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Elevated testosterone levels and social ranks in female rock hyrax

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Abstract

In mammals, males maintain significantly higher testosterone (T, 'the male hormone') levels than females throughout the year and are typically dominant over females. Our study of the cooperatively breeding rock hyrax (*Procavia capensis*) demonstrated a distinct exception. In most hyrax social groups that we studied, adult females were at the highest social rank within the group and showed higher than or equal T levels to males. To our knowledge, this is the first reported instance of adult female mammals demonstrating higher T levels than adult males. However, although T levels significantly correlated with rank in males, in females such correlations were not detected, suggesting a more complex interplay between behavior and endocrine factors in this species.

Keywords: Agonistic interactions; Female dominance; Rock hyrax; Social hierarchy; Testosterone levels; Hair-testing

Introduction

In most mammals, males are the dominant sex. Female dominance is rare and is typical of only lemurs (Kappeler, 1990; van Schaik and Kappeler, 1996; Pochron et al., 2003) and spotted hyenas (*Crocuta crocuta*; Kruuk, 1972; Frank et al., 1985). Male dominance ranks have been found to correlate with both age and body size (reviewed by Malyon and Healy, 1994), as well as with male androgen levels (reviewed by Bouissou, 1983), all of which affect fighting ability. The androgen testosterone (T) is considered 'the male hormone'. This may be the reason why the role of androgens in female vertebrates has been, until recently, mostly ignored (Staub and De Beer, 1997), despite the fact that both genders produce androgens in the gonads and adrenal tissue and metabolize them in peripheral tissues.

The few studies that have tested T levels in adult females have shown that these were significantly lower than in males, year round (elephants, Rasmussen et al., 1984; spotted hyenas, *Crocuta crocuta*, Frank et al., 1985; Glickman et al., 1987; Glickman et al., 1992; Goymann et al., 2001; humans, Longcope, 1986; California ground squirrels, *Spermophilus beecheyi*, Holekamp and Talamantes, 1991; Greylag geese, *Anser anser*, Hirschenhauser et al., 1999; placental sharks, the carcharhinids, Rasmussen et al., 1999; European moles, *Talpa europaea*, Whitworth et al., 1999; ring-tailed lemurs, *Lemur catta*, von Engelhardt et al., 2000; fossas, *Cryptoprocta ferox*, Hawkins et al., 2002). Since T is generally assumed to be associated with dominance and aggression, and since hierarchy is often determined by agonistic interactions (Mazur and Booth, 1998), higher female T levels may perhaps be expected in social systems where females are dominant. However, although in ring-tailed lemurs (*L. catta*), females dominate males in all social contexts, their androgen levels are significantly lower than those in males (von Engelhardt et al., 2000). Spotted hyena (*C. crocuta*) females are also dominant and more aggressive than males (Kruuk, 1972; Frank et al., 1985; Glickman et al., 1992), and juvenile female T levels in this species are as high as those of the juvenile males. However, after the age of 27 months, once the animals are sexually mature, male T levels are significantly higher (Glickman et al., 1992).

In human males, high levels of T promote dominance behavior, sometimes in the form of aggression (Mazur and Booth, 1998). In men, T both affects and responds to behavior. T levels rise in the face of a challenge and after winning, and decline in losers after a competition (Mazur and Booth, 1998). In human females, no such responses have been detected (Mazur et al., 1997). T levels in women are significantly lower (one-tenth; Longcope, 1986) than the levels measured in men,

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and its association with female aggression or status is a matter of dispute (Mazur and Booth, 1998; Christiansen, 2001).

In the literature, the basic social unit of the co-operatively breeding rock hyrax (*Procavia capensis*) is a group of females monopolized by a territorial male, with peripheral males loosely associated with the colony (Hoeck, 1975; Hoeck et al., 1982; Fourie and Perrin, 1987). Observations of agonistic interactions in hyrax groups in Israel have suggested female dominance (Koren, 2000). The social hierarchy in hyrax society (Koren, 2000) and its unique hormonal profile (Kirkman et al., 2001) make this species an interesting model for the study of the functional significance of androgens in females. Our objectives were to determine long-term T levels in adult male and female rock hyrax, assess social rank within groups, and evaluate the relationship between T levels and dominance ranks.

