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Seasonal changes in testosterone and corticosterone levels in four social classes of a desert dwelling sociable rodent

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Abstract

Animals have to adjust their physiology to seasonal changes, in response to variation in food availability, social tactics and reproduction. I compared basal corticosterone and testosterone levels in free ranging striped mouse from a desert habitat, comparing between the sexes, breeding and philopatric non-breeding individuals, and between the breeding and the non-breeding season. I expected differences between breeders and non-breeders and between seasons with high and low food availability. Basal serum corticosterone was measured from 132 different individuals and serum testosterone from 176 different individuals of free living striped mice. Corticosterone and testosterone levels were independent of age, body weight and not influenced by carrying a transmitter. The levels of corticosterone and testosterone declined by approximately 50% from the breeding to the non-breeding season in breeding females as well as non-breeding males and females. In contrast, breeding males showed much lower corticosterone levels during the breeding season than all other classes, and were the only class that showed an increase of corticosterone from the breeding to the non-breeding season. As a result, breeding males had similar corticosterone levels as other social classes during the non-breeding season. During the breeding season, breeding males had much higher testosterone levels than other classes, which decreased significantly from the breeding to the non-breeding season. My results support the prediction that corticosterone decreases during periods of low food abundance. Variation in the pattern of hormonal secretion in striped mice might assist them to cope with seasonal changes in energy demand in a desert habitat.

Keywords: *Rhabdomys pumilio*; Breeding; Helper; Philopatry; Group-living; Drought; Food; Cooperative breeding

Introduction

Studies of the seasonal changes in hormone levels are important to understand how physiology and ecology interact (Reeder and Kramer, 2005a; Romero, 2002; Wikelski and Ricklefs, 2001). Energy demands change for individuals over time, as they get older, reach maturity, change their social tactic or because of seasonal changes in food availability. These changes in energy demand might be regulated hormonally. Therefore, field studies of hormone levels including individuals of both sexes, different social classes and in different seasons can help us to understand how physiology, behavior and ecology interact (Reeder and Kramer, 2005a).

Glucocorticoids are one major class of hormones that enable individuals to respond to situations with high energy demands. Glucocorticoids are secreted by the adrenal gland and regulate the availability of energy by influencing glucogenesis, glucose use, and fat and protein metabolism (Reeder and Kramer, 2005b). Glucocorticoids are stress responsive and high levels of glucocorticoids indicate that the individual is in an energetically demanding situation (Reeder and Kramer, 2005b; Romero, 2002). Several field studies found increased glucocorticoid levels during the breeding season (reviewed in Reeder and Kramer, 2005a; Romero, 2002) indicating the high costs of breeding. This is especially the case in breeding female mammals, which typically have higher glucocorticoid levels than males, probably due to the high costs of pregnancy and lactation (Reeder and Kramer, 2005a; Strier et al., 2003). In sum, the

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hypothesis exists that glucocorticoid levels change seasonally as a function of both demand and availability of energy, contributing to an individualized optimal energy budget.

An important finding of previous field studies is that glucocorticoid levels not only change over short periods in response to stress, but even basal glucocorticoid levels can differ according to differences in season, ecology and life history, probably to provide individuals with the optimal amount of energy (Reeder and Kramer, 2005b; Romero, 2002; Wingfield, 2003). In the present study, I tested the following three predictions using correlative field data: 1. Breeding individuals have higher glucocorticoid levels than non-breeders, as breeding is energetically expensive. 2. Breeding females have higher glucocorticoid levels than breeding males, as lactation and pregnancy are especially expensive. 3. Glucocorticoid levels decline during the season of food shortage, as it would be difficult for individuals to meet high energy demands during this season. This effect should also be found in non-breeders, indicating that it is independent of breeding. Therefore, I expected glucocorticoid levels to vary as a function of breeding and food availability.

Glucocorticoids are not the only hormones affecting metabolism and reproduction. Androgens also influence the metabolic rate and are important for reproductive physiology and behavior (Baum, 1992; Wikelski and Ricklefs, 2001; Wingfield et al., 2000). In male primates, testosterone levels are higher during the breeding season (reviewed in Strier et al., 1999). Therefore, when studying seasonal changes in glucocorticoid levels it is of advantage when one can measure androgens at the same time (Reeder and Kramer, 2005a). While this has been done for males of a few species, very little data exist for females (Reeder and Kramer, 2005a). As androgens are also important in females (Staub and Beer, 1997), seasonal changes in androgen levels can also be expected in females, but these have seldom been investigated.

