyle, during IGEs, groups engage in one or more joint vocal displays (‘howling bouts’) that are accompanied by vigorous behavioural displays, including breaking or shaking branches and chases. Resident males who have sired offspring in the group are the primary participants in howling bouts [57], but other males and females participate in 67% and 72% of the calls, respectively [57,58]. IGEs among tufted capuchin monkeys involve long-distance chases (500 m or less) that occasionally escalate into direct face-offs between opposing groups [6,55,56]. Due to the species-specific nature of intergroup contests, we use separate behaviours to assess individual participation in collective defence. Among black howler monkeys, we examine whether the duration of calling by sire males, and whether non-sire males and females joined in or not, and subsequently the duration of their participation is influenced by numerical superiority and intergroup dominance rank. Among tufted capuchin monkeys, we examine whether individuals were more likely to participate in chases according to numerical asymmetries.

If group members differ in their assessment of neighbouring groups, we would predict that dominant or sire males are more likely to respond aggressively to an opposing group when their group is numerically superior or socially dominant over the encountered group. Similarly, the likelihood of participation by females and subordinate males may increase when their group is numerically superior to or socially dominant over the rival group, when the probability of winning the contest is higher. Alternatively, females and subordinate males may participate more when groups are evenly matched, when increased individual participation may be critical in determining which group has a competitive advantage [10].

Additionally, in black howler monkeys, clear intergroup dominance relationships have not been identified previously, but all group members significantly increase their group defence efforts during IGEs; relative to spontaneous or response calls to distant groups, individuals are more likely to vocalize and continue to vocalize for longer when in visual contact with a rival group [57,58,64]. Due to pronounced dimorphism in the vocal apparatus, loud calls produced by females are acoustically distinct from those produced by males [65], providing a reliable indicator of the sex of the calling individual. Consequently, numeric assessment of competing groups might not be based solely on the relative number of adult males per group but may instead reflect the relative number of both adult males and females. Similarly, because intergroup dominance relationships in tufted capuchin monkeys are driven primarily by asymmetries in adult male group size—and not the total number of adult individuals [6], individual participation should be affected solely by relative male group sizes, and not the asymmetry in total group size.

2. Material and methods

(a) Black howler monkeys

S.V.B. observed five social groups with contiguous home ranges at Palenque National Park, Mexico (17°28′ N, 92°03′ W) during a
28-month study. Groups ranged in size between two and four adult and subadult males, one and three adult females, and their offspring (electronic supplementary material, table SII). The five study groups had two to five neighbouring groups, including one to three study groups and one to four non-study groups. An IGE was scored whenever a neighbouring group was within visual contact of the focal group (50 m or less) [7,64,66]. We collected data on howling bouts using all-occurrence sampling throughout IEGs. For each howling bout, we recorded the start and end times and, whenever possible, the participation (i.e. roaring or barking, being vigilant, branch breaking or shaking, throat-rubbing or chasing opponents) of all adult and subadult males and all adult females simultaneously via instantaneous scan samples at 1-min intervals. We considered successive howling bouts to be independent if all group members were silent for at least 10 min before resuming howling [7,64,66]. The focal group was considered to ‘win’ a howling bout against a neighbouring group when they displaced the opposing group or the opposing group retreated more than 50 m within the first hour. The focal group was considered to ‘lose’ when the reverse occurred. When both groups remained in the area for more than 1 h without displacements, the outcome was labelled a ‘draw’. Because separate howling bouts during the same IGE did not always result in the same outcome, we determined an outcome per howling bout instead of per IGE.

We fitted generalized linear mixed models (GLMMs) to assess how male and female participation was influenced by intergroup dominance and numerical asymmetry. The focal group was considered dominant over a neighbouring group when they won more howling bouts than they lost (electronic supplementary material, table SII). We included two distinct fixed variables for numerical asymmetry in the models. Both variables were categorical based on whether the focal group was at numerical advantage or numerical disadvantage, or the groups were evenly matched. One was calculated from the relative number of both adult and subadult males and females. The other was calculated from the relative number of both adult and subadult males and females.

