Sexually opposite effects of testosterone on mating success in wild rock hyrax

Lee Koren, a,b Yishai Weissman, a,b Inbar Schnitzer, a Rosanne Beukeboom, a Einar Bar Ziv, b Vlad Demartsev, c,d, f Adi Barocas, e, f Amiyaal Ilany, a, e and Eli Geffen. c, e

a The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan 52900, Israel, bMitarani Department of Desert Ecology, Ben-Gurion University of the Negev, Sde Boker, 8499000, Israel, c School of Zoology, Tel Aviv University, Tel Aviv 69978, Israel, d Biology Department, University of Konstanz, Konstanz, Germany, e San Diego Zoo’s Institute for Conservation Research, Escondido, CA 92027, USA, and f Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford, UK

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INTRODUCTION

Although males and females share traits, their motivations and needs may be different, due to life-history disparities that lead to divergent selection pressures. Proximate mechanisms underlying differences between the sexes include hormones that mediate the development and activation of suites of traits. Testosterone is associated with morphological features, physiological processes, and social behaviors in both sexes. However, even if present in similar concentrations in the circulation, testosterone often affects males and females differently. We combined behavioral mating observations of the wild polygynandrous rock hyrax (Procavia capensis) with hair testosterone that represents long-term integrated levels. We found that whereas copulation success increases with the rise in testosterone in males it decreases in females. We did not find an association between testosterone and choosiness in either sex. However, we found that males with higher testosterone mate-guarded females with lower testosterone. Our findings show disassortative mating and mate-guarding in respect to testosterone and provide clues to the cost of testosterone for females, in terms of copulation success. These results open up intriguing questions relating to the role of testosterone in mediating a similar trade-off in male and female reproductive success.

Key words: androgens, disassortative mating, mate-guarding, mating strategy, mating success, sex differences

Address correspondence to L. Koren. E-mail: lkc.koren@biu.ac.il.
Testosterone may also impact fitness by affecting social signal detection (van Honk and Schutter 2007), mate choice (McGlothlin et al. 2004; Raveh et al. 2014; de Jong et al. 2017), interfering with pair bonds and parental care (Dufty 1989; Paternostro 1994; Reed et al. 2006). All of these costs are expected to be especially challenging for breeding females, which need to choose the right mate, copulate, produce offspring, and develop maternal behavior. As such, testosterone is often described as a physiological mediator of the trade-offs between reproduction, survival, and parental effort (Ketterson and Nolan 1992; Ketterson and Nolan 1999; Hau 2007; McGlothlin et al. 2007; Koren et al. 2012), which are central to life-history theory (Sterns 1992; Roff 1993).

Because of its role as a physiological mediator and intersexual variability, testosterone is a potential candidate for studying assortative mating criteria. Here, we studied whether testosterone is involved in mate choice and copulation success in a wild mammal, the rock hyrax (Procavia capensis). Sex differences in the effects of testosterone on mating is especially intriguing in this species since male and female circulating and hair testosterone levels are similar year round (Koren et al. 2006; Koren and Geffen 2009a). In the past, we found that whereas male testosterone is positively associated with social status, with more dominant males possessing higher testosterone levels (Koren et al. 2002; Koren and Geffen 2009a), in females the association is inverse. More dominant females possess lower testosterone levels than low ranking females (Koren and Geffen 2009a), suggesting that testosterone may be costly to breeding females. Here, we examined whether testosterone is related to maternal status, and predicted that what has been found for humans (Kuzawa et al. 2010), females that are mothers would have lower testosterone levels. Rock hyraxes are social, living in mixed-sex groups consisting of 7–20 (average 9 ± 4) females with their pups, 1–2 resident males and late dispersing males (Koren et al. 2006; Koren and Geffen 2009a). Hyraxes in our study area mate polygynandrously (Bar Ziv et al. 2016). In the short (i.e., 1–3 weeks) mating season, both sexes mate with multiple partners, but females are more choosy, rejecting more copulation attempts than males (Bar Ziv et al. 2016). We expect choosiness to be related to testosterone in both sexes (Johnstone et al. 1996; McGlothlin et al. 2004). In our study area, resident males are mostly dispersers from outside the research area and remain with a social group for an average of 3.1 years and a maximum of 5 years. Bachelor males, in contrast, are mostly local, and associate with females of several social groups (Koren et al. 2008). Based on these previous findings and the potential costs of testosterone (Folstad and Karter 1992), along with the Challenge Hypothesis that predicts varying testosterone responses to mating, breeding, or territorial behavior (Wingfield et al. 1990; Hirschenhauser et al. 2004), we expected resident males to have higher testosterone levels than bachelor males.

