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Androgens and social status in female rock hyraxes

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Androgens have been linked to social behaviour in males across many vertebrate species. Despite the lack of gender specificity in steroid hormones, the association of androgens with behaviour in females remains obscure. We analysed steroid hormone levels in male and female rock hyraxes, *Procavia capensis,* and found strong ties between androgens and cortisol in females but not in males, despite the latter being the sex that usually shows this association. In the past we have shown that both female and male hyraxes have similar testosterone levels. In the present work, we found a significant interaction between testosterone levels and social status. Testosterone levels differed only between lower-ranking males and females, with females showing higher levels. Furthermore, dominant females had significantly lower testosterone levels than subordinate females. No association was detected between litter size and female rank, testosterone or cortisol levels. At this stage, we can only hypothesize that the assumed detrimental effects of high circulating androgen levels, reflected in the hair samples, influence the reproductive output or the offspring survival of subordinate females in some other ways, which require further investigation to be revealed.

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Androgens, whose role in the male endocrine system has been well documented, apparently play a significant role in females as well, such as enhancing follicle development and providing the required substrate for oestrogen biosynthesis (Walters et al. 2008). Androgens may therefore directly and indirectly regulate the degeneration and resorption of immature follicles in the ovary. Recent genetic studies have shown that the androgen receptor (a nuclear receptor which is activated by the binding of testosterone or dihydrotestosterone) function is essential for maintaining age-related female fertility through the optimization of the conditions for follicular growth (Walters et al. 2008). In female spotted hyaenas, *Crocuta crocuta*, levels of the androgen androstenedione (A4) are consistently higher than in males, particularly during early infancy, and A4 is implicated as a lead player in physical development and aggressive behaviour (Glickman et al. 1987; Goymann et al. 2001). In birds, maternal androgens deposited in eggs have been shown to affect the behaviour, growth, morphology, immune function and survival of the offspring (Groothuis et al. 2005). Taken together, the above findings suggest that androgens play multiple roles in females, including in reproduction.

Previously, we reported that females of the social rock hyrax, *Procavia capensis*, which are on average more dominant than males,

possess average testosterone (T) levels as high as in males (Koren et al. 2006). To our knowledge, this is the first reported instance in a mammal in which adult females have similar T levels to those in the males. The large variance observed in female hyrax hormone levels (Koren et al. 2006) implies that some individuals possess high androgen levels whereas others maintain lower levels. In several mammals, high-ranking individuals maintain elevated stress hormone levels (reviewed by Creel 2001). Furthermore, in many vertebrates, dominant and more aggressive males show increased T levels during the mating season, which contribute to regulating territorial and sexual behaviours such as aggressive displays (Ketterson & Nolan 1992; Ros et al. 2004; Chastel et al. 2005; Kabelik et al. 2006). Seasonal changes in male androgen levels in relation to aggressive social events have been explained by the challenge hypothesis (Wingfield et al. 1990). Consequently, the temporal changes in levels of androgens are an outcome of a trade-off between the amount of parental care needed for reproductive success and the aggressiveness essential for maintaining social status. The positive relationship between social dominance and T has been widely documented in social vertebrate males (e.g. Sapolsky 1982; Creel et al. 1997; Kraus et al. 1999; Muller & Wrangham 2004; Hirschenhauser & Oliveira 2006), yet this association in females is ambiguous (Christiansen 2001). High T levels are known to have costs, such as higher energetic demands, reduced fat stores, interference with parental care, and increased risk of injury from increased activity and aggression (Wingfield et al. 2001; Glickman et al. 2006). All of these costs are expected to be especially problematic for

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breeding females, which require sufficient energy reserves for reproduction and the ability to develop maternal behaviour. Androgens may negatively affect female fecundity in vertebrates by delaying both the onset of female reproduction and embryo implantation (Ketterson et al. 2005; Rutkowska et al. 2005; Browne et al. 2006).

