**Effects of group size and contest location on the outcome and intensity
of intergroup contests in wild blue monkeys**

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Intergroup contests determine access to resources and influence the evolution of group living in social species. Asymmetries in resource holding potential and payoffs should influence the outcome and intensity of such contests. We evaluated predictors of contest outcome and intensity using data collected over 40 months from 6 groups of wild blue monkeys (*Cercopithecus mitis*). We found increased odds of winning when a group was larger than and used the contest site more than its opponent, and when contests occurred closer to its home range center while farther from the opponent's center. However, a larger difference in group size (across five pairs of opposing groups) did not predict a greater proportion of contests won by the larger group. Some evidence suggested increased odds of a draw when group sizes were more similar. Additionally, contests were longer and more aggressive when groups were more similar in size and when the contest site was similarly central in both groups' home ranges. Contests were also more aggressive when the opposing groups' use of the contest site was more similar. Overall, asymmetries in resource holding potential (i.e. group size) and/or payoffs related to the contest's location influenced a group's competitive advantage, the likelihood of a draw, and the intensity of intergroup contests. Although comparable data are limited, it seems clear that both types of asymmetries can play a role in determining the outcome and intensity of intergroup contests, and that the relative power of each may vary across species.

KEYWORDS: Intergroup agonism; intergroup dominance; between-group competition; resource holding potential; payoff asymmetries; territoriality; space use

In group-living animals, the outcomes of intergroup contests determine access to vital resources such as food, mates, and refuge. Game theory models of animal contests predict that competitive outcomes may reflect asymmetries between contestants in resource holding potential (RHP), in the payoffs gained by winning, or in both (Hammerstein, 1981; Baker, 1983; Enquist & Leimar, 1987; Riechert, 1998). In the context of intergroup contests, group size is a commonly used measure of RHP, and numerical superiority increases a group's chances of winning in various taxa (Sillero-Zubiri & Macdonald, 1998; Kitchen et al., 2004; Palmer, 2004; Radford & du Plessis, 2004; Benadi et al., 2008; Crofoot et al., 2008; Mosser & Packer, 2009; Harris, 2010; Markham et al., 2012; Scarry, 2013; Cassidy et al., 2015). However, larger groups do not always prevail because payoff asymmetries can overwhelm asymmetries in RHP (Hammerstein, 1981; Riechert, 1998; Crofoot et al., 2008; Markham et al., 2012; Scarry, 2013).

Payoff asymmetries may relate to the relative frequency of use of a contest site by opposing groups if each group uses particular areas of its home range proportionally to how much it values those areas. Such a correlation could arise if certain areas contain critical resources or preferred habitat. In addition, unequal use may drive information asymmetries that influence how much each group values an area (Enquist & Leimar, 1987). For example, repeated use of an area could provide knowledge that enhances foraging efficiency or predator avoidance (Crofoot et al., 2008; Tinbergen, 1957). Location-based payoff asymmetries may affect competitive outcomes if groups are more motivated to persist or take risks when contests occur in areas that they value more than their opponent does (Enquist & Leimar, 1987). Differential use of an area, perhaps over extended periods of varying length, may indicate a site's relative value to opposing groups. Yellow baboon (*Papio cynocephalus*) groups, for example, were more likely to win contests in areas they used more heavily than an opponent group during the 9-12

month period before a contest, though not when frequency of use was calculated over a 3-6 month period only (Markham et al., 2012). Familiarity with an area, resulting from frequent use, may also directly influence a group's competitive ability (Harris, 2010).

Payoff asymmetries might also relate to a contest's location relative to the center vs. periphery of opposing groups' home ranges. If a group values the center of its home range more than the peripheries, a payoff gradient may occur along an edge-center axis. Defense of central areas may yield higher payoffs than defense of peripheral areas if groups spend more time in home range centers, if centers contain more resources or a discrete resource such as a nest or refuge, and/or if intraspecific competition at peripheries decreases the value of such areas (Ydenberg et al., 1986; Giraldeau & Ydenberg, 1987; Stewart et al., 1997; Crofoot et al., 2008). Additionally, territory centers may be more valuable to animals if the loss of the territory center to a competitor is more likely to result in the loss of the whole territory, compared to the loss of an equal-sized area at the periphery (Giraldeau & Ydenberg, 1987). For example, white-faced capuchin (*Cebus capucinus*) groups have greater odds of winning contests that occur closer to the center of their home range (Crofoot et al., 2008).

In principle, certain location-based outcomes could also reflect arbitrary conventions that settle conflicts (Hammerstein, 1981; Kokko et al., 2006). Some animals demonstrate "ownership" conventions for portable resources, such that one individual will "respect" (i.e., not challenge) a conspecific's possession of an object, such as a food object, regardless of relative dominance status (Kummer & Cords, 1991). In a similar way, contesting individuals or groups may behave as if particular areas of habitat "belong" to one or the other. In two-player contests of this sort, the first to arrive at a given contest location appears to gain a "psychological" competitive advantage, even in the absence of payoff asymmetries (i.e., the "prior-residence

effect”; Kokko et al., 2006). For example, when researchers manipulated the location of repeated contests involving pairs of male dart-poison frogs (*Dendrobates pumilio*), a territory resident generally defeated an intruder, even if he had been defeated by the same opponent in a prior contest on the opponent’s territory (Baugh & Forester, 1994). Arbitrary conventions in the context of territorial contests may be exemplified by extremely stable territory boundaries, as reported in several taxa (Klopfer & Jolly, 1970; Janes, 1984; Greenberg & Gradwohl, 1986; Price et al., 1986). Opposing individuals or groups may respect landmarks as indicators of territory boundaries because landmarks provide a visual cue that is obvious to both parties (Mesterton-Gibbons & Adams, 2003).

While empirical studies often focus on factors that predict contest wins vs. losses, “draws” are a type of competitive outcome that has been largely ignored. Draws should be more likely when the cost of continued fighting to both parties equals or exceeds the benefit of obtaining or maintaining exclusive access to a resource (Papaj & Messing, 1998; Preuschoft & Paul, 2000). If groups with greater RHP and location-based payoffs have increased odds of winning contests, intergroup contests should be more likely to end in a draw when opposing groups have similar RHPs and payoffs. In chacma baboons (*Papio cynocephalus ursinus*), for example, some evidence suggests that draws are more likely when groups have similar numbers of males and when contests occur in areas of high intergroup range overlap (Kitchen et al., 2004).

Asymmetries in RHP and payoffs may influence not only the outcome but also the intensity (i.e., duration and/or level of aggression) of intergroup contests. To date, only a few studies have examined the factors affecting intergroup contest intensity. Contest duration and the degree or probability of aggressive escalation may increase when RHP or payoffs to opponents

are more similar, according to predictions based on game theory (Riechert, 1998; Radford & du Plessis, 2004). When RHP is more similar, groups may have a harder time assessing their relative competitive power, leading to increased contest intensity. Likewise, if opponents have similar payoffs, they may also have similar motivation to escalate aggression. Thus, contests increase in intensity because neither rival concedes. In contrast to game theory models, however, contestants in some species escalate contests when they have greater RHP than their opponents (Rohwer, 1975; Keys & Rothstein, 1991; Silk, 2002; Wilson et al., 2012). Individuals or groups may use their superior RHP to intimidate an opponent when they are in an advantageous position, thus reducing the occurrence of future contests and their associated costs.

In this study, we examined intergroup contests in a population of blue monkeys (*Cercopithecus mitis*). These forest-dwelling monkeys live in groups that typically comprise one adult male, multiple philopatric females, and young. In high- and intermediate-density populations, neighboring groups show variable degrees of home range overlap and interact with each other regularly. These interactions often occur at feeding sites, are typically antagonistic, and involve primarily the females (Rudran, 1978; Cords, 2002; 2007; Payne et al., 2003). By contrast, in a low-density population in Uganda, groups have not been reported within 500 m of each other, and it is possible that intergroup contests do not occur (Butynski, 1990). While the determinants of which group wins contests have not been investigated systematically, group fissions suggest that group size differences play a role in between-group competition, at least over the long run: after a fission, new daughter groups fight frequently, and the larger daughter group invariably acquires a larger portion of the original home range (Cords, 2012).