Methods

Study site and animals

Adult rock hyraxes (*P. capensis*) were studied between March and August over 5 consecutive years (1999–2003) in the Ein Gedi Nature Reserve (31°28′N, 35°24′E). Two deep gorges (David and Arugot) constitute the Reserve, which is located west of the Dead Sea in the Judean Desert. Animals were caught using live box traps and anesthetized with ketamine hydrochloride. Each animal was individually marked using ear tags and a collar. Body length, from base of the skull to tip of the tail, and head diameter (at eye level) were measured for each animal as size indicators. Weight and body girth were also measured, but were not used as size indicators since females are pregnant almost two-thirds of the year (approximately 230 days; Mendelssohn, 1965; Millar, 1971). Groups were assigned using two criteria. First, by observing the animals during emergence from their burrows at dawn; members of each social group share the same sleeping quarters (Koren, 2000). Second, we used multidimensional scaling (PROXCAL, Busing, 1998; implemented in SPSS version 10, SPSS Inc., Chicago, IL) to map out groups based on the frequency of association between each pair of individuals. We used the chi-square distance as the measure of association between pairs of individuals as our data were composed of counts.

Captive hyrax from zoos around Israel and a group of animals from the northern part of Israel were also sampled as a reference population (see details below).

Dominance rank determination

Hyraxes are diurnal, facilitating field observations. We observed the hyraxes for 5 days each week, from March to August during four consecutive years (2000–2003), for a total of 3200 h. Parturition takes place in the spring (March–April) followed by the mating season (July–August), a period of intense social interplay. From September to March, the rate of social conflicts is considerably reduced (L.K. personal observation). Agonistic interactions that involved display by one hyrax and evasive action by a second were observed using 10 × 42 binoculars and a telescope with × 50 and × 75 magnifications (C5 Spotting Scope, Celestron, USA). Pairwise interaction counts were set as a matrix of encounters and used for individual rank assignment following the Batchelder–Bershad–Simpson (BBS) scaling method (Jameson et al., 1999; http://caspar.bgsu.edu/~software/Java/1Hierarchy.html). This scaling method was chosen since it provides dominance predictions for all pairings of animals, based on outcomes of a small number of interactions. It assumes that the outcome of a given encounter between two animals is independent of the outcomes of previous encounters, and that the distribution of dominance interactions is normal (Jameson et al., 1999). The scale reflects both the order and magnitude of dominance rank for each individual animal relative to the rest of the group. We found that ranks maintained the same order, whether assigned according to group members only, clumping groups with the bachelor males, or sorting the animals by sex. Ranks were not assigned to the captive animals or to those sampled at Korazim because the behavior of these groups was not studied.

Hair collection and testosterone determination protocol

Hormonal extraction from hair samples offers a number of advantages over alternative sources. Hair is safe, readily available, and easy to store and transport. Hair sampling does not involve pain or possible infection, and the analysis is unaffected by the momentary stress of capture (Yang et al., 1998; Koren et al., 2002). Yang et al. (1998) showed that T measured in hair is significantly correlated with T found in serum. Hormones are deposited in the growing hair by the internal blood vessel that nourishes it, and are subsequently embedded in the hair. Hair samples thus offer an integrated record of hormonal levels over time (about 3 months in our case, considering our sampling protocol and mammalian moult patterns; Maurel et al., 1986), and circumvent short-term fluctuations in hormonal levels.

Hyraxes in our study site live in stable social groups for long periods of time (years; L.K. personal observations). We measured several months of accumulation of T within the hair column. In our hyrax social groups, individuals kept their hierarchical position as long as group composition remained unchanged (L.K. personal observations); thus, rank reflects a long-term trend. Likewise, T concentration in hair reflects long-term trends, making both variables comparable. Urine and feces are difficult to sample reliably in free-ranging hyraxes because they deposit in common latrines.

