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LETTERS

Intrasexual competition and sexual selection in cooperative mammals

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In most animals, the sex that invests least in its offspring competes more intensely for access to the opposite sex and shows greater development of secondary sexual characters than the sex that invests most[1,2]. However, in some mammals where females are the primary care-givers, females compete more frequently or intensely with each other than males[3–5]. A possible explanation is that, in these species, the resources necessary for successful female reproduction are heavily concentrated and intrasexual competition for breeding opportunities is more intense among females than among males. Intrasexual competition between females is likely to be particularly intense in cooperative breeders where a single female monopolizes reproduction in each group[6]. Here, we use data from a twelve-year study of wild meerkats (*Suricata suricatta*), where females show high levels of reproductive skew, to show that females gain greater benefits from acquiring dominant status than males and traits that increase competitive ability exert a stronger influence on their breeding success. Females that acquire dominant status also develop a suite of morphological, physiological and behavioural characteristics that help them to control other group members. Our results show that sex differences in parental investment are not the only mechanism capable of generating sex differences in reproductive competition and emphasize the extent to which competition for breeding opportunities between females can affect the evolution of sex differences and the operation of sexual selection.

Meerkats (*Suricata suricatta*) breed cooperatively in groups of 3–50 in the arid savannahs of southern Africa. In each group, a single dominant female (who usually either inherits her position in her natal group or acquires it as a founding member of a new group) monopolizes reproduction, producing up to four litters of 3–7 pups per year for up to ten years, though subordinate females breed occasionally[7]. Over 90% of pups born to dominant females are fathered by the group's dominant male, who is usually an immigrant or founding member of the group[8]. As in other mammals, breeding females invest more heavily in producing and rearing young than males, paying the costs of gestation and lactation as well as making a larger contribution than breeding males to provisioning dependent young[9,10]. Subordinate females, too, contribute more to provisioning and guarding dependent young than subordinate males[11].

Although reproductive skew is pronounced in both sexes, female meerkats gain larger reproductive benefits from acquiring dominant status than males. The average number of pups surviving to 12 months produced by 33 dominant females during their period of tenure was 17.0 (range = 0–65), whereas the average number of pups fathered by 53 dominant males was 8.9 (range = 0–42; Mann Whitney U test, $W = 2{,}070.5$; $N = 33{,}53$; $P = 0.037$; Fig. 1a). In both sexes, individual differences in breeding success depend primarily on the number of months for which individuals hold the dominant breeding position in their group (Fig. 1b), but the average tenure of females that acquire dominant status and breed at least once (31.5 months) is longer than that of males (17.4 months) (Hazard Ratio ± 95% Confidence Interval (CI) = 1.85 ± 0.31; $P = 0.041$; Fig. 1c). Sex differences in reproductive tenure occur partly because dominant females are less commonly replaced by competitors before their death and partly because dominant males are more likely to leave the group following the death of their partner than dominant females: although 80% of 'widows' retain their status for at least six months after the death of their partner and commonly breed with a

