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ADAPTIVE SIZE MODIFICATION BY DOMINANT FEMALE MEERKATS

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Abstract.—In species of cooperative insects that live in large groups, selection for increased fecundity has led to the evolution of an increased body size among female reproductives, but whether this is also true of cooperative vertebrates is unknown. Among vertebrates, morphological modification of female breeders has only been documented in a single species; in naked mole rats (*Heterocephalus glaber*), acquisition of alpha status is associated with a significant increase in body size through an elongation of the lumbar vertebrae. Here we provide evidence of morphological modification among breeding females of a cooperative carnivore, the meerkat (*Suricata suricatta*), and demonstrate that this modification is likely to be adaptive. The same female meerkats were significantly larger when they were dominant than when they were subordinate. This increased body size was not explained by differences in age, foraging efficiency, or investment in offspring care, but may have arisen, in part, through increased levels of hormone that govern bone growth. Increases in body size are likely to result in fitness benefits, for large females delivered larger litters and had heavier offspring, both of which are known to correlate positively with measures of breeding success in meerkats. Our results suggest that the acquisition of alpha status in female meerkats is associated with an adaptive increase in body size and hence that morphological modification of female vertebrates may be more widespread than has been previously supposed.

Key words.—Eusocial, fecundity, morphological modification, naked mole-rat, progesterone, vertebrate.

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The caste system of social insects, in which individuals that carry out different activities are morphologically distinct, represents a pinnacle in social evolution (Wilson 1971; Maynard-Smith and Szathmáry 1995). In some species, the differences between castes are substantial, with reproductive females being an order of magnitude or larger than nonreproductives (Wilson 1971). The degree to which reproductive females are morphologically modified in social insects is, in part, associated with group size, with modification being greater in species of larger groups than those of smaller groups (Bourke 1999). One explanation is that selection for increased body size (and resulting fecundity) is stronger in species of large groups since many helpers are able to raise many offspring, whereas selection against increased body size is weaker, because corresponding costs of foraging and parenting are lower or absent (Alexander et al. 1991; Bourke 1999; Peeters and Ito 2001). However, it is currently unclear whether morphological modifications are a general feature of highly cooperative animals and, if so, whether a positive relationship between group size and the extent to which breeders are morphologically modified is also apparent in vertebrates.

Unequivocal evidence that female breeders can be modified in vertebrates is provided by a single species. In female naked mole rats (*Heterocephalus glaber*), acquisition of alpha rank (and hence reproductive status) is associated with a significant increase in body size, achieved by an elongation of the lumbar vertebrae (O'Riain et al. 2000a). Dominant females are also larger or heavier than mature subordinates in groups of Damaraland mole rats (*Cryptomys damarensis*; Bennett and Jarvis 1988), common mole rats (*C. hottentotus*; Bennett 1989), dwarf mongooses (*Helogale parvula*; Creel and Creel 1991), and meerkats (*Suricata suricatta*; Clutton-Brock et al. 2001a). However, with the exception of naked mole rats, it is unclear whether such differences are a consequence of age or a result of larger individuals having an increased likelihood of becoming dominant. Furthermore, the adaptive significance of being a large reproductive female has yet to be established in cooperative vertebrates.

The aim of this study is to determine whether or not dominant females are morphologically modified in the meerkat, one of the most cooperative vertebrates known, and to establish whether being a large reproductive female is likely to afford fitness benefits. Meerkats are small (<1 kg), carnivorous mongooses that live in groups of up to 50 individuals in arid regions of southern Africa. A dominant female is the principal breeder in each group (Clutton-Brock et al. 2001a; Griffin et al. 2003), delivering up to four litters per year of between three and eight pups per litter (Russell et al. 2003a). Subordinates may aid the dominant female by allosuckling, babysitting, and provisioning her pups, as well as by clearing out ''bolt-holes'' and scanning for predators (Clutton-Brock et al. 2002). The presence of helpers has significant benefits for the dominant female: through provisioning food, helpers improve the growth, condition, and survival of her offspring (Clutton-Brock et al. 2001b, Russell et al. 2002); and through reducing her energetic expenditure in pup care (Scantlebury et al. 2002; Clutton-Brock et al. 2004),

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helpers improve her condition and subsequent fecundity (Russell et al. 2003a).

Subordinate females may attempt to reproduce from twelve months of age (Clutton-Brock et al. 2002), but their attempts are generally suppressed by the dominant. Dominant females enforce suppression behaviorally, through evicting subordinates from the group or killing their offspring (Clutton-Brock et al. 2001a; O'Riain et al. 2000b), but may also enforce it physiologically (Young 2003; Carlson et al. 2004). Subordinates can only attain alpha status upon the death of the current dominant (56% of the 25 dominance acquisitions observed), or by dispersing to become a dominant in a new group (44% of observations). Either way, acquisition of alpha status is strictly age related, with older subordinates always succeeding in gaining dominance over younger subordinates, and females virtually never losing alpha status once established.

