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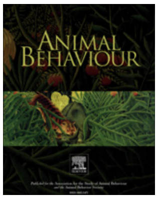

Intergroup conflict: ecological predictors of winning and consequences of defeat in a wild primate population

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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.

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 subordinance 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 ± 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 ± 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 with 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)