Male testosterone has been linked with copulation success (Alatalo et al. 1996) and attractiveness (Enstrom et al. 1997) in other species. Thus, we expected that hyraxes with higher testosterone would have higher copulation success, and that both males and females with higher testosterone would be less choosy in regard to mates (McGlothlin et al. 2004). To contend with females mating with multiple partners, males in polygynandrous systems may use alternative mating tactics such as mate-guarding to increase their fertilization success. The propensity to male mate-guard has been shown to be related to testosterone in several vertebrates (Wingfield et al. 2001; Onyango et al. 2013). In hyraxes, resident males tend to mate guard females that were mothers in previous years, while bachelor males rarely mate-guard (Bar Ziv et al. 2016). However, since mate-guarding prevents promiscuity, we expected that males with higher testosterone would mate-guard less and copulate with more females. The underlying basis for our hypotheses is that testosterone will enhance copulation success for both sexes at the cost of choosiness, parental behavior, and mate-guarding.

**MATERIALS AND METHODS**

We have been studying rock hyraxes in the Ein Gedi Nature Reserve (31°28′N, 35°24′E) since 1999. For this study, we used the data set from Bar Ziv et al. (2016), in which mating-related events were observed during 1999–2012 (Bar Ziv et al. 2016). We added to this dataset integrated hair testosterone levels of the males and females that were involved in the mating behaviors.

**Field procedures**

Our detailed field procedures have been previously published (e.g., Koren et al. 2008; Barocas et al. 2011; Bar Ziv et al. 2016). Briefly, we capture hyraxes annually via live box traps (Tomahawk Live Trap Co.), and individually mark them using subcutaneous transponders (DataMars SA), earrings, and numbered collars (collar weight 5 g; range of 0.125–0.2% of hyrax body weight). These allow us to individually identify hyraxes from a distance of up to 100 m using 10X42 binoculars (Monarch, Nikon) and a telescope with up to ×75 magnification (Fieldscope ED82, Nikon). Mating behaviors in this study were scored exactly as on a previous study of this hyrax population by Bar Ziv et al. (2016). Copulation included mounting and repetitive pelvic thrusts. For a behavior to be scored as rejection, a hyrax approached another of the opposite sex, and the latter reacted aggressively and retreated. In mate guarding, a male closely followed a female during the mating season, for at least 24 h, and up to several days.

**Ethical statement**


**Hair testosterone**

We measured long-term integrated testosterone levels from 20 mg hair of male and female rock hyraxes (Koren et al. 2002; Koren et al. 2006; Koren and Geffen 2009a). Hair samples were collected in the spring, before the mating season. Since hyrax hair shows continuous growth throughout the year, and cut hair fully regrows within 1–2 months of cutting, we conclude that hair samples represent integrated concentrations relevant to the premating season (late winter-early spring).

Hair was cut from the same area of the body, to avoid inconsistencies in gland distribution, hair color, and growth. In the lab, hair samples were washed twice with isopropanol (Romatic Ltd.), dried, and depending on the year, either left whole (N = 30) or ground to a fine powder (N = 122; 25 Hz, 200 MM, Retsch). Hair samples were sonicated with 1 mL methanol (Sigma-Aldrich Israel Ltd.) and incubated overnight. The following day, methanol was evaporated to dryness under a stream of nitrogen and reconstituted.
using the commercial zero standard from the testosterone enzyme-linked immunosorbent assay (ELISA) kit (DRG International, Inc., item no. EIA-1559). The kit was previously validated for hyrax hair (Koren et al. 2006, 2008; Koren and Geffen 2009a, 2009b), and all samples were run in duplicate. Samples were distributed randomly (using the assign random command in excel) across plates designated for males and females. Here, running six duplicates of a pool of hyrax hair on the same plate gave an intra-assay variability of 4.69%. Duplicates of a pool that was quantified on nine different days gave an interassay coefficient of variation of 6.16%. Serial dilutions of the hyrax hair pool showed parallelism with the provided kit standards (ANOVA; \( P = 0.67 \)), and linearity was demonstrated between 1 and 40 mg hair. Recovery was calculated to be 101.9% through the addition of a known amount of testosterone standard to the pool.

