

Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population

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In many social species, competition between groups is a major factor proximately affecting group-level movement patterns and space use and ultimately shaping the evolution of group living and complex sociality. Here we evaluated the factors influencing group-level dominance among five social groups of wild baboons (*Papio cynocephalus*), in particular focusing on the spatial determinants of dominance and the consequences of defeat. When direct conflict occurred between conspecific baboon groups, the winning group was predicted by differences in the number of adult males in each group and/or groups that had used the areas surrounding the encounter location more intensively than their opponent in the preceding 9 or 12 months. Relative intensity of space use over shorter timescales (3 and 6 months) was a poor predictor of the interaction's outcome. Losing groups, but not winning groups, experienced clear short-term costs. Losing groups used the area surrounding the interaction less following an agonistic encounter (relative to their intensity of use of the area prior to the interaction). These findings offer insight into the influences and consequences of intergroup competition on group-level patterns of space use.

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Intergroup competition occurs in many social species and is considered a major factor shaping the evolution of group living and complex sociality. Comparable to factors influencing the outcome of individual-level contests, important determinants of dominance in group-level competition include asymmetries in both fighting abilities and perceived resource value. In intergroup conflicts, advantages in fighting ability (or 'resource holding potential') are most commonly associated with group size such that larger groups have a competitive advantage relative to outnumbered opponents (Maynard Smith & Parker 1976). However, asymmetries in fighting ability alone are insufficient to explain situations in which dominance roles reverse. For example, among territorial species, residents are thought to place a higher value on the area being contested than are intruders, and thus residents have more to gain from winning and/or more to risk by defeat (Enquist & Leimar 1987). Ownership advantage may also reduce to arbitrary conventions, such as 'residents always win', in territorial species (Maynard Smith & Parker 1976; Kokko et al. 2006).

In situations characterized by overlapping home ranges rather than discrete territories, interpreting perceived resource value for

each contestant is complicated when both groups in a pairwise encounter utilize the area surrounding an interaction (i.e. when there is ambiguity in defining 'resident' versus 'intruder'). Previous studies typically have overcome this challenge by considering the relative distance between an interaction location and each contestant's nest site or home range centre: resources are considered more valuable when close to a central reference point (e.g. Steller's jay, *Cyanocitta stelleri*: Brown 1963; ocellated antbird, *Phaenostictus mcleannani*: Willis 1973; eastern chipmunk, *Tamias striatus*: Elliott 1978; capuchin monkey, *Cebus capucinus*: Crofoot et al. 2008). For many species, however, areas used intensively may be highly valued regardless of their location in the home range. An alternative approach, therefore, is to measure directly asymmetric use of the area surrounding the interaction location with the prediction that intensity of use is a marker for the contestant's value of a resource (Crofoot et al. 2008).

In this study, we investigated group-level power asymmetry, or dominance, in wild baboons, *Papio cynocephalus*. Baboons, like many other cercopithecine primates, live in discrete, stable multimale-multifemale social groups. Multiple social groups consisting of 20–100 individuals (Estes 1991) make up a single population, and the home ranges of neighbouring groups overlap extensively (e.g. Altmann & Altmann 1970; Shopland 1982; A. C. Markham, V. Guttal, S. C. Alberts & J. Altmann, unpublished data). Limited and concentrated resources essential to survival,

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such as waterholes and sleeping sites, occur within regions of overlap. Baboons are obligate users of both: drinking from waterholes is a near-daily necessity, and sleeping groves of adequate size provide safety from nocturnal predators. In the Amboseli basin of Kenya, any single group utilizes multiple waterholes and groves in their home ranges (i.e. baboons are 'multiple central place foragers'; sensu Chapman et al. 1989; McLaughlin & Montgomerie 1989). Typically, resource size and group intolerance are believed to limit simultaneous use of a resource to members of a single group, suggesting that groups rely upon temporal mechanisms to partition the landscape. How the outcomes of intergroup contests both influence and are influenced by group-level patterns of space use has not been investigated.