In the first GLMM, we assessed patterns of male participation in general. Given that it was not always feasible to record the participation of each resident male throughout the entire bout because they sometimes moved out of view for periods of time, we first calculated per howling bout the percentage of scans each male was out of view; we excluded from the analyses those bouts for which we lost sight of at least one male for more than 20% of the scans. We then calculated the total number of scan samples in which each male was observed to participate for those howling bouts for which sufficient data were collected (N = 121). The response variable included in the model represents per howling bout the mean number of scans in which resident adult and subadult males participated. In order to assess how adult female participation was influenced by intergroup dominance and numerical asymmetry, we ran a GLMM excluding howling bouts for which any adult female was out of view for more than 20% of the scans (N = 116). For these howling bouts, we calculated the mean number of scans that all adult females participated as the response variable in the models. To further assess the influence of intergroup dominance and numerical asymmetry on the disparate participation of males who had sired offspring in the group versus those that had not [57], we ran two additional GLMMs. The response variable for the first GLMM was the mean number of scans in which sire males participated (N = 1−2 males per group); while that of the second was the mean number of scans for non-sire males (N = 1−2 males per group). Paternity analyses for 19 offspring in the five study groups were conducted in CERVUS v. 3.0 (details are provided in [57]). Because non-sire males and females frequently did not participate, we conducted a two-part analysis to assess female and non-sire male participation. The response variable of the first GLMM (with a binomial error structure and a logit-link function) indicated per howling bout whether females (or non-sire males) participated (i.e. yes or no), while that of the second GLMM (with a Gaussian error structure) represented per bout the mean number of scans in which resident females (or non-sire males) participated when at least one female (or non-sire male) participated. We also fitted a GLMM with a binomial structure (and logit-link function) to assess whether the outcome of howling bouts was influenced by either the relative number of resident males or total adult group size.

All continuous response variables of the GLMMs explained above were square-root transformed to obtain normally distributed data (Shapiro tests, p > 0.05). All models included focal group ID, neighbouring group ID and IGE ID as random factors. For each analysis, we started with a saturated model that included all predictor variables (intergroup dominance rank, numerical asymmetry in male group size and numerical asymmetry in adult group size). Using the ‘ dredge’ function of the MuMln package [67] in R v. 3.1.1 [68], we fitted all subset models of this global model and identified the model with the lowest AICc as the ‘best-fit model’. We used multimodel inference to calculate Aikake weights (wi) and evidence ratios (ER) of these best-fit models [69,70]. To incorporate the uncertainty inherent in selecting a single best-fit model [69], however, we also employed an information theoretic approach to make unbiased inferences about the effects of all biologically relevant predictor variables (versus only variables included in the best-fit model). We ranked the candidate models by their AICc and calculated the Akaike weight (wi) of each model [69]. From a confidence set that included all models with ΔAICc < 4, we calculated unconditional parameter estimates and standard errors, using the zero method of model averaging [69,71] from a confidence set. The unbiased parameter estimates from this model-averaging procedure, as well as the 95% confidence set of models for each analysis, are available in the electronic supplementary material.

(b) Tufted capuchin monkeys
C.J.S. conducted all-day follows of four habituated groups at Iguazú National Park, Argentina (25°40′S, 54°30′W), over a 20-month period (June–December 2007, June 2008–August 2009). In addition to the focal groups, seven partially habituated groups resided in the study area and interacted with the focal groups on occasion. At Iguazú, tufted capuchin monkeys live in variably sized groups of five to 44 independently locomoting individuals [72], including one to five adult and subadult males and up to 14 adult females accompanied by juveniles and dependent infants. Including all possible dyadic interactions, focal groups encountered asymmetries in male group size ranging from a numerical disadvantage of three males to a numerical advantage of three males (electronic supplementary material, table SIII and figure S1). We included all interactions—either visual or vocal—between members of the focal group and extragroup individuals as IGEs (N = 115 encounters). At the onset of an encounter, we began ad libitum sampling of individual behavioural responses (N = 440 records). Because the identity of the individuals that we could observe depended on the observer’s position relative to the group prior to the encounter, and not on the behavioural response of the individual, we have no reason to expect a bias towards participation or deflection. We categorized behavioural responses according to two dichotomous variables:

**Participation versus deflection.** Participants included all individuals that moved towards the other group, maintaining proximity.
during at least a portion of the chase. Although this definition permits a degree of lagging during participation, individuals that arrived at the location only after all members of the opposing group had fled were not considered to have participated.

**Fleeing versus remaining.** All individuals that retreated following initial contact were considered to have fled from the neighbouring group, whether or not they participated briefly; however, individuals that simply failed to participate (i.e. remained in a constant location) were not considered to have fled.

Although we recorded the outcome of dyadic intragroup aggression ad libitum, we were unable to collect sufficient records to construct complete intragroup dominance hierarchies in order to assign cardinal ranks to individuals [73,74]. Instead, adult females were classified as high-, mid- and low-ranking depending on whether or not aggression was received from and/or directed to other female group members. These categories correspond to distinct socio-spatial subgroups which differ in their access to food resources [75] and central foraging positions [75,76]. Adult and subadult males were classified simply as alpha or subordinate. Comprehensive paternity analyses have not yet been conducted (but see [63]); however, the alpha male maintains priority-of-access in mating [76,77] and is the likely sire of the majority of infants born during his tenure.