We addressed the key question that emerged from the findings of Koren et al. (2006): can females maintain high T levels without compromising their reproductive output? While individuals may regulate their androgen levels physiologically, they can also remove themselves from social situations that may increase androgen and stress hormone levels (e.g. high-ranking positions, which are often associated with elevated fight frequency). To answer the above question in female rock hyraxes, we examined the association of androgens and stress hormones with social rank and reproductive output, since in many mammals, high-ranked females are more reproductively successful than lower-ranked females (Ellis 1995; Creel et al. 1997; Clutton-Brock et al. 2006). Considering the general trend between rank and androgens, we hypothesized that high-ranked females would have higher androgen levels than lower-ranked females.

METHODS

Study Animals

The rock hyrax is an African social mammal belonging to the ancient Afrotheria lineage (Springer et al. 1997). We studied rock hyraxes at the Ein Gedi Nature Reserve (31°28′N, 35°24′E), which is located west of the Dead Sea in the Judean Desert, Israel. The reserve comprises two deep gorges, David and Arugot. Rock hyraxes in Ein Gedi live in large, mixed-sex groups that include several males and 10–20 females with their pups. Observations of agonistic interactions suggest female dominance, which is established by winning aggressive interactions and claiming priority for preferred sitting sites (Koren et al. 2006). Hyraxes are seasonal breeders (mating in July–August in our study site) with a long gestation period of approximately 230 days and a litter size ranging from one to six (Mendelssohn 1965). All females over 2 years of age (i.e. adults) in our study site gave birth annually in March (L. Koren, unpublished data).

Study periods in the field averaged 6 months each year, from February to August (i.e. a month before parturition until the end of the mating period), over 7 consecutive years (1999–2005). Hyraxes were caught using live box traps, placed in natural crevices. Traps were set before first light (approximately 90 min before dawn) and operated until noon, with inspections every 2 h. Newly trapped animals were anaesthetized with ketamine hydrochloride (0.1 ml/kg intramuscular injection), weighed, measured, photographed, and individually marked using small (1 cm) cylindrical subcutaneous transponders (DataMars SA, Bedano-Lugano, Switzerland) that were inserted into the neck region and remained there for the duration of this long-term ongoing study (monitored annually). All measurements were recorded in situ, and the animals were returned to the traps for full recovery (3 h), and thereafter released at the capture site. Animals resumed full normal activity following their release. Permits for capturing, handling and marking the hyrax were issued and reviewed annually by the Israeli Nature and Parks Authority.

The subjects of this study comprised 62 adult males and 59 adult females. We set three criteria by which to classify an animal as adult: (1) animals that were older than 2 years; (2) males that were out of their natal group; and (3) females that had given birth at least once. To facilitate individual identification of the animals from a distance, we fitted adults that weighed over 2.3 kg with numbered collars (collar weight 5 g; range 0.125–0.2% of hyrax body weight). We did not observe any injuries to the neck from the long-term (i.e. 7 years) presence of the collars. Both internal and visual markers have been successfully used since 1999.

All births at Ein Gedi are in the spring, with pups first observed in March. The birth year for all hyraxes native to the study site was known since they were captured as pups. Body weight (BW) was the best predictor of known age in 89 males and 131 females using linear fit (age was normalized using the Box–Cox transformation; normalized male age $= 0.971 + 1.681\,\text{BW}$, $F_{1,88} = 1092.6$, $R^2 = 0.925$, $P < 0.0001$; normalized female age $= 0.721 + 1.989$ BW, $F_{1,130} = 2147.3$, $R^2 = 0.943$, $P < 0.0001$; Koren 2006). Using the above equations, we estimated the age of immigrants and individuals born before our study began in 1999.

