Animal Behaviour 113 (2016) 49–58

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 24 May 2015
Initial acceptance 24 June 2015
Final acceptance 21 October 2015
Available online
MS. number: A15-00445R

Keywords:
between-group competition
intergroup agonism
intergroup dominance
payoff asymmetry
resource-holding potential
space use
territoriality

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 and used the contest site more than its opponent, and when contests occurred closer to the group's home range centre while farther from the opponent's centre. 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. In addition, 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.

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), or the payoffs gained by winning, or both (Baker, 1983; Enquist & Leimar, 1987; Hammerstein, 1981; 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 (Benadi, Fichtel, & Kappeler, 2008; Cassidy, MacNulty, Stahler, Smith, & Mech, 2015; Crofoot, Gilby, Wikelski, & Kays, 2008; Harris, 2010; Kitchen, Cheney, & Seyfarth, 2004; Markham, Alberts, & Altmann, 2012; Mosser & Packer, 2009; Palmer, 2004; Radford & du Plessis, 2004; Scarry, 2013; Sillero-Zubiri & Macdonald, 1998). However, larger groups do not always prevail because payoff asymmetries can overwhelm asymmetries in RHP (Crofoot et al., 2008; Hammerstein, 1981; Markham et al., 2012; Riechert, 1998; 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 that they used more heavily than an opponent group during the 9–12 month period before a contest, although not when frequency of use was calculated over a 3–6 month period only

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http://dx.doi.org/10.1016/j.anbehav.2015.11.011

(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 centre versus periphery of opposing groups' home ranges. If a group values the centre of its home range more than the peripheries, a payoff gradient may occur along an edge–centre axis. Defence of central areas may yield higher payoffs than defence of peripheral areas if groups spend more time in home range centres, if centres 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 (Crofoot et al., 2008; Giraldeau & Ydenberg, 1987; Stewart, Anderson, & Macdonald, 1997; Ydenberg, Giraldeau, & Kramer, 1986). In addition, territory centres may be more valuable to animals if the loss of the territory centre 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 centre 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, López-Sepulcre, & Morrell, 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 (Greenberg & Gradwohl, 1986; Janes, 1984; Klopfer & Jolly, 1970; Price, Broughton, Boutin, & Sinclair, 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 versus 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 (Radford & du Plessis, 2004; Riechert, 1998). 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 (Keys & Rothstein, 1991; Rohwer, 1975; Silk, 2002; Wilson, Kahlenberg, Wells, & Wrangham, 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, neighbouring 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 (Cords, 2002, 2007; Payne, Lawes, & Henzi, 2003; Rudran, 1978). 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 centre of its home range while farther from the opponent's centre. 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 to 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.

In addition, 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.