We aimed to identify the factors affecting contest outcome and intensity in a high-density population of blue monkeys using an extensive data set (864 contests over 39 months). We

predicted that a group would have increased odds of winning (1) when it was larger than its opponent, (2) had used the contest site more frequently than its opponent prior to the contest (i.e., had higher “site occupancy”), and (3) when the contest occurred closer to the center of its home range while farther from the opponent’s center. We assessed multiple time periods of prior site occupancy (1, 3, and 6 months before a contest) because we did not know *a priori* which might be most relevant to the animals themselves. If the value of a resource corresponds with the length of time that it has been used and defended, and value predicts a group’s odds of winning a contest (Bradbury & Vehrencamp, 1998), evaluating site occupancy over a longer period should provide stronger results (e.g., Markham et al., 2012). It also seems possible, however, that animals would emphasize more recent use when assessing the value of a contest site, as short-term use is likely to be tied to current resources more strongly than long-term use.

Additionally, we predicted that the odds of a draw would be higher (1) when groups were more similar in size, (2) when site occupancy was more symmetrical, and (3) when contests occurred at sites that were similarly central in both groups’ home ranges. As before, we evaluated site occupancy for multiple periods before each contest.

Finally, we looked beyond contest outcomes to two measures of contest intensity: duration of the contest and level of aggression. We predicted that contest duration and level of aggression would increase (1) when groups were more similar in size, (2) with greater symmetry in frequency of use of the contest site, and (3) when the contest site was similarly central in both groups’ home ranges. We again examined site occupancy over multiple time frames.

METHODS

Study Population

We studied six groups of blue monkeys (*Cercopithecus mitis stuhlmanni*) inhabiting the Kakamega Forest, Kenya. This rainforest (ca. 2000 mm annual rainfall; Mitchell et al., 2009) supports a high-density population (ca. 170-220 individuals/km²; Fashing & Cords, 2000) which has been studied for >35 years (Cords, 2012). There is substantial home range overlap, with a group sharing as much as 50% of its annual home range with neighboring groups (Cords, 2002; 2007). Nevertheless, descriptive accounts suggest groups defend stable territorial boundaries (Cords, 2002), with overlapping ranges occurring when groups trespass undetected by their neighbors.

As part of the long-term study of individually identified animals, a team of field assistants (including MC) followed each study group on a near-daily basis, with follows lasting from 1-11 hours/group/day across a 40 month period (September 2010 through December 2013). On each day, observers recorded the presence of each group member they detected, and these records allowed us to assess daily group size. Observers sometimes missed seeing all group members because they were typically dispersed in the thick foliage of the forested environment. When there were gaps in the record for any female or for any juvenile male <7 years old, we assumed that the animal was present during the gap because females are strictly philopatric, never leaving their natal group, and males typically emigrate as sub-adults at the age of 7 years (Ekernas & Cords, 2007). We did not make such an assumption for males $\geq$ 7 years old. The mean total size of the six study groups varied from 9.1-49.8 individuals. In conjunction with long-term reproductive records, we also knew the age of each group member present on any given day. We could thus specify the number of individuals in particular age-sex classes, such as the total number of non-infant females and the total number of females older than 5 years.

Intergroup Contests

While following the study groups, the observer team recorded the location, duration (in minutes), level of aggression, and outcome (win, loss, draw) of all intergroup contests they detected. We defined an intergroup contest as any occasion on which individuals of at least one group responded, invariably agonistically, to members of another group. Such responses included unilateral retreat, vocalizations (alarm and threat), non-vocal threats, chasing, and occasionally contact aggression (pushing, grabbing, biting). Adult (parous) and old juvenile (≥ 5 years) females are the main participants in these contests, although other group members occasionally join in (Cords, 2007). The group's adult male rarely participates in intergroup contests, and in the exceptional cases, his involvement is usually brief (Cords, 2007).

When an intergroup contest occurred, observers noted its start time according to their perception of typical behavioural responses (as noted above) of their focal group or the opposing group. They also noted the contest's location on a 50 m x 50 m gridded map of the study area and scored the maximum level of aggression on an ordinal scale. From least to most aggressive, categories included: (1) contests in which one group silently retreated from another's approach, even though there had been no vocalizations or other threats (level 1 aggression); (2) contests with unilateral vocalizations only (level 2); (3) contests with bilateral vocalizations only (level 3); (4) contests including both vocal and non-vocal threats (but no phalanxes) or vocal threats only if one group fled (level 4); (5) contests in which group members formed shoulder-to-shoulder opposing phalanxes, always with vocal threats, but no contact aggression (level 5); and (6) contests with contact aggression (level 6). Observers also noted contest end time, which we defined as the cessation of all responses of the opposing groups for at least 10 minutes. A group might engage in more than one contest with a given opponent on a single day: in our sample, $33 \pm 23\%$ ($X \pm SD$) of contests per group-pair occurred on days when there were other contests with

the same opponent, but only 12% of these occurred at the same location *and* within one hour of each other. We recorded a group as losing a contest if it retreated from the contest site and winning if the opposing group retreated within 10 minutes of the last agonistic interaction (most responses were immediate). If aggression ceased and neither group retreated, or both retreated simultaneously, we recorded the outcome as a draw.

Because we needed to assess relative site occupancy of an area at least 1 month prior to a contest occurring at that location, we used 39 months (October 2010 through December 2013) of intergroup contest records in our analyses. In this period, we recorded 1436 intergroup contests involving at least one study group. However, we limited analyses to the 864 contests in which both opponents were study groups, as it was only for these groups that we had sufficient records of group composition and ranging patterns for our analyses. We also wanted to ensure that observer presence did not affect contest outcome (unhabituated non-study groups sometimes fled from observers).

Home Range Use

To quantify home range use, we used location records associated with focal animal samples that were part of the long-term behavioural monitoring. The field team collected focal samples on adult females on each observation day, never repeating a given individual on a given day, and balancing by individual across the morning, midday, and afternoon hours. Home ranges were fairly small, ca. 49 ha ($X \pm SD$: 195.5 ± 59.5 grid cells, range: 121-270, $N = 6$), and observers located groups by starting at the edge of the home range closest to the last group sighting and crisscrossing the area (using established trails) until the animals were located. This search procedure made it unlikely that location records were biased toward the home range center. At the end of each 30 minute sample, the observer recorded the 50 m x 50 m mapped grid

cell occupied by the focal subject. We recorded 32 514 location records over the course of the study, with a mean $\pm$ SD of 4.9 ± 2.1 observations per group per day on days where the group was observed (GN group: 7421 total records, $X \pm$ SD (Range) = 6.7 ± 2.5 (1-15) per day; GSAA group: 5869 total, 5.1 ± 2.5 (1-13) per day; GSB group: 1574 total, 2.1 ± 0.9 (1-4) per day; GSC group: 4735 total, 4.2 ± 2.3 (1-13) per day; TWN group: 3708 total, 3.3 ± 1.7 (1-9) per day; TWS group: 9207 total, 7.7 ± 3.4 (1-20) per day). We used these location records to identify each group's home range, including any grid cell that was occupied at least once. We did not include unoccupied cells as part of a group's home range, even when they were completely surrounded by occupied cells. Such cells were rare ($X \pm$ SD: 1.3 ± 2.0 cells per home range, range: 0-5, $N = 6$). Five of six islands of non-use included just a single cell, and all six occurred 1 grid cell in from the home range edge.

To assess site occupancy, we calculated the proportion of location scores for a given group in each grid cell of its home range. As observers occasionally specified a grid cell location on the boundary of 2 or 4 cells, we weighted the observations accordingly: that is, we gave a weight of 0.5 to each cell if a location record was on the boundary of 2 cells and a weight of 0.25 if the record was on the common point of 4 cells. We compiled site occupancy records for periods of 1, 3, and 6 months before each intergroup contest, with the earliest records of site occupancy occurring 1 month before the first contest in our data set. Data sets decreased in size as the time frame for assessing site occupancy increased.