**Statistical analysis**

To determine the effect of age, residency status, and maternal experience on long-term, integrated testosterone levels in males and females, we applied linear mixed models. Residency status (i.e., resident or bachelor) and maternal experience (i.e., mother or nonmother; Bar-Ziv et al. 2016) were set as fixed effects; age of males or females as covariates; and individual identity as the random effect. Hair processing method (i.e., ground or whole) and year were also added as fixed effects to these models. Because testosterone levels did not distribute normally, we used the Box-Cox transformation. Linear mixed models were fitted using program JMP (version 14, SAS, Inc.). Last, we calculated the total effect for each variable in the model, which is a measure of relative contribution of that factor both alone and in combination with the other factors (Saltelli 2002). The total effect size is calculated via Monte Carlo sampling, and is independent of the model type and fitting method.

We looked at each copulation-related event as a separate case. For each observation, we determined whether an individual copulated or was rejected by its partner. Thus, each event was either a successful copulation or not (i.e., a binary variable). Similarly, whether mate-guarding was performed or absent followed each event. We used a logistic regression model within the framework of the generalized estimating equations (GEE) to test the effect of hair testosterone level in females and males (independent variables) on copulation success, rejection, and mate-guarding (Table 1). We used the same approach also to test the effect of testosterone levels on the initiation of sexual interactions in males and females. GEE is an extension of generalized linear models (GLM) for correlated data (i.e., mixed model design). In our models, copulation success and mate-guarding were both binary variables that were set as the dependent variables; the annual hair testosterone levels for each male and female pair were set as covariates; and male and female identities were set as random effects. The “No” level in copulation success or mate-guarding was set as the reference category. Wald \( \chi^2 \) statistics was used to test the significance of each effect. GEE model fitting was performed using SPSS (version 24, SPSS, Inc.).

To control for the variance in testosterone levels due to the processing method and year, we used standardized regression residuals (i.e., residuals divided by their SE) as the male and female testosterone concentration predictor for the analyses presented in Table 1. We selected to use residuals as our covariates in the above logistic regressions because our sample size was small, especially for the mate-guarding analysis. Thus, using residuals allowed us to construct the minimal model (i.e., \( T_{\text{male}} + T_{\text{male}} + T_{\text{female}} \times T_{\text{male}} + \text{random effect} + \text{error} \); Table 2) required to the combined effect of testosterone of both sexes on copulation success and mate-guarding frequency.

**RESULTS**

We extracted testosterone for 39 females and 39 males that had been observed by Bar-Ziv et al. (2016). Overall, we had testosterone data for 86 different female–male combinations that had participated in 199 mating-related events, composed of 140 bachelor-female and 59 resident-female combinations. Our dataset included 69 male and 84 female annual hair testosterone values.

Hair testosterone was only significantly affected by year (linear mixed model; females \( P = 0.011 \); and males \( P = 0.044 \); Table 1). Our analysis showed that resident male hair testosterone levels did not differ from those of bachelors (Table 1), despite their higher social ranking (Wald \( \chi^2 = 9.4, P = 0.002 \)). No interaction was found between male residency status and age (\( P = 0.972 \)). Females that had previously been mothers did not differ than nonmothers in hair testosterone level (Table 1). No significant interaction between maternal experience and female age was detected (\( P = 0.127 \); Table 1).

We analyzed copulation success using 335 events in which either copulation (\( n = 93 \)) or rejection (\( n = 242 \)) were observed. For 129

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**Table 1**

(A) The effect of year, hair processing method, male residency status, and male age on male hair testosterone level and (B) the effect of year, hair processing method, maternal experience, and female age on female hair testosterone level

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Estimate</th>
<th>df</th>
<th>( F )</th>
<th>( P )</th>
<th>Total effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Male effects (( n = 63 ))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>8.35</td>
<td>4.2</td>
<td>( 0.001 )</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Hair processing method</td>
<td>-1.8</td>
<td>1.49</td>
<td>0.6</td>
<td>0.455</td>
<td>0.06</td>
</tr>
<tr>
<td>Male residency status</td>
<td>0.9</td>
<td>1.50</td>
<td>0.7</td>
<td>0.395</td>
<td>0.02</td>
</tr>
<tr>
<td>Male age</td>
<td>0.9</td>
<td>1.48</td>
<td>2.09</td>
<td>0.155</td>
<td>0.06</td>
</tr>
<tr>
<td>Male residency status × Male age</td>
<td>0.0</td>
<td>1.48</td>
<td>0.0</td>
<td>0.972</td>
<td></td>
</tr>
<tr>
<td>B. Female effects (( n = 520 ))</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>7.68</td>
<td>2.2</td>
<td>( 0.044 )</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Hair processing method</td>
<td>4.1</td>
<td>1.71</td>
<td>0.6</td>
<td>0.452</td>
<td>0.10</td>
</tr>
<tr>
<td>Maternal experience</td>
<td>1.3</td>
<td>1.68</td>
<td>0.4</td>
<td>0.522</td>
<td>0.11</td>
</tr>
<tr>
<td>Female age</td>
<td>1.2</td>
<td>1.64</td>
<td>1.2</td>
<td>0.285</td>
<td>0.15</td>
</tr>
<tr>
<td>Maternal experience × Female age</td>
<td>1.7</td>
<td>1.68</td>
<td>2.4</td>
<td>0.127</td>
<td></td>
</tr>
</tbody>
</table>