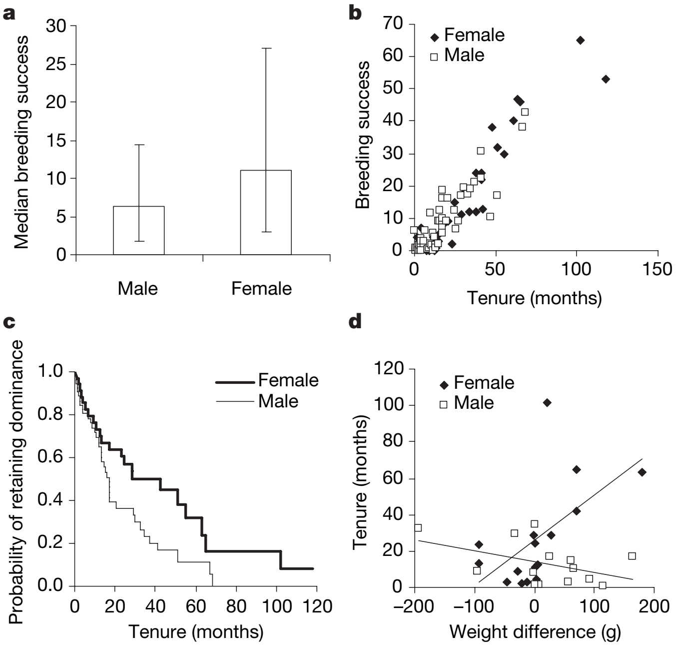

Figure 1 | Dominance and breeding success in males and females. **a**, Breeding success (offspring surviving to 12 months) of 33 dominant females and 53 dominant males. Graph shows medians and interquartile range. **b**, The influence of dominance tenure on breeding success in 33 dominant females (linear regression: $F_{1,32} = 226.44$, $P < 0.001$, $R^2 = 87.6$) and 53 dominant males (linear regression: $F_{1,52} = 185.91$, $P < 0.001$, $R^2 = 78.1$). **c**, Kaplan–Meier estimates of the probability of dominant females ($N = 33$) and males ($N = 53$) retaining their status after different periods of time. **d**, The relationship between the difference in body weight between the dominant and the heaviest same-sex competitor and tenure in dominant females ($N = 16$) and dominant males ($N = 14$).

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new partner, only 25% of 'widowers' do so (chi-square, $\chi^2_1 = 8.17$; $N = 15$ females, 12 males; $P < 0.004$).

As a result of the longer tenure of females, fewer females than males breed as dominants and standardized variance (variance/mean^2) in estimates of lifetime breeding success is larger in females than males (females = 6.13; 95% CI = 3.66,11.28; $N = 59$; males=3.98; 95% CI=2.23,6.71; N=59; see Supplementary Methods for details). Because the benefits of acquiring dominance status are greater for females than for males (Fig. 1a) females would be expected to compete more intensely with each other for dominant positions. As predicted, subordinate females of all ages initiate (Generalized Linear Mixed Model (GLMM): $\chi^2_1 = 10.09$; $P < 0.001$) and receive more aggression (GLMM: $\chi^2_1 = 19.77$; $P < 0.001$) than males of similar age and status (Fig. 2a, b). Subordinate females are also more frequently submissive than subordinate males (GLMM: $\chi^2_1 = 427.66$; $P < 0.001$; Fig. 2c). Though males and females do not differ in the frequency with which they win play fights as pups, as they grow older, females win a greater proportion of play fights than males (GLMM age*sex: $\chi^2_2 = 13.77$; $P = 0.001$; Fig. 2d).

Traits affecting competitive ability also have a stronger influence on the acquisition of dominance in females than in males. When subordinate females compete for the dominant position, older individuals usually win, but where there is no difference in age or younger individuals win, those that acquire dominant status are heavier than those that fail to do so (paired *t*-test: $t_{13} = 2.60$; $P = 0.023$; Fig. 3a). After the effects of body mass have been allowed for, daughters of dominant females are also more likely to acquire dominant status than those of subordinates (GLMM: $\chi^2_1 = 3.84$; $P = 0.050$; Fig. 3b). Older subordinate males usually win contests for dominant status but, where this is not the case, winners are not consistently heavier than losers (paired *t*-test: $t_{10} = 0.08$; $P = 0.94$; Fig. 3a) and the sons of dominant mothers are no more likely to acquire dominant status than those of subordinates (GLMM: $\chi^2_1 = 0.15$; $P = 0.70$; Fig. 3b), generating a significant interaction between the effects of sex and mother's dominance status on the probability of acquiring dominance status (GLMM: $\chi^2_1 = 6.62$, $P = 0.010$).