Position of Contest Site on an Edge-center Axis

The home ranges we measured were generally consistent across the years of study, with 22-50% of grid cells differing between years ($N = 2$ pairs of years compared in each of 6 groups; we used only data from full years, 2011-2013, for this comparison). We therefore used a

composite home range spanning the entire study period when we identified where the grid cell of a given intergroup contest was located on an edge-center axis. We chose to assess distance from home range edge rather than distance from home range center because the irregular shapes of some groups' home ranges made it easier to assess the edge unambiguously. Furthermore, using distance from the edge allowed us to assess the relative distance of invasion of both groups into each other's home ranges (see Data Analysis, "relative edge score"). Assessing distance from the center would not have permitted this assessment.

We assigned an "edge score" to grid cells in and around a group's home range based on the cell's distance from the home range boundary, measured in terms of grid cells (Fig. S1). Specifically, we defined a boundary cell as any cell within the home range that shared a flat edge with a cell that was not part of the home range (i.e., a cell with no location record): boundary cells received an edge score of zero. We assigned progressively more positive edge scores to cells inside the home range as their distance from the boundary increased. For example, we scored cells inside the home range as +1 if they shared a flat edge with at least one boundary cell, +2 if they shared a flat edge with +1 cells, and so on. Thus, cells that were closer to the center of a group's home range had higher edge scores. Scores for cells outside the home range became progressively more negative as their distance from the boundary increased. For example, we assigned scores of -1 to cells outside the home range that shared a flat edge with one or more boundary cells, -2 if they shared a flat edge with -1 cells, and so on. Intergroup contests occurred outside a group's home range on rare occasions. Such records could reflect the fact that (1) our method of specifying home ranges provided an *approximation* (based on location records), and/or that (2) home range is defined as the area in which normal daily activities occur (i.e.,

foraging, mating, rearing young; Burt, 1943), whereas at least some of the contests represent unusual events that occurred outside of a group's home range.

This research was entirely noninvasive and was carried out with approval from the Institutional Animal Care and Use Committee of Columbia University (protocols AAAB0178 and AAAD9003).

Data Analysis

In all of our analyses, predictors included difference in group size, difference in edge score, and difference in site occupancy. We calculated these differences using the perspective of a randomly assigned analytical focal group for one dependent variable (win vs. loss), and the absolute value of the difference for the other dependent variables (draw vs. decided, contest duration, and level of aggression). We calculated relative site occupancy for periods of 1, 3, and 6 months before an intergroup contest and ran separate analyses to see how these different time frames affected our results. To facilitate interpretations, we centered all predictor variables by subtracting their mean values (Schiegg, 2010).

For each dependent variable, we created a model containing the three predictor variables and all possible two-way interactions. To evaluate alternative plausible (and correlated) measures of relative group size (i.e., difference in total group size, difference in the number of females excluding infants, and difference in the number of adult females combined with the number of old juvenile females ("adult plus old juvenile females")), we used second-order Akaike Information Criteria (AICc) values to assess which measure provided the best fit model. For this purpose, we used the largest data sets (when relative site occupancy was calculated over a 1-month time frame). We used the same group size variable in subsequent analyses in which relative site occupancy was collated over 3 and 6 months. We calculated variance inflation

factors (VIFs) to assess collinearity in each of our models. In all instances, VIFs were low (1.00-1.33).

We used likelihood ratio tests to compare each final model to a model with no fixed effects or interactions, thus verifying the statistical significance of the final model; we expected significant differences. We describe specific models for each dependent variable below.

Win vs. loss: To analyse factors that predicted a group's odds of winning vs. losing, we included only intergroup contests in which the outcome was decided. We used conditional logistic regression (Stata 13.1), with data clustered by the identity of the two interacting groups ($N = 5$ unique "group-pairs," each with multiple contests). Within each cluster, we randomly assigned one group as the focal group for all contests. Conditional logistic regression is sensitive to variation within each cluster and accounts for unmeasured factors that are constant for each group-pair that may affect which group wins. Particularly, it does not assume that model intercepts (i.e., unmeasured group-pair specific factors that may influence the dependent variable) are independent of predictors, and thus prevents the possibility that such factors confound the predictors' effects.

We also examined whether greater average discrepancies in group size were associated with larger win-loss asymmetries across the 5 group-pairs. Here, we calculated the average difference in the number of adult plus old juvenile females for each group-pair, as well as the proportion of decided contests in which the larger group won, using data from the entire study period. In four of five group-pairs, one group was consistently larger than its opponent. In the remaining case, each group had a numerical advantage at different times. We split the data for this group-pair into two sets of contests to reflect this inconsistency.

Draw vs. decided: We used a similar approach to the win-loss analyses to assess which factors predicted the odds that a contest ended in a draw. Because there was no asymmetry in the roles played by opposing groups in a draw – i.e., both groups either retreated simultaneously or held their position – there was no need to assign a focal group to each contest, and we calculated relative group size, relative site occupancy, and relative edge score as the absolute value of the difference between the two groups' values. Otherwise, we followed the same procedure as described above for conditional logistic regression analyses of win-loss outcomes.

Contest duration: To analyse variation in contest duration (a continuously varying dependent variable), we ran generalized linear mixed models in Stata 13.1. Again, we used the absolute value of differences in group size, site occupancy, and edge score as predictors. We also included group-pair as a random effect to account for variation among group-pairs and repeated measures within each such pair. To reduce the effect of outliers, we transformed the dependent variable, taking the log of one plus the recorded duration.

Level of aggression: Level of aggression was an ordinal dependent variable, so we used the ordered logit regression `meglm` function in Stata 13.1, with ordinal family and logit link function. Here again, the predictors were absolute value of differences in group size, site occupancy, and edge score, and we included group-pair as a random effect.

RESULTS

Win vs. Loss

Across all pairs of interacting groups, both groups won at least some of the contests; for the group that won more often, the mean percentage of wins was 69% (range: 57-93% across 5 group-pairs, with 3-218 contests each). For win vs. loss models, the group size variable that produced the best fit model was the number of adult plus old juvenile females (Table 1).

When we examined site occupancy prior to a contest, all final models differed significantly from null models (likelihood ratio tests: 1-month: $\chi^2 = 56.93$, $P < 0.001$; 3-month: $\chi^2 = 57.93$, $P < 0.001$; 6-month: $\chi^2 = 38.28$, $P < 0.001$). However, we found that the different time frames for assessing site occupancy produced somewhat different outcomes. For 1 or 3 months of site occupancy, groups had greater odds of winning when they contained more adult plus old juvenile females than their opponent, used the contest site more frequently than their opponent, and when contests occurred closer to the center of their home range and farther from the center of the opponent's home range (Table 2; Fig. 1). The two location measures, difference in site occupancy and difference in edge score, were not strongly correlated (Pearson $r = 0.292$, $N = 864$). For models based on 1-month site occupancy, there was also a significant interaction effect: the effect of relative edge score on the odds of winning decreased when groups diverged more in the number of adult plus old juvenile females (Table 2). This same interaction was almost significant for 3 months of site occupancy. For 6 months of site occupancy, results were similar, except that relative group size was no longer a significant predictor, and there was no interaction effect between relative edge score and relative group size.

Across group-pairs, the difference in the number of adult plus old juvenile females was unrelated to the proportion of decided contests in which the larger of the two groups won (Pearson $r = -0.193$, $N = 6$, 2-tailed $P = 0.714$). That proportion was less than 50% for half of the six data points. In the group-pair where numerical advantage was inconsistent over time, one group (GSAA) was more likely to win regardless of whether it had the numerical advantage. These findings show that at another level of analysis (i.e., when one compares different group-pairs), asymmetries in group size had a limited effect in predicting which group won most often.