Model parameters were estimated using linear mixed models where male and female identities were set as random effect, and \( P \) values were estimated using permutations. Effect size was calculated using the total effect approach. \( n \) = number of events observed. Significant effects are indicated in bold.
events, we had testosterone levels for both male and female partners. The dataset for the copulation success was composed of 40 male and 60 female annual hair testosterone values. We detected a significant effect of both male and female hair testosterone on copulation success. In addition, the fully factorial model revealed that the interaction between testosterone levels in males and females was significant (Wald $\chi^2 = 5.9$, $P = 0.013$; Table 2). Copulation success increased with higher testosterone in males (estimate = 0.42), but decreased in females (estimate = -0.82; Table 2, Figure 1a). In other words, females with the lowest testosterone levels and males with the highest testosterone levels demonstrated the highest copulation success (Figure 1a). The effect size of testosterone levels on female copulation success was almost five times greater than that of males (Table 2).

To address concerns about the possible effect of the testosterone processing method, we repeated the above regression analysis for ground hair data alone. In this sub-dataset we had a sufficiently large dataset (i.e., 91 cases), and testosterone values were only controlled for the year effect. This analysis showed a rather similar trend to that observed in Table 2. We found that with the rise in annual hair testosterone levels, copulation success decreases in females (estimate $=-1.33$, Wald $\chi^2 = 4.8$, $P = 0.028$) and increases in males (estimate $=0.61$, Wald $\chi^2 = 8.0$, $P = 0.005$). The interaction between male and female annual hair testosterone levels was not significant (Wald $\chi^2 = 0.1$, $P = 0.751$).

We did not find testosterone levels to be involved in initiation of sexual interactions in either sex. Both males and females were found in both roles, as initiator and as receiver, in different events, and the testosterone levels between the two roles did not differ (Wald $\chi^2 = 0.5$, $P = 0.479$ and Wald $\chi^2 = 0.6$, $P = 0.437$ for males and females, respectively). Testosterone levels were not associated with multiple mating, that is, the number of partners in males (Wald $\chi^2 = 0.02$, $P = 0.876$), nor in females (Wald $\chi^2 = 0.9$, $P = 0.333$). Testosterone levels were not associated with rejection rates, in both sexes (Wald $\chi^2 = 0.6$, $P = 0.456$ and Wald $\chi^2 = 1.6$, $P = 0.202$ for males and females, respectively).

Lastly, we had testosterone data for both sexes in 20 successful copulatory events, of which mate-guarding was observed in eight. Females with low testosterone were the most likely to be mate-guarded by males with high testosterone (Figure 1b). However, our model also revealed mate-guarding on high-testosterone females by low-testosterone males (Figure 1b), as indicated by the significant interaction effect between testosterone level and sex (Table 2).