While energy demands change from the breeding to the non-breeding season, energy availability in the form of food can also change seasonally. This is especially the case in extreme environments, such as deserts. The present study was conducted in the Succulent Karoo desert in South Africa where cold and moist winters are followed by hot and dry summers. While specialized desert species do show interesting and fascinating physiological adaptations, it is equally important to understand how non-specialized species can cope with such an environment. The study species was the African striped mouse (*Rhabdomys pumilio*), a diurnal murine rodent that occurs in many areas of southern Africa, including moist grasslands and desert habitats (Schradin, 2005). The striped mouse does not show specific physiological adaptations to living in a desert (Christian, 1979).

Materials and methods

Study species

The striped mouse shows extraordinary flexibility in its social system, ranging from solitary to extended family groups with communal breeding (Schradin, 2005; Schradin and Pillay, 2005b). At my study site, mice typically form extended families with one breeding male, one to four breeding females and their philopatric offspring of both sexes which can remain at their natal group long after reaching adulthood (Schradin and Pillay, 2004b). Males participate in infant care (Schradin and Pillay, 2003) and females often rear their offspring cooperatively (Schradin and Pillay, 2004b). Social groups consist of 8–30 adult individuals of both sexes after the breeding season (Schradin and Pillay, 2004b). The breeding season is during the 3–4 month spring period (August to November) and mice usually do not breed during the season of their birth but only in the following year when they are 10–12 months old (Schradin and Pillay, 2005a). Females breed either in their natal group or disperse at the start of the following breeding season, while most males disperse when they are 6–12 months old (Schradin, unpubl.). Striped mice of one group share one nest and territory but forage solitarily (Schradin, 2006). While striped mice of one group interact amicably with one another forming an egalitarian social system without apparent dominance hierarchy, they react aggressively towards mice from neighboring groups (Schradin, 2004).

Study area and period

The study was conducted in Goegap Nature Reserve near Springbok in the Northern Cape Province, South Africa (S 29 41.56, E 18 1.60; for pictures of the field site see www.stripedmouse.com). The vegetation type is classified as Succulent Karoo (Cowling et al., 1999). The area is arid, with an average rainfall of 160 mm p.a. (Rösch, 2001). Most rain falls in winter (May to August, −1 to 20°) followed by spring (September to November, −1 to 30°) with maximum plant growth, mainly consisting of annuals and perennials. This seasonal plant growth restricts the duration of the breeding season of striped mice (Schradin and Pillay, 2006). Spring is followed by a long dry season (summer; December to April, 10–45 °C) when food abundance decreases and mice loose considerable body mass (Schradin and Pillay, 2005a). The study took place during the 2005 and 2006 breeding seasons (August to November) and the 2007 dry season (March). All parts of the study were approved by the animal ethics committee of the University of the Witwatersrand (animal ethical clearance no. 2004/87/2A and 2005/82/4).

Trapping and marking of animals

Striped mice were trapped using locally produced metal live-traps (26×9×9 cm^3; similar in design to Sherman traps), baited with a mixture of bran flakes, currants, sea salt and salad oil. Traps were placed in the shade under bushes where the mice were nesting (revealed by radio-tracking). Traps were checked at least every hour and trapping took place during mornings and afternoons, but not during the hottest time in the middle of the day. Trapped mice were sexed, weighed and individually marked with ear tags (National Band and Tag Co., USA). I also marked individuals with hair dye (Rapido, Pinetown, South Africa) to aid with individual recognition during behavioral observations (see pictures on www.stripedmouse.com).

Radio-tracking

Radio-tracking was performed using an AOR 8000 wide range receiver and a Telonics RA-14 K antenna. Individuals were equipped with radio transmitters (Holohil, Canada). Radio collars weighed 2.5 to 4.5 g, which represented less than 10% of body weight. Mice were radio-tracked 3–5 times/week to determine nesting sites. During the breeding season, all breeding males and approx. 75% of breeding females of the 12 focal groups had transmitters. During the non-breeding season, one breeding female per group had a transmitter. Transmitters did not influence hormone levels (see Results).