We first examine whether the acquisition of alpha status is followed by an increase in body size and weight by examining whether (after controlling for age) the same individuals are larger and heavier when dominant than when a mature subordinate. Second, we investigate whether differences in body size may be explained by changes in foraging efficiency or investment in pup care, or whether it may be influenced by changes in levels of estradiol and progesterone, two of the hormones most involved with bone growth in mammals. Finally, we investigate the relationship between body size and fecundity in meerkats, and hence determine whether increasing body size is likely to be adaptive.

MATERIALS AND METHODS

The study was carried out in 17 groups of meerkats between September 1993 and May 2002 in farmland near Vanzylsrus in the Northern Cape of South Africa (26°58′S, 21°49′E). The number of individuals in each group (excluding pups) ranged from four to 44 (mean = 19), and all individuals were habituated to close observation (<1 m). Details of climate and habitat are provided elsewhere (Clutton-Brock et al.1999; Russell et al. 2002). During each group visit (every one to five days), we recorded the identities of group members and determined their reproductive and dominance status (for further details, see Clutton-Brock et al. 2001a). Reproductive status (i.e., pregnant or nonpregnant) was determined from the first month of pregnancy by visual inspection and changes in body weight, with the reliability of such methods having been confirmed using ultrasound imaging. The acquisition of dominance status can be easily determined through observation, for dominant females alone ''anal mark'' and evict other females from their group. All individuals included in this study were born during the study period and so were of known age (± 5 days). Details of all statistical terms and procedures introduced below are presented at the end of the Methods in the section entitled Statistical Analyses.

Morphological Modifications

Whether female meerkats show morphological modifications with the acquisition of dominance status was investigated by examining the size and weight of the same females when both subordinate and dominant, after controlling statistically for changes in age. Because all individuals were measured both as a subordinate and as a dominant, we exclude the possibility that dominants are larger or heavier than subordinates because large, heavy subordinates are more likely to become dominant. In addition, we reduce the likelihood that any rank related differences in size or weight are a consequence of differences in foraging efficiency by restricting measures to individuals over 18 months old. This is the age when foraging efficiency levels off in meerkats (Clutton-Brock et al. 2003) as well as the age at which the youngest female attained dominance status in this study (548 days).

We used two measures of body size to investigate whether or not acquisition of alpha status is associated with an increase in size: head width (zygomatic arch) and body length (bottom of neck to base of tail). Measurements were obtained from captured and anesthetized animals (see O'Riain et al. 2000b for details). Skull width was measured with vernier callipers (± 0.1 mm), whereas body length was measured using a tape-measure (± 1 mm) with the animal face down. Overall, 84 measurements (of each morphometric) were obtained from 13 individuals that obtained alpha status in 12 groups, 35 measurements were obtained when individuals were subordinate, and 49 when they were dominant. When individuals were subordinate they ranged in age from 567 to 1287 days (mean = 770), whereas when they were dominant they ranged from 646 to 2737 days (mean = 1079).

Measures of body weight were based on morning, preforaging weights, collected during periods of nonbreeding (i.e., when females were nonpregnant and dependent pups were absent). Weights were obtained by coaxing individuals onto electronic top-pan balances (± 1 g) using crumbs of hard-boiled egg (Clutton-Brock et al. 2001a). Overall, we obtained 1914 weights from 17 individuals that acquired alpha status in 14 different groups. When individuals were subordinate (n = 1017 weights), they ranged in age from 550–1298 days (mean = 771), whereas when they were dominant (n = 897 weights), their ages ranged from 592–2081 days (mean = 1054).

Whether or not individuals were relatively larger or heavier as dominants was investigated using general linear mixed models. In each analysis, dominance status was fitted as the main fixed effect, while individual age and group size were fitted as covariates. Individual identity was fitted as a random term in each analysis to control for repeated measures of the same individuals (2–12 measures per individual for the two body size analyses and 33–230 measures per individual for the body weight analysis).

Mechanisms of Size Differences

Acquisition of alpha status could be associated with increased growth rates if, when dominant, females have greater resource intake rates because their foraging efficiency is higher or their investment in pup care is lower. Foraging efficiency may increase among dominants, because they spend little time scanning for predators (Clutton-Brock et al. 2004). Investment in pup care may decrease among dominants, because they appear to contribute less to offspring care than subordinate females (Clutton-Brock et al. 2004), and offspring care is energetically costly (Russell et al. 2003b).