Fur Coverage

Many hyraxes in Ein Gedi have only partial fur coverage, owing to an irritation of the skin, mostly on the hindquarters of the animal. The cause of this skin disorder is unknown, but is suspected to be the result of bites by hippoboscid flies (e.g. *Lipoptena* sp.), which cause a similar skin condition in the local ibex, *Capra ibex nubiana* (Theodor & Costa 1967). We found no evidence of embedded mites under the skin (scabies) or flea infestation. A similar-looking skin condition (mange) is known to affect body condition in several mammals (e.g. Skerratt 2003). Because androgens may suppress the immune system (Folstad & Karter 1992), and the skin is a major target of androgens, where receptors are imbedded in the epidermis, dermis, sebaceous glands and hair (Alesci & Bornstein 2000), it is reasonable to link hair coverage, androgens and body condition. Thus, we used hyrax fur coverage as a proxy for the resistance of individuals to parasites and infection. Individual physical condition was estimated by the percentage hair loss on the back of the animal, which we assessed by calculating the bold area from photographs. For statistical purposes, fur coverage was normalized by an arcsine transformation.

Social Hierarchy

We recorded behavioural observations on five social groups over a 5-year period (2000–2004; a total of 430 observation days and approximately 3000 h; by L.K.) using 10×42 binoculars and a telescope with ×50 and ×75 magnifications. Most observations were in the morning from first light to noon, when hyraxes in Ein Gedi retreat to their shelters. We recorded all agonistic interactions among individuals (all occurrences; Altmann 1974), and specified the initiator, recipient and outcome. For the social hierarchy analysis we considered only agonistic interactions: those that involved display by one individual (i.e. approaching, biting, pushing or chasing) and resulted in an evasive action being taken by a second animal (i.e. running away or retreating from its position). We prepared a matrix of encounters for each group using all pairwise dominance interactions observed during a given field season. For each interaction, the winner (i.e. the hyrax that remained in place or chased away another) was placed in the row, and the loser (i.e. the displaced or chased hyrax) in the column of the matrix. David's score (DS; Gammell et al. 2003), which scales the wins and losses of an individual by the scores of its opponents, was calculated as $DS = w + w_2 - l - l_2$, where w represents an individual's proportion of wins over group members, w_2 is the summed proportions of wins of the animals with which it interacted, l is the proportion of an individual's losses and l_2 is the proportion of its rival's losses. All proportions were weighted by the number of interactions between dyads (Excel macros from H. de Vries, Department of Behavioural Biology, Utrecht University, The Netherlands). We used the David's scores calculated annually to rank individuals such that the highest score was ranked as 1, the second score as 2, etc. Annual ranking

values closely reflect the David's scores standardized per annum ($r_{55} = -0.86$, $P < 0.0001$).

Hormone Levels

We measured the basal levels of steroid hormones that had accumulated over a period of a few months in the hair of male and female rock hyraxes. Hormones are deposited in a growing hair shaft by the blood vessel that feeds it. Davenport et al. (2006) showed experimentally that hair testing accurately depicts significant and prolonged changes in endogenous hormone levels (i.e. cortisol in this case). They exposed rhesus macaques, *Macaca Mulatta*, to a prolonged stressful situation, and showed that within a few weeks a sharp increase in cortisol was detected in the hair. We cut full hair length once a year in the pre-mating period (April–July), from the back leg of trapped hyraxes in the field. The shaved area regained full hair cover within a month. In addition to T, we also examined the individual profiles of the androgen A4, which is considered a weak androgen since it has a low affinity for androgen receptors and weak peripheral androgenic effects. Despite this, A4 can be a potent organizer of anatomical and behavioural differentiation, able to mimic the effects of T on T-responsive neural systems (Villalba et al. 1999). It is also a precursor of T, other androgens and oestrogens. Because cortisol (C) is strongly associated with stress situations, and many such situations are also associated with elevated T (e.g. fighting), a link between C and T is expected. Consequently, we measured C as well.