To examine the effect of numerical asymmetries on the probability of individual participation and flight, we fitted GLMMs with logit-link functions because both response variables were binomially distributed. We first ran analyses including relative male group size as a categorical variable (i.e. numerical advantage, numerical disadvantage, evenly matched). Intergroup dominance relationships are predicted by relative male group size; groups with more males consistently win encounters against neighbouring groups with fewer males [6], which prevented us from identifying separate effects of male group size asymmetry and group rank. Because there is a non-zero probability that the numerically smaller group will win if the asymmetry in male group size is minimal (±1 male [6]), we ran a second analysis including relative male group size as a continuous variable. Due to the strong correlation between male and female group sizes [6], we could not include measures of both the asymmetry in male group size and total group size in a single model (variance inflation factor = 4.7). Using a subsample of the records of participation representing only encounters between focal groups, we ran separate analyses for male and total group size asymmetries and used multimodel inference to assess which measure of relative group size better predicted individual participation.

To control for repeated measures of groups and individuals, we included individual identity as a random factor nested within group identity in all models. We also included the group dyad because individual response may be affected by identity of the encountered group and variation in intergroup social relationships unrelated to between-group contest competition (e.g. male relatedness, prior history of interaction). Given the marked intragroup dominance effects on behaviour, we included individual dominance class as a covariate, fitting separate models for males and females because our definitions of rank categories were sex-specific. Thus for each analysis, the saturated model included numerical asymmetry (categorical or continuous), individual rank and an interaction term.

### 3. Results

#### (a) Black howler monkeys

We recorded a total of 110 IGEs involving the study groups (electronic supplementary material, table SI). These occurred on average every 5.0 ± s.e. 1.7 observation days, and lasted on average 3.27 ± s.e. 0.25 h (median = 2.4 h, range = 9 min–11.6 h), during which the study groups engaged in one to seven howling bouts per IGE (N = 207 bouts, mean = 1.9 ± s.e. 0.1 bouts, median = 2 bouts; electronic supplementary material, tables SI and SII). The outcome of howling bouts was not influenced by the relative number of males (GLMM estimate numerical advantage versus even: −0.09 ± s.e. 0.68, z = −0.13, p = 0.898; numerical disadvantage versus even: −0.03 ± 0.68, z = −0.04, p = 0.969) or of both males and females (numerical advantage versus even: 0.78 ± 0.48, z = 1.64, p = 0.102; numerical disadvantage versus even: 0.58 ± 0.68, z = 1.04, p = 0.296). Adult and subadult males participated, on average, for 11.9 ± s.e. 0.8 min, although the duration of participation by sire males was generally longer (sires: 16.0 ± 1.0 min versus non-sires: 6.0 ± 0.7 min). Females were observed to participate for a mean of 6.0 ± 0.7 min.

The best AIC model for male participation yielded a significant effect of male numeric asymmetry (w0 = 0.48, ER = 2.22; electronic supplementary material, table SIV). Resident males participated more frequently when the groups were evenly matched than when a numerical asymmetry was present (numerical advantage versus even: −1.25 ± 0.48, t0.2,10 = −2.57, p = 0.013; numerical disadvantage versus even: −1.19 ± 0.48, t0.2,5 = −2.51, p = 0.015; figure 1a). Even though both sire and non-sire males participated most when male numeric odds were symmetric (figure 1b,c), these patterns were not statistically significant (sire: w0 symmetry = 0.26; non-sire: w0 symmetry [categorical] = 0.16; w0 symmetry [continuous] = 0.09; all p > 0.05; electronic supplementary material, tables SV and SVI). Mean participation by males, in general, and sires and non-sires, in particular, was not influenced by numeric asymmetry based on the relative adult group size between the rival groups or by intergroup dominance rank (all p > 0.05; electronic supplementary material, tables SIV–SVI). Similar to males, the best AIC model for female participation included male numeric asymmetry as the only predictor (electronic supplementary material, table S VII). Decisions by females to join a howlingbout were not influenced by male numeric asymmetry (w0 symmetry [categorical] = 0.18; all p > 0.05); however, during howling bouts in which at least one female participated, the mean duration of female participation was longer when the focal group had an equal number of resident males as the rival group (w0 symmetry [continuous] = 0.31; all p > 0.05; electronic supplementary material, table S VII). Numeric asymmetry based on the relative adult group size and intergroup dominance rank did not significantly influence female participation (all p > 0.05; electronic supplementary material, tables S VII).