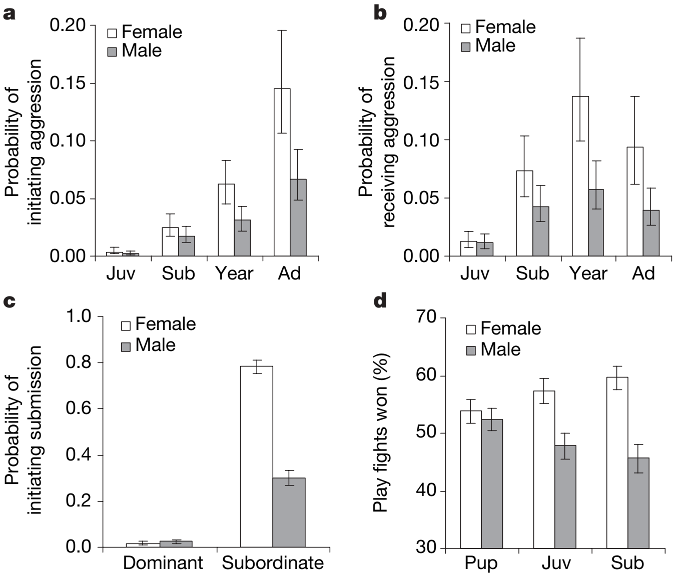

Figure 2 | Sex differences in aggression and submission. a, **b**, Probability that male and female subordinates of different age categories initiate or receive aggression during a breeding attempt (juvenile, 3–6 months; sub-adult, 6–12 months; yearling, 12–24 months; adult, >24 months). **c**, Probability that dominant and subordinate males and females >1 yr will initiate submission. **d**, The percentage of play fights involving opposite sexed pups (1–3 months), juveniles (3–6 months) and subadults (6–12 months) won by each sex ($N = 28$ females, 24 males); graphs show the predicted means (± s.e.m) derived from GLMMs in which group, litter and individual identity were included as random terms. Sample sizes are provided in Methods.

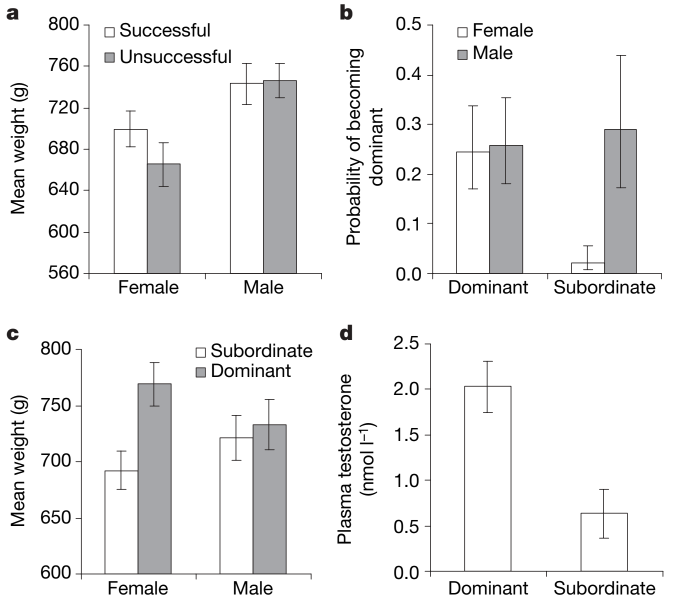

Figure 3 | The acquisition and maintenance of dominance status. a, Mean body mass in the three months before a dominance change of females ($N = 13$) and males ($N = 10$) that successfully acquired dominant status compared with an older, or same-aged unsuccessful competitor. **b**, Proportion of daughters and sons born to dominant ($N = 97$ daughters, 104 sons) or subordinate ($N = 23$ daughters, 20 sons) mothers that acquired dominant status. **c**, Mean mass (g) of females ($N = 13$) and males ($N = 8$) three months before becoming dominant, and six months after becoming dominant. **d**, Plasma testosterone concentrations (nmol l^{-1}) of dominant ($N = 12$) and subordinate ($N = 13$) adult females during pregnancy. All graphs show means ± s.e.m.