We measured T and C in all study years, and A4 from 2002. Hair from each individual was tested in duplicates in a double-blind experimental set-up. The sampling and extraction protocols follow the steps in Koren et al. (2002, 2006). We detected hormones using the ELISA method (human plasma kits for T and A4, and human saliva kits for C; DRG International, Mountainside, NJ, U.S.A.) and validated kits for use by demonstrating parallelism between serial dilutions of hyrax hair and the standard curves generated with kit calibrators. Kit specificity was assessed by the manufacturer according to Abraham's method. Cross-reactivity of the T antiserum is 100% for T, 1% for A4 and less than 0.9% with any other naturally occurring steroid hormones; A4 antiserum has 100% cross-reactivity with A4 and $\leq$0.01% with any other naturally occurring steroid hormones; C antiserum has cross-reactivity of 100% for C and 60% with prednisolone, 29% with corticosterone, 3% with cortisone and less than 1% with any other naturally occurring steroid hormones. All samples collected for each year were analysed as a single batch. To compare levels between years, hormone values from each microplate were standardized. The average coefficient of variation for six replicates performed in the same assay (intra-assay) was 4.6%, and when one sample was analysed over 6 consecutive days (interassay) the coefficient of variation was 8.3%. We ruled out the influence of external factors (e.g. through hyraxes rubbing against each other), by comparing hair washed with 10% Sodium dodecyl sulphate with unwashed hair in six males and 14 females. These hair samples were collected in the field from hyraxes that were members of social groups. Hormone levels of washed and unwashed samples were highly correlated ($r_{16} = 0.724$, $P = 0.0006$).

Our results generated by the immunoassay approach were further validated by the use of liquid chromatography–mass spectrometry (HPLC/MS/MS). The hair (20 mg) from 10 hyraxes was minced into 2–3 mm pieces and thoroughly mixed, to overcome potential differences in levels along the hair shaft. The mixture was divided into 12 glass vials and incubated overnight at 40 °C on a shaker with 1 ml Soerensen buffer (38.8 ml KH_2PO_4 (9.07 g/litre) and 61.2 ml Na_2HPO_4 (11.87 g/litre)) at pH 7.6. Standards were obtained by adding 50 µl of 0.25–20 ng/ml T in methanol solution to 20 mg of blank (human female) hair. To each sample, 50 µl of

deuterated T (5 ng/ml) as an internal standard was added. After incubation, the solutions were transferred into clean tubes and centrifuged. The supernatant was placed on C18 bound-elute columns (activated with 3 ml of methanol and rinsed with 3 ml of deionized water). Columns were rinsed with 1 ml of deionized water followed by 1 ml of deionized water: methanol (90:10, v/v) and then dried for 30 min. T was eluted three times with 0.5 ml methanol, which was then evaporated to dryness under nitrogen. The residue was reconstituted in 50 µl mobile phase (75% methanol:acetonitrile (60:40): 25% ammonium acetate 10 mM). We injected 10 µl of each sample into a column (Phenomenex Luna Torrance, CA, U.S.A.; 5 µM; C18; 100 A; 150 × 4.6 mm) using an HPLC system consisting of an LC binary pump and a thermo autosampler (Agilent 1100 Santa clara, CA, U.S.A.). The flow rate was 0.6 ml/min, with a linear gradient of 10 mM ammonium acetate from 5 to 25% and a methanol:acetonitrile (60:40) solution from 95 to75%. The run time was 10 min. The retention time of T was 5 min 45 s. The HPLC/MS/MS method detected T in the hair. The results obtained by the ELISA method were highly correlated with those obtained by the HPLC/MS/MS method ($r_9 = 0.843$, $P < 0.01$).

Statistical Analysis

We used general linear models (GLM) to test the effect of sex, age and social status (independent variables) on each of the four hormones measured (dependent variables). Relationships between standardized untransformed hormones were linear, and pairwise Pearson correlations were evaluated by permutations. A sequential Bonferroni correction was applied to address multiple comparisons. Standardized T was normally distributed. Standardized C and A4 were normalized and linearized by a log (hormone)^2 transformation. To eliminate pseudoreplicates we used each hyrax only once per analysis. For animals that were recaptured in multiple years, we used the first full dataset, where all information (hormones and social status) was available.