Our study addressed three specific objectives. First, we evaluated total group size and composition (number of adult males and number of adult females) as predictors of dominance in group-level interactions. If philopatry influences participation in intergroup aggression (e.g. Cheney 1987; Isbell 1991), the number of adult females (the nondispersing sex in this species) would be a stronger predictor of dominance than total group size or number of adult males. However, adult male baboons are reported to exhibit more aggressive displays and be more actively involved in intergroup conflict relative to other sex-age classes (e.g. Maxim & Buettner-Janusch 1963; Stoltz & Saayman 1970; Paterson 1973; Cheney & Seyfarth 1977), suggesting asymmetries in the number of adult males may determine an interaction's outcome. We therefore predicted that differences in the number of adult males would be a better predictor of dominance than differences in total group size or number of adult females.

Second, we evaluated relative space use in the area surrounding the interaction location as a predictor of dominance over four timescales (3, 6, 9 and 12 months) prior to the interaction. This approach offered novel, empirical insight into the theory that resource value is correlated with long-term use, specifically that the probability of winning is influenced by the duration of tenure (reviewed in Bradbury & Vehrencamp 1998).

Third, we analysed the spatial consequences of agonistic interactions over the same four timescales for winners and losers by comparing space use in the area surrounding an interaction before and after the encounter. Theoretical and empirical research on individual-level agonisms suggests that losers should avoid areas of agonistic interaction if prior experience reliably predicts future conflict (reviewed in Stamps & Krishan 2001). Yet, to the best of our knowledge, spatial consequences of defeat have not been studied in group-level contests. We predicted that the losing group would show avoidance of the area (relative to its former use) following the interaction whereas space use patterns of the winning group would be unaltered.

METHODS

This study was part of ongoing research on baboons, *Papio cynocephalus*, living within the Amboseli ecosystem, a semi-arid short-grass savannah that straddles the Kenya–Tanzania border (Alberts & Altmann 2012). The data presented here represent a 9-year period from August 2000 to October 2009, and focused on five social groups. All baboons within the study population were individually identifiable by field researchers of the Amboseli Baboon Research Project (ABRP), and each group was the focus of detailed observations several days each week. Consequently, demographic data were typically accurate to within a few days. Details on assessing maturational milestones relevant to calculating the number of adult males and females are provided by Alberts & Altmann (1995) and Gesquiere et al. (2007), respectively. Complete details on monitoring effort and data collection protocols can be accessed online (<http://www.princeton.edu/~baboon/>).

For this study, we used observer-recorded data on decided agonistic interactions between group pairs ($N = 222$). Decided agonistic interactions were defined as contests in which only one group displayed clear dominance over another group and/or in which only one group displayed clear subordination in response to another group. For each dyadic agonistic interaction, ABRP observers recorded group identities, date, time and dominant/subordinate group-level behaviours. Specifically, the behaviours we considered in assessing interactions included direct aggression ($N = 3$; 1.3%), chasing ($N = 11$; 5.0%), spatial displacement ($N = 200$; 90.1%) and blocking access to discrete ecological resources ($N = 8$; 3.6%). To ensure independence of observations, we included only one agonistic interaction per dyad-day in our analyses (i.e. agonistic interactions have a daily resolution). Dyad-days were defined as days in which at least one of the two groups involved in the agonistic interaction was the focus of observation. For the 9-year period of this study (August 2000–October 2009), we had a total of 18 691 dyad-days, and the observation days had an average \pm SE duration of 4.4 ± 0.03 h ($N = 5520$).

