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Social 'predators' within a multilevel primate society

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Group living confers a variety of benefits to individuals, particularly in predator detection and defence. Hamilton's selfish herd hypothesis (Hamilton 1971, *Journal of Theoretical Biology*, **31,** 295–311) posits that individuals come together to reduce their own risk of predation, and numerous studies have shown that predators affect both the grouping and spacing patterns of their prey. We suggest that this hypothesis is also useful for understanding group responses to a very different threat: that posed by nonbreeding, potentially infanticidal males. In such cases, males may act as a predator-like force on the grouping patterns of breeding individuals. We hypothesized that nonbreeding males, like predators, can affect the spacing patterns of conspecifics. Specifically, we examined the effect of bachelor males on both the grouping and spacing patterns of gelada, *Theropithecus gelada*, reproductive units. First, we demonstrated that the number of bachelors was positively correlated with the number of animals in a group. Second, and more importantly, we found that bachelors exerted an acute pressure on the spacing of individuals; as bachelors approached, breeding individuals moved closer to their nearest neighbours. By approaching other breeding individuals, reproductive males and females may dilute the costs of associating with bachelor males.

Predator detection and defence are often invoked as benefits of group living. However, the costs and benefits of predator protection are not shared equally among group members. For example, predators generally target the nearest individual, making marginal individuals the most probable targets. Hamilton's (1971) 'selfish herd' hypothesis posits that an individual's risk of predation is positively related to its distance to conspecific neighbours. In other words, widely spaced individuals should be targeted more often by predators (Quinn & Cresswell 2006; Wood & Ackland 2007). Hamilton (1971) suggested that by simply moving towards conspecifics, an individual reduces its risk of predation. Recent experimental (De Vos & O'Riain 2010) and naturalistic (Quinn & Cresswell 2006) studies support the central tenets of the selfish herd hypothesis in both mammalian and avian species.

Conspecifics may also pose a threat that is similar to predation. In many mammals, social units are composed of one male and several females. Unattached males mount challenges to males in mixed-sex units. Bachelors pose two direct types of threats to the fitness of breeding individuals: (1) they may replace the dominant breeding male, effectively ending his reproductive tenure; (2) they may commit infanticide, reducing the fitness of breeding males and females. The 'bachelor threat' hypothesis predicts that breeding males associate and form coalitions to avoid harassment, cuckoldry, risk of take-over (male replacement) and infanticide from unattached bachelor males (Rubenstein 1986). For example, the presence of bachelor males is the main cause of herding behaviour by stallion plains zebra, *Equus burchelli* (Rubenstein & Hack 2004), and has affected the evolution of multilevel societies in some colobine primates (Grueter & van Schaik 2010). In these taxa, bachelors have a predator-like effect on the grouping behaviour of individuals within core social units.

Here we examine the effect of bachelor males on the grouping and spacing patterns of a gregarious Old World monkey, the gelada, *Theropithecus gelada*. We also seek to determine whether breeding male geladas collectively defend their social group from bachelor intrusion. Gelada diet is composed nearly entirely of grasses (>90%), an abundant and evenly distributed resource that facilitates large social aggregations (Dunbar & Dunbar 1975; Kawai 1979). Geladas live in a fluid society composed of four levels: (1) the reproductive unit: 1–12 related females with their dependent offspring, one dominant 'leader' male, and possibly one or more subordinate 'follower' males that spend 100% of their time

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together; (2) the team: two to three units that spend at least 90% of their time together; (3) the band: a collection of 5–30 units that spend at least 50% of their time together; and (4) the community: a collection of all of the units in an area (as many as >100 units) that spend at least some time together (Dunbar & Dunbar 1975; Kawai et al. 1983; Snyder-Mackler et al., in press). In addition, bachelor groups, comprising 2–15 mature bachelors and subadult males (Dunbar 1984), are loosely associated with reproductive units (often more than 20 m away). Reproductive units and bachelor groups fission (to form smaller groups) and fuse (to form a larger group) with each other during the day to form temporary 'herds' that may consist of reproductive units and bachelor groups from multiple bands (Dunbar & Dunbar 1975; Kawai et al. 1983). Leader males regularly solicit chases ('yelping chases'; Dunbar & Dunbar 1975) from bachelors, and previous research suggests that leader males that engage in more chases are less likely to be replaced (Dunbar 1984). However, it is unknown whether leader males act collectively during these chases in a coalitionary fashion to defend the herd from bachelors.