Draw vs. Decided

Overall, 421 of 823 (51%) intergroup contests ended in a draw, and the percentage of draws ranged from 39% to 57% across the 5 group-pairs ($N = 7$ -498 contests each). In a comparison of different group size variables, the best fit model for this data set included the difference in total group size (Table 1).

The odds of a draw increased when groups were more similar in total size, no matter which time frame we used to assess site occupancy (Table 3; Fig. 2). However, models were not significantly different from a null model for any time frame (1-month: $\chi^2 = 9.16$, $P = 0.165$; 3-month: $\chi^2 = 9.97$, $P = 0.126$; 6-month: $\chi^2 = 9.55$, $P = 0.145$). Given these results, we conducted post-hoc univariate analyses to assess the effect of relative group size on the odds of a draw, using datasets for 1-, 3-, and 6-month relative site occupancy. In each case, contests had significantly lower odds of ending in a draw when there were larger differences in group size (odds ratios: 0.092 – 0.093, Wald $P < 0.03$), and all models differed significantly from null models (1-month: $\chi^2 = 6.17$, $P = 0.013$; 3-month: $\chi^2 = 6.31$, $P = 0.012$; 6-month: $\chi^2 = 5.26$, $P = 0.022$).

Contest Duration

Overall, the mean $\pm$ SD duration of intergroup contests was 28.4 ± 24.0 min (range: 1-175, $N = 848$), with averages across the 5 group-pairs ranging from 18.8 ± 16.6 to 31.7 ± 26.5 min ($N = 7$ -513 contests each). For models of contest duration, the group size variable that produced the best fit model was the difference in number of adult plus old juvenile females (Table 1).

Contests were longer when groups had more similar numbers of adult plus old juvenile females, and this result held for all three site occupancy time frames (Table 4). When we assessed site occupancy for periods of 1 and 3 months before a contest, contests were also longer

when the contest site was similarly central in both groups' home ranges. However, the final model differed significantly from the null model only for the 1-month time frame (1-month: $\chi^2 = 16.56$, $P = 0.011$; 3-month: $\chi^2 = 12.36$, $P = 0.055$; 6-month: $\chi^2 = 10.57$, $P = 0.103$).

Level of Aggression

While contests included all levels of aggression, the intermediate levels were more common. The median score across group-pairs was 4 ($N = 857$), and contests were distributed as follows: 1% at level 1 (silent retreat), 10% at level 2 (unilateral vocalizations), 19% at level 3 (bilateral vocalizations), 41% at level 4 (vocal and non-vocal threats), 16% at level 5 (phalanxes), and 13% at level 6 (contact aggression). The median level of aggression for each group-pair was also 4 ($N = 7\text{-}519$ contests per group-pair). For models of aggression level, the group size variable in the best-fit model was the relative number of adult plus old juvenile females (Table 1).

No matter which time frame we used to assess site occupancy, contests reached higher levels of aggression when opposing groups had more similar numbers of adult plus old juvenile females and when the contest site was similarly central in both groups' home ranges (Table 5). The effect of asymmetries in site occupancy, however, depended on the time frame: when we assessed site occupancy for a period of 1 month before a contest, contests between groups with more similar site occupancy reached higher aggressive levels. By contrast, relative site occupancy for periods of 3 and 6 months before a contest did not predict level of aggression on its own (Table 5). When we assessed site occupancy for a period of 6 months before a contest, however, there was a significant interaction between relative site occupancy and relative edge score, such that the effect of relative site occupancy on the level of aggression decreased as relative edge score increased. Likelihood ratio tests revealed significant differences between our

final and null models for all time frames that we used to assess site occupancy (1-month: $\chi^2 = 19.71$, $P = 0.003$; 3-month: $\chi^2 = 14.95$, $P = 0.021$; 6-month: $\chi^2 = 15.41$, $P = 0.009$).

DISCUSSION

Overall, we found that RHP and/or location-based payoff asymmetries predicted the outcome (win, loss, draw) and intensity (contest duration and level of aggression) of between-group contests in blue monkeys. Groups generally had greater odds of winning when they were larger than their opponent, used the contest site more than their opponent, and when the contest occurred closer to the center of their home range while farther from the opponent's center. Similarly, intergroup contests had greater odds of ending in a draw when groups were more similar in size. Contests were generally longer and more aggressive when groups were more similar in size and when contests occurred at sites that were similarly central in both groups' home ranges. Additionally, contests were more aggressive when the opposing groups used the contest site to similar degrees in the month prior to the contest. Overall, these findings matched our predictions.

Win vs. Loss

The fact that winning depended on asymmetries in both RHP and location-based payoffs suggests that blue monkey groups exhibit "partial site-dependent dominance" (Brown & Crofoot, 2013). In addition, the fact that the relative number of adult plus old juvenile females produced the best fit model supports previous reports that these individuals are the primary participants in intergroup contests (Cords, 2007).

Other studies have documented how asymmetries in RHP influence a group's competitive advantage (e.g., McComb et al., 1994; Sillero-Zubiri & Macdonald, 1998; Palmer, 2004; Benadi et al., 2008; Mosser & Packer, 2009; Cassidy et al., 2015). Only a few, however,

have considered whether a group's competitive advantage reflects *both* RHP and payoff asymmetries. In chacma baboons, yellow baboons, white-faced capuchins, and green woodhoopoes (*Phoeniculus purpureus*), both superior RHP and location-based payoff asymmetries increase a group's chance of winning contests (Kitchen et al., 2004; Radford & du Plessis, 2004; Crofoot et al., 2008; Markham et al., 2012).

In blue monkeys, the contest location variables, reflecting differences between groups in occupancy of a contest site and its position on an edge-center axis in the two home ranges, were more consistently important predictors of wins and losses than numerical superiority. It is possible that location-based payoff asymmetries overshadowed the effects of asymmetries in RHP when site occupancy was assessed over a longer period (6 months). In addition, data pooled for each group-pair across the entire study period suggested limits on the effects of group size differences at another level of analysis: there was no relationship between the average difference in group size and the proportion of decided contests won by the larger group. In fact, the larger group won less than half of the decided contests in half of the group-pairs. These results contrast with the finding that relative group size generally predicted the winner of intergroup contests *within* a group-pair, suggesting that there are likely to be other unmeasured factors, specific to the group-pairs, that influence how group-size asymmetries affect the odds of winning. Such factors might include physical strength, experience, or the personalities of individual group members, which could influence their participation in contests. In gray wolves (*Canis lupus*), pack composition can diminish the effects of relative pack size (Cassidy et al., 2015). Specifically, smaller packs that contain more old individuals or more males occasionally defeat larger packs. Packs with older animals may have an advantage because these pack members are more experienced, and packs with more males probably contain more aggressively motivated

individuals (Cassidy et al., 2015). Future work might help determine what untested factors are important for different group-pairs of blue monkeys.

While numerical superiority and relative site occupancy also predicted a group's competitive advantage in yellow baboons, differences in group size seemed to have a more consistent effect than contest location on the winner of intergroup contests (Markham et al., 2012), contrary to the pattern in blue monkeys. Baboon groups were more likely to win if they had used the contest site more heavily than their opponent for a period of 9 or 12 months before the contest, but not if they had used the site more frequently for 3 or 6 months before the contest (Markham et al., 2012). For blue monkeys, the time frame used to assess site occupancy did not affect its importance in predicting wins vs. losses, suggesting that blue monkeys value areas of both short- and long-term use. These dissimilarities in the relative importance of group size and site occupancy coincide with species differences in territoriality. Specifically, yellow baboons are non-territorial, with groups showing extensive home range overlap (Markham et al., 2012; 2013), whereas blue monkeys in East Africa are reported to be territorial (Cords, 2002; 2007). This comparison matches the expectation that location-based payoff asymmetries should play a greater role than relative RHP in predicting a group's competitive advantage for territorial species, while relative RHP should be more important than location-based payoff asymmetries for non-territorial species (Sugiura et al., 2000; for a possible exception, however, see Cassidy et al., 2015).