#### (b) Tufted capuchin monkeys

We recorded both the relative male group sizes and behaviour of at least one identifiable individual during 88 of the 115 observed encounters (76.5%). On average, we could determine the behaviour of 5.1 ± s.e. 3.2 individuals per encounter (range = 1–14), producing a total of 440 records of individual participation and/or flight behaviour.

Relative male group size was the only predictor of female participation included in the best-fit model, whether measured categorically (w0 = 0.68, ER = 2.89) or continuously (w0 = 0.72,
ER = 2.89). Males were more likely to participate when their group had a numerical advantage than when they had a numerical disadvantage (numerical advantage versus numerical disadvantage: 1.85 ± 0.52, RR = 1.33, t = 3.59, p < 0.001; figure 2a; electronic supplementary material, table SVIII); however, the male participation did not differ clearly between symmetric and asymmetric contests (even versus numerical advantage: −0.77 ± 0.86, RR = 0.93, t = −0.89, p = 0.37; even versus numerical disadvantage: 1.08 ± 0.82, RR = 1.33, t = 1.33, p = 0.18). Instead, males were sensitive to the absolute disparity in male group size (w asymmetry (continuous) = 1.00). Each incremental change in the asymmetry affected the probability of male participation, with male participation becoming more likely as the numerical odds increasingly favoured the focal group (asymmetry [continuous]: 0.45 ± 0.14, t = 3.24, p = 0.001; figure 2b; electronic supplementary material, table SVIII). This pattern of participation and defection was mirrored in the analysis of flight behaviour. Males were more likely to flee when their group was outnumbered than when the groups were evenly matched or the focal group had a numerical advantage (even versus numerical disadvantage: −1.96 ± 1.06, RR = 0.42, t = −1.85, p = 0.06; numerical disadvantage versus numerical advantage: −5.06 ± 0.88, RR = 0.03, t = 5.72, p < 0.001). For all asymmetries, no rank effects were apparent in the probability of participation (w rank = 0.24; electronic supplementary material, table SIX) or flight (subordinate versus dominant: −0.94 ± 0.59, RR = 0.48, t = −2.12, p = 0.03).

Overall, females were less likely to participate in intergroup aggression than males (males versus females: 1.74 ± 0.34, RR = 1.54, t = 5.09, p < 0.001). Yet the sexes did not differ in their sensitivities to the asymmetry in male group size (sex × asymmetry [continuous]: −0.12 ± 0.15, t = −0.85, p = 0.40), and the asymmetry in male group size was similarly the only variable included in the best-fit models predicting female participation, whether measured categorically (w0 = 0.74, ER = 2.83; even versus numerical disadvantage: 0.33 ± 0.80, RR = 1.25, t = 0.41, p = 0.68; numerical advantage versus numerical disadvantage: 1.82 ± 0.35, RR = 2.42, t = 5.13, p < 0.001; figure 2c; electronic supplementary material, table SX) or continuously (asymmetry: 0.49 ± 0.10, t = 4.84, p < 0.001, w0 = 0.74, ER = 3.86; figure 2d; electronic supplementary material, table SX). Like males, females were more likely to flee from an IGE when their group was at a numerical disadvantage, relative to encounters with a numerical advantage (numerical advantage versus numerical disadvantage: −6.28 ± 1.44, RR = 0.007, t = −4.34, p < 0.001; electronic supplementary material, table SX); however, low sample size prevented categorical comparisons of flight responses during symmetric contests. Rank effects on the probability of participation were not apparent in females (w rank = 0.22). Patterns of individual participation were best explained by the asymmetry in male group size rather than the asymmetry in total adult group size (ER = 10.48).

4 Discussion

Although relative group size may provide individuals with a means to assess the competitive ability of rivals, the distribution of this assessment strategy is unclear (table 1), in part because many other factors can affect individual participation [11,12,45,46,50]. Nevertheless, both black howler and tufted capuchin monkeys appear to assess numerical asymmetries in male group size in decisions to participate in intergroup contests. Vocal displays by both male and female black howler...
monkeys were longest when they encountered a neighbour with an equal number of resident males. In the absence of a clear dominance hierarchy among neighbouring groups (i.e. frequent undecided encounters and low directional consistency), these more prolonged displays may be necessary for rival groups with matching competitive abilities to assess one another [78]. Because individuals have both vocal and visual contact with opponents during IGEs in black howler monkeys, they can reliably assess the number of participants in a competing group and adjust their investment according to participation by group mates and opponents over the course of a single IGE and across different IGEs.