Hair samples for the T analyses were obtained from three hyrax populations: (1) Ein Gedi (n = 119); (2) Zoos around Israel (captive hyraxes; n = 27); (3) Korazim (32°54′N, 35°32′E), a site in northern Israel (n = 32). For the purpose of comparison, we also sampled blood from all the individuals collected at the Korazim site. The T analyses for populations 2 and 3 aimed to test whether the hormonal patterns observed are site-dependent. Since rock hyraxes reach sexual maturity by 16 months of age (Millar, 1971), only individuals at least 2 years old were sampled. As the field study started in 1998, and all births in Ein Gedi are between March and April (Koren, 2000), we were able to classify all animals as either under or over 2 years of age. The ages for the captive hyrax were known since all births are recorded. In Korazim, adult hyraxes were size selected. Since all hyrax births take place during the spring, at least three size classes can be identified, making size difference an effective tool to distinguish between adults and juveniles.

Hair samples were cut at skin level, and consistently sampled from the same area on the body, the upper hind leg. Samples were placed in dry vials for independent analysis in two laboratories: in the Hospital for Sick Children in Toronto, Canada and at the Institute for Nature Conservation Research, Tel-Aviv University, Israel. Paired t test across individuals showed no significant difference between the results obtained at the two laboratories ($t = 0$, $df = 56$, $P > 0.99$). The protocol for obtaining T is based on methanol extraction and sonication (for complete details see Koren et al., 2002). Briefly, each sample consisted of 20–50 mg of hair, which was accurately weighed (maximal weighing error ± 0.1 mg) into a glass vial, and then minced into 3–4 mm pieces with fine scissors. Methanol was added and the vials were sonicated for 30 min, and incubated overnight at 50°C with gentle shaking. The methanol was then pipetted off into glass tubes and evaporated to dryness under a stream of nitrogen. Each of the samples was then reconstituted with phosphate buffered saline (PBS; pH 7.0).

In order to determine whether hormonal trends are representative of circulating blood levels, we took blood samples from the hyraxes in the village of Korazim. One ml of blood was placed in a microfuge tube containing 100 μl EDTA. Plasma was subsequently removed and frozen. T was detected and quantified from both hair extractions and from blood samples using a commercial T detection ELISA (solid phase enzyme linked immunoassay) kit (ALPCO Diagnostics, USA), following the manufacturer's protocol. The test is highly specific for T and cross-reactivity with other steroids is less than 1% for the kit. The lowest detectable level of T that can be distinguished from the zero standard was assessed to be 0.069 ng/ml. Average inter-assay CV was 3.72%. All samples were tested in duplicates, with an average intra-assay CV of 6.8%. All routine validations for the hyrax hair-testing were executed successfully by the Motherisk laboratory in the Hospital for Sick Children in Toronto, Canada (Koren et al., 2002; Koren et al., in preparation).

Unlike serum or saliva, T from hair needs to be extracted by solvents, sonicator, and other manual steps. Despite the accuracy of the assay, slight variations in the extraction protocol between sets of samples influence the final concentrations detected. In other words, T levels obtained in two different assays are not comparable as concentrations. They are a relative measure, comparable to samples tested in the same microplate. Since hair-testing can only be used as a comparative tool between the samples analyzed simultaneously on the same microplate, animals from each social group (males and females) were essayed together. In order to compare between groups, T level values from each microplate were standardized.

Results

We defined six social groups in Ein Gedi, four in the Arugot site (Fig. 1) and two at the David site. Five groups were composed of two adult males, between 7–15 adult females and their juvenile offspring and pups. In addition to the two adult males, group 1, in Arugot, had two sub-adult males that were born in the group and were at a transient stage of joining the bachelors, already sleeping in the bachelor burrows. Group 2, in Arugot, was composed of seven bachelor males that shared sleeping areas separate from the mixed-sex groups, but foraged with them during the daytime (Koren, 2000). Females in estrus mated with both bachelor and resident males.

