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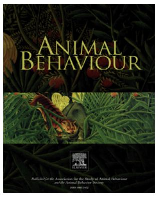

Formidable females and the power trajectories of socially integrated male vervet monkeys

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Sexual conflict theory expects females to avoid nonoptimal mating attempts by males. Although female vervet monkeys, *Chlorocebus pygerythrus*, can resist direct mating attempts, higher-ranking males still have more mating opportunities than lower-ranking ones. We presume that rank-related access reflects male–male competition that may conflict with female reproductive objectives. We extend an earlier report of codominance in this species to show that powerful females can undermine the restrictions imposed through male–male competition by improving the dominance rank of preferred male associates. We found that the dominance hierarchies of the sexes were comprehensively interdigitated and that males who had more female spatial associates, and who groomed with well-connected females, were more likely improve their Elo-ratings, which we use as an index of male power. The effects of partner number and integration, which predicted the probability of the initiation of aggression by lower-ranking males, suggest that association with females offered the prospect of protected threat if this likelihood increased. Although female rank and aggression were not directly consequential for males, we argue that female power and influence are intertwined and that both stem from the strength of female reproductive control.

Reproductive conflict between the sexes can be characterized as resistance by one sex to attempts by the other to coerce them into matings that may not optimize offspring viability (Gowaty, 2004); that is, for one sex to undercut the other's choice of mates. Where competition between males selects for size and weaponry, and males are larger than females, male curtailment of female choice has two components: direct monopolization of females and the suppression of reproductive access by male rivals. These generally work in conjunction insofar as a male that can control female movement should also be able to control access to them (Andersson & Simmons, 2006). However, even where females can, to a greater or lesser extent, evade immediate control by males, the ability of males to inhibit rivals, either directly, through interference (Wong & Candolin, 2005), or indirectly, through 'psychological castration' (Creel, Dantzer, Goymann, & Rubenstein, 2013; Henzi, 1981; Kraus, Heistermann, & Kappeler, 1999), will still circumscribe the expression of female mate choice.

Female vervet monkeys, *Chlorocebus pygerythrus*, face the latter predicament. Although they are able successfully to resist mating attempts by males (Freeman, 2012; Keddy, 1986), higher-ranking males nevertheless mate more frequently than do lower-ranking ones (Freeman, 2012; Keddy, 1986; Struhsaker, 1967). This suggests either that females cannot prevent high-ranking males from mating, despite their ability to resist in some circumstances, or that they actively prefer higher-ranking males and are less likely to resist their mating attempts.

Female resistance to male mating attempts is facilitated by the intrinsic difficulties of sexual monopolization in an arboreal habitat (Henzi & Lawes, 1987), but it may also occur because some females, despite being much smaller and with less impressive weaponry, appear to outrank some males (Struhsaker, 1967). To the extent that this observation of 'codominance' (Hemelrijk, Wantia, & Isler, 2008) or hierarchical integration is generalizable, it also offers the possibility that some, if not all, females are in a position to intervene and influence the dominance rank of males to the females' benefit (Raleigh & McGuire, 1989; see also Surbeck & Hohmann, 2013, for bonobos, *Pan paniscus*). That is, if higher-ranking males can reduce the mating opportunities of subordinates independently of their attempts at monopolization, then a female who improves or helps

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sustain the rank of a favoured male will also improve her reproductive access to him. As this is clearly also in the interests of the assisted males, we might expect them to cooperate and to promote affiliation with females.

If females are codominant, then we might expect them to express their influence in two, nonmutually exclusive, ways. First, they may aggressively target particular, nonpreferred males. In many other taxa, recipients of repeated aggression have higher physiological stress levels (Creel et al., 2013), and are susceptible to the rank loss associated with 'winner–loser' effects (Chase, Tovey, Spangler-Martin, & Manfredonia, 2002; Franz & Alberts, 2015; Silk, 2002). Second, females might provide agonistic support for preferred males. They could do so directly, by intervening in male–male aggression as males do (Young, Majolo, Schülke, & Ostner, 2014), or indirectly, where the mere possibility of support prevents the escalation of a contest and increases a male's extrinsic power (Berghänel, Ostner, & Schülke, 2011; Surbeck & Hohmann, 2013; Surbeck, Mundry, & Hohmann, 2011; Wittig et al., 2007) allowing them to win dyadic encounters with higher-ranking opponents. Importantly, of course, this coincides with the interests of most males, aligning the reproductive strategies of the sexes more closely and making social integration valuable to both parties. It follows, therefore, that, to the extent to which it increases the probability of effective support, social integration should be beneficial to males.

Here, after demonstrating extensive female codominance in our population, we use estimates of male power trajectories, derived from Elo-ratings (Albers & de Vries, 2001; Neumann et al., 2011), across successive 6-month blocks centred on the mating and birth seasons, and social network (SN) estimates of male–female affiliation to assess the following predictions. (1) Females exert a direct influence on male power trajectories by targeting males aggressively, with males who receive more frequent aggression from females being more likely to have a negative power trajectory. (2) The stronger a male's integration into the female network, the more frequently he will (i) receive agonistic support from them, (ii) initiate aggression against higher ranked opponents and (iii) win dyadic agonistic encounters up the hierarchy, (iv) leading to positive power trajectories.