Behavioral observations

Nests were observed in the mornings and afternoons to record group composition. Observations were made from a distance of 5–10 m. Mice were habituated to and not disturbed by the presence of observers (Schradin, 2006; Schradin and Pillay, 2004b). Mice spend 30–45 min at the nest in the morning before leaving to forage and in the evening before withdrawing into the nest (Schradin et al., 2007) and nest observations lasted for the entire period mice were present. I recorded all individuals at the nest, recognized by the individual hair dye marking.

Determination of breeders versus philopatrics

Mice were categorized either as breeders or as philopatric by a combination of trapping, behavioral observations and radio-tracking. Philopatric individuals were young adults that were trapped as juveniles (<30 g) at the nest of one group and subsequently observed only with this group but not at other nests of other groups and not trapped more than 100 m away from their natal nest. The striped mouse is socially polygynous with one non philopatric adult males living with a group of one to four closely related females that are philopatric to their natal territory (harem defense polygyny; Schradin and Pillay, 2004b). These non natal males are called breeding males and were always the heaviest males of the group. Breeding males are thought to breed with the females of their group during the breeding season, while philopatric males are assumed not to breed with the females of their natal group due to the reported inbreeding avoidance in this species (Pillay, 2002). However, in how far extra-group paternity occurs, i.e. whether females mate with the breeding and philopatric males of neighboring groups, remains so far unknown but is currently under research. Breeding females had perforated vagina, were lactating, obviously pregnant and/or showed a body mass loss of >10 g within less than 2 weeks (indicating birth). During the non-breeding season, females were regarded as breeding females that had bred during the previous breeding season. Groups consisted of one breeding male, 1–4 breeding females and several philopatric adults of both sexes.

Blood collection

Mice emerge in the morning from their nest and bask as a group for about half an hour, before leaving alone to forage (Schradin et al., 2007). Blood samples were always collected during this morning period to control for possible circadian rhythms of hormone excretion. Mice were trapped at their nests during the morning shortly after they became active. Mice were anaesthetized with di-ethyl ether and a blood sample of about 250 µl was taken from the retro-orbital sinus. Corticosterone levels are known to rise quickly in rodents that are trapped (Fletcher and Bonnstra 2006), which is why samples had to be taken within 3 min to obtain basal levels (Romero and Reed 2005). Thus, traps were watched from a distance of 10 m and as soon as a mouse entered a trap, it was removed, anaesthetized and a blood sample was taken. In this way, samples could be collected within 1.5–3 min after mice entered traps. Time between catching and sampling did not effect corticosterone levels (see Results), meaning that samples were taken before a stress response occurred. Furthermore, breeding females that were sampled when traps were only checked after 45 min, showed a stress response with corticosterone levels about double as high as breeding females sampled as described above (Schradin, unpubl. data), indicating that I measured basal corticosterone levels in this study. Each morning, one nest was trapped. Additionally, some samples were obtained from traps checked after 45 min at a second nest. These samples were only used for testosterone measurements. Blood samples were left at room temperature for 1 hour and then centrifuged for 10 min. The resulting serum was pipetted and frozen in aliquots of 20 µl for corticosterone and 50 µl for testosterone at −15 °C at the research station in the field and at −20 °C at the University of Zurich. Mice seemed unaffected by blood sampling and readily re-entered traps, such that their eyes could be examined when trapped the next afternoon or morning, without any indication of damage found (see also Schradin and Pillay, 2004a).

The anesthetic, di-ethyl ether, can act as a stressor and affect corticosterone levels (Tohei et al., 1997; Raff et al., 2003). To determine the possible effects of di-ethyl ether on hormonal profiles, I compared corticosterone levels in ten captive male mice kept in Zurich (Switzerland), when they were anaesthetized with ether, and when they were anaesthetized with methoxyflurane (Medical Developments International limited, Springvale, Australia). Methoxyflurane was used as it could have been used without an evaporator in the field (in contrast to e.g. halothane) and there is no indication that it leads to an increase of corticosterone levels in laboratory mice (pers. commun. M. Arras, Institute for Laboratory Animal use, University of Zurich). The time period between the two samples was three days. Half of the individuals were first anaesthetized with ether, the other half with methoxyflurane. Males did not have higher corticosterone levels when anaesthetized with ether (221±53.7 ng/ml) than when anaesthetized with methoxyflurane (194±23.6 ng/ml; $p>0.9$, paired $t_9=0.083$).