We compared the rates of weight change of the 17 individuals when subordinate and when dominant during periods of nonbreeding and breeding (pre- and postpup weaning), although we were unable to calculate weight changes for all individuals when both subordinate and dominant for all periods. Short-term changes in weight were calculated (grams/day) using slopes obtained from regressions of weight and age for each individual (when subordinate and dominant) during each of the three periods. Overall, we obtained 247 rates of weight change, 66 during periods of nonbreeding and 181 during periods of breeding (82 during preweaning periods and 99 during postweaning periods). We conducted a general linear mixed model analysis in which rate of weight change was fitted as the response term, dominance/breeding status, age, and group size were fitted as fixed effects and individual identity was fitted as a random term (repeated measures per individual 6–34). During periods of nonbreeding, dominance/breeding status refers to whether an individual was subordinate or dominant and whether or not it had been breeding in the previous event. During periods of pup care, it refers to whether an individual was subordinate or dominant and whether or not it was breeding in a current event.

Alternatively, dominance-mediated differences in body size or weight may be influenced by differences in levels of hormones that govern bone growth. Two of the most important hormones influencing aspects of bone growth in female mammals are estrogens and progesterone (Prior 1990; Schmidt et al. 2000; Lindberg et al. 2001). We obtained measurements of both hormones from small blood samples taken under license from nonpregnant anesthetized animals. Plasma was separated from the blood on the day of collection using a centrifuge, and immediately frozen at −40°C. Details of estradiol assay procedures are described briefly because they are published elsewhere (Carlson et al. 2004), although details of progesterone assay procedures are given in more detail. Estradiol assays were conducted on blood samples from 33 individuals, 24 subordinates and nine dominants, whereas progesterone assays were conducted on blood from 29 individuals, 22 subordinates and seven dominants. Subordinates ranged in age from 365 to 1665 days (mean = 732), whereas dominants ranged from 548 to 2040 days (mean = 1357). The effect of dominance status on levels of circulating estradiol and progesterone were investigated using Mann Whitney *U*-tests, because the variance distributions of subordinates and dominants were unequal.

Plasma samples were assayed for estradiol using Coat-a-Count Estradiol kits (Diagnostic Products Corp., Los Angeles, CA). Assay sensitivity was 10pg/ml. Intra- and interassay coefficients of variation for a pool of meerkat plasma were 5.2% and 6.7%, respectively. Levels of plasma estradiol did not vary with increasing capture-to-bleed time (Spearman rank correlation, $r_s = 0.11$, $n = 22$, $P = 0.64$), although capture-to-bleed times ranged from three to 38 minutes.

Plasma samples were assayed for progesterone using Coat-a-Count Progesterone kits (Diagnostic Products Corp.). Serial dilutions of meerkat plasma were parallel to the standard curve ($P > 0.05$). Accuracy, calculated as the percent recovery of known amounts of progesterone added to each standard curve point, was 95.5% ($n = 5$). Assay sensitivity was 0.1ng/ml. Cross-reactivity with other hormones was 9.0% for 5 α-pregnan-3,20-dione and <5% for testosterone, pregnenalone, 5 β-pregnan-3,20-dione, medroxy-progesterone, 17 α-hydroxy-progesterone, estradiol, and 11-deoxy-corticosterone. Briefly, 25 μl of meerkat plasma and 75 μl of assay dilutent were added to antibody-coated test tubes, 1 ml ^{125}I-progesterone was then added and the assay was incubated for 3 h at room temperature. The assay was decanted before counting each tube for one minute in a gamma counter. Intra- and interassay coefficients of variation for a pool of meerkat plasma were 5.7% and 7.9%, respectively. Levels of plasma progesterone did not vary with increasing capture-to-bleed time (Spearman rank correlation, $r_s = 0.018$, $n = 29$, $P = 0.93$), although capture-to-bleed times ranged from four to 38 minutes.

Body Size and Fitness

We investigated whether or not body size is related to measures of fitness among females. Two components of fitness were investigated: (1) litter size at birth, and (2) mean pup weights at weaning. These two measures have been shown to have long-term ''fitness'' consequences in meerkats (Clutton-Brock et al. 2001b; Russell et al. 2002, 2003a). In the two analyses, we fitted the response term to a normal error structure in a general linear model. Fixed, potential explanatory, terms fitted included maternal age, body length, body weight, and head width. Age and weight were averaged at conception, between 60 and 80 days before the birth of the litter, although measures of body length and head width were obtained and averaged within a three-month period before and/or after litter delivery.

Litter sizes at birth are difficult to obtain in cooperative mammals because mothers usually give birth underground so we estimated these using a portable ultrasound scanner (for further details, see Russell et al. 2003a). In total, we obtained 34 scans from 19 females in eight groups approximately 14 days prepartum (range 4–30 days), but in only 28 of these was body size data available. The number of days between scanning and birth was initially fitted as a covariate, but we found no evidence to suggest that this significantly influenced litter sizes at scanning ($F_{1,26} = 0.07$, $P = 0.80$).