Females that acquire dominant status show a suite of behavioural and morphological changes that are reduced or absent in males. They increase in body mass whereas males do not (Fig. 3c), generating a significant interaction between the effects of dominance status on changes in body mass between the two sexes (Linear Mixed Model (LMM): $\chi^2_1 = 4.63$; $P < 0.031$). During pregnancy, dominant females also show higher levels of circulating testosterone than subordinates (General Linear Model (GLM): $F_{1,25} = 9.64$; $P = 0.005$; Fig. 3d), whereas males that acquire dominant status show no consistent increase in testosterone[12]. Dominant females are also more frequently aggressive to other group members than dominant males (GLMM: $\chi^2_3 = 9.56$; $P = 0.021$), especially in late pregnancy when they direct aggression at older subordinate females, whom they commonly evict from their groups[7,13]. These changes probably help to secure their position, for the tenure of dominant females increases with the difference between their average body weight and that of the heaviest subordinate female in the group (GLM: $F_{1,15} = 5.39$, $P = 0.037$). In contrast, there is no consistent association between the breeding tenure of dominant males and the difference between their weight and that of the heaviest subordinate male (GLM: $F_{1,13} = 1.89$, $P = 0.20$), generating a significant interaction between the effects of sex and relative body mass on dominance tenure in the two sexes (GLM: $F_{1,29} = 6.52$, $P = 0.017$; Fig. 1d).

Our results show that female meerkats that acquire dominant status have longer breeding tenures and gain greater reproductive benefits than males. A possible reason for the longer tenures of breeding females is that, once a dominant female is established, her potential competitors are natal animals that she can suppress or evict before they become serious rivals[13], whereas the principal competitors of dominant males are either mature immigrants or members of other groups whose development they cannot control. Females are also more likely to retain their position after the death of their partner because they commonly attract immigrant males from other groups, who are tolerated by their resident subordinate sons (who will eventually disperse to breed). In contrast, dominant males that lose their partners are not accepted as mates by natal females (who are commonly their daughters) and cannot attract unrelated female immigrants because these are not tolerated by resident subordinate females[13]. The greater benefits of acquiring dominance status may explain why females compete more intensely with each other for breeding opportunities throughout their lives and why traits enhancing competitive ability show greater development in dominant females than in dominant males.

Variation in female breeding success is unusually large in other cooperative or eusocial breeders[6], and females are often more frequently aggressive than males. High levels of reproductive skew, long breeding lifespans and intense intrasexual competition for breeding opportunities are characteristic of females in many eusocial insects[14,15]. Similarly, in naked mole-rats (*Heterocephalus glaber*), which live in colonies of up to a hundred or more with a single breeding female in each colony who breeds several times each year[16], dominant females are more aggressive than other group members. Like dominant female meerkats, they show higher levels of testosterone than subordinates[17] as well as a secondary period of growth after attaining dominant status, which is reduced or absent in males[18]. Although the reproductive tenure of dominant animals in natural populations of naked mole-rats is not known, captive breeding females can maintain their status for over twenty years[19] and variance in female breeding success is likely to be high. Intense intrasexual competition combined with greater development of secondary sexual characters in females also occurs in a number of other vertebrates that do not breed cooperatively. In several of these species, successful reproduction depends on access to scarce or concentrated resources and females compete intensively with each other for these. For example, in spotted hyenas (*Crocuta crocuta*), where females are larger and more aggressive than males, females compete more intensely than males for social rank, which affects their access to resources as well as the survival of their dependent progeny[3] but has little effect on breeding success in males[20]. Dominant females develop high testosterone levels in late pregnancy and their offspring are more competitive[21] and achieve higher status than those of subordinates[22]. Similarly, in clown fishes (*Amphiprion*), protandrous females compete for access to scarce sea anemones that provide safe breeding sites and are larger and more frequently aggressive than males[23,24] and in *Eclectus* parrots (*Eclectus roratus*), females are brighter than males, and compete intensely for scarce nesting holes[25].