RESULTS

In adult males, the androgens T and A4 were weakly correlated with each other ($r_{47} = 0.34$, $P = 0.017$; Fig. 1), but following a sequential Bonferroni correction (which set $\alpha < 0.008$) this correlation was no longer significant. In adult females, however, androgens were highly correlated with each other ($r_{47} = 0.59$, $P = 0.0001$; Fig. 1) and with C levels ($r_{58} = 0.61$, $P = 0.0002$ and $r_{47} = 0.43$, $P = 0.002$ for T and A4, respectively; Fig. 2). These correlations in females still held true after a sequential Bonferroni correction. In males, no significant correlation was found between C and T ($r_{61} = 0.23$, $P = 0.07$) or A4 ($r_{47} = 0.28$; $P = 0.05$; Bonferroni correction $\alpha < 0.01$). Even after we removed one clear outlier (5.7 SD), the association between C and A4 remained nonsignificant ($r_{46} = 0.36$; $P = 0.015$; Bonferroni correction $\alpha < 0.008$; Fig. 2).

No association was found, in either sex, between morphometric parameters (body length, girth and head diameter) and hormone levels (males: T: $r_{45} = 0.23$; C: $r_{45} = 0.08$; A4: $r_{32} = 0.07$; $P \geq 0.200$ in all cases; females: T: $r_{47} = 0.07$; C: $r_{47} = 0.11$; A4: $r_{37} = -0.02$; $P \geq 0.448$ in all cases.). Steroid levels were independent of age in males (T: $F_{1,108} = 1.11$, $P = 0.294$; A4: $F_{1,91} = 0.01$, $P = 0.951$; C: $F_{1,104} = 0.69$, $P = 0.408$) and females (T: $F_{1,116} = 3.51$, $P = 0.064$; A4: $F_{1,91} = 3.33$, $P = 0.071$; C: $F_{1,110} = 0.06$, $P = 0.806$). Furthermore, we did not detect an interaction between sex and age in any of the hormones (T: $F_{1,224} = 0.25$, $P = 0.617$; A4: $F_{1,189} = 1.42$, $P = 0.234$; C: $F_{1,214} = 0.59$, $P = 0.442$).

To test for costs associated with elevated androgen levels, we used fur coverage as a proxy for the resistance of individuals to parasites and infections. Adult fur coverage ranged between 60 and 100% ($\overline{X} \pm SD = 90 \pm 12.6\%$), with males having significantly fuller
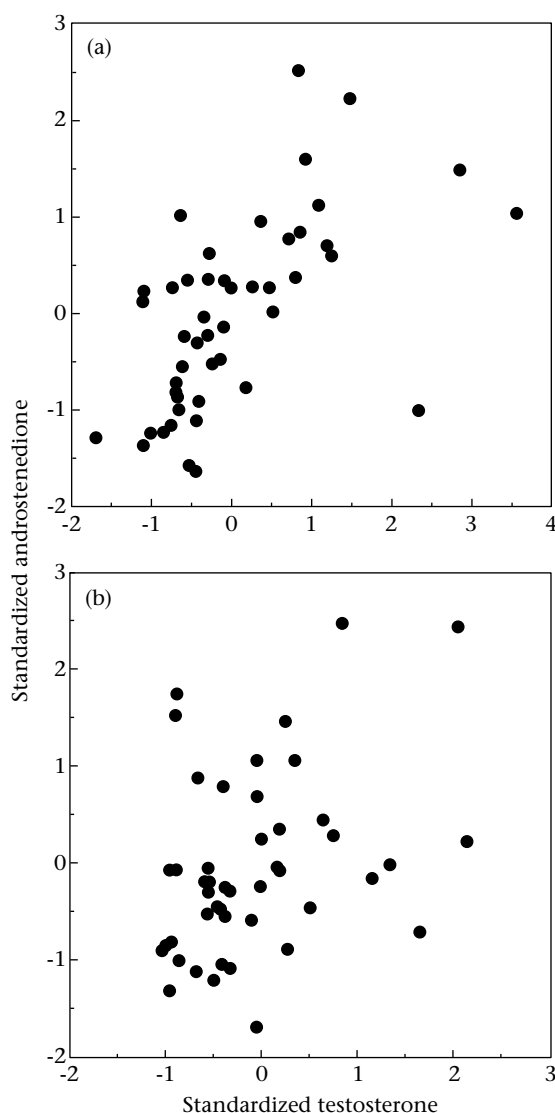
Figure 1. Relationship between standardized androstenedione and testosterone levels in (a) adult females and (b) adult males.