Mean weights of pups in litters were calculated when pups were aged between 25 and 30 days. After one month, the weight of pups is significantly influenced by the number of helpers present in the group (Clutton-Brock et al. 2001b, Russell et al. 2002), but this is not the case before this age (Russell et al. 2003a). Pup weights were obtained from 33 litters delivered by 14 females in eight groups, but in only 25 were body size data available. Additional terms fitted as covariates were litter size and the average age at which pups were weighed, but neither was found to influence the weight of pups at weaning ($F_{1,22} = 2.91$, $P = 0.10$ and $F_{1,22} = 0.92$, $P = 0.86$, respectively).

Statistical Analyses

Analyses were conducted in Genstat 5, Release 4.1 (GENSTAT, Rothamsted Experimental Station, Harpenden, U.K.). All analyses (except hormones) were initially conducted using linear mixed models. Linear mixed models are similar to

TABLE 1. Linear mixed model showing effect of body size, age, and dominance status on female body weight ($n = 84$ measurements (35 when subordinate, 49 when dominant) from 13 individuals obtaining dominance status in 12 groups. Statistics arise from forward step-wise procedure built in this order presented. Effects indicate direction of relationship and are presented after setting the mean of the covariate to zero.

Model term	Wald statistic	df	*P*-value	Effect	SE
Body length	39.96	1	<0.0001	13.38	1.17
Head width	16.77	1	<0.001	20.31	5.12
Age (log fit)	5.51	1	0.019	49.13	20.99
Dominance status	0.26	1	0.61	5.19	12.83
Constant				761	13.06

generalized linear model (GLM), except that they allow both fixed and random terms to be fitted. Fixed terms included the explanatory term(s) of interest, as well as potentially confounding covariates such as age and group size. All covariates were fitted as linear, logarithm and quadratic functions, but no quadratic fits attained significance. With the exception of the results presented in Table 1 in which a stepwise forward elimination technique was used, potential explanatory (fixed) terms were entered in each analysis and subsequently dropped until the model only included those terms whose elimination would have significantly reduced the explanatory power of the model. The significance of fixed terms in linear mixed models is calculated using maximum likelihoods and is assessed by their Wald Statistics, which are distributed as χ^2 for each term fitted last in the model. Thus, all *P*-values reported (except those in Table 1) are presented after controlling for all other significant terms in the model, and hence all potential confounding covariates that were entered. Random terms take into consideration repeated sampling of the same individual (Schall 1991). Where the random term had a negative component of variance (indicating that it explained none of the variance in the model), it was dropped and an equivalent linear (nonmixed) model was conducted instead.

RESULTS

Morphological Modifications

Females continue to grow throughout their adult life. Older females had longer bodies than younger females (GLM: linear effect, $\chi^2 = 15.67$, df = 1, $P < 0.001$), but did not have wider skulls ($\chi^2 = 2.68$, df = 1, $P = 0.10$). No effect of group size was found on either morphometric ($\chi^2 = 0.66$, df = 1, $P = 0.42$ and $\chi^2 = 1.64$, df = 1, $P = 0.20$, respectively). Females also continued to gain significant weight during adulthood (GLM, logarithm function, $\chi^2 = 495.80$, df = 1, $P < 0.0001$), and were heavier in larger groups than in smaller groups (log function, $\chi^2 = 6.85$, df = 1, $P = 0.009$).

After controlling for significant age and group size effects (where appropriate), we found that females increase in size following acquisition of alpha status. Females had longer bodies (Fig. 1a; $\chi^2 = 6.66$, df = 1, $P = 0.010$) and wider skulls (Fig. 1b; $\chi^2 = 6.13$, df = 1, $P = 0.013$) when they were dominant compared with when they were subordinate. Consequently, females were found to be significantly heavier when they were dominant than when they were subordinate (Fig. 1c; $\chi^2 = 113.57$, df = 1, $P < 0.0001$). Finally, restriction of the body weight dataset to the six months before the acquisition of alpha status and the six months following its acquisition revealed that body weight increased more rapidly after alpha status was attained than before it was attained (Fig. 1d; dominance status × days: $\chi^2 = 12.56$, df = 1, $P < 0.001$). This increase in weight was evident after controlling for the age of the individuals when they attained alpha status ($\chi^2 = 79.45$, df = 1, $P < 0.0001$) and their current breeding status (see below). The evidence suggests that accelerated weight gain following acquisition of alpha status reflects a period of accelerated body growth rather than increased body condition (see below and Discussion).