The effects of the two measures of location-based payoff asymmetries were independent in our study, as relative site occupancy and relative edge score were not strongly correlated. In other words, blue monkeys do not have greater odds of winning intergroup contests that occur closer to their home range center because of high frequency of use of this area. Instead, payoff

asymmetries possibly arise because resource value at home range peripheries is reduced by competition with neighboring groups, or home range centers may contain higher densities of resources than peripheries. Crofoot et al. (2008) proposed a similar explanation for white-faced capuchin groups that had greater odds of winning contests in home range centers.

When we considered site occupancy for just 1 month before a contest we saw an interaction effect, such that smaller groups were more likely to defeat larger groups when contests occurred closer to the center of their home range, but less able to win at sites that were similarly central to both groups' home ranges. Furthermore, larger groups could defeat smaller groups even in the center of the smaller groups' home ranges if their numerical superiority was substantial enough. A similar pattern occurs in white-faced and tufted capuchins (*Sapajus nigritus*; Crofoot et al., 2008; Scarry, 2013). In white-faced capuchins, this pattern seems to result from a collective action problem at home range peripheries: capuchins appear to value the center of their home range more than the edges, increasing the likelihood that individuals will not participate in contests that occur near home range peripheries (Crofoot et al., 2008; Crofoot & Gilby, 2012). Thus, numerical odds are effectively more symmetrical when a contest occurs closer to the center of the smaller group's home range and farther from the home range center of the larger group (Crofoot & Gilby, 2012). The possibility that blue monkeys also experience a collective action problem at home range peripheries merits further study.

Draw vs. Decided

If group size reflects RHP and superior RHP confers a competitive advantage, the increased odds of a draw when opponent groups were more similar in size is consistent with the idea that more evenly matched groups should have a harder time reaching a decided outcome. Comparable results are limited but suggest similar patterns in other taxa. Kitchen et al. (2004)

found that a subset of contests between two chacma baboon groups were more likely to end in a draw when groups had more similar numbers of males. Furthermore, dyadic contests between male Barbary macaques (*Macaca sylvanus*) were more likely to end in a draw when individuals had more similar RHPs (Preuschoft & Paul, 2000). Although not all group members participate in intergroup contests in blue monkeys (Cords, 2007), our finding that difference in total group size provided the best fit model suggests that all group members together provide a visual cue of RHP to the opposing group.

Contest Duration

Game theory predicts that a larger difference in RHP should lead to a quicker settlement of disputes. Our finding that contests were shorter when groups were more discrepant in size matches these predictions, as well as patterns in other species (reviewed in Riechert, 1998). In green woodhoopoes, for example, the length of short (<5 min) intergroup vocal rallies increases when groups are more similar in size (Radford & du Plessis, 2004). Furthermore, the fact that the relative number of adult plus old juvenile females was the best group size variable for models of contest duration (as well as wins vs. losses) is consistent with previous research showing that these individuals are the main participants in intergroup contests (Cords, 2007).

The finding that contests were shorter with greater asymmetries in edge score is expected if a group values the periphery of its home range less than the center, and is therefore likely to retreat sooner from contests in more peripheral locations. When the contest site is similarly central in both groups' home ranges, however, opposing groups should place equal value on the area, and should be similarly likely to retreat or concede. This situation would thus increase contest duration.

Level of Aggression

Similar to the results for contest duration, we found that intergroup contests were more aggressive when groups were more similar in size. Also similar to models for contest duration, and to models for wins vs. losses, the fact that the relative number of adult plus old juvenile females produced the best fit models for level of aggression reaffirms the notion that these individuals are the primary participants in intergroup contests (Cords, 2007). Groups of more similar size may have a harder time visually assessing numerical advantage, causing them to resort to increased aggression. A similar positive correlation between RHP symmetry and aggressive level occurs in dyadic contests in other species, including male house sparrows (*Passer domesticus*), velvet swimming crabs (*Necora puber*), and jumping spiders (*Euophrys parvula*; Møller, 1987; Wells, 1988; Smith et al., 1994). Some group-living species show the opposite pattern, however. For example, parties of male chimpanzees (*Pan troglodytes*) are more likely to escalate contests if they outnumber opponents from a neighboring community (Wilson et al., 2012). By harassing a smaller group when it has a more marked numerical advantage, a larger group may reinforce dominance over its opponent and ultimately reduce net energetic costs by reducing the frequency or intensity of future contests. Unlike intergroup contests in blue monkeys that are rarely, if ever, lethal, parties of male chimpanzees benefit when an opponent group is much smaller because they can then commit lethal attacks, which gives them even greater advantages in future contests (Wilson & Wrangham, 2003). This apparent difference in the ability to kill conspecific opponents may explain the differences between patterns of escalation in blue monkeys and chimpanzees. Lastly, there are other species that show no relationship between group size asymmetry and escalated aggression: groups of chestnut-crowned babblers (*Pomatostomus ruficeps*) are more likely to *approach* neighboring groups

when they have the numerical advantage, but group size does not predict the probability that an encounter escalates to fighting (Sorato et al., 2015).

Contests were also more aggressive when the opposing groups used the contest site (in the previous month) to a similar extent, and when the site was similarly central in both groups' home ranges. These patterns may occur because opponents value such sites equally, making both groups less likely to retreat or concede than they would be in cases where large location-based payoff asymmetries exist, thus increasing the level of aggression. The negative interaction between relative site occupancy and relative edge score suggests that the importance of each predictor decreases with an increase in the other, at least when site occupancy is based on the 6 months preceding a contest.

Conclusion

This study demonstrates that RHP and/or location-based payoff asymmetries can predict the outcome (win, loss, draw) and intensity (contest duration and level of aggression) of between-group contests in blue monkeys. Contrary to patterns found in non-territorial species like baboons (Markham et al., 2012), however, asymmetries in location-based payoffs seemed to be more consistent predictors of a group's competitive advantage in these territorial monkeys. This study contributes to an understanding of the evolution of group living by assessing how asymmetries in both RHP and location-based payoffs influence contests between groups. Although comparable data are limited, it seems clear that both types of asymmetries can play a role in determining the outcome and intensity of intergroup contests, and that the relative power of each may vary across species.

REFERENCES

- Baker, R. R. (1983). Insect territoriality. *Annual Review of Entomology*, 28, 65-89.
- Baugh, J. R., & Forester, D. C. (1994). Prior residence effect in the dart-poison frog, *Dendrobates pumilio*. *Behaviour*, 131, 207-224. DOI: 10.1163/156853994X00442
- Benadi, G., Fichtel, C., & Kappeler, P. (2008). Intergroup relations and home range use in Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Primatology*, 70, 956-965. DOI: 10.1002/ajp.20588
- Bradbury, W. J., & Vehrencamp, L. (1998). *Principles of animal communication*. Sunderland: Sinauer Associates.
- Brown, M., & Crofoot, M. (2013). Social and spatial relationships between primate groups. In E. Sterling, E. Bynum, & M. Blair (Eds.), *Primate ecology and conservation* (pp. 151-176). Oxford: Oxford University Press.
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, 24, 346-352. DOI: 10.2307/1374834
- Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high-and low-density subpopulations. *Ecological Monographs*, 1-26. DOI: 10.2307/1943024
- Cassidy, K. A., MacNulty, D. R., Stahler, D. R., Smith, D. W., & Mech, L. D. (2015). Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behavioral Ecology*, 26, 1352-1360. DOI: 10.1093/beheco/arv081
- Cheney, D. L. (1987). Interactions and relationships between groups. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primate societies* (pp. 267-281). Chicago: University of Chicago Press.