Hormone assays: Testosterone was measured in a total of 194 samples from 81 females and 95 males. Corticosterone was measured in 147 samples of 65 females and 67 males. All samples were analyzed in the EIA laboratory of the Zoological Institute, University of Zurich. Commercial kits from IBL Hamburg were used for both hormones. Procedures were as stated in the kit manuals. However, due to very high corticosterone levels, samples were diluted 1:100. In some cases, the available sample volume for testosterone measurements were too small and had to be diluted 1:1 with the zero standard, the measured value then being multiplied by two before statistical analyses.

For both hormones, serial dilution of striped mouse sample pools (2 for each hormone) paralleled the standard curve and the slopes were not different. Intra- and inter-assay variability was determined with two pools from wild striped mice that had low and medium values of the hormones. Eight measurements were done for intra-assay and five for inter-assay variability. For corticosterone, intra-assay variability was 8.3 and 10.0% for the medium and low pool respectively. Inter-assay variability was 6.4 and 2.3%. For testosterone, intra-assay variability was 9.9 and 6.9% for the medium and low pool respectively. Inter-assay variability was 12.9 and 12.8%. Recovery of samples added to the standards curve was 95.9% for one corticosterone sample and 100.8% and 98.9% for two testosterone samples.

Statistical analysis

The software packages Instat 3.05 and SAS 9.1.3 were used. Data are presented as mean±SD. To explain corticosterone and testosterone levels, general linear mixed models (GLMM) were fitted to normal data using REML (SAS, proc MIXED). For both hormones, social class (philopatric male, philopatric female, breeding male or breeding male), season (breeding or non-breeding season) and whether or not mice carried a transmitter were entered as fixed categorical effects into the model, while the time it took to take the blood sample (in seconds) and body weight (in g) were entered as continuous covariates into the model. Individual identity was introduced as a random effect on the intercept as some animals were measured repeatedly. For testosterone, additionally trapping technique (whether traps were emptied immediately after capture or checked after 45 min) was included as a categorical fixed effect. For both testosterone and corticosterone, hormone data were log-transformed before analysis. In all GLMMs, residuals were accepted as being normally distributed when Shapiro–Wilk statistics yielded $p>0.05$. Error degrees of freedom (df) were calculated using the Satterthwaite method. Effects were tested using type III (simultaneous) modeling, i.e. in multiple effects models parameters for each independent variable are corrected for all other fixed effects in the model. Differences between the least square means (function LSMEANS in SAS) of multiple categories were compared posthoc using *t*-tests.

For each hormone, a second GLMM was done with the subset of the data for which the level of the other hormone was known as well. Thus, in a second model for corticosterone testosterone was used as an additional fixed effect, but with a lower total sample size ($N=108$ instead of $N=147$). For testosterone, in a second model corticosterone was included as fixed effect, but with a lower total sample size than in the first model ($N=148$ instead of $N=194$).

Results

Basal corticosterone serum levels

Basal corticosterone was not influenced by weight, age of individuals, time until the blood sample was taken (1.5 to 3.0 min) and whether or not mice were carrying transmitters (Table 1). Season, social class and their interaction were significant (Table 1). Breeding males had the lowest corticosterone values that were significantly different from philopatric males ($t_{115}=3.16$, $p=0.002$), philopatric females ($t_{113}=2.74$, $p=0.007$) and breeding females ($t_{115}=-5.04$, $p<0.0001$; Fig. 1). Philopatric males, philopatric females and breeding females did not differ in corticosterone levels (all $p>0.3$). Breeding males were the only social class that showed an increase of corticosterone levels from the breeding to the non-breeding season ($t_{111}=-3.91$, $p=0.0002$;

Table 1
General Linear Mixed Model explaining corticosterone values

Variable	DF	Den DF	*F* value	*p*
Weight	1	114	0.24	0.63
Age	1	114	0.70	0.40
Season	1	115	5.05	**0.027**
Time until blood was taken	1	103	1.18	0.28
Social class	3	113	8.62	**<0.0001**
Carrying a transmitter	1	85.2	0.00	0.96
Interaction season and social class	3	105	14.78	**<0.0001**

DF = degrees of freedom, Den DF = denominator degrees of freedom for *F*, calculated using the Satterthwaite method.