We ranked dominance in two neighboring social hyrax groups in Arugot (groups 1 and 3) based on 67 and 59 agonistic interactions, respectively, and in one group in David (group 5; Table 1) based on 21 agonistic interactions. These also included interactions with the bachelor males from outside the group (e.g., in Arugot, group 2). Individuals of group 4 had too few agonistic interactions to allow reliable ranking. Antagonistic interactions were observed between females (30%), between males (31%), and between the sexes (39%). In Arugot, females were found to be the highest-ranking members in both groups and during all years (Table 1). The older male ranked within the first three dominant animals, below a female or two, and the younger of the two males in the group was among the lowest-ranking members in both groups. In David, however, the top-ranking hyraxes were males. Overall, female rank was significantly higher than males in Arugot (Mann–Whitney test, $Z = 2.1$, $P = 0.036$, $n = 28$ females and 17 males), but equal ranking between the sexes was observed in David (Mann–Whitney test, $Z = 0.57$, $P = 0.569$, $n = 5$ females and 7 males). Sexual size dimorphism in the Ein Gedi hyrax population was not apparent in the four morphometric variables we measured (body length, head diameter, weight, and body girth; $t < 1.52$, $df = 36$, $P > 0.13$ for all variables).

In the Ein Gedi population of hyrax, average female T levels were higher than males across the groups and the years (with the exception of 1999; Fig. 2a). However, only in the Arugot 2000 sample, was the mean T level in females found to be significantly higher than that of males (Mann–Whitney test, $Z = 1.98$, $P = 0.048$ for 2000, and $Z \leq 1.15$, $P \geq 0.248$ for other years and sites). In males, T levels highly correlated with dominance rank (Spearman rank correlation, $r_s = 0.903$, $Z = 2.71$, $P = 0.007$; Fig. 3) and to a lesser extent with body length ($r_s = 0.609$, $Z = 1.82$, $P = 0.068$). In females, however, T levels correlated with neither rank ($r_s = 0.124$, $Z = 0.45$, $P = 0.653$; Fig. 3) nor body length ($r_s = 0.049$, $Z = 0.22$, $P = 0.824$).

On average, during the first month at a site, we were able to sample about 75% of the population. The rest of the individuals (i.e., trap-shy) were trapped during the following months. To accommodate for a monotonic increase in T over the entire mating and breeding periods (Millar and Glover, 1973), we tested for the effect of sampling time and sex using multiple

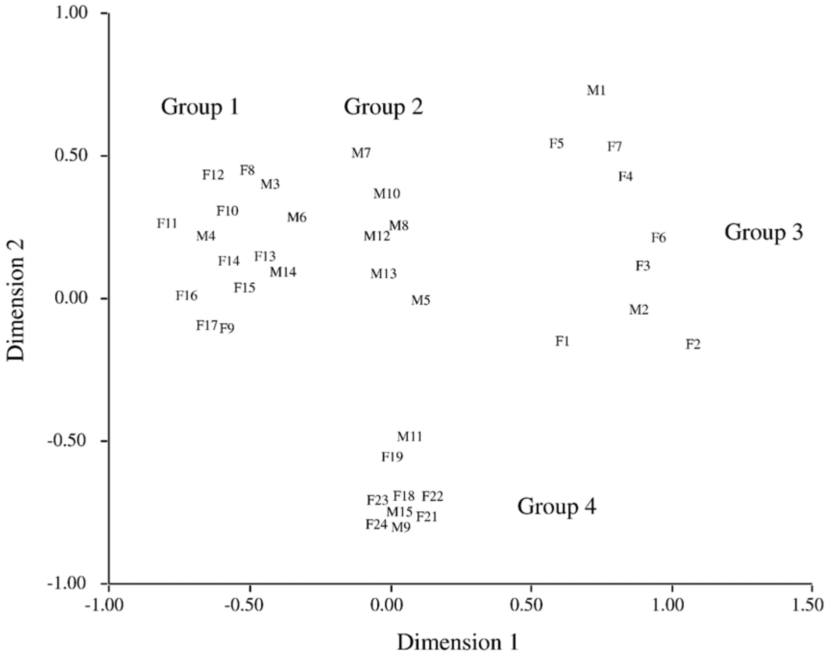

Fig. 1. Multidimensional scaling of associations between all study animals in Arugot during 2000. This configuration, based on the chi-square distance, has a stress factor of 0.069 and accounted for 93.1% of the observed variance. Males and females are indicated by M and F, respectively.

