Comparative Biochemistry and Physiology, Part A 308 (2025) 111911

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Short communication: Elevated testosterone correlates with enhanced innate immune function in a cooperatively breeding rodent

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ARTICLE INFO

Editor: Michael Hedrick

Keywords:
Damaraland mole-rat
Cortisol
Endocrine-immune axis
Immunocompetence handicap hypothesis

ABSTRACT

In many vertebrates, elevated testosterone is believed to compromise the immune function, reflecting a trade-off between reproduction and survival. However, such trade-offs may potentially be relaxed in cooperative breeders, where social conflict and sexual selection are reduced. We investigated the relationship between testosterone, cortisol, and innate immunity in captive male Damaraland mole-rats (*Fukomys damarensis*), a eusocial rodent with minimal aggression-driven reproductive competition. Using microbial killing assays (MKAs) and white blood cell counts as proxies of immune function, we found that urinary testosterone concentration was positively correlated with immune strength. Males with higher urinary testosterone concentrations exhibited significantly greater antimicrobial capacity and elevated total white blood cell counts. However, urinary testosterone was unrelated to independent immune cell differentials. While, reproductive status, age, body mass, and urinary cortisol concentrations had a limited effect on any immune metric. These findings, while correlative, challenge traditional endocrine-immune trade-off models and infer that, in this species, testosterone may signal condition rather than impose immunosuppressive costs.

1. Introduction

The immune and endocrine systems are deeply intertwined, with well-established evidence demonstrating that reproductive hormones modulate immune function through a complex web of signalling interactions (Kelley, 1988). Among these, androgens (such as testosterone) and glucocorticoids (such as cortisol) have received considerable attention for their roles in mediating life-history trade-offs between reproduction and survival (Crespi et al., 2025; Crespi et al., 2013; Muehlenbein and Bribiescas, 2005). In many vertebrates, elevated testosterone is classically associated with reproductive success via the promotion of aggression, territoriality, and dominance, but it is often linked to reduced immunocompetence—a central tenet of the immunocompetence handicap hypothesis (ICHH) (Roberts et al., 2004). This trade-off suggests that only high-quality individuals can afford the immunosuppressive costs of testosterone while maintaining reproductive dominance (O'Brien et al., 2018; Roberts et al., 2004). The stress-linked ICHH refines this theory by incorporating the role of cortisol as a mediator of immune suppression (Moore et al., 2011; Roberts et al., 2007). As testosterone levels rise, stress-related hormonal cascades can also be activated, which in turn lead to chronic cortisol exposure and further downregulation of the immune responses. These frameworks are supported in many mammalian taxa, particularly in species with strict dominance hierarchies, where high-ranking males secure reproductive access at the cost of reduced immunity and elevated physiological stress (Esattore et al., 2024; Roberts et al., 2004; Smyth et al., 2018).

Yet, exceptions to this pattern are emerging (O'Brien et al., 2018; Rogovin et al., 2015; Snyder et al., 2025), particularly in cooperative breeders, where complex social structures and division of reproductive roles decouple testosterone's conventional link with aggression. In the Damaraland mole-rat (*Fukomys damarensis*), a subterranean, eusocial rodent, reproduction is monopolised by a single breeding female and male, while the majority of colony members remain reproductively suppressed (Bennett and Faulkes, 2000). This species presents an ideal natural system for testing the ICHH and its extensions, as reproductive status is socially regulated and not experimentally induced (Hart et al., 2022; Jacobs et al., 2021).

Intriguingly, breeding female Damaraland mole-rats exhibit elevated testosterone levels alongside enhanced immune function, challenging traditional predictions that testosterone is inherently