Table 2
General Linear Mixed Model explaining testosterone values

Variable	DF	Den DF	*F* value	*p*
Weight	1	148	0.87	0.35
Age	1	143	0.18	0.67
Season	1	152	23.39	**<0.0001**
Sampling technique	1	153	0.62	0.43
Time until blood was taken	1	153	0.05	0.82
Social class	3	143	7.63	**<0.0001**
Carrying a transmitter	1	145	2.48	0.12
Interaction season and social class	3	152	0.83	0.48

DF = degrees of freedom, Den DF = denominator degrees of freedom for *F*, calculated using the Satterthwaite method.

Fig. 1). In contrast, breeding females ($t_{79.8}=-3.27$, $p=0.0016$), philopatric males ($t_{108}=-3.721$, $p=0.0003$) and philopatric females ($t_{112}=-2.86$, $p=0.005$) showed a decrease from the breeding- to the non-breeding season (Fig. 1).

When using the sub-sample with available testosterone data for the final GLM used above including testosterone as a co-variable, results remained unchanged with season ($F_{1,90.7}=6.00$, $p=0.02$), social class ($F_{3,89.5}=6.53$, $p=0.0005$) and their interaction ($F_{3,81}=12.16$, $p<0.0001$) being the only significant variables. Testosterone had no effect on corticosterone levels ($F_{1,93.8}=0.36$, $p=0.55$).

Testosterone

Serum testosterone levels were not influenced by weight, age of individuals, the way of sampling (whether traps were emptied immediately after capture or checked after 45 min), time it took until the blood sample was taken and whether or not mice were carrying a transmitter (Table 2). Both season and social class had a significant effect, but their interaction was not significant (Table 2), as in all classes testosterone declined from the breeding to the non-breeding season (Fig. 2). Breeding males had significantly higher testosterone levels than philopatric males ($t_{136}=-3.13$, $p=0.002$), philopatric females ($t_{148}=-3.49$, $p=0.0006$) and breeding females ($t_{143}=4.45$, $p<0.0001$; Fig. 1). There was no difference in testosterone levels between philopatric males, philopatric females and breeding females (all $p>0.26$).

When using the sub-sample with available testosterone data for the final GLM used above including corticosterone as a co-variable, results remained unchanged with season ($F_{1,131}=19.50$, $p<0.0001$) and social class ($F_{3,124}=6.10$, $p=0.0007$) being the only significant variables. Corticosterone had no effect on testosterone levels ($F_{1,127}=0.26$, $p=0.61$).

Discussion

Both corticosterone and testosterone levels differed as a function of season and social class. Important co-factors such as age and body weight that potentially influence hormone levels in field studies could be ruled out. Thus, this study yielded important results regarding how changes in the physiology might help individual striped mice to meet seasonally changing energy demands in the Succulent Karoo desert.

Exclusion of co-factors as an explanation of variation in hormone levels

Hormone levels in wild ranging animals can be influenced by a wide range of factors. In this study, I could include many co-variables. Neither carrying a transmitter nor age and weight