regression. Standardized T was the dependent variable, and date (i.e., number of days since first capture) and sex (scored as zero and one) were the independent variables. We detected a significant association between standardized T and the sampling time only in Arugot during 2003 ($r^2 = 0.427$, $F_{(2,9)} = 3.36$, $P = 0.085$; partial standardized regression coefficient = 0.640, $t_{(9)} = 2.53$, $P = 0.032$) and in David during 2002 ($r^2 = 0.306$, $F_{(2,17)} = 3.74$, $P = 0.045$; partial standardized regression coefficient = 0.546, $t_{(9)} = 2.68$, $P = 0.016$). Standardized T was independent of sex in these years, suggesting that the rise in T over time cannot explain the observed T levels in both sexes. Significant association between standardized T and sex, but not with sampling time, was detected only in Arugot during 2000 ($r^2 = 0.169$, $F_{(2,17)} = 2.86$, $P = 0.074$; partial standardized regression coefficient for sex = −0.365, $t_{(28)} = 2.10$, $P = 0.044$). Standardized T levels were independent of both sampling time and sex in Arugot during 1999 and 2002 and in David during 2003.

To determine whether the level of T we observed in female hyraxes was widespread or only a local phenomenon confined to our population in Ein Gedi, we sampled two other hyrax populations. The first consisted of hyraxes from five zoos around Israel. T analysis revealed that female T levels were not statistically different from those of males ($Z = 1.15$, $P = 0.248$; Fig. 2b). The second population was sampled at Korazim in northern Israel. For this population, we analyzed T levels from both hair and plasma (see Methods), and found the concentration to be similar for males and females (hair: $Z = 0.63$, $P = 0.527$; plasma: $Z = 0.44$, $P = 0.659$; Fig. 2b). Further, female plasma T levels were higher, though not statistically different, than those of males (female average ± SD in ng/ml = 1.59 ± 2.87; males = 0.86 ± 0.55). Finally, plasma and hair T were significantly correlated ($r_s = 0.48$, $Z = 2.67$, $P = 0.007$).

Table 1
Hierarchical ranking and sex for individuals of three social hyrax groups in Ein Gedi

Group ID	Year	Social rank				
		1	2	3	4	5
1	2000	f (2.18)	f (1.08)	m (1.04)	f (0.80)	f (0.31)
1	2002	f (0.75)	f (0.75)	f (0.75)	f (0.75)	f (−0.75)
1	2003	f (3.50)	f (1.50)	f (1.50)	f (0.75)	f (−0.46)
3	2000	f (1.44)	m (1.18)	f (0.75)	f (0.36)	f (0.32)
3	2001	f (1.37)	f/m (−0.37)	m (−2.63)	f (−4.50)	f (−4.50)
3	2002	f (3.93)	f (2.07)	f (2.07)	m (−0.07)	m (−1.93)
5	2002	m (3.05)	f (1.25)	f (1.25)	f (1.25)	m (0.95)
5	2003	m (1.40)	m (0.80)	m (0.75)	f (−0.70)	m (−0.75)

Numbers indicate the order of rank, where one is the most dominant group member. The first five ranks are displayed. The sex of each ranked individual is indicated by the letters f and m for female and male, respectively. BBS ranks are shown in parentheses.

Discussion

The most significant finding of this study is that the average T levels in female rock hyraxes are higher or equal to those of males. In nearly all of the social groups sampled, females did not have lower average T levels than males. In one case, average female T was even significantly higher than in males. To our knowledge, our data represent the first case of elevated T levels in adult mammalian females. We also found that females are the dominant sex in most hyrax social groups in Ein Gedi. Despite the fact that females ranked higher than males, the lack of correlation between T and rank suggests that female dominance in the hyrax may be influenced by additional factors, independent of or interacting with their high T levels.