Location of each agonistic interaction was determined by cross-referencing group identity, date and time with observer-recorded global positioning system (GPS) location data. Observers recorded half-hourly GPS locations of focal groups during each day of observation. Groups rarely travelled in areas that were inaccessible to observers; therefore, GPS data were not spatially biased to times/locations for which observers were able to follow the animals. For a subset of interactions ($N = 25$), GPS data were coincident with the time of the interaction. In other cases ($N = 182$), we used Esri ArcGIS 9.2 (Environmental Systems Resources Institute, Inc., Redlands, CA, U.S.A.) and the Hawth's Tools extension (Beyer 2004) to calculate straight-line displacements from GPS readings taken within 15 min before and after the interaction; interaction location was estimated along this line based on the time of the interaction and assuming constant travel speed. As a third and final source of locational information, in seven cases we were able to use known coordinates of specified sleeping groves or waterholes referenced in observer-recorded notes about the interaction. We were not able to determine the interaction's location in eight cases.

Half-hourly GPS location data were also used to determine each group's intensity of use in the area surrounding each interaction location. Observers recorded an average \pm SE of 115 ± 1.5 GPS readings per group in each calendar month of this study ($N = 630$ group-months). Intensity of prior use was assessed independently for each of the two groups participating in the interaction. For each group we calculated intensity of use as the proportion of that group's total GPS locations that were within 500 m of the interaction location over four timescales preceding and following the interaction date: 3, 6, 9 and 12 months.

Ethical Note

All project protocols complied with regulations in Kenya (Republic of Kenya Research Permits NCST/5/002/R/776 to J.A. and NCST/5/002/R/777 to S.C.A.) and in the United States (Princeton University IACUC 1649), and adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

Statistical Analyses

To test for determinants of dominance between a pair of groups, we randomly selected one group from each intergroup interaction as the focal subject for analysis. Accounting for repeated observations of each group-pair, we used generalized estimating equations (GEE) to test whether difference in demographics and relative intensity of use (focal group's intensity of use/opponent's intensity of use) predicted the interaction's outcome (i.e. whether the focal group won or lost)

over four timescales (3, 6, 9 and 12 months) prior to the interaction. Three demographic predictors were evaluated: differences in total group size (focal group size – opponent's group size), differences in the number of adult males (adult males in focal group – adult males in opponent group) and differences in the number of adult females (adult females in focal group – adult females in opponent group). Because these three predictors were highly correlated, we tested the effects of each in three separate models. We selected the single best model at each timescale using quasi-likelihood under the independence model criterion (QIC), which compares the adequacy of several models and identifies the model that best explains the variance of the dependent variable as that with the lowest QIC value (Pan 2001; Tsai et al. 2011). Additionally, we calculated QIC weights to determine the relative predictive ability of the models tested by normalizing each model based on its QIC value relative to the QIC value of the best model (Burnham & Anderson 2002).

For evaluating the effects of an encounter's outcome over the same four timescales, we used a Wilcoxon signed-ranks test to determine whether each group's intensity of use in the months following an interaction differed significantly from the intensity of use prior to the interaction. Intensity of use before and after the interaction was tested separately for winners and losers. All statistical tests were run individually for each timescale (3, 6, 9 and 12 months) and were performed in SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.). The alpha value for statistical significance was set to 0.05 for all analyses.

RESULTS

The average \pm SE difference in total group size during 222 interactions (where group size was measured on the day of the interaction) was 29.6 ± 1.1 individuals (range 1–78). The average \pm SE difference in the number of adult males was 5.2 ± 0.2 males (range 0–13), and the average \pm SE difference in the number of adult females was 9.1 ± 0.35 females (range 0–26). Based on locational information and associated notes, the majority of intergroup agonistic interactions (143 of 222) occurred in apparent conflict over either waterholes ($N = 54$; 24.3%) or sleeping groves ($N = 89$; 40.1%). Field records for the remaining 79 interactions (35.6%) provided no explicit reference to waterholes and/or sleeping groves in the context of the interaction. Although intergroup agonisms varied in intensity of aggression and/or submission, no instances of wounding were observed in this 9-year period.