In contrast, among tufted capuchin monkeys, wherein the outcome of contests is reliably determined by relative male group size [6], the willingness of both males and females to participate systematically increased with increasing relative male group size. In contests with groups that were numerically superior, however, males and females were unlikely to participate, and almost invariably retreated if the opposing group had a surplus of two or more males (probability of winning to 15% or less [6]). Consequently, during encounters involving moderate asymmetry in male group sizes (i.e. difference in male group size of two or more), defection by any single male decreases the likelihood of winning by only 5–10% [6]. Given the high-intensity aggression during IGEs that is associated with unstable intergroup relationships [56], investing energy in chasing numerically inferior groups may serve as a low-cost mechanism to reinforce existing dominance relationships through intimidation [79]. In accordance with this suggestion, among white-faced capuchin monkeys (Cebus capucinus), in populations where stable intergroup dominance hierarchies are not apparent, numerical asymmetries do not appear to influence male participation [11]. When intergroup hierarchies, determined by the relative number of males and/or females [53], are pronounced, then individual strategies—albeit distinct from those of tufted capuchin monkeys—reflect numeric odds (table 1; [12]), suggesting that predictability of contest outcomes may mediate individual assessment strategies in capuchin monkeys.

While black howler and tufted capuchin monkeys show distinct responses to variation in numerical odds, within each species, males and females converge in assessment strategies of the relative costs of participation in collective group defence, despite the pay-off asymmetries that arise due to sex differences in parental investment and body size. These parallel responses most likely reflect the nature of the contested resources; in both black howler and tufted capuchin monkeys, reduced access to feeding resources due to encroachment by neighbouring groups is the primary threat, and both males and females compete to maintain long-term access to space and resources [6,64]. In contrast, in response to simulated

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**Figure 2.** Probability of participation in intergroup aggression by tufted capuchin monkeys. Male participation as a function of the asymmetry in male group size measured (a) categorically or (b) continuously. Female participation as a function of the asymmetry in male group size measured (c) categorically or (d) continuously.
intrusions by unfamiliar males (versus familiar males from neighbouring groups)—who are competing primarily with resident males over group membership and the corresponding access to reproductive opportunities, black howler monkeys demonstrated sex- and rank-based differences in patterns of numerical assessment (table 1; [8–10]).

Notably, although females participated in both species, individual assessments of the relative competitive ability of neighbours were based on male group size, and not on total adult group size, suggesting that the additional competitive ability conferred by adult female participation has little effect on the balance of power between competing groups in either species [80,81]. Nevertheless, female participation may be critical in stimulating resident males’ contribution to defence efforts given the potential collective action problem [42,82]. Among black howler monkeys, the vocal nature of group defence combined with high cohesion enables females to monitor the contribution or defection by resident males, and howling bouts last significantly longer (i.e. males howl for longer) when females join in the vocal display [58]. Similarly, participation during long-distance chases in capuchin monkeys may allow females to monitor male behaviour, thereby ensuring continued engagement by males (audience effect [11,83]), especially if participation in collective resource defence is being traded for mating access or social tolerance.

The sensitivity to numerical asymmetries displayed by both black howler and tufted capuchin monkeys suggests that—in these species—cooperative resource defence is not readily threatened by free-riders, rather individuals adjust their levels of participation to the expected cost–benefit trade-offs. In black howler monkeys, the free-riding problem associated with collective group defence is primarily overcome because of asymmetric distribution of benefits that accrue to different males [57]; the most active participants (sire males) are those that benefit the most at the least cost (cf. ‘privileged groups’ [42]). As such, collective group defence in black howler monkeys may have evolved principally through mutualism; individuals can accrue higher benefits through coordinated group defence as the joint activities of several individuals may be more effective than the lone action of a single individual (i.e. by-product mutualism [84]). Similarly, among tufted capuchin monkeys, dominant males are the preferred sociosexual partner [62,76,85,86]; yet, despite these asymmetric benefits to male reproductive success, no rank effects are apparent. High levels of participation by subordinate males may nevertheless be maintained if resident males gain benefits through inclusive fitness [87] or through reproductive queuing and delayed reciprocity (cf. cooperative breeders [88]). To date, few studies of intergroup contests have examined the individual differences in contribution to collective defence in relation to a wide range of pay-off asymmetries that may exist among group members [39,46]. Such analyses are crucial to understand whether interspecific variation in the utility of numerical asymmetries reflects patterns of defection and free-riding (cf. unconditional laggards in lions [25]) or the correlation between the number of privileged individuals within the group and relative group size.

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