The male rock hyrax, a seasonal breeder with intraabdominal testes, has interested several endocrinology-oriented researchers in the 1970s. Unfortunately, these studies did not include females, whose T levels were not measured. Millar and Glover (1973) showed that T levels in the male hyrax featured annual fluctuations, like in other seasonal breeders, reaching a climax that coincides with the peak of testes development. Neaves (1973) went further to correlate Leydig (androgen producing) cell volume with plasma T level. In his study of *Procavia habessinica*, testis weight and plasma T levels increased 5-fold during the breeding season. A similar trend is observed during the musth period in the elephants (Rasmussen et al., 1984; see below), which are phylogenetically closely related to the hyrax. We analyzed hair collected over a 6-month period, which included the mating season (July–August), from free-ranging male and female hyrax. Because hair accumulates T over time, daily or short-termed peaks are smoothed out, yet longer-term elevations in hormone concentrations are reflected in a comparative analysis between the sexes. Since T levels can also be subject to biotic factors influenced by seasonality, such as food availability (Millar and Fairall, 1976), even in animals that are not seasonal breeders, we controlled for the sampling time in our statistical analysis. Similar trends in T level between the sexes were obtained whether standardized values or data controlled for time were used. The analysis of two additional hyrax populations, northern Israel and captives, further supports our conclusions.

Our findings contrast previous reports from Africa noting that the social system in the rock hyrax (*Procavia johnstoni*) is composed of a group of females monopolized by a dominant male (Hoeck, 1975; Estes, 1991). Hoeck et al. (1982) reported that peripheral males were always observed sitting alone, never huddling together with the female groups, and that the highest-ranking peripheral male takes over a territory when a territorial male disappears. Our observations showed that, in Ein Gedi, peripheral males often aggregated at night in fixed locations, and later shared a common sleeping space. Moreover, these males were also seen huddling with females at different periods of the day. In all groups we studied, the males that replaced the highest-ranking males when they disappeared were not the highest-ranking bachelors. Further, whereas Fourie and Perrin (1987) claimed that there is no evidence of bachelor groups, we observed a bachelor group for several years.