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https://doi.org/10.1016/j.cbpa.2025.111911
Received 15 May 2025; Received in revised form 26 July 2025; Accepted 26 July 2025
Available online 28 July 2025

immunosuppressive (Wallace et al., 2023a, 2023b). Unlike in other mammals (Smyth et al., 2018), dominant females in this species appear to maintain high immunocompetence, potentially due to the cooperative nature of their social environment, reduced reproductive competition, and stable dominance Wallace et al., 2023a, 2023b). In males, breeding individuals also display higher testosterone and similar cortisol levels relative to their non-breeding counterparts (Wallace et al., 2023a, 2023b), but without a corresponding increase in aggression (Lutermann et al., 2013). Instead, testosterone in breeding males appears linked to mating effort and potentially to increased body condition, energy balance, and a readiness for dispersal (Lutermann et al., 2013; Scantlebury et al., 2006; Wallace et al., 2023a, 2023b), factors that may facilitate enhanced immune function rather than compromise it. Moreover, some non-breeding males with higher body mass and better condition also show elevated testosterone, independent of aggression or dominance (Wallace et al., 2023a, 2023b). This suggests that in cooperative systems like that of Damaraland mole-rats, testosterone and cortisol may not signal social conflict, but rather reflect metabolic state and reproductive readiness. These dynamics raise the possibility that testosterone's relationship with immunity is context-dependent, modulated by social environment, stress physiology, and life-history strategy.

Here, we investigate the interplay between testosterone, cortisol, and innate immune function in captive-bred male Damaraland mole-rats, aiming to evaluate predictions from the ICHH and the stress-linked ICHH. We compared innate immune responses between breeding and non-breeding males using multiple immune proxies, including in vitro bacterial growth inhibition assays (measured via microbicidal killing assays, MKAs) and white blood cell differentials. This approach allows us to assess immunocompetence relative to hormonal profiles in a social system where reproductive dominance is not maintained through aggression, but instead arises within a cooperative framework. In such a system, social buffering and reduced intra-sexual conflict may decouple the typical trade-offs between immune function and reproductive investment. By examining these dynamics, our study seeks to refine current evolutionary models of hormone-mediated immunity and provide new insights into the complex regulation of immune function in a cooperative breeding mammal.

2. Materials and methods

This study was conducted using twenty-six adult male Damaraland mole-rats (Fig. S1), housed in the captive mole-rat research facility at the University of Pretoria. The animals were sourced from ten outbred and independent captive-bred colonies and included ten breeding males and 16 non-breeding males. All individuals were maintained under standardised environmental conditions (Grenfell et al., 2024), which are detailed in the Supplementary Material. Prior to sample collection, each mole-rat was weighed and identified using a subcutaneous passive integrated transponder tag. Experimental procedures were approved by the animal ethics committee of the University of Pretoria (NAS017–2021 and NAS022/2021).

Detailed protocols are provided in the Supplementary Materials. In brief, whole blood was collected from the dorsal tarsal vein of the hindfoot from all twenty-six individuals. Haematological analyses included the measurement of total white cell count ($x10^9$/L), segmented neutrophils ($x10^9$/L), lymphocytes($x10^9$/L), eosinophils($x10^9$/L), basophils ($x10^9$/L) and monocytes ($x10^9$/L). The relative proportions of segmented neutrophils, lymphocytes, eosinophils, basophils, and monocytes were expressed as percentages (%) of the total white cell count. To evaluate innate immune function, MKAs were performed on a subset of 20 individuals, comprising ten breeding males and ten non-breeding males. These assays measured the ability of each animal's blood to inhibit the growth of *Escherichia coli* in vitro. Antimicrobial capacity was quantified as the percentage (%) of *E. coli* bacteria killed during the microbicidal killing assay. This was calculated using the following formula: [1 – (Positive control CFU – Inoculated sample CFU)/ Positive control CFU]. The positive control represented the bacterial concentration prior to interaction with blood.

Urinary steroid hormone [testosterone (ng) and cortisol (μg)] concentrations of all twenty-six individuals were quantified, using Coat-A-Count radioimmunoassay kits (Diagnostic Products Corporation, Los Angeles, California, USA), following the manufacturer's instructions, and normalised to creatinine content, expressed as hormone levels per milligram of creatinine, in order to account for variation in urine concentration (See Supplementary Materials for further detail).

Due to ethical constraints limiting blood sampling to 1 % of an animal's body mass (body mass range: 106-235 g), the available blood volume (1.0–2.3 ml) was prioritised for immunological assays (microbicidal killing activity and white blood cell counts), particularly in smaller individuals. To minimise potential stress-induced alterations in circulating hormone levels during sampling, we assessed urinary steroid hormones as non-invasive proxies of endocrine activity. Urinary steroid measurements are widely used in mammals and provide an integrated measure of hormonal output over time, rather than a single time-point snapshot. Previous studies in rodents and other mammals have demonstrated that urinary testosterone and cortisol concentrations correlate with circulating blood levels (e.g., Thorpe et al., 2012; Scott et al., 2024), supporting the validity of this approach in our study species.