METHODS

Study Site and Subjects

Data were collected between March 2012 and September 2015 at the Samara Private Game Reserve, South Africa (32°22′S, 24°52′E), on three groups (PT, RBM, RST) of wild, fully habituated and individually recognizable vervet monkeys occupying semiarid riverine woodland (Pasternak et al., 2013). Group composition varied across the three groups and the study period ($N_{\text{RBM Males}}$: 7–17; $N_{\text{RBM Females}}$: 10–14; $N_{\text{RST Males}}$: 10–15; $N_{\text{RST Females}}$: 17–18; $N_{\text{PT Males}}$: 4–10; $N_{\text{PT Females}}$: 8–11). Each group was followed for 10 h per day. In winter, daylight hours (0730–1730) coincided with our 10 h sampling period. During the longer daylight period in summer, we balanced our daily follows so there were equal numbers of days that began at dawn (0400 hours) and finished 10 h later in mid-afternoon, and days that terminated at 1900 hours and began 10 h earlier in the mid-morning.

Behavioural Data Collection

We used scan sampling (Altmann, 1974) at 30 min intervals to record the general activity (resting, moving, foraging or allogrooming) of each adult group member and the identities of all its neighbours within a 2 m radius, across each study day. Each scanning period lasted a maximum of 10 min to ensure as many animals as possible were sampled (i.e. to permit researchers to identify animals beyond the researchers' immediate vicinity), and most individuals were recorded in each scan ($N_{\text{total}} = 290\,019$ scans. The mean number of scans/animal/6-month block (±SD) were: $\text{RST}_{\text{Males}} = 305.10 \pm 220.54$; $\text{RST}_{\text{Females}} = 351.94 \pm 274.71$; $\text{RBM}_{\text{Males}} = 379.22 \pm 224.25$; $\text{RBM}_{\text{Females}} = 479.43 \pm 309.58$; $\text{PT}_{\text{Males}} = 418.66 \pm 255.41$; $\text{PT}_{\text{Females}} = 580.18 \pm 399.06$). Additionally, for records of allogrooming, we recorded both the identity of the partner and the direction of grooming. Agonistic behaviours, the identities of participants and the outcomes were recorded ad libitum. While we certainly did not see all agonistic encounters, we have no reason to suspect any systematic bias in the sampling.

Dominance Rankings

We divided the 42-month study period into seven consecutive 6-month blocks centred on either the mating (March–August) or the birth (September–February) season. Data from ongoing, ad libitum observations of decided dyadic agonism ($N_{\text{Male–Male}} = 2486$; $N_{\text{Male–Female}} = 1219$; $N_{\text{Female–Female}} = 4040$) were then used to construct both sex-specific and intersexual (hereafter 'integrated') dominance hierarchies for all adults in each 6-month period. This allowed us to estimate the proportion of group members of the opposite sex that each individual outranked. To do so, we determined the number of individuals of the opposite sex that ranked below the target individual and divided this by the total number of individuals of the opposite sex in that 6-month period/group.

For each troop, in each time period, dominance rank was expressed as a standardized normalized David's score, using the R package 'DomiCalc' (Schmid & de Vries 2013) in R 3.2.2 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Standardization enables direct comparison across groups of different size (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013). Using decided dyadic agonism, we determined the level of aggression each male received from females over each 6-month block. As our study site is situated in open, semiarid riverine woodland with generally high visibility, we are confident we missed very few agonistic interactions and that there was no systematic bias in the likelihood of detecting encounters. We also controlled for observer effort (number of observers per group per scan day; range 1–3) and for the presence of each individual animal in the group on each scan day (based on daily group census of an individual animal's presence/absence within the group). We used the R package 'steepness' (Leiva & De Vries, 2011) to estimate the slopes of dominance hierarchies and 'Domicalc' to determine directional consistency and *h*' as an estimate of linearity (Table 1).

Male Power Trajectories

To determine changes in male power over time (hereafter power trajectories), we estimated each male's power trajectory across each 6-month block by determining Elo-ratings (Albers & de Vries, 2001; Neumann et al., 2011), using the R package 'EloRating' (Neumann & Kulik, 2014). A male's Elo-rating is described by a value that increases or decreases depending on the outcome of contests between rated males. After each aggressive interaction, the winner takes points from the loser, with the difference in the current ratings of the loser and winner dictating the number of points that are gained or lost. For example, in a contest between a high-rated winner and low-rated loser, only a few points will be transferred as the winner began with a high probability of winning (reflected in their higher rating), whereas if the low-rated individual wins, a larger number of points are transferred to reflect the lower probability that this would occur. The number of points that can be won or lost is