Our analyses suggest that, although greater parental investment by female mammals commonly leads to intense competition between males for access to mates and to strong selection favouring competitive ability in males[1,26], competition for reproductive opportunities between females can also generate strong selection pressures favouring competitive ability. In extreme cases, these may be capable of reversing the usual direction of sex differences in behaviour and morphology. Strong selection for competitive ability in females may sometimes be associated with greater variance in breeding success among females than among males[6], but qualitative differences in the determinants of breeding success in males and females may also lead to divergent selective pressures on particular traits in the two sexes, and to sex differences in competitive behaviour and morphology[27]. For example, the larger size and greater aggressiveness of females in spotted hyenas does not necessarily indicate that variation in breeding success is greater in females and could also occur because size and aggressiveness have a stronger effect on the breeding success of females than males. The relative benefits of successful competition are also likely to vary throughout the reproductive cycle in both sexes, and sex differences in competitiveness may also change[28]. As a result, although sex differences in parental investment and associated indices (including the operational sex ratio, the opportunity for sexual selection and comparative Bateman gradients) may usually predict the direction of sex differences in behaviour and morphology, they will not always do so and exceptions may be more common than is currently appreciated.

Finally, our results illustrate the limitations of current definitions of sexual selection. Although Darwin[29] sometimes described sexual selection as a consequence of intrasexual competition for breeding opportunities and sometimes as a consequence of intrasexual competition for mates, it is now commonly used to refer to selection operating through intrasexual competition for mates or mating opportunities[2,30]. Unlike males, females more commonly compete with each other for opportunities to conceive or rear young (or for resources that allow them to do so, including male care) than for access to gametes produced by the opposite sex, so that current definitions of sexual selection[1] exclude the consequences of many important forms of intrasexual competition between females. An alternative approach is to return to Darwin's broader description of sexual selection as a process operating through intrasexual competition for reproductive opportunities, providing a conceptual framework that is capable of explaining the evolution of pronounced secondary sexual characters in females as well as in males.

METHODS

Study site. Data were collected at the Kuruman River Reserve, South Africa (26° 58′ S, 21° 49′ E), between October 1993 and May 2005. Descriptions of habitat, climate and study population are provided elsewhere[13]. All animals in the study population were habituated to close observation and most could be weighed before the morning foraging session without the need for capture.

Breeding success. The breeding success of 33 dominant females and 53 dominant males was measured as the number of pups surviving to 12 months produced during their tenure. As dominant males sire over 90% of pups born to dominant females and 45% of pups born to subordinate females (G.S. *et al.*, submitted) we assumed that 90% of pups born to dominant females and 45% of pups born to subordinate females were fathered by the resident dominant male during his tenure.

Statistical analysis. Multivariate analyses were performed in Genstat 5 (Release-4.2, Lawes Agricultural Trust, Rothamsted, Harpenden, UK). Where multivariate analyses were required, GLMs were used. Where necessary, LMMs and GLMMs were used to take into account repeated sampling within individuals, breeding attempts or groups. Random terms were retained in the model unless variance components were found to be zero. All statistical tests are two-tailed. Anderson-Darling tests were used to test for normality.

Dominance tenure. Tenure was measured from the date on which an individual acquired dominance to the date that dominance ended or observations ceased. Survival analysis (Cox's proportional hazards regression) was used to compare the probability of losing dominance for females ($N = 33$) and males ($N = 53$) from 21 social groups. To investigate the influence of relative weight at the start of the dominance period on the tenure of male ($N = 14$) and female ($N = 16$) dominants, dominance tenure was log transformed and fitted as the response term in a GLM. The differences in the mean non-breeding weights of dominants and their largest competitor in the two months around a dominance change, and the sex of the dominant individual, were fitted into the model as the main terms of interest. The number of competitors and group size at the start of dominance, and whether or not the dominant was the oldest individual in the group, were included as covariates but had no significant influence ($P > 0.05$).