Mechanisms of Size Differences

One explanation for our results is that individuals show increased growth after attaining dominance status as a result of improved foraging efficiency. In contrast, we found little evidence to suggest that this is the case. First, individuals appeared to have similar levels of foraging efficiency when subordinate and as when dominant (Fig. 2a). During periods of nonbreeding, when dependent pups were absent, individuals had similarly low levels of weight gain when they were subordinate as when they were dominant if they had not bred in the previous attempt, and similarly higher levels if they had bred. Thus, weight gains during periods of nonbreeding are likely to be caused by compensation for the costs of reproduction rather than differences in foraging efficiency (for similar results among helpers, see also Russell et al. 2003b). Moreover, because weight changes were similarly high when individuals were subordinate (and had bred) versus dominant (and had bred), individuals appear to suffer similar costs of breeding irrespective of their dominance status.

Another possibility is that individuals suffer reduced costs during breeding attempts when they are dominant compared with when they are subordinate. However, the costs of reproduction appeared to be greater than those of helping (Fig. 2b). During the preweaning period, females lost significantly more weight when dominant and breeding than when subordinate and not breeding, suggesting that the costs of lactation are greater than the costs of babysitting. This suggestion is emphasized further by the finding that when females were subordinate and breeding they lost similar amounts of weight as when they were dominant and breeding, and substantially more weight than when they were subordinate and not breeding. Similarly, we found no evidence to suggest that females gained more weight during postweaning periods when they were dominant than when they were subordinate, although, in this case, females gained significantly more weight when dominant and not breeding than when subordinate and not breeding. This is presumably because helping is energetically costly (Russell et al. 2003b) and subordinates contribute more than dominants to raising the litters of others (Clutton-Brock et al. 2004).

A final explanation for our results is that female meerkats, as is the case among naked mole rats, have higher levels of hormones that induce bone growth when they are dominant compared with when they are subordinate. In line with this possibility, we found that dominant females had significantly higher plasma concentrations of estradiol (Fig. 2c; Mann

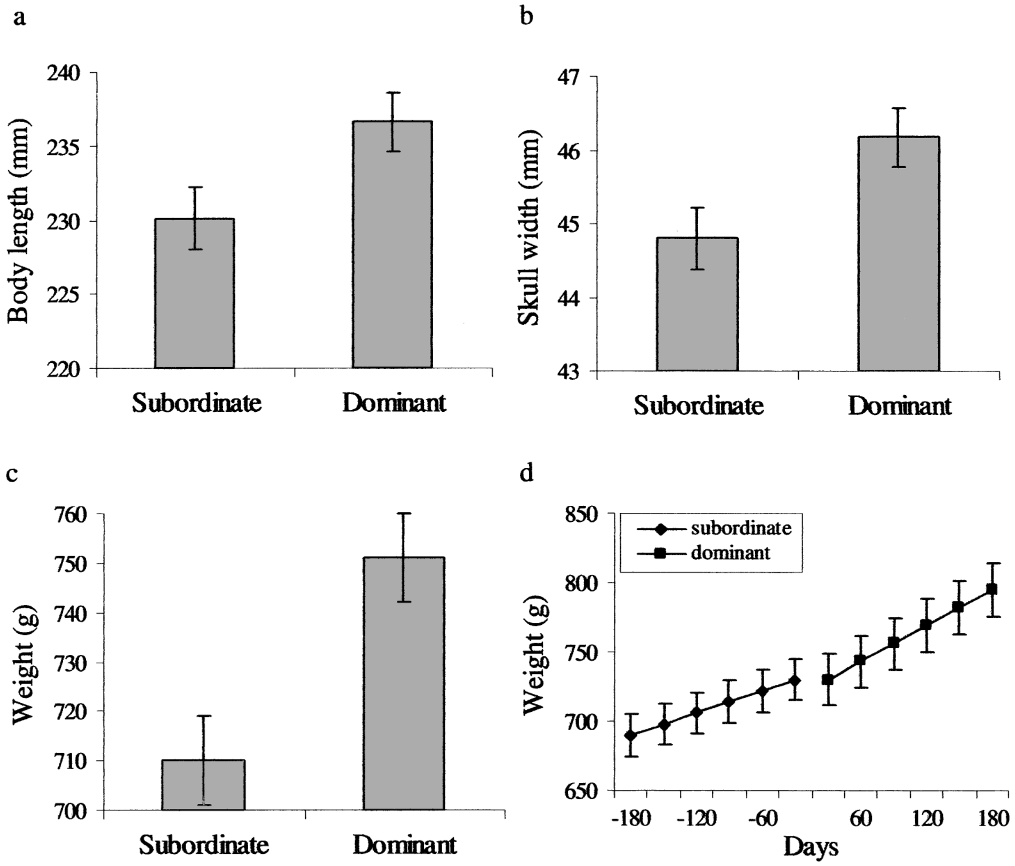

FIG. 1. Morphological modifications of breeders. Effect of attaining alpha status on: (a) body length, (b) head width, (c) body weight, and (d) growth in the first six months. Results are presented after controlling for differences in age and group size (a–c) and differences in age, group size, and breeding status (d) where necessary. Individual identity constituted significant random terms in both analyses ($P < 0.05$). Graphs show mean ±1 SE. Note that (c) shows results without controlling for body size (see Table 1) and (d) shows predicted relationship calculated from the model.