- 590 Cords, M. (2002). Friendship among adult female blue monkeys (*Cercopithecus mitis*).
 591 *Behaviour*, 139, 291-314. DOI: 10.1163/156853902760102681
- 592 Cords, M. (2007). Variable participation in the defense of communal feeding territories by blue
 593 monkeys in the Kakamega Forest, Kenya. *Behaviour*, 144, 1537-1550. DOI:
 594 10.1163/156853907782512100
- 595 Cords, M. (2012). The 30-year blues: What we know and don't know about life history, group
 596 size, and group fission of blue monkeys in the Kakamega Forest, Kenya. In P. M.
 597 Kappeler & D. P. Watts (Eds.), *Long-term field studies of primates* (pp. 289-311).
 598 Springer Berlin Heidelberg.
- 599 Crofoot, M. C., Gilby, I. C., Wikelski, M. C., & Kays, R. W. (2008). Interaction location
 600 outweighs the competitive advantage of numerical superiority in *Cebus capucinus*
 601 intergroup contests. *Proceedings of the National Academy of Sciences*, 105, 577-581.
 602 DOI: 10.1163/156853907782512100
- 603 Crofoot, M. C., & Gilby, I. C. (2012). Cheating monkeys undermine group strength in enemy
 604 territory. *Proceedings of the National Academy of Sciences*, 109, 501-505. DOI:
 605 10.1073/pnas.1115937109
- 606 Ekernas, L. S., & Cords, M. (2007). Social and environmental factors influencing natal dispersal
 607 in blue monkeys, *Cercopithecus mitis stuhlmanni*. *Animal Behaviour*, 73, 1009-1020.
 608 DOI: 10.1016/j.anbehav.2006.11.007
- 609 Enquist, M., & Leimar, O. (1987). Evolution of fighting behaviour: the effect of variation in
 610 resource value. *Journal of Theoretical Biology*, 127, 187-205. DOI: 10.1016/S0022-
 611 5193(87)80130-3

- 612 Fashing, P. J., & Cords, M. (2000). Diurnal primate densities and biomass in the Kakamega
 613 Forest: an evaluation of census methods and a comparison with other forests. *American*
 614 *Journal of Primatology*, 50, 139-152. DOI: 10.1002/(SICI)1098-
 615 2345(200002)50:2<139::AID-AJP4>3.0.CO;2-N
- 616 Giraldeau, L. A., & Ydenberg, R. (1987). The center-edge effect: the result of a war of attrition
 617 between territorial contestants?. *The Auk*, 535-538.
- 618 Greenberg, R., & Gradwohl, J. (1986). Constant density and stable territoriality in some tropical
 619 insectivorous birds. *Oecologia*, 69, 618-625. DOI: 10.1007/BF00410372
- 620 Hammerstein, P. (1981). The role of asymmetries in animal contests. *Animal Behaviour*, 29, 193-
 621 205. DOI: 10.1016/S0003-3472(81)80166-2
- 622 Harris, T. R. (2010). Multiple resource values and fighting ability measures influence intergroup
 623 conflict in guerezas (*Colobus guereza*). *Animal Behaviour*, 79, 89-98. DOI:
 624 10.1016/j.anbehav.2009.10.007
- 625 Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and
 626 ranging behavior among primates. *Behavioral Ecology*, 2, 143-155. DOI:
 627 10.1016/j.anbehav.2009.10.007
- 628 Janes, S. W. (1984). Influences of territory composition and interspecific competition on red-
 629 tailed hawk reproductive success. *Ecology*, 862-870. DOI:
 630 10.1016/j.anbehav.2009.10.007
- 631 Keys, G. C., & Rothstein, S. I. (1991). Benefits and costs of dominance and subordination in
 632 white-crowned sparrows and the paradox of status signalling. *Animal Behaviour*, 42, 899-
 633 912. DOI: 10.1016/S0003-3472(05)80142-3

- 634 Kitchen, D. M., Cheney, D. L., & Seyfarth, R. M. (2004). Factors mediating inter-group
 635 encounters in savannah baboons (*Papio cynocephalus ursinus*). *Behaviour*, *141*, 197-218.
 636 DOI: 10.1163/156853904322890816
- 637 Klopfer, P. H., & Jolly, A. (1970). The stability of territorial boundaries in a lemur troop. *Folia*
 638 *Primatologica*, *12*, 199-208. DOI: 10.1159/000155289
- 639 Kokko, H., López-Sepulcre, A., & Morrell, L. J. (2006). From hawks and doves to self consistent
 640 games of territorial behavior. *The American Naturalist*, *167*, 901-912. DOI:
 641 10.1086/504604
- 642 Kummer, H., & Cords, M. (1991). Cues of ownership in long-tailed macaques, *Macaca*
 643 *fascicularis*. *Animal Behaviour*, *42*, 529-549. DOI: 10.1016/S0003-3472(05)80238-6
- 644 Markham, A. C., Alberts, S. C., & Altmann, J. (2012). Intergroup conflict: ecological predictors
 645 of winning and consequences of defeat in a wild primate population. *Animal behaviour*,
 646 *84*, 399-403. DOI: 10.1016/j.anbehav.2012.05.009
- 647 Markham, A. C., Guttal, V., Alberts, S. C., & Altmann, J. (2013). When good neighbors don't
 648 need fences: temporal landscape partitioning among baboon social groups. *Behavioral*
 649 *ecology and sociobiology*, *67*, 875-884. DOI: 10.1007/s00265-013-1510-0
- 650 McComb, K., Packer, C., & Pusey, A. (1994). Roaring and numerical assessment in contests
 651 between groups of female lions, *Panthera leo*. *Animal Behaviour*, *47*, 379-387. DOI:
 652 10.1006/anbe.1994.1052
- 653 Mesterton-Gibbons, M., & Adams, E. S. (2003). Landmarks in territory partitioning: a
 654 strategically stable convention? *The American Naturalist*, *161*, 685-697. DOI:
 655 10.1086/374203

- 656 Mitchell, N., Schaab, G., & Wägele, W. (2009). Kakamega Forest ecosystem: An introduction to
 657 the natural history and the human context. BIOTA East Africa Report 5. *Karlsruher*
 658 *Geowissenschaftliche Schriften A*, 17, 1–56.
- 659 Møller, A. P. (1987). Variation in badge size in male house sparrows *Passer domesticus*:
 660 evidence for status signalling. *Animal Behaviour*, 35, 1637-1644. DOI:
 661 10.1016/S0003-3472(87)80056-8
- 662 Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African
 663 lion, *Panthera leo*. *Animal Behaviour*, 78, 359-370. DOI:
 664 10.1016/j.anbehav.2009.04.024
- 665 Palmer, T. M. (2004). Wars of attrition: colony size determines competitive outcomes in a guild
 666 of African acacia ants. *Animal Behaviour*, 68, 993-1004. DOI:
 667 10.1016/j.anbehav.2004.02.005
- 668 Papaj, D. R., & Messing, R. H. (1998). Asymmetries in physiological state as a possible cause of
 669 resident advantage in contests. *Behaviour*, 135, 1013-1030. DOI:
 670 10.1163/156853998792913546
- 671 Payne, H. F., Lawes, M. J., & Henzi, S. P. (2003). Competition and the exchange of grooming
 672 among female samango monkeys (*Cercopithecus mitis erythrarchus*). *Behaviour*, 140,
 673 453-471. DOI: 10.1163/156853903322127931
- 674 Preuschoft, S., & Paul, A. (2000). Dominance, egalitarianism, and stalemate: an experimental
 675 approach to male-male competition in Barbary macaques. In P. M. Kappeler (Ed.),
 676 *Primate males: Causes and consequences of variation in group composition* (pp. 205-
 677 216). Cambridge University Press.