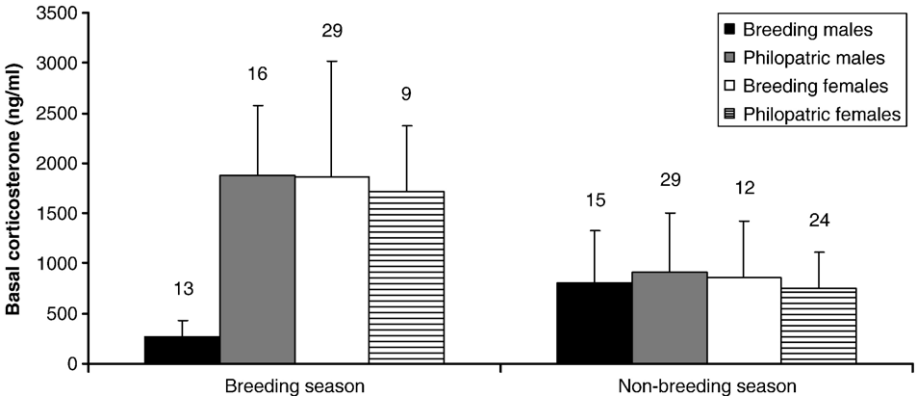

Fig. 1. Basal serum corticosterone levels during the breeding season (left) and the non-breeding season (right) in breeding and philopatric non-breeding males and females. Means ± SD are shown, samples sizes above bars. During the breeding season, breeding males had significantly lower corticosterone values than all other social classes ($p<0.007$), but this difference disappeared during the non-breeding season, when breeding males showed a significant increase ($p=0.0002$) and all other classes a significant decrease of corticosterone values ($p\leq0.005$).

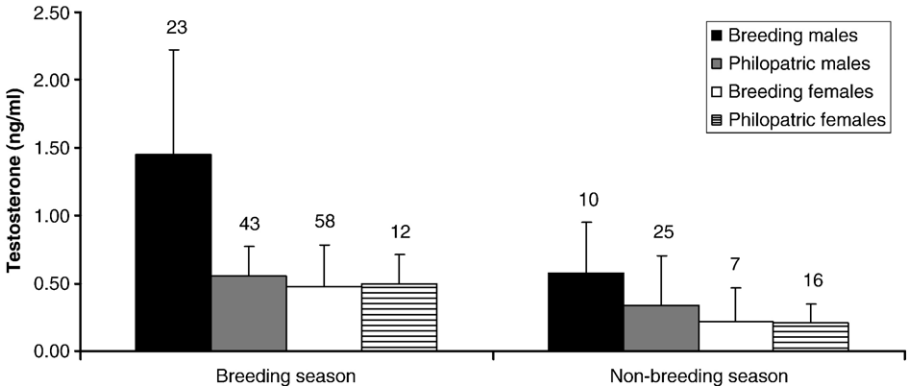

Fig. 2. Testosterone serum levels during the breeding season (left) and the non-breeding season (right) in breeding and philopatric non-breeding males and females. Means ± SD are shown, samples sizes above bars. Breeding males had significantly higher testosterone levels than all other classes ($p \leq 0.002$), which did not differ from each other. Testosterone declined significantly from the breeding to the non-breeding season ($p < 0.0001$).

influenced hormone levels. This might be surprising, as e.g. breeding males differed from philopatric males significantly in hormone levels and in both age and body mass. However, the range of body mass and age was high for both social categories (breeding males: 6–19months, 49–87 g; philopatric males 1–7.5months, 21–66 g) and the analysis, correcting for the effect of social category, did not find an effect of age or body mass within social categories. Importantly, I collected blood samples in a time period short enough to avoid a stress response, thus measuring basal hormone levels. Furthermore, whether mice were sampled immediately or whether traps were only checked after 45 min did not influence testosterone levels, which is in contrast to other studies (Boonstra et al., 2001; Place and Kenagy, 2000).

Glucocorticoid levels: influences of social class and season

Corticosterone levels were about 50% lower during the non-breeding season in females that bred during the previous breeding season (breeding females). This is in accordance with the hypothesis that lactation and pregnancy are energetically demanding for female mammals. However, in my study, non-breeders of both sexes had the same corticosterone levels as breeding females. This result could be explained in two alternative ways. 1. Glucocorticoid levels are increased during the breeding season in all three classes due to reasons independent of breeding, for example due to the increased food availability. 2. Breeding females have increased corticosterone levels for other reasons than philopatric males and females. Breeding females could have a higher energy demand due to the costs of breeding while philopatric individuals could be permanently stressed. Group living in striped mice is mainly due to a high populations density, making dispersal and obtaining their own breeding territory impossible for young adult males and females (Schradin, 2005). Being forced to stay at home and abstain from breeding until the next breeding season could be extremely stressful. Once the breeding season is over, this stressor disappears, as breeding is impossible, and glucocorticoid levels could decrease to normal basal levels.