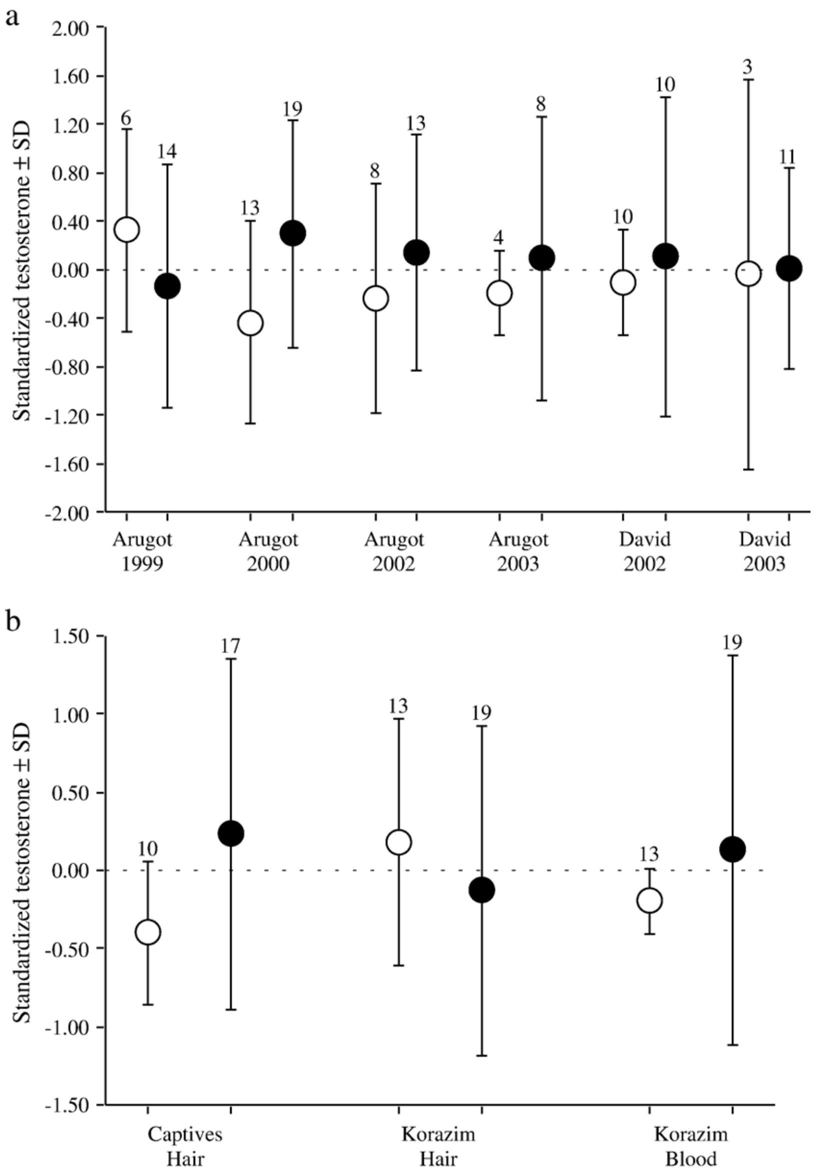

Fig. 2. Mean standardized (±SD) testosterone levels measured in hair of adult female (solid circles) and male (open circles) rock hyrax in the Ein Gedi Nature Reserve (a), and in captivity and in the Korazim populations (b). Sample size is indicated above bars.

In our study groups, more than half of the observed agonistic interactions involved females. Female rock hyraxes are no larger than males, yet females were dominant in the social hierarchy, some ranking higher than the males. These observations contrast with previous reports that females rarely embark upon agonistic interactions, having no apparent dominance among themselves (Hoeck et al., 1982). The mechanisms that promote their dominance are yet to be determined. For comparison, female spotted hyenas are larger than males (Kruuk, 1972) and stable female dominance is attributed, among other factors, to female coalitions, maternal rank inheritance, and male dispersal (Smale et al., 1993; Jenks et al., 1995).

In males, androgens are known to be correlated with aggression and dominance (Bouissou, 1983; Mazur and Booth, 1998). Male hyraxes compete among themselves fiercely during the mating season. Their dominance rank is correlated with and can be used to explain their T levels. In males, rank and T level were independent of residency within a mixed-sex or unisex group (Fig. 3), and can be explained by the fact that females in estrus mated with many partners, both bachelor and resident males (L.K. personal observations). The high testosterone levels that we measured in female hyraxes may explain the lack of mating choosiness, typical of mammalian male sexual behavior (McGlothlin et al., 2004), or may serve as a survival tactic to mask paternity and protect offspring from the threat of possible infanticide. Significant correlation between dominance rank and T was documented in both sexes of the naked mole-rat (Clarke and Faulkes, 1997). In that eusocial mammal, queens are at the top of the female hierarchical ladder and have the highest level of T among females. In some species, elevated female T levels have been shown to facilitate male-typical behaviors such as aggression and mate choosiness (reviewed in McGlothlin et al., 2004). In female hyraxes, as is the case with human and most other mammalian females, the association between T levels and