- Price, K., Broughton, K., Boutin, S., & Sinclair, A. R. E. (1986). Territory size and ownership in red squirrels: response to removals. *Canadian Journal of Zoology*, 64, 1144-1147. DOI: 10.1139/z86-172
- Radford, A. N., & du Plessis, M. A. (2004). Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour*, 68, 803-810. DOI: 10.1016/j.anbehav.2004.01.010
- Riechert, S. E. (1998). Game theory and animal contests. In L. A. Dugatkin & H. K. Reeve (Eds.), *Game theory and animal behavior* (pp. 64-93). Oxford: Oxford University Press.
- Rohwer, S. (1975). The social significance of avian winter plumage variability. *Evolution*, 593 - 610. DOI: 10.2307/2407071
- Rudran, R. (1978). *Socioecology of the blue monkeys (Cercopithecus mitis stuhlmanni) of the Kibale Forest, Uganda*. Smithsonian Institution Press.
- Scarry, C. J. (2013). Between-group contest competition among tufted capuchin monkeys, *Sapajus nigritus*, and the role of male resource defence. *Animal Behaviour*, 85, 931-939. DOI: 10.1016/j.anbehav.2013.02.013
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103-113. DOI: 10.1111/j.2041-210X.2010.00012.x
- Silk, J. B. (2002). Practice random acts of aggression and senseless acts of intimidation: the logic of status contests in social groups. *Evolutionary Anthropology*, 11, 221-225. DOI: 10.1002/evan.10038
- Sillero-Zubiri, C., & Macdonald, D. W. (1998). Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *Journal of Zoology*, 245, 351-361. DOI: 10.1111/j.1469-7998.1998.tb00110.x

- 701 Smith, I. P., Huntingford, F. A., Atkinson, R. J. A., & Taylor, A. C. (1994). Strategic decisions
 702 during agonistic behaviour in the velvet swimming crab, *Necora puber* (L.). *Animal*
 703 *Behaviour*, 47, 885-894. DOI: 10.1006/anbe.1994.1120
- 704 Sorato, E., Gullett, P. R., Creasey, M. J., Griffith, S. C., & Russell, A. F. (2015). Plastic
 705 territoriality in group-living chestnut-crowned babbler: roles of resource value, holding
 706 potential and predation risk. *Animal Behaviour*, 101, 155-168. DOI:
 707 10.1016/j.anbehav.2014.12.012
- 708 Stewart, P. D., Anderson, C., & Macdonald, D. W. (1997). A mechanism for passive range
 709 exclusion: evidence from the European badger (*Meles meles*). *Journal of Theoretical*
 710 *Biology*, 184, 279-289. DOI: 10.1006/jtbi.1996.0248
- 711 Sugiura, H., et al. (2000). Variation in intergroup encounters in two populations of Japanese
 712 macaques. *International Journal of Primatology*, 21, 519-535. DOI:
 713 10.1023/A:1005448120967
- 714 Tinbergen, N. (1957). The functions of territory. *Bird Study*, 4, 14-27.
- 715 Wells, M. S. (1988). Effects of body size and resource value on fighting behaviour in a jumping
 716 spider. *Animal Behaviour*, 36, 321-326. DOI: 10.1016/S0003-3472(88)80001-0
- 717 Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review*
 718 *of Anthropology*, 363-392. DOI: 10.1146/annurev.anthro.32.061002.120046
- 719 Wilson, M. L., Kahlenberg, S. M., Wells, M., & Wrangham, R. W. (2012). Ecological and social
 720 factors affect the occurrence and outcomes of intergroup encounters in chimpanzees.
 721 *Animal Behaviour*, 83, 277-291. DOI: 10.1016/j.anbehav.2011.11.004

- 722 Ydenberg, R. C., Giraldeau, L. A., & Kramer, D. L. (1986). Interference competition, payoff
723 asymmetries, and the social relationships of central place foragers. *Theoretical Population*
724 *Biology*, 30, 26-44. DOI: 10.1016/0040-5809(86)90023-7

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Figure 1. Likelihood of winning as a function of differences in (a) group size (adult plus old juvenile females), (b) site occupancy (assessed for three time frames), and (c) edge score. Groups with more adult plus old juvenile females, higher site occupancy, and higher edge scores had greater odds of winning. Figures do not include contests for which there was no difference in these predictors. Asterisks show differences that were significant (see Results: Win vs. Loss for details).

Figure 2. Frequencies of draws vs. decided outcomes as a function of relative group size. When groups were more similar in total size, the odds of a draw were higher. The data pictured come from the dataset in which spatial use was assessed for a period of 1 month before a contest.

Table 1. Second-order Akaike Information Criterion (AICc), Δ AICc, and Akaike weight (w_i) for models comparing how well three group size measures predicted the outcome (win vs. loss, draw vs. decided) and intensity (duration, level of aggression) of intergroup contests. Relative site occupancy was calculated for a period of 1 month before a contest. The group size measures were relative number of all group members (Total group), relative number of females, excluding infants (Total females), and relative number of adult plus old juvenile females (AF OJF).

Relative group size variable	AICc	Δ AICc	w_i
<i>Win vs. Loss</i>			
Total group	463.434	10.872	0.004
Total females	465.215	12.653	0.002
AF OJF	452.562	0	0.994
<i>Draw vs. Decided</i>			
Total group	1102.146	0	0.640
Total females	1104.097	1.951	0.241
AF OJF	1105.525	3.379	0.118
<i>Contest Duration</i>			
Total group	768.465	3.918	0.123
Total females	774.083	9.536	0.007
AF OJF	764.547	0	0.870
<i>Level of Aggression</i>			
Total group	2616.458	6.233	0.041
Total females	2616.625	6.400	0.038
AF OJF	2610.225	0	0.922

Table 2. Effects of relative number of adult plus old juvenile females (AF OJF), relative site occupancy, and relative edge score on the odds of winning intergroup contests, as indicated by conditional logistic regressions.

Predictor	Odds Ratio $\pm$ SE	Z	P	95% CI
<i>Win vs. Loss</i>				
<i>Time frame: 1 month (N = 402)*</i>				
AF OJF	1.097 $\pm$ 0.048	2.10	0.036	1.006, 1.196
Site occupancy	1.213 $\pm$ 0.063	3.72	<0.001	1.096, 1.343
Edge score	1.285 $\pm$ 0.092	3.50	<0.001	1.117, 1.479
Edge score $\times$ AF OJF	0.974 $\pm$ 0.009	-2.98	0.003	0.957, 0.991
Site occupancy $\times$ Edge score	1.004 $\pm$ 0.020	0.21	0.835	0.965, 1.045
AF OJF $\times$ Site occupancy	1.005 $\pm$ 0.006	0.89	0.373	0.994, 1.016
<i>Time frame: 3 months (N = 380)*</i>				
AF OJF	1.128 $\pm$ 0.055	2.48	0.013	1.026, 1.241
Site occupancy	1.361 $\pm$ 0.108	3.88	<0.001	1.165, 1.591
Edge score	1.293 $\pm$ 0.099	3.35	0.001	1.112, 1.503
Edge score $\times$ AF OJF	0.982 $\pm$ 0.009	-1.92	0.055	0.964, 1.000
Site occupancy $\times$ Edge score	0.996 $\pm$ 0.030	-0.14	0.890	0.938, 1.057
AF OJF $\times$ Site occupancy	1.007 $\pm$ 0.010	0.78	0.436	0.989, 1.026
<i>Time frame: 6 months (N = 348)*</i>				
AF OJF	1.085 $\pm$ 0.054	1.65	0.100	0.985, 1.196
Site occupancy	1.264 $\pm$ 0.120	2.46	0.014	1.049, 1.523
Edge score	1.273 $\pm$ 0.111	2.76	0.006	1.073, 1.511
Edge score $\times$ AF OJF	0.984 $\pm$ 0.011	-1.49	0.136	0.963, 1.005
Site occupancy $\times$ Edge score	0.978 $\pm$ 0.031	-0.70	0.482	0.919, 1.041
AF OJF $\times$ Site occupancy	1.011 $\pm$ 0.012	0.92	0.356	0.987, 1.036

*Denotes a significant difference from a null model without predictors. See Results: Win vs. Loss for details.

Table 3. Effects of relative number of all group members (Total group), relative site occupancy, and relative edge score on the odds of an intergroup contest ending in a draw, as indicated by conditional logistic regressions.