Similar to the large aggregations of many ungulate species, it is hypothesized that the enormous size of gelada herds (>1000 individuals) is a response to predation risk (Crook 1966). However, the largest aggregations of geladas are often found at midday (Snyder-Mackler et al., in press), and most gelada predators are crepuscular or nocturnal (e.g. spotted hyaenas, *Crocuta crocuta*, and leopards, *Panthera pardus*). Therefore, with very few predators during the daytime, we asked whether there were any factors that could affect gelada grouping and spacing throughout the day? We hypothesized that bachelors function as 'social predators' in gelada society because bachelors regularly harass leader males (which can result in male replacement: Dunbar 1984) as well as unit females (which can result in infanticide: Dunbar & Dunbar 1975; Mori et al. 1997; Beehner & Bergman 2008). Specifically, we predicted that the presence and proximity of bachelors would influence the grouping and spacing patterns of breeding individuals and that leader males should collectively defend the gelada herd from encroaching bachelors. First, larger groups of geladas should form in response to increased bachelor presence, after controlling for weather variables (i.e. rainfall and temperature) that are known to influence group size (Hunter 2001). Second, the presence of bachelors should cause bands to fuse together forming larger herds throughout a given day, so that individuals may dilute their own risk of associating with bachelor groups. Third, as bachelors approach reproductive units, those units, as well as the individuals within them, should move closer together. Finally, leader males should collectively chase away bachelor males that get too close to the herd.

METHODS

Study Species and Location

Data were collected from a population of wild geladas in the Simien Mountains National Park, Ethiopia from January 2009 to April 2011 as part of the University of Michigan Gelada Research Project. Their Afroalpine habitat includes few trees, facilitating high visibility of study animals. We collected regular observations from 229 individually recognized adults (48 unit males, 123 unit females, 58 bachelor males) across 19 units (Snyder-Mackler et al., in press). Because of severe human encroachment, most of the natural predators of geladas, such as the spotted hyaena and leopard, are rare in the Simiens ($N = 2$ observed instances of predation, 2006–2011). All observers were trained for 6 weeks on data collection methods, including training with estimating known distances and interobserver reliability checks for distance estimates.

Weather Data

Weather data were collected using a La Crosse WS-2315U weather station (La Crosse Technology; La Crosse, WI, U.S.A.). Daily maximum and daily minimum temperatures (°C) were recorded in addition to daily rainfall data (mm). Mean monthly rainfall was calculated as the average of rainfall from the previous 30 days.

Relationship between Bachelor Number and Herd Size

Each morning ($N = 381$ days), observers counted all individuals as they ascended from the sleeping cliffs. Only fully mature bachelors were included in counts for bachelor groups (i.e. subadult males were excluded; for male age estimates and descriptions, see Beehner et al. 2009). Because of the high visibility conditions and spatial contiguity of the gelada herd, we counted bachelors as 'present' if they were located within 0.5 km of the herd.

First, we wanted to examine the relationship between the number of bachelors and herd size. We ran five separate correlations that addressed the relationship between the number of bachelors present at a sleeping cliff, the monthly rainfall, the daily maximum temperature and the herd size: (1) number of bachelors versus herd size; (2) number of bachelors versus rainfall; (3) number of bachelors versus temperature; (4) herd size versus rainfall; and (5) herd size versus temperature. In these analyses, we did not include bachelors in our counts of herd size, and because our data were not normally distributed, we used a nonparametric Spearman's rank correlation coefficient.

Second, to establish a causal argument (i.e. does the number of bachelors cause larger herd sizes or do larger herd sizes attract more bachelors?), we then examined how bachelor number and herd size changed in response to the number of bachelors and herd size on consecutive days (hereafter, termed 'previous day' and 'subsequent day'). We used only pairs of consecutive days in which we observed the same band on both days ($N = 71$ pairs of days). We ran two separate multiple linear regressions to test the effect of bachelor number and herd size on the subsequent day's bachelor number and herd size. In both models the number of bachelors and herd size were entered as predictor variables. The two models differed in their outcome variables. We used bachelor number on the subsequent day as the outcome variable for one model and herd size on the subsequent day as the outcome variable in the other. All predictor variables were *z*-transformed prior to analysis to reduce collinearity.

Effect of Bachelors on the Fissioning and Fusing of Herds

Next, we examined whether the presence of bachelors influenced a herd's probability of fissioning from or fusing with other geladas. We ran a generalized linear model using data from 113 fission and fusion events during the study period. We entered bachelor number and herd size prior to the fission or fusion event as predictor variables (in addition to rainfall and maximum daily temperature). We included the number of animals in the herd ('herd size') as a predictor because there is probably an upper and lower limit to gelada aggregation size, such that larger groups are more likely to fission and smaller herds are more likely to fuse (i.e. a herd composed of only a few units is much more likely to fuse with another herd than to fission into independent units). We entered the subsequent fission or fusion event as a binomial outcome variable.