### DISCUSSION

Our analysis of the relationship between testosterone and copulation success in both sexes revealed opposite trends. Whereas testosterone was positively associated with copulation success in males, in females it was negatively associated, so that females with higher testosterone obtained lower copulation success. In the past, we found that higher testosterone levels are associated with higher social rank in males, but lower social rank in females (Koren et al. 2002; Koren and Geffen 2009a). Combining these two studies suggests on one hand disassortative mating concerning testosterone levels whereas high testosterone males and low testosterone females mate, and assortative mating concerning social rank, with successful high-ranking male–female copulations. Since there are no sex differences in testosterone levels in hyraxes (Koren et al. 2006) and they are considered high (Gustafson and Shemesh 1976), our predictions were mixed. On one hand, we expected testosterone to be related to copulation success in an opposite manner in the two sexes. On the other, we suspected that considering hyrax circulating levels, male and female copulation success will show similar trends. High female testosterone in hyrax may be a by-product of high male testosterone, having co-evolved as a consequence of selection on males for increased levels (Møller et al. 2005). Since selection differs between the sexes, a trait that is beneficial for one sex may be detrimental for the other sex (Rice 1992), even in monomorphic species. For example, if male and female testosterone levels are correlated, elevation of male testosterone may be constrained (Ketterson et al. 2005). Intersexual genetic correlation may also be the origin of the negative effects associated with high female testosterone levels (Clotfelter et al. 2004). These may be alleviated via decoupling testosterone from behavior (Jawor et al. 2006) through a loss of sensitivity (i.e., receptors) to the high circulating levels, or modification of sex hormone binding globulin levels. These processes may be mediated by specific genes whose expression is sexually dimorphic (Peterson et al. 2013). Although we found that high female testosterone has a fitness cost via copulation, additional fitness-related parameters, such as maternal behavior, may be hardwired in a way that precludes the effects of testosterone. For example, in dark-eyed juncos (Junco hyemalis), testosterone-implanted females displayed a change in some aspects of parental behavior but did not reduce offspring provisioning (O’Neal et al. 2008), despite observed trade-offs in males (Ketterson and Nolan 1992; Wingfield and Farner 1993).

### Table 2

The effect of hair testosterone level in females ($T_{female}$) and males ($T_{male}$), controlled for the hair processing method and year, on copulation success and mate guarding

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate</th>
<th>Wald $\chi^2$</th>
<th>df</th>
<th>$P$</th>
<th>Total effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copulation success ($n = 129$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_{female}$</td>
<td>-0.815</td>
<td>14.9</td>
<td>1</td>
<td>$&lt;0.001$</td>
<td>0.986</td>
</tr>
<tr>
<td>$T_{male}$</td>
<td>0.419</td>
<td>6.8</td>
<td>1</td>
<td>0.009</td>
<td>0.221</td>
</tr>
<tr>
<td>$T_{female} \times T_{male}$</td>
<td>-0.508</td>
<td>5.9</td>
<td>1</td>
<td>0.015</td>
<td></td>
</tr>
<tr>
<td>Mate guarding ($n = 20$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$T_{female}$</td>
<td>19.760</td>
<td>16.9</td>
<td>1</td>
<td>$&lt;0.0001$</td>
<td>0.794</td>
</tr>
<tr>
<td>$T_{male}$</td>
<td>1.018</td>
<td>0.1</td>
<td>1</td>
<td>0.786</td>
<td>0.238</td>
</tr>
<tr>
<td>$T_{female} \times T_{male}$</td>
<td>-60.108</td>
<td>22.8</td>
<td>1</td>
<td>$&lt;0.0001$</td>
<td></td>
</tr>
</tbody>
</table>

Model parameters were estimated using logistic regression mixed model where male and female identities were set as random effect. Effect size was calculated using the total effect approach, $n$ = number of events observed. Significant effects are indicated in bold.
Male hyrax generally fit the vertebrate dogma where males with high testosterone, or with exaggerated ornamentation that reflect high testosterone, have higher copulation (Ketterson and Nolan 1992; Zuk et al. 1995; Enstrom et al. 1997; Martin et al. 2013) and reproductive success (Garamszegi et al. 2005), especially in mammals not demonstrating paternal care (Hirschenhauser and Oliveira 2006). It is also well documented that androgens such as testosterone respond to the social environment and prepare the individual for competitive situations. For example, male testosterone levels can rise by merely watching a fight, without actively participating in it (Oliveira et al. 1996; Mazur et al. 1997; Oliveira 1998). However, we found opposite to our prediction that male residence status was not related to testosterone levels, corroborating our previous observations that resident males do not mate more than bachelors (Bar Ziv et al. 2016). It is possible that sociality restrains resident male testosterone, with its need to interact with group females nonaggressively (Holekamp and Smale 1998; East et al. 2003). Testosterone is essential in physiological processes in both sexes (Staub and DeBeer 1997; Wingfield et al. 2001). However, the costs of testosterone may outweigh the benefits (Cain and Ketterson 2013; Goymann and Wingfield 2014), as testosterone has costs in terms of parental behavior and survival (Ketterson and Nolan 1992; Clark and Galef 1999), and has been suggested as a mechanism modulating the trade-offs between mating and parental efforts. In females, the fitness costs involved with high testosterone levels are expected to be substantial, and although testosterone is essential to maintaining age-related female fertility (Walters et al. 2008), it may be deleterious to fitness and reproduction in many ways (Clotfelter et al. 2004; McGlothlin et al. 2004; van Honk and Schutter 2007; O’Neal et al. 2008; Cain and Ketterson 2013; Gerlach and Ketterson 2013; Rosvall 2013). In the dataset used for this study, we did not find a relationship between female age (i.e., proxy for survival), and testosterone levels, but year had a significant effect of testosterone. In the future, as our database will grow, we will be able to assess these effects, including abiotic parameters (e.g., rainfall). Currently, we are studying hyrax reproductive success and parental behavior. Combining these data will provide a framework to study the role of testosterone in mediating fitness-related behaviors. We hypothesize that dominant female hyraxes, which were older, and had lower testosterone levels.