Group dominance was predicted by asymmetries in the number of adult males, particularly when relative differences in the number of adult males were large (Fig. 1). Although comparable results were found for asymmetries in total group size and number of adult females, differences in the number of adult males produced lower QIC values at all timescales examined (Table 1). Because the number of adult males predicted the observed outcomes better than either total group size or number of adult females, we focus hereafter exclusively on the number of adult males.

In analyses of the subset of interactions for which location could be determined ($N = 214$), the number of adult males was a significant determinant of dominance at all timescales; groups with more males experienced competitive advantages. Furthermore, space use was a significant determinant of dominance; groups that used the area surrounding the location more intensively than their opponent in the preceding 9 or 12 months were more likely to win the encounter. In contrast, more recent space use (i.e. over shorter timescales, 3 and 6 months) did not predict dominance. Table 2 provides summary statistics of the GEE at all timescales examined.

Groups that won interactions did not significantly change their intensity of use following an interaction at any of the four timescales examined. In contrast, groups that lost interactions used the area surrounding the interaction less in the 3 months following an

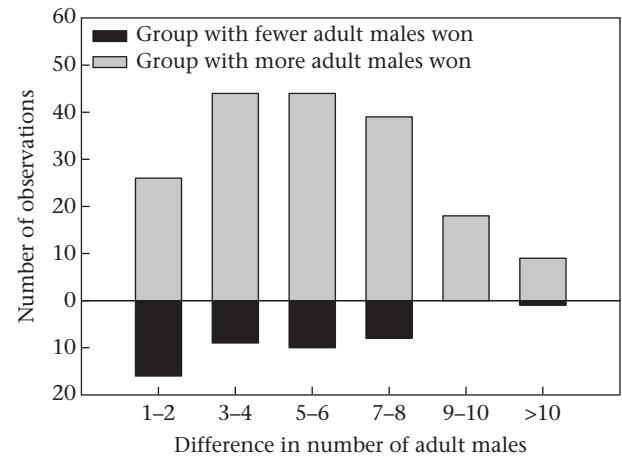


Figure 1. Relationship between group dominance in baboons and asymmetries in the number of adult males present in each group during intergroup encounters.

agonistic encounter (relative to their intensity of use of the area 3 months prior to the interaction); there were no significant changes in intensity of space use over longer timescales (6, 9 or 12 months) for groups that lost interactions (Table 3). For consistency, we used nonparametric tests in these analyses because data were not normally distributed at some timescales. Nevertheless, parametric analyses also indicated no significant change in space use for dominant groups at any timescale. However, they suggested significant avoidance of the interaction location for subordinate groups at all timescales; this effect for subordinate groups was strongest within 3 months after the encounter (Fig. 2), parallel to the results of the nonparametric tests.

DISCUSSION

This study demonstrates that success in contests between neighbouring groups of wild baboons was determined by asymmetries in both the number of adult males and space use patterns. Competitive advantages were experienced by groups with more

Table 1

Quasi-likelihood independence model criterion (QIC), Δ QIC and model weights for the three models tested for their ability to predict outcomes of baboon intergroup interactions at each timescale (3, 6, 9 and 12 months)

Demographic predictor	QIC	Δ QIC	Model weight
Timescale: 3 months			
Difference in number of adult males	191.11	0.00	0.962
Difference in total group size	197.60	6.48	0.038
Difference in number of adult females	212.78	21.66	0.000
Timescale: 6 months			
Difference in number of adult males	205.83	0.00	0.831
Difference in total group size	209.02	3.19	0.169
Difference in number of adult females	222.39	16.56	0.000
Timescale: 9 months			
Difference in number of adult males	208.76	0.00	0.952
Difference in total group size	214.78	6.02	0.047
Difference in number of adult females	227.31	18.55	0.000
Timescale: 12 months			
Difference in number of adult males	209.12	0.00	0.954
Difference in total group size	215.20	6.08	0.046
Difference in number of adult females	228.13	19.01	0.000

At each timescale, Δ QIC is the difference between a model and the model with the lowest QIC value, and the model weight is the normalized value of the model based on its Δ QIC value. All models were tested with relative intensity of use as an additional predictor variable (see text).