Predictor	Odds Ratio $\pm$ SE	Z	P	95% CI
<i>Draw vs. Decided</i>				
<i>Time frame: 1 month (N = 823)</i>				
Total group	0.930 $\pm$ 0.029	-2.33	0.020	0.875, 0.989
Site occupancy	0.988 $\pm$ 0.034	-0.34	0.736	0.923, 1.058
Edge score	1.069 $\pm$ 0.060	1.18	0.238	0.957, 1.194
Edge score $\times$ Total group	0.994 $\pm$ 0.007	-0.81	0.419	0.981, 1.008
Site occupancy $\times$ Edge score	1.007 $\pm$ 0.023	0.32	0.749	0.964, 1.053
Total group $\times$ Site occupancy	0.997 $\pm$ 0.005	-0.71	0.475	0.987, 1.006
<i>Time frame: 3 months (N = 767)</i>				
Total group	0.930 $\pm$ 0.030	-2.29	0.022	0.873, 0.990
Site occupancy	1.032 $\pm$ 0.055	0.59	0.553	0.929, 1.147
Edge score	1.076 $\pm$ 0.065	1.22	0.223	0.956, 1.210
Edge score $\times$ Total group	0.994 $\pm$ 0.007	-0.88	0.381	0.980, 1.008
Site occupancy $\times$ Edge score	0.985 $\pm$ 0.034	-0.45	0.653	0.921, 1.053
Total group $\times$ Site occupancy	0.997 $\pm$ 0.007	-0.41	0.680	0.983, 1.011
<i>Time frame: 6 months (N = 694)</i>				
Total group	0.931 $\pm$ 0.031	-2.12	0.034	0.871, 0.995
Site occupancy	0.953 $\pm$ 0.068	-0.67	0.502	0.829, 1.096
Edge score	1.141 $\pm$ 0.078	1.94	0.053	0.998, 1.304
Edge score $\times$ Total group	1.005 $\pm$ 0.010	0.52	0.602	0.986, 1.024
Site occupancy $\times$ Edge score	1.000 $\pm$ 0.042	0.01	0.992	0.922, 1.085
Total group $\times$ Site occupancy	0.990 $\pm$ 0.010	-1.08	0.280	0.971, 1.009

Note: no model differed significantly from a null model without predictors (Likelihood Ratio Tests, see

Results: Draw vs. Decided for details).

Table 4. Effects of relative number of adult plus old juvenile females (AF OJF), relative site occupancy, and relative edge score on the duration of intergroup contests, as indicated by generalized linear mixed models with group-pair as a random effect.

Predictor	Coef. $\pm$ SE	Z	P	95% CI
Contest Duration				
<i>Time frame: 1 month (N = 848)*</i>				
AF OJF	-0.011 $\pm$ 0.004	-3.08	0.002	-0.018, -0.004
Site occupancy	-0.004 $\pm$ 0.006	-0.62	0.536	-0.016, 0.008
Edge score	-0.022 $\pm$ 0.010	-2.21	0.027	-0.041, -0.002
Edge score $\times$ AF OJF	-0.003 $\pm$ 0.002	-1.55	0.122	-0.006, 7.4×10^{-4}
Site occupancy $\times$ Edge score	0.004 $\pm$ 0.005	0.88	0.379	-0.005, 0.013
AF OJF $\times$ Site occupancy	$2.4 \times 10^{-4} \pm 0.001$	0.22	0.826	-0.002, 0.002
Intercept	0.004 $\pm$ 0.003			8.2×10^{-4} , 0.019
<i>Time frame: 3 months (N = 790)</i>				
AF OJF	-0.010 $\pm$ 0.004	-2.62	0.009	-0.017, -0.002
Site occupancy	-0.008 $\pm$ 0.009	-0.90	0.370	-0.025, 0.009
Edge score	-0.021 $\pm$ 0.010	-1.97	0.049	-0.041, -7.5×10^{-5}
Edge score $\times$ AF OJF	-0.002 $\pm$ 0.002	-1.31	0.190	-0.006, 0.001
Site occupancy $\times$ Edge score	0.001 $\pm$ 0.007	0.14	0.889	-0.013, 0.015
AF OJF $\times$ Site occupancy	$-2.0 \times 10^{-4} \pm 0.002$	-0.12	0.902	-0.003, 0.003
Intercept	0.004 $\pm$ 0.003			8.1×10^{-4} , 0.019
<i>Time frame: 6 months (N = 717)</i>				
AF OJF	-0.009 $\pm$ 0.004	-2.32	0.020	-0.017, -0.001
Site occupancy	-0.011 $\pm$ 0.011	-0.99	0.322	-0.032, 0.010
Edge score	-0.018 $\pm$ 0.011	-1.58	0.114	-0.040, 0.004
Edge score $\times$ AF OJF	-0.003 $\pm$ 0.002	-1.42	0.157	-0.007, 0.001
Site occupancy $\times$ Edge score	0.009 $\pm$ 0.009	1.03	0.305	-0.009, 0.027
AF OJF $\times$ Site occupancy	0.002 $\pm$ 0.002	0.89	0.373	-0.002, 0.006
Intercept	0.005 $\pm$ 0.004			0.001, 0.022

*Denotes a significant difference from a null model without predictors. See Results: Contest Duration for details.

Table 5. Effects of relative number of adult plus old juvenile females (AF OJF), relative site occupancy, and relative edge score on the level of aggression of intergroup contests, as indicated by generalized linear mixed models with group-pair as a random effect.

Predictor	Coef. $\pm$ SE	Z	P	95% CI
Level of Aggression				
<i>Time frame: 1 month (N = 857)*</i>				
AF OJF	-0.036 $\pm$ 0.014	-2.51	0.012	-0.064, -0.008
Site occupancy	-0.064 $\pm$ 0.029	-2.16	0.031	-0.121, -0.006
Edge score	-0.106 $\pm$ 0.049	-2.19	0.029	-0.201, -0.011
Edge score $\times$ AF OJF	-0.003 $\pm$ 0.009	-0.33	0.738	-0.020, 0.014
Site occupancy $\times$ Edge score	0.001 $\pm$ 0.024	0.04	0.968	-0.046, 0.048
AF OJF $\times$ Site occupancy	-0.009 $\pm$ 0.006	-1.63	0.104	-0.020, 0.002
Intercept	0.010 $\pm$ 0.022			1.3×10^{-4} , 0.732
<i>Time frame: 3 months (N = 799)*</i>				
AF OJF	-0.027 $\pm$ 0.013	-2.14	0.033	-0.052, -0.002
Site occupancy	-0.061 $\pm$ 0.044	-1.40	0.161	-0.147, 0.024
Edge score	-0.110 $\pm$ 0.052	-2.12	0.034	-0.211, -0.008
Edge score $\times$ AF OJF	-0.005 $\pm$ 0.009	-0.49	0.624	-0.023, 0.014
Site occupancy $\times$ Edge score	-0.046 $\pm$ 0.037	-1.24	0.216	-0.118, 0.027
AF OJF $\times$ Site occupancy	-0.010 $\pm$ 0.008	-1.26	0.208	-0.026, 0.006
Intercept	0.001 $\pm$ 0.014			7.4×10^{-16} , 1.4×10^9
<i>Time frame: 6 months (N = 728)*</i>				
AF OJF	-0.032 $\pm$ 0.012	-2.73	0.006	-0.056, -0.009
Site occupancy	-0.023 $\pm$ 0.052	-0.43	0.665	-0.125, 0.079
Edge score	-0.120 $\pm$ 0.056	-2.14	0.033	-0.230, -0.010
Edge score $\times$ AF OJF	-0.005 $\pm$ 0.011	-0.46	0.647	-0.026, 0.016
Site occupancy $\times$ Edge score	-0.089 $\pm$ 0.044	-2.01	0.045	-0.176, -0.002
AF OJF $\times$ Site occupancy	-0.017 $\pm$ 0.011	-1.59	0.113	-0.038, 0.004
Intercept	$3.5 \times 10^{-28} \pm 5.5 \times 10^{-15}$			0.000, 0.000

*Denotes a significant difference from a null model without predictors. See Results: Level of

Aggression for details.