Figure 1
The probability of copulation success (a) and mate guarding (b) as a function of standardized testosterone residuals in male and female rock hyraxes. Actual observations are superimposed on the model so that absence and presence of copulation (a) and mate-guarding (b) are denoted by empty and filled circles, respectively. The color codes denote the probability of copulation success or mate-guarding. These probability spaces are predicted by the logistic regression.
(Koren and Geffen 2009a) may be more fertile, as high levels of testosterone are maladaptive for breeding females (Ketterson et al. 2005; Rutkowska et al. 2003; Browne et al. 2006). In addition, our results suggest that low-testosterone females may be more attractive possibly due to their higher social status (Koren and Geffen 2009a), or to their maternal status, both of which may trade-off with testosterone. Mate choice is likely associated with both male and female hormonal profiles (Kidd et al. 2013). Experimental studies have shown that high female testosterone may alter the females’ propensity to choose higher-quality mates (McGlothlin et al. 2004; de Jong et al. 2017). However, in the hyrax, we did not detect an association between testosterone and initiation or rejection rate, which may be related to choosiness, and testosterone levels were not associated with multiple mating, that is, the number of partners in either sex. Since testosterone may play different roles in mediating reproduction and fitness as well as social status (Koren and Geffen 2009a) in males and females, multiple generations need to be studied to uncover the full impact of testosterone on fitness.

Finally, we found that, contrary to what we had predicted, testosterone was associated with dissociative mate-guarding. We predicted that high-testosterone males would copulate more and mate-guard less than low-testosterone males. However, we found that high-testosterone males were more likely to mate-guard than low-testosterone males, and that they mate-guarded females with low testosterone. Mate-guarding is an attempt to manipulate female reproduction. Since hyrax oestrus is synchronized, a single male cannot monopolize all the females in the group. By mate-guarding females with low testosterone, which are likely high-ranking (Koren and Geffen 2009a) and experienced at raising pups (Bar Ziv et al. 2016), males invest in females that will potentially produce viable, high-quality offspring. However, females with high testosterone may be at an advantage due to the lack of mate-guarding, which enables them to mate with multiple males rather than be monopolized by the resident males. It is therefore possible that although high-testosterone females mate less, they may have more mating possibilities. In addition, we found that males with low testosterone tried to mate-guard females with high testosterone, suggesting that young males may practice mating-related behaviors with females that are less choosy, or less desirable to high-testosterone, dominant males. This may also suggest that hyraxes maximize mating opportunities from the available mate pool in their sexual networks (Bar Ziv et al. 2016), based on their testosterone level. Although the interaction that we detected for mate guarding was significant, our sample size was very small (i.e., 20 cases), and verification of these results with a larger dataset is required.

Our long-term studies integrating androgens, social status and mating behavior suggest that testosterone is linked to multiple aspects of sexual behavior in both males and females. Assessing the fitness advantages of complex testosterone/mating strategy interactions offers insight into the traits that are related to mate choice, and to the mechanisms that drive sexual selection. At this stage, we have uncovered multiple indications that testosterone challenges female reproduction via behavioral and social paths that may shape both male and female mate choice. Ultimately, a more comprehensive view is needed to understand how males and females achieve reproductive success (Zeh and Zeh 2003), and how their strategies affect one another.

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Authors contributions: L.K. designed the project. L.K., A.I., A.B., E.B.Z., and V.D. collected mating-related observations in the field 1999–2012. Y.W. and L.S. extracted and quantified testosterone. R.B. contributed to the organization of data. E.G. analyzed and interpreted the data. L.K. drafted the article and all authors commented on it.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Koren et al. (2019).

**Handling editor:** Michael Tahorsky

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