Whitney U test, $W = 300$, $n = 9{,}24$, $P < 0.0001$) and progesterone (Fig. 2d; $W = 142$, $n = 7{,}22$, $P = 0.048$) than subordinate females.

Body Size and Fitness

Increasing body size appears to be associated with fitness benefits among female meerkats. We have previously shown that litter sizes at birth and pups weight at weaning are both positively influenced by maternal weights at conception, but are neither influenced by maternal age nor group size (Russell et al. 2003a). Here we show that variation in the two fitness correlates can be explained additionally by variation in female body length, but not head width. We found a positive relationship between female body length and litter sizes at birth (Fig. 3a; $F_{1,27} = 6.70$, $P = 0.015$, $R^2 = 0.35$), with longer females being significantly more likely to deliver a litter above average size ($F_{1,28} = 5.15$, $P = 0.023$). Longer bodied females also produced pups that were heavier at weaning (Fig. 3b; $F_{1,23} = 4.65$, $P = 0.042$, $R^2 = 0.31$). In contrast, we found no additional effects of female head width on either fitness correlate (litter size: $F_{1,26} = 0.03$, $P = 0.86$; pup weights: $F_{1,22} = 0.05$, $P = 0.82$). Statistics presented above are reported after controlling for significant effects of maternal weight at conception (litter size: $F_{1,27} = 5.00$, $P = 0.034$; mean pup weights: $F_{1,23} = 6.90$, $P = 0.015$).

DISCUSSION

Female meerkats increase in size after attaining alpha status. The same females were significantly larger and consequently heavier as dominants than as subordinates after correcting for their greater age. These effects were unlikely to have been caused by differences in foraging efficiency or investment in pup care, but may have been influenced by increases in estradiol and progesterone levels among dominants. Increases in size are likely to be adaptive, for body length was significantly and positively associated with litter sizes at birth and pup weights at weaning, both of which are known to have beneficial effects on breeding success. Our results suggest that morphological modifications are adaptive in mammals, and more widespread than has previously been supposed.

We provide the first evidence of morphological modifications in a carnivorous mammal. Female meerkats had significantly longer bodies and significantly wider skulls as dominants than as subordinates. Differences in body size were found despite comparisons of the same females as sub-