3. Data analysis

All statistical analyses were performed using R Studio (version 4.5.0) and GraphPad Prism (version 8.4.3). Data are presented as the mean value accompanied by the standard error of the mean. A threshold of statistical significance was set at a probability value of 0.05 or lower.

Normality and homogeneity of variance for all dependent variables was assessed using the Shapiro-Wilk test and Levene's test, respectively. These variables included antimicrobial capacity, total white cell count, and the proportions of segmented neutrophils, lymphocytes, monocytes, eosinophils, and basophils.

Each response variable was analysed using separate mixed-effects models. Fixed effects in the models included the interaction between the reproductive status and urinary steroid hormone concentration (either testosterone or cortisol). Age and body mass were included as covariates. These models were implemented using the *lme4* package in R (Bates et al., 2015).

For proportional data, including antimicrobial capacity and immune cell differentials, generalised linear mixed-effects models were fitted using a beta distribution and a logit link function. These models were implemented using the glmmTMB package in R (Brooks et al., 2017). Variables with approximately normal distributions, such as total white cell count, were analysed using linear models implemented through the lme4 package. Assumptions of model fit were validated using diagnostic plots, and overdispersion was checked where appropriate.

4. Results

Urinary testosterone concentration was the only significant predictor of immune strength among the variables tested in male Damaraland mole-rats. Elevated urinary testosterone concentrations were significantly associated with enhanced immune function, as indicated by increased antimicrobial capacity (Fig. 1A) and elevated total white blood cell count (Fig. 1B; Table 1). In contrast, antimicrobial capacity and total white blood cell count were not significantly influenced by reproductive status, age, body mass, or urinary cortisol concentrations (Table 1).

Urinary testosterone and cortisol concentrations were not significantly associated with the relative proportions of any specific immune cell types (Table S1). Similarly, monocyte, eosinophil, and basophil differentials were not influenced by reproductive status, age, or body mass (Table S1). However, age and body mass did significantly predict

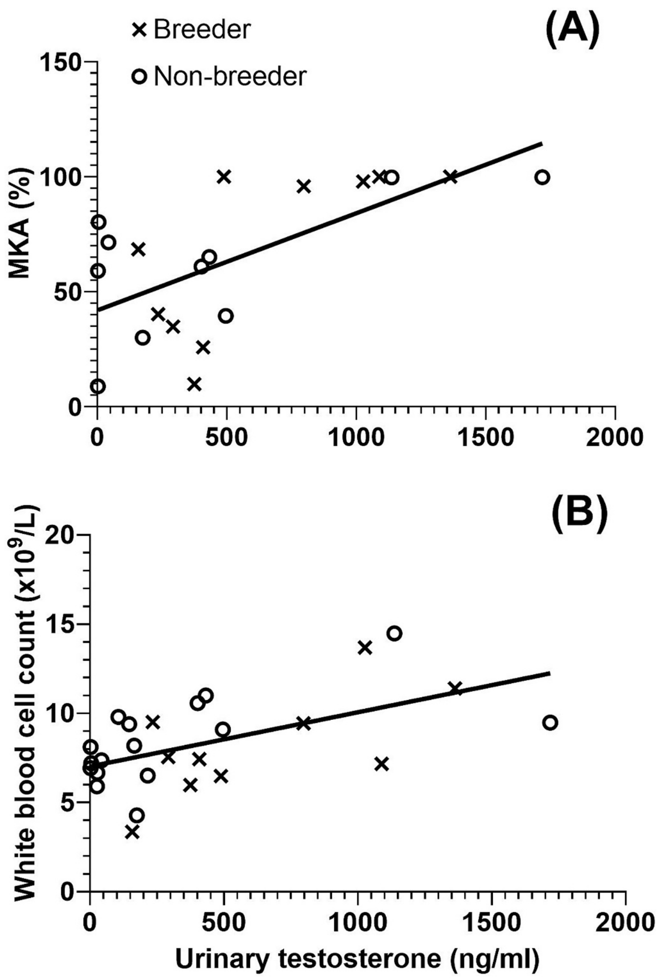

Fig. 1. Positive relationship between urinary testosterone concentration (ng/mL) and (A) antimicrobial capacity (MKA%) and (B) total white blood cell count ($\times10^9$/L) in male Damaraland mole-rats. Breeders are represented by × and non-breeders by ○.