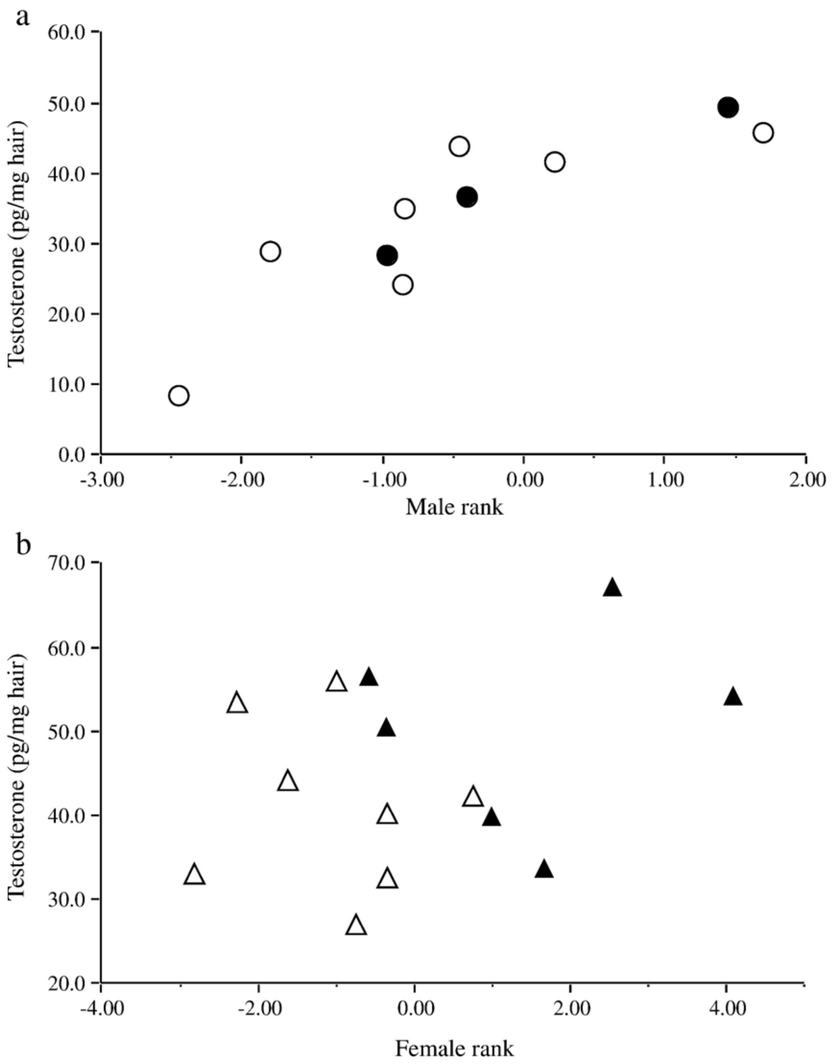

Fig. 3. Dominance rank (BBS scaling method) versus testosterone levels in the wild Ein Gedi hyrax. Data represent adult members of two neighboring social groups and adult male bachelors in their vicinity. (a) Males ($r_s = 0.903$, $P = 0.007$). Open circles are members of the bachelor group; solid circles are members of mixed-sex social groups. (b) Females ($r_s = 0.124$; $P = 0.653$). Open triangles are members of group 1; solid triangles are members of group 2.

dominance is more obscure (Staub and De Beer, 1997; Mazur and Booth, 1998; Christiansen, 2001).

Although female spotted hyenas and ring-tailed lemurs dominate over males in almost every social situation, regardless of size, T levels in adult females are not higher than in adult males (Glickman et al., 1992; von Engelhardt et al., 2000). In fact, we could not find a single report of a placental mammal in which adult females have equal, or higher, levels of T than males. In the female-dominated society of African elephants, a sister taxon to the hyracoidea (Afrotheria; Springer et al., 1997), males have higher serum T levels than females (Rasmussen et al., 1984). Even during the non-musth periods, mean T levels in African (1.40 ± 2.31 ng/ml) and Asian (2.63 ± 1.78 ng/ml) elephant males are significantly higher than in African (0.22 ± 0.16 ng/ml; $Z = 2.52$; $P = 0.012$) and Asian (0.08 ± 0.02 ng/ml; $Z = 1.95$; $P = 0.052$) females (based on data in Rasmussen et al., 1984). During musth, T levels are increased 5–10-folds in males. However, in both the elephant and the hyrax, circulating progesterone is relatively low during pregnancy, an unusual phenomenon in placental mammals, whereas 5 alpha − DHP and 5 alpha − PO are 8–20 times higher than progesterone (Heap et al., 1975; Hodges et al., 1997; Kirkman et al., 2001). Kirkman et al. (2001) suggested that in the hyrax 5 alpha − DHP binds to the progesterone receptors in the uterus where it triggers the physiological mechanisms that support pregnancy. Considering the unique hormonal system in the hyrax, it is possible that dominance in females is mediated through other androgen metabolites. In two different mammalian species, in the spotted hyenas and in fossas, adult females had elevated levels of other androgens (androstenedione; Glickman et al., 1987; Glickman et al., 1992; Goymann et al., 2001 and dihydrotestosterone; Hawkins et al., 2002; respectively), but not of T.

The fact that in female rock hyraxes the high T levels do not correlate with dominance rank, as opposed to the situation in males, opens up intriguing questions as to the role that T plays in females. The mechanisms that allow females to intercept the 'male hormone' and continue with their reproductive cycle as well as the behavioral repercussions of high T levels in females pose exciting new twists to the old-school rules of hormones and the genders to which they have been assigned.

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