Aggression and submission. We recorded all incidences of aggression and submission *ad libitum* during daily watches of groups during three-month periods following the birth of a litter. Aggression was defined as an occasion when an individual growled at, hip-slammed, bit or chased another individual. Submission was defined as an occasion when an individual emitted a peeping vocalisation, accompanied by a characteristic crouched posture. Whether or not a subordinate individual was seen to give or receive aggression from any other group member during a breeding attempt was fitted as the binomial response term (1 = Yes, 0 = No) in two separate GLMMs with 1 as the binomial denominator. The age category (juvenile, subadult, yearling or adult) and sex of the individual were fitted as the main terms of interest and group size was fitted as a covariate. In two further models, we fitted whether or not an individual older than 12 months gave aggression or submission to at least one other individual older than 12 months (of either sex) during a breeding attempt as the binomial response term (1 = Yes, 0 = No). The status of the individual (dominant male, dominant female, subordinate, male or subordinate female) was fitted as the main term of interest and group size was fitted as a covariate. Only individuals who were present on all days on which data were collected were included in these analyses. Analyses of aggression were conducted on 1,457 periods of potential aggression, involving 335 individuals ($N = 42$ dominants and 324 subordinates) during 143 breeding attempts in 14 groups. Analyses of submission were conducted on 3,653 periods of potential submission involving 515 individuals ($N = 71$ dominants, 495 subordinates) in 374 breeding attempts and 23 groups. Group, individual and litter identity were included as random terms in all models.

Play fights. Bouts of play wrestling were recorded *ad libitum* between April 1999 and November 2002. For each wrestling bout, the individual that ended up on top was considered the 'winner'. We fitted the number of play fights won by each individual in each age category as the binomial response in a GLMM, with the total number of play fights observed as the binomial denominator. We included the age category of the individual (pup, juvenile or subadult) and the sex of the individual as fixed effects. Analysis was conducted on 52 individuals ($N = 28$ females, 24 males) from nine litters in seven groups, all of whom were observed in all three age categories. Individual, litter and group identity were included as random terms.

Influence of mother's dominance status. We included all offspring that survived to one year that could have reached four years of age before 01/04/05 in the analysis. Data were available from 97 daughters and 104 sons born to 15 dominant mothers, and 23 daughters and 20 sons and born to 19 subordinate mothers. Whether or not offspring attained dominance before 01/04/05 ($1 = \text{Yes}$, $0 = \text{No}$) was fitted as the binomial response term in a GLMM, with 1 as the binomial denominator. The sex of the offspring and the dominance status of the mother were included as the main fixed effects. Mean weight at 12 months (between 365 and 395 days) was included as a covariate, but was found to be non-significant ($P > 0.05$). Group and mother's identity were included as random terms.

Changes in body weight on attaining dominance. To investigate whether individuals became heavier after attaining dominance, we compared measures of body mass ($N = 103$) for 21 individuals ($N = 13$ females, 8 males) who acquired dominant status during the course of the study, using a LMM. Only the weights of non-pregnant females were included. Dominance status and sex were fitted as the main terms of interest. Age was included as a significant covariate (LMM: $\chi^2_1 = 16.18$, $P < 0.001$) and group size was included but was found to be non significant ($P > 0.05$). Individual identity was included as a random term.

Hormonal analyses. Blood samples for hormonal analysis were collected from 25 females during the early stages of pregnancy ($N = 12$ dominant, 13 subordinate) living in 11 social groups between January 2006 and April 2006. Methods of hormonal analysis are described elsewhere[12]. The testosterone concentration for each female ($\text{nmol}\,\text{l}^{-1}$) was fitted as the normally distributed response term in a GLM, with dominance status (dominant or subordinate) as the main term of interest. Oestrogen concentration ($\text{pmol}\,\text{l}^{-1}$) was included as a covariate and was found to have a significant positive influence (GLM: $F_{1,25} = 8.89$, $P = 0.007$). Female age and pregnancy stage (in days) were also included as covariates but were found to be non-significant ($P > 0.05$).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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