Table 2

Results from a generalized estimating equation (GEE) testing the effects of asymmetries between groups of baboons that interacted (number of adult males in the focal group minus number of adult males in the other group) and each group's relative intensity of space use in the area surrounding the interaction's location (focal group intensity of use/other group's intensity of use) on the probability of winning across four timescales (3, 6, 9 and 12 months)

	Estimate	Wald χ^2_1	P
Timescale: 3 months			
Intercept	0.123	0.245	0.620
Difference in number of adult males	0.297	94.849	<0.001
Relative intensity of use	0.008	0.010	0.918
Timescale: 6 months			
Intercept	0.031	0.028	0.868
Difference in number of adult males	0.285	78.134	<0.001
Relative intensity of use	0.025	2.627	0.105
Timescale: 9 months			
Intercept	0.051	0.093	0.761
Difference in number of adult males	0.277	61.107	<0.001
Relative intensity of use	0.028	4.072	0.044
Timescale: 12 months			
Intercept	0.041	0.061	0.806
Difference in number of adult males	0.278	62.333	<0.001
Relative intensity of use	0.026	4.108	0.043

Statistically significant results are shown in bold.

adult males and/or groups that had used the areas surrounding the interaction location more intensively than their opponents in the preceding 9 or 12 months. Interestingly, shorter-term intensity of use was not a significant predictor of dominance.

The influence of group size on contest outcome is well established (e.g. Nagel 1973; McComb et al. 1994; Crofoot et al. 2008). However, few studies have evaluated whether differences in group composition provide a competitive advantage (but see Hamilton et al. 1975; Mosser & Packer 2009) despite recognition that aggressive involvement in intergroup encounters is not necessarily shared equally amongst group members (reviewed in Cheney 1987). In primates, female aggression during intergroup encounters is commonly reported in species characterized by female philopatry (Cheney 1987; Isbell 1991; but see Okamoto & Matsumura 2002). However, in baboons, males are more likely than females to engage actively in intergroup interactions (e.g. Maxim & Buettner-Janusch 1963; Stoltz & Saayman 1970; Paterson 1973; Cheney & Seyfarth 1977). This male-biased participation in baboons may be explained by the high

Table 3

Results from a Wilcoxon signed-ranks test to determine whether baboons' intensity of space use in the months following an intergroup interaction differed significantly from their intensity of space use prior to the interaction across four timescales (3, 6, 9 and 12 months)

	N	Z	P
Timescale: 3 months			
Winning group	214	-1.596	0.110
Losing group	214	-3.186	0.001
Timescale: 6 months			
Winning group	214	-0.807	0.420
Losing group	214	-1.841	0.066
Timescale: 9 months			
Winning group	214	-0.323	0.747
Losing group	214	-1.721	0.087
Timescale: 12 months			
Winning group	214	-0.305	0.761
Losing group	214	-1.776	0.076

Statistically significant results are shown in bold.

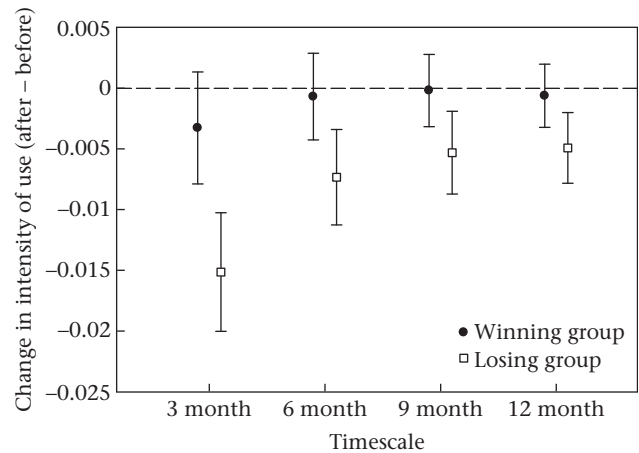


Figure 2. Mean \pm SE change in the intensity of space use by winning and losing groups of baboons before and after intergroup interactions. See text for details.