variation in neutrophil and lymphocyte proportions (Table S1). Older and heavier males exhibited lower relative neutrophil counts and a corresponding increase in lymphocyte proportions, indicating a potential age- or size-related shift in immune investment (Table S1).

5. Discussion

Our results challenge conventional expectations in vertebrate endocrinology by demonstrating that testosterone is positively associated with innate immune function in male Damaraland mole-rats. In contrast to predictions from the ICHH and the stress-linked ICHH (Crespi et al., 2025; Crespi et al., 2013; Muehlenbein and Bribiescas, 2005; Roberts et al., 2004), males with higher urinary testosterone concentrations exhibited greater innate immune strength, primarily evidenced by enhanced bacterial killing capacity in the MKA and elevated total white cell counts. Neither cortisol concentrations, nor reproductive status (breeding vs. non-breeding) had a measurable impact on any immune proxy, and no consistent patterns were observed in immune cell proportions. These findings suggest that, in this cooperative breeder, testosterone may be associated with immune function in a way that differs from other mammalian species, whether solitary or social, where it is often linked to immunosuppression or no effect (Crespi et al., 2025; Crespi et al., 2013; Muehlenbein and Bribiescas, 2005; Roberts et al., 2004; Barnard et al., 1998; Klein et al., 1997).

This atypical endocrine–immune relationship may be attributable to

Table 1
Fixed effects from models testing the effect of the interaction between reproductive status [Breeder vs Non-breeder] and urinary steroid hormone concentration [testosterone (ng/mg) or cortisol (μg/mg)] on antimicrobial capacity (MKA%) and total white blood cell count (x10^9/L) in male Damaraland mole-rats, with age and body mass included as covariates.

Variable	*Z*-value	*P*-value
MKA		
Breeding status	0.76	0.45
Urinary testosterone	3.00	0.003*
Body mass	−0.19	0.85
Age	1.08	0.28
Breeding status*Urinary testosterone	−1.02	0.31
Breeding status	−1.36	0.17
Urinary cortisol	−1.09	0.27
Body mass	0.08	0.94
Age	−0.22	0.83
Breeding status*Urinary cortisol	1.04	0.30
White blood cells		
Breeding status	0.57	0.58
Urinary testosterone	2.52	0.02*
Body mass	−0.34	0.73
Age	−1.38	0.18
Breeding status*Urinary testosterone	−1.00	0.33
Breeding status	−0.07	0.94
Urinary cortisol	0.18	0.86
Body mass	−0.66	0.52
Age	−1.67	0.11
Breeding status*Urinary cortisol	−0.29	0.76

* Indicates statistical significance ($p < 0.05$).

the unique social and reproductive structure of Damaraland mole-rats. In this species, dominance is not maintained through chronic aggression, but instead emerges from incest avoidance and stable, cooperative interactions within a colony (Bennett et al., 2022). As such, elevated testosterone in breeding males likely reflects reproductive readiness and increased mating effort, rather than heightened social conflict (Wallace et al., 2023). Furthermore, high testosterone was also observed in some non-breeding males (Fig. S2). Scantlebury et al. (2006) proposed that certain non-breeders may prioritise self-maintenance over cooperative tasks, resulting in a positive energy balance and improved physiological condition, which could contribute to increased testosterone levels. Thus, one possibility is that in this species, testosterone serves as a proxy for overall health and energetic status rather than imposing a physiological cost (parameters not looked at in this study). In individuals with abundant energetic resources, simultaneous investment in reproductive hormones and immune function may be possible, thereby mitigating the classical trade-off between reproduction and survival (Demas et al., 2012). Moreover, the lack of association between cortisol and any immune parameters suggests that chronic stress is potentially not a major driver of immunocompetence in these animals, at least under captive conditions. This observation further challenges the expectations of the ICHH, which posits that glucocorticoid-mediated stress suppresses immunity in tandem with rising testosterone.