fur than females ($t_{95} = 2.4$, $P = 0.02$). Fur coverage was independent of social status ($F_{1,25} = 1.3$, $r^2 = 0.05$, $P = 0.26$ and $F_{1,22} = 1.4$, $r^2 = 0.06$, $P = 0.24$ for females and males, respectively). In adult males, androgen levels were not significantly correlated with fur coverage, while in adult females we detected a weak negative association between A4 and fur coverage ($F_{1,35} = 4.15$, $R^2 = 0.11$; $P = 0.048$). Females with higher androgen levels had less fur coverage.

Females had an average $\pm$SD of 1.9 ± 0.8 pups per litter (range 1–4). Since each pup was observed to suckle from a single female, we used this criterion to cluster pups to mothers. We found no association between litter size and T levels (Spearman rank correlation; $r_S = 0.259$, $N = 27$, $P = 0.193$), C levels ($r_S = 0.23$, $N = 27$, $P = 0.153$) or female social rank ($r_S = 0.231$, $N = 27$, $P = 0.247$).

Androgen Levels and Social Status

To test for an interaction between sex and social status in androgen levels of adult hyraxes, we fitted a GLM using social rank (David's score) and sex as the independent variables. Significance between the sexes in T was only marginal, with females showing higher levels than males ($F_{1,45} = 4.0$, $P = 0.052$). However, we

detected a significant interaction between rank and sex. Testosterone levels differed between the sexes only for the subordinate ranks, with females showing higher levels. Testosterone was high in the low-ranked females and low in the high-ranked females ($F_{1,45} = 6.5$, $P = 0.015$; Fig. 3), a trend not observed in males ($F_{1,21} = 5.7$, $r^2 = 0.21$, $P = 0.027$ and $F_{1,22} = 0.7$, $r^2 = 0.03$, $P = 0.408$ for females and males, respectively). Essentially, dominant females had lower T levels than subordinate females, as T levels were inversely related to dominance parameters. Finally, the association between rank and A4 or C was nonsignificant in both sexes (ANCOVA: $F_{3,27} = 1.6$, $P = 0.207$ and $F_{3,43} = 1.1$, $P = 0.366$, respectively).

DISCUSSION

The main finding in this study was the association between T levels and social status in female rock hyraxes, a trend not observed in males. We hypothesized that high-ranked females would maintain high androgen levels, yet found the opposite trend: females with low social status had higher T levels than females with high social status. We also expected higher-ranking females to have a higher reproductive output. However, the above hypothesis was not supported by our results. Higher-status hyrax females did not have a higher reproductive output. It is possible that the consequences of maintaining higher social status may not be expressed via reproductive output, but through other prominent factors such as pup survival or neonate sex ratio. Currently, we do not have sufficient data to evaluate these possibilities.

The association between rank and androgens observed in the rock hyrax in some ways resemble that reported for the spotted hyaena (Glickman et al. 1987). However, in infant female hyaenas, the androgen A4 is two to four times higher than in prepubertal and adult females. Towards adulthood, it drops sharply in females, yet stays consistently higher than in males. Glickman et al. (1987) attributed the ability of the ovary to produce such high levels of A4 to critical developments in the social life of the spotted hyaena. Intense intersibling aggression and siblicide are characteristic at this early age at the communal den. These authors hypothesized that elevated A4 levels in infant females, which are the dominant and more aggressive sex in the spotted hyaena society, may organize or activate the elements of aggressive behaviour. In our rock hyrax society, females are also at the top of the ranking order (Koren et al. 2006). However, in contrast to the situation in the spotted hyaena, androgen levels in the rock hyrax were independent of age in both males and females. This finding implies that the observed link in females between social status and T is rank related, and not a result of a confounding effect of individual morphological or chronological state.