degree of sexual dimorphism in body size (Altmann et al. 1993) and canine size (Walker 1984) characterizing the species: individuals of the smaller sex and/or individuals lacking 'weaponry' (e.g. large canines) may be unlikely to challenge rivals (Packer & Pusey 1979). Because aggressive involvement in intergroup encounters is not shared equitably, we predicted that differences in the number of adult males would be a stronger determinant of dominance than differences in total group size or number of adult females. Our results support this prediction, suggesting that a group's fighting ability is best assessed by numerical differences in the age–sex class most likely to be actively involved in the encounter.

Although intergroup agonistic interactions in our population occasionally escalated to physical aggression, most observed displays of dominance involved one group displacing another in the absence of physical conflict. The dominance of a group measured by its ability to displace others at discrete resources has been noted previously in several baboon populations (e.g. Altmann & Altmann 1970; Saayman 1971; Nagel 1973; Hamilton et al. 1975, 1976; Maples et al. 1976; Rasmussen 1979; Sugarwara 1979).

Among primates, contests between groups are most likely to intensify to extreme, even lethal, aggression in situations when groups temporarily fission into smaller subgroups such that imbalances of power vary across time (reviewed in Crofoot & Wrangham 2010). For example, 'warfare' between male subgroups of neighbouring communities has been studied extensively in the fission–fusion society of chimpanzees, *Pan troglodytes*. Although the number of members in each subgroup reliably predicts dominance in chimpanzees, variability in subgroup composition and size contributes to the likelihood that chimpanzee conflicts will escalate (Manson & Wrangham 1991). In contrast, the multimale-multifemale groups in baboon society are remarkably stable over time. As a result, each baboon group may be able to assess its fighting ability relative to its neighbour over long timescales. However, the effect of temporary subgroup formation (wherein stable groups occasionally fission and range separately for several hours) on the propensity for violence and/or dominance has not yet been evaluated. We do not know of any attempt to do so and the data available from our studies are not adequate to address this topic.

In addition to the effects of adult male numerical superiority, we demonstrated that intensity of space use surrounding the interaction location was a significant predictor of dominance: groups with fewer adult males than the opponent's group were occasionally able to win contests if they had used the interaction area more intensively than their opponent in the preceding 9 or 12 months. We are aware of only one study that similarly evaluated effects of both group size and

location on the outcome of group-level agonistic interactions. Comparable to our findings, Crofoot et al. (2008) observed that the effects of numerical superiority on intergroup dominance patterns in capuchin monkeys vary across space. We agree with their interpretation that this tendency of relative 'residents' to win contests, despite numerical disadvantages, may be an important mechanism by which a range of group sizes is maintained within a population.

Despite recognition that intensity of space use confers a competitive advantage in contests between animals, we know of no empirical studies that have explicitly addressed the timescale over which space use influences contest outcome. We found that intergroup dominance was predicted by long-term space use (space use over shorter timescales was a poor predictor of the interaction's outcome), perhaps reflecting the periodicity of resource/space use, a possibility that is beyond our current ability to evaluate. In contrast, spatial consequences of defeat primarily consisted of short-term site avoidance by subordinate groups. Together, these findings have important implications for the ways in which intergroup dominance and space use are interrelated. If intergroup encounter rates were higher in some species or under some conditions, we postulate that the repeated negative reinforcement may be more long-lasting and result in more spatial separation between groups. To the best of our knowledge, theoretical studies demonstrating that frequency of interaction influences spatial overlap among solitary animals (e.g. Jetz et al. 2004) have not yet been extended to empirical research on species obligated to group living.

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