The lack of consistent patterns in immune cell differentials also suggests that the primary immune benefit associated with elevated testosterone is a general increase in immune cell production and function, rather than a shift in specific leukocyte populations. Together, these findings point to a system in which testosterone supports, rather than constrains, immune performance, an outcome that likely reflects the interplay of social cooperation, reproductive suppression, and energetic condition unique to this cooperative breeder. However, as older and heavier males exhibited lower relative neutrophil counts and a corresponding increase in lymphocyte proportions, this indicates a potential age- or size-related shift in immune investment (Yung, 2000) that warrants further investigation. Two additional mechanisms worth considering involve the interaction between dehydroepiandrosterone (DHEA) and innate immunity, and between testosterone and the hypothalamic–pituitary–adrenal (HPA) axis, respectively. A recent review by

Buendía-González and Legorreta-Herrera (2022) highlights the complex relationships among testosterone, DHEA, and the immune system. While the testosterone–immune relationship was the focus of this study, work on DHEA in Damaraland mole-rats has so far proved inconclusive (unpublished data), and further investigation is needed to understand the role of adrenal-derived DHEA in this species. Additionally, Handa et al. (1994) demonstrated in laboratory rats that elevated testosterone can inhibit HPA axis activity, thereby preventing glucocorticoids from suppressing reproductive and immune function. If similar mechanisms operate in Damaraland mole-rats, testosterone-mediated suppression of cortisol could indirectly enhance immune function by mitigating glucocorticoid-induced immunosuppression. However, as these findings derive from laboratory rodents under controlled conditions, their applicability to wild or cooperatively breeding species remains uncertain. Future studies examining the dynamic interactions among testosterone, cortisol, and immunity in natural populations will be valuable for clarifying these relationships.

It is important to note that our study examined only innate immunity, which has relatively low developmental costs, but high activation costs compared to adaptive immunity (McDade et al., 2016). As such, the associations we observed between testosterone and innate immune function may not apply to adaptive responses, which involve higher developmental investment, but lower activation costs once established (McDade et al., 2016). These differing energetic dynamics could also influence cortisol levels and their interaction with immune function. Future studies incorporating measures of adaptive immunity are needed to clarify how testosterone shapes the broader immune landscape in Damaraland mole-rats. Moreover, the balance between innate and adaptive immune investment is likely modulated by social-ecological factors such as food availability. In the highly cooperative social system of Damaraland mole-rats, where group living and resource sharing reduce individual energetic constraints, males may be better able to invest simultaneously in reproduction and immunity. This makes the species a particularly valuable model for exploring how endocrine–immune trade-offs are shaped by ecological and social contexts.

Given these unusual patterns, Damaraland mole-rats offer a promising model for studying the endocrine regulation of immunity in social mammals. Their reproductive division of labour, high tolerance of close kin, and lack of aggression-driven hierarchy provide a natural context in which to test and refine classic life-history trade-offs. Future studies on wild colonies of Damaraland mole-rats and employing experimental manipulations of testosterone levels will be crucial to confirm this pattern across the species and disentangle causality in the observed hormone–immune associations, respectively. Additionally, expanding this research to other African mole-rat species with varying social structures will provide valuable comparative insights. Unlike traditional rodent models, this species allows for the examination of hormone–immune relationships in the absence of confounding competitive behaviours, making it ideally suited for dissecting the true physiological roles of androgens in vertebrate immunity.

CRediT authorship contribution statement

K.M.E. Wallace: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **S.N. Venter:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **N.C. Bennett:** Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **D.W. Hart:** Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The project was funded by the SARChI chair for Mammal Behavioural Ecology and Physiology, South Africa, # 64796, for the DST-NRF awarded to NCB. A special thanks to Dr. Yolandi Rautenbach, Carien Muller and the rest of the Clinical Pathology team at the Department of Companion Animal Clinical Studies, Faculty of Veterinary Science, University of Pretoria, for conducting the haematological analysis for this project. We would like to extend our sincere thanks to the three anonymous reviewers for their constructive feedback and helpful suggestions, which have greatly improved the quality of this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2025.111911.

Data availability

Data will be made available on request.

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