In many social vertebrates, dominant and aggressive males have higher T than subordinate males (Sapolsky 1982; Ketterson & Nolan 1992; Creel et al. 1997; Kraus et al. 1999; Muller & Wrangham 2004; Wingfield 2005; Hirschenhauser & Oliveira 2006). In the hyrax, despite earlier analysis with a small subset of males (Koren et al. 2006), we did not detect a significant association between rank and androgens. However, in this study, female social status was negatively associated with androgen levels (both T and A4): low-ranking females had higher T and A4 than high-ranking females. Androgens are known to have profound effects on females. For example, in different avian systems, experimentally elevated T has a negative effect on female fecundity and delays the onset of female reproduction (Ketterson et al. 2005; Rutkowska et al. 2005). In fur seals, *Callorhinus ursinus*, androgens have been shown to delay embryo implantation (Browne et al. 2006). How do female hyraxes bypass the reproductive interference of high androgen levels (Glickman et al. 2006) and reproduce every year, regardless of rank (Koren 2006)? Soma et al. (1999) and Wingfield et al. (2001) suggested
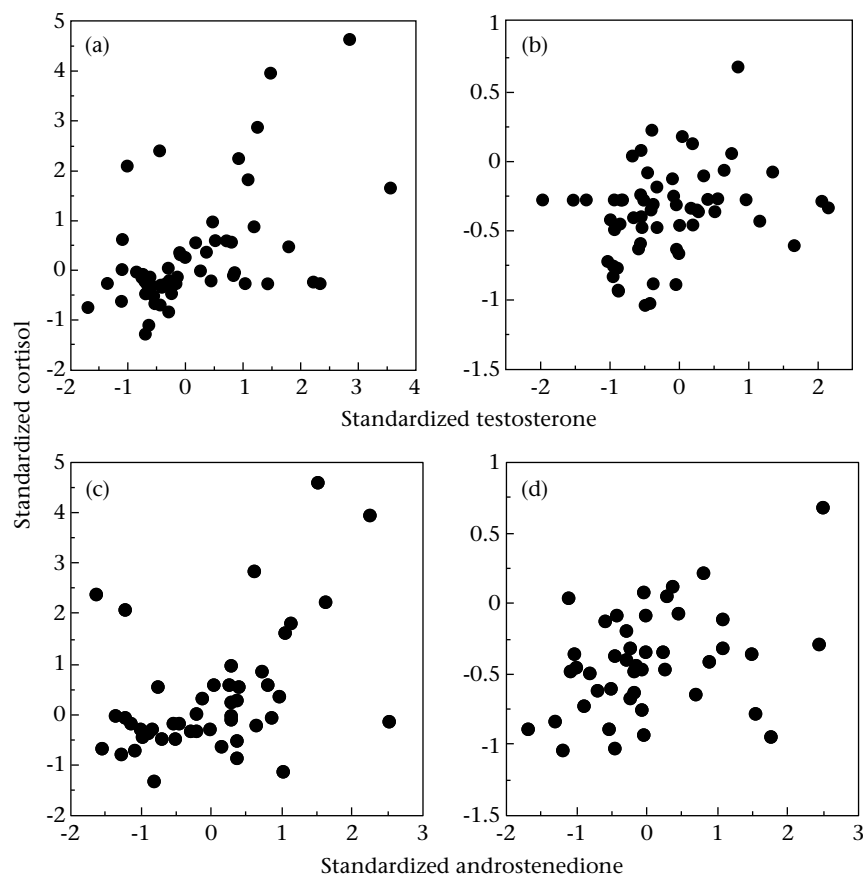
Figure 2. Relationship between (a, b) standardized cortisol and testosterone levels and (c, d) standardized cortisol and androstenedione levels in (a, c) adult females (b, d) and males.

several ways in which individuals may cope with high T, such as possessing hormone-binding proteins that prevent circulating androgen levels from rising, or by acquiring insensitivity to the behavioural effects of high androgen levels by downregulating

Figure 3. Standardized testosterone in females (●) and males (□) as a function of social status. Linear fit is indicated by the solid line for females and by the dashed line for males. The bar at the bottom of each figure indicates social status (high status is indicated by low social-rank values).

receptors and enzymes. Female hyraxes may use these mechanisms to reproduce despite their high androgen levels.