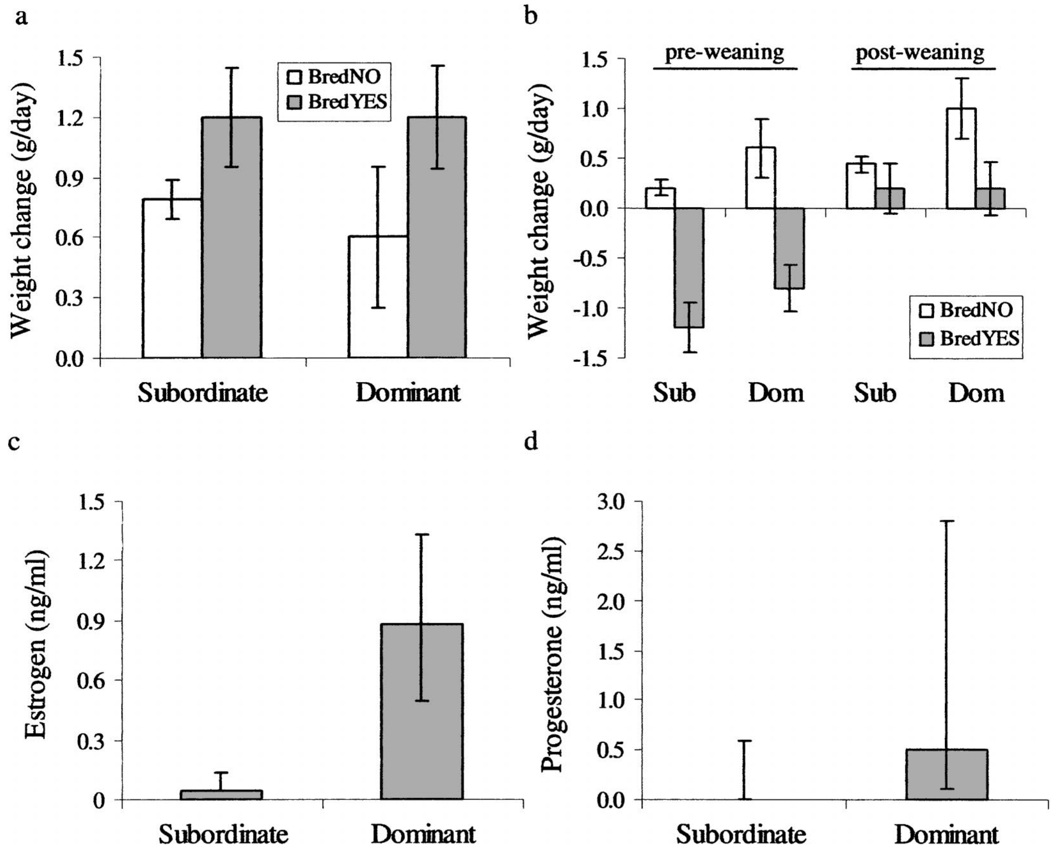

FIG. 2. Potential mechanism behind morphological modification. Effect of dominance status on: (a) rates of weight change (g/day) during periods of nonbreeding, (b) rates of weight change (g/day) during breeding (pre- and postweaning) periods, (c) plasma concentration of estradiol, and (d) plasma concentration of progesterone. Figures a–b show means ± one standard error whereas c–d show medians ± interquartile ranges. BredNo and BredYes refer to whether or not females had bred in the previous attempt (a), or were breeding in a current attempt (b). Sub and Dom refer to subordinate and dominant. Results presented in Figures a–b are shown after controlling for significant repeated measures of individual ($P < 0.05$) positive effects of group size ($\chi^2 = 6.18$, df = 1, $P = 0.013$), but not age ($\chi^2 = 1.42$, df = 1, $P = 0.23$). Figures a–b show short term changes in body weight that are likely to reflect fluctuations in net resource intake rates, and are shown separately for clarity.

ordinates and as dominants and despite controlling for potential effects of age. Thus, our results can neither be explained by larger subordinates having an increased probability of attaining alpha status nor simply by a linear continuation of growth. In addition, further analysis revealed that body weight increased more quickly in the six months after attaining dominance than in the six months before it was attained. Two findings suggest that this result reflects a period of accelerated body growth rather than increased condition. First, we found no evidence to suggest that females should gain more condition as a dominant than as a subordinate (Fig. 2a,b, and see below). Second, significant differences in body weight within individuals when subordinate and dominant disappear after controlling the greater age and body size of individuals when dominant (Table 1).

Only one other study has provided evidence of a morphological modification in a cooperative vertebrate. Using X-ray imaging, O'Riain et al. (2000a) showed that female naked mole rats increase the length of their lumbar vertebrae to achieve a significant increase in body size following the acquisition of alpha status. However, dominant females have been reported to be larger than old subordinates in a number of other cooperative mammals (Bennett and Jarvis 1988; Bennett 1989; Creel and Creel 1991). Such studies only provide circumstantial evidence to suggest that morphological modifications occur in other cooperative mammals, because one cannot rule out the possibility that such effects are a consequence of differences in age or larger individuals having higher probability of attaining dominance. Nevertheless, current evidence raises the possibility that modifications may be more widespread in cooperative mammals than has previously been supposed.

In cooperatively breeding insects, the probability of a female becoming a queen is often determined by conditions experienced during early development, and morphological differences between queens and workers are established (in part) prior to acquisition of reproductive status (Wilson 1971; Thorne 1997; Peeters and Ito 2001). In contrast, in cooperative vertebrates acquisition of alpha status is generally determined by age, and morphological differences between dominant and subordinate females appear to arise following the acquisition of alpha status (O'Riain et al. 2000a; this study). Perhaps the simplest way in which dominant females could become larger in vertebrates is if the acquisition of