The striped mouse is a cooperatively breeding species and philopatric individuals of both sexes act as helpers at the nest, participating in nest defense, nest building and allo-parental care (Schradin and Pillay, 2004b). In most cooperatively breeding species, breeders have higher glucocorticoid levels than helpers, probably because breeders are dominant and suppress helpers (Creel et al., 1996; Sands and Creel, 2004). This is apparently not the case in the striped mouse, since breeding males had the lowest glucocorticoid levels and helpers did not differ from breeding females. In contrast to species with a clear dominance hierarchy, the striped mouse is egalitarian and there is no indication that breeders dominate helpers nor that a dominance hierarchy exists (Schradin and Pillay, 2004b). If increased glucocorticoid levels in breeders of cooperatively breeding species are due to social dominance, one would expect this effect to occur only in despotic and not in egalitarian species. Thus, the absence of increased glucocorticoid levels in breeders of the egalitarian cooperatively breeding striped mouse supports the hypothesis that increased glucocorticoid levels in breeders of cooperatively breeding species are a result of social stress.

My study demonstrates the importance of including both sexes and different social classes into one study. Looking at the data of breeding males alone, one could conclude that they are more stressed and have increased glucocorticoid levels during the non-breeding season, maybe due to food shortage. However, when comparing them to other social classes it becomes clear that their non-breeding glucocorticoid levels are not abnormally high, but instead they show remarkably low levels during the breeding season. Interestingly, breeding males were also the only class that showed an increase of corticosterone levels from the breeding to the non-breeding season. As a result, breeding males had similar corticosterone levels during the non-breeding season when compared to all other classes. This indicates that the corticosterone secretion of breeding males differed significantly from other individuals.

Testosterone levels: influences of social class and season

While breeding males had by far the lowest corticosterone levels during the breeding season, they also had the highest testosterone levels. As both glucocorticoids and androgens are known to increase the availability of energy for the organism (Baum, 1992; Wikelski and Ricklefs, 2001), it is possible that

the high testosterone levels are sufficient to increase metabolism during the breeding season. Thus, in contrast to the other social classes, breeding males might not need an increase of basal corticosterone levels. Another explanation could be that testosterone has an inhibitory effect on corticosterone secretion (Place and Kenagy, 2000) which would also explain why breeding males are the only social class that show an increase instead of decrease of corticosterone levels from the breeding to the non-breeding season, when testosterone levels decline (for a similar effect in *Octodon degu* see Soto-Gamboa et al., 2005). However, I did not find a significant influence of testosterone on corticosterone in my analysis, weakening support for this hypothesis. But if testosterone has only an inhibitory effect over a certain threshold level that is only achieved in breeding males, the statistical power (sample size) of this study might have been too low. An experimental study under standardized laboratory conditions would be needed to test the hypothesis that testosterone inhibits corticosterone levels in striped mice.

Breeding male mammals often show an increase of testosterone levels during the breeding season (Lynch et al., 2002; Place and Kenagy, 2000) and I found the same for the striped mouse. In species where breeding is associated with high male–male competition this can be explained by the challenge hypothesis (Wingfield et al., 1990) and testosterone is often increased in association with territorial aggression (Archawaranon and Wiley, 1988; Marler and Moore, 1988). Breeding striped mouse males are territorial (Schradin, 2004) and patrol territory boundaries (Schradin, 2006). Thus, testosterone correlates positively with male aggression in the striped mouse, but whether testosterone increases male aggression, or whether male aggression increases testosterone levels is unknown (Wingfield, 2005).

In this study, female breeders had relatively high testosterone values, comparable to the ones of philopatric males and females. Breeding females and helpers showed a significant decrease from the breeding to the non-breeding season. Testosterone might not be the most important androgen in female rodents (Degtyar and Kushlinskii, 2000), but my study provides further evidence that testosterone plays an also important role in female physiology (Staub and Beer, 1997).

Conclusions

There were three important findings of this study, 1. The physiology of breeding males reacted differently compared to three other social classes and cannot be interpreted without reference to the other classes. 2. There was no clear association between high glucocorticoid levels and breeding as found in many other species. 3. In this egalitarian cooperatively breeding species, breeders did not have higher glucocorticoid levels than helpers, which support the hypothesis that in despotic cooperative breeders, increased glucocorticoid levels might be due to social dominance. The non-specialized striped mouse demonstrated physiological plasticity that is likely to enable it to survive in the Succulent Karoo desert and meet changing energy demands and seasonal changes in energy availability. While the data presented in this study are correlative and need careful discussion, they provide biological meaningful hypothesis and thus open the avenue for experimental testing under laboratory conditions that mimic the natural situation.

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