It is well established that hormones act differently in males and females (Mazur et al. 1997; Jawor et al. 2006). Only in female hyraxes were T and C levels positively correlated. In humans, with a rise in C levels resulting from a stressful event (or an expectation of such), T significantly declines in males and increases in females. Despite the opposite trends, both reactions, however, may have the same function, suppressing fertility to increase survival (Christiansen 2001). Generally, individuals with high T are expected to take greater risks, which can induce high stress and C levels (Schoech et al. 1999) that keep the fight or flight mechanism continuously operating (Creel et al. 1996). Glucocorticoids are highly oxidized toxic and mutagenic molecules, which at high levels (typical of chronic stress) can have detrimental effects on metabolism, vascular function, growth, tissue repair, immune defences, reproduction and neuron health (von Holst 1998; Sapolsky 2000; Jasnow et al. 2001). High T can also impose costs that reduce lifelong fitness (Wingfield et al. 2001). Roberts et al. (2004) suggested, in regard to integration of C and T, that the two hormones may offset one another by competing for common binding sites, or by sharing binding proteins that keep them from circulating at high levels. This may also be a mechanism by which female hyraxes manage simultaneously high T and C. However, our present results do not allow us to distinguish between the above hypotheses, and additional experimental work is required to resolve this question.

From our estimates of fur coverage as a proxy for body condition, females with high androgen levels appeared in worse body condition than females with lower levels. Fur coverage is a body condition 'bulletin board', representing high maintenance levels when it appears healthy (Folstad & Karter 1992). However, A4 accounted for
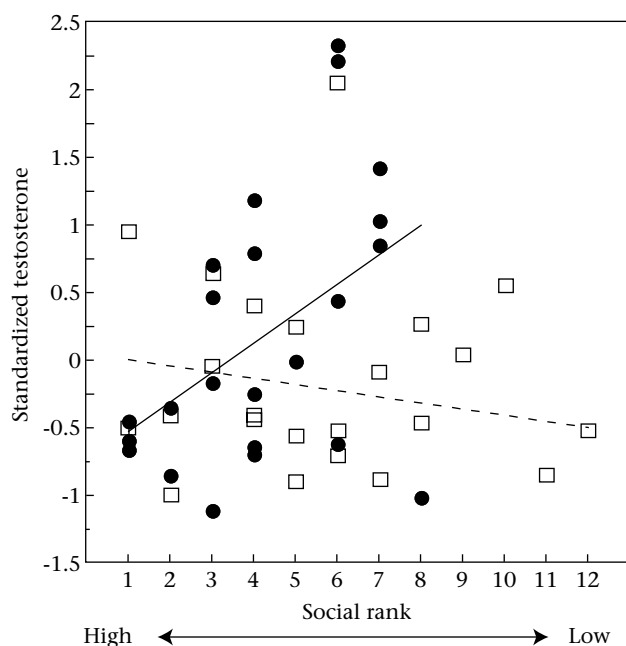
only 11% of the variance in fur coverage, thus making hyrax fur coverage a poor predictor of androgen levels. None the less, androgens and body condition were associated only in female hyraxes, and not in males. This observation could be explained as females being more sensitive to an increase in androgens, because the cost in females is higher in terms of survival and reproduction.

Since relationships involving hormones are very complex, influenced by almost every possible endogenous and exogenous factor and subject to vast individual differences (Guimont & Wynne-Edwards 2006), social contexts (Gruenewald et al. 2006) and species peculiarities, it is important to assess the fitness advantages of dominants over subordinates among female rock hyraxes, in the context of their individual hormone levels. At this stage, we can only speculate that subordinate female hyraxes are at a disadvantage relative to their dominant counterparts, by having higher androgen levels and a less favourable body condition. The role that androgens play in female mammals is still an open question, and one that requires more data on the level of androgens in females, relative to males, in a wide range of mammalian systems.

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