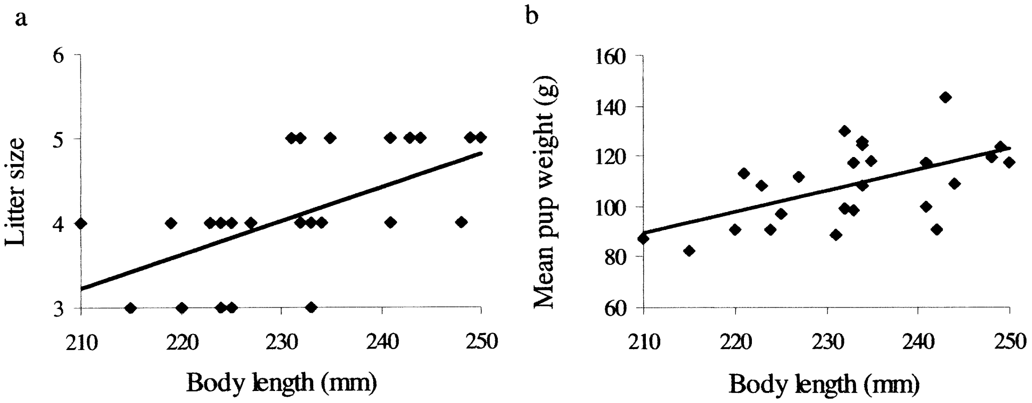

FIG. 3. Body size and fitness correlates. Effect of body length on: (a) litter sizes at birth, and (b) pup weights at weaning. Individual identity was a negative component of variance ($P = 0.99$).

alpha status is associated with net increases in resource intake rates. In contrast, we found little evidence for this possibility. First, rates of weight change during periods of nonbreeding were unaffected by dominance status after controlling for whether or not a female had bred in the previous event. This suggests that females do not have greater rates of resource intake as dominants than as mature subordinates. Second, during preweaning periods, breeding females lost significantly more weight than nonbreeding females, suggesting that the costs of lactation are greater than the costs of babysitting (see also Scantlebury et al. 2002), although during postweaning periods, rates of weight change were only greater among dominant females that were currently nonbreeding, presumably because they contribute little to raising the litters of others (Clutton-Brock et al. 2004). Given that females breed considerably more frequently as dominants and weight loss is higher when breeding, it is highly improbable that females incur reduced energy expenditure as dominants than as subordinates. Finally, as indicated above, dominance-related differences in weight disappear after controlling for the greater size and age of individuals when they are dominant (Table 1), suggesting that increases in body size are unlikely to be explained by net increases in resource intake rates.

Alternatively, increases in body size may be achieved by increases in levels of hormone that influence bone growth. Two hormones that have the greatest impact on bone growth in female mammals are estrogens and progesterone (Prior 1990; Schmidt et al. 2000; Lindberg et al. 2001). O'Riain et al. (2000a) suggested that morphological modifications may occur in naked mole rats as a result of increasing levels of circulating estradiol or progesterone that transpire when females become pregnant. Like naked mole rats, dominant female meerkats have higher levels of circulating estradiol and progesterone, but unlike the mole rats, 76% of the female meerkats that become dominant have bred as a subordinate (this study). The evidence from meerkats suggests that pregnancy is not sufficient to account for modification. An alternative explanation is that modification following the acquisition of alpha status arises as a consequence of increases in hormone-mediated bone growth following release from physiological suppression.

Increases in body size achieved following the acquisition of alpha status are likely to be adaptive in female meerkats. First, increases in body length were positively associated with an increased probability of individuals producing litters of greater than average size and pups of greater weight at weaning. Thus, by increasing in size, females are either able to accommodate more offspring or larger offspring (Sherman et al. 1999; Leutenegger 1982). Second, and perhaps more importantly, by increasing in size and consequently weight (Fig. 1a–c; Table 1), alpha females increase the dominance asymmetry between themselves and subordinates, leading to more efficient control of reproduction (Clutton-Brock et al. 2001a; Young 2003). This is obviously beneficial for the dominant female but may also be so for nonbreeding group members because contributing to cooperation may be costly (Russell et al. 2003b), and offspring growth rates and survival are reduced when the number of offspring (and not carers) increase (Clutton-Brock et al. 2001b; Russell et al. 2002).

In order for morphological modifications to be adaptive, the reproductive benefits of increases in size must outweigh any corresponding energetic or survival costs. In social insects, the most morphologically modified species are those in which both benefits to queens of suppressing subordinate reproduction and worker numbers are high (Bourke 1999), whereas costs to the queen of foraging and parenting are low (Thorne 1997; Peeters and Ito 2001). Such circumstances are also likely to explain the greater degree of morphological modification found in naked mole rats compared with meerkats. In naked mole rats, colony sizes are the largest known for vertebrates (up to 300), and acquisition of alpha status is associated with full control over reproduction, as well as reduced foraging costs and vulnerability to predation (Lacey and Sherman 1997). In contrast, meerkat groups are smaller (up to 50), and acquisition of alpha status is associated with incomplete control over reproduction and smaller reductions in the costs of foraging or vulnerability to predation, although it is associated with substantial reductions in the cost of parenting (Scantlebury et al. 2002; Russell et al. 2003a; Clutton-Brock et al. 2004). Further studies in cooperative vertebrates will elucidate the generality of morphological modifications, and enable the generalization of the associating factors across cooperative breeders as a whole.

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