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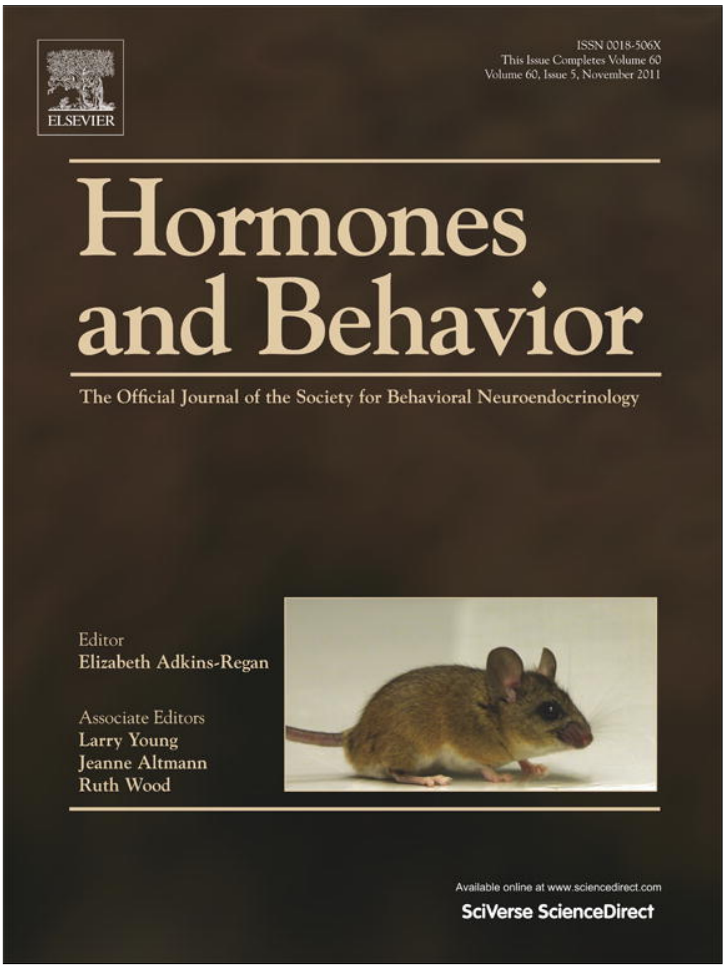

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Hormone levels of male African striped mice change as they switch between alternative reproductive tactics

Carsten Schradin *, Chi-Hang Yuen

Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

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ABSTRACT

Alternative reproductive tactics occur when individuals of the same species follow alternative ways to maximize reproductive success. Often younger and smaller males follow tactics that result in lower fitness than that of dominant larger males. The relative plasticity hypothesis predicts that hormone levels change as males change tactics, but direct tests of this hypothesis are missing. It has been demonstrated in a number of studies that males following different tactics also differ in hormone levels (unpaired data), but not that individual males change their hormone levels as they change tactic (paired data). We compared hormone levels in the same individuals before and after they changed their tactic, using field samples collected over a period of 6 years. We studied male striped mice (*Rhabdomys pumilio*) following three alternative reproductive tactics: 1. alloparental philopatric males; 2. solitary roaming males, and 3. group-living dominant breeders. Testosterone levels increased and corticosterone levels decreased when philopatric males became roamers or breeders. The increase in testosterone levels tended to be higher in philopatric males that became roamers than in philopatric males that became breeders. Testosterone levels decreased when roamers became breeders. Prolactin levels increased when males of any other tactic became breeders. Thus, males significantly changed their hormone profiles as they changed tactics. These results are in agreement with the hypothesis that changes in hormone levels are associated with the switch from one alternative reproductive tactic to another.

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Introduction

Males can differ in the way they maximize their reproductive success, using so called alternative reproductive tactics (ARTs; Taborsky et al., 2008). ARTs can be fixed for life, or they can be plastic with individuals being able to switch between tactics (Gross, 1996). Plastic tactics are found particularly in species with single strategies where all males follow similar decision rules (Schradin and Lindholm, 2011). In such species, tactics often differ in their fitness payoffs, with the tactic chosen being dependent on individual and environmental conditions (Schradin and Lindholm, 2011). The most competitive individuals follow the tactic that yields the greatest fitness payoff, called the bourgeois tactic. Less competitive males, which are often smaller and younger than the bourgeois males, make the best of a bad job (Dawkins, 1980) by following an alternative tactic with low reproductive success (often called the sneaker or satellite tactic) but are able to change to the bourgeois tactic when they grow larger (Gross, 1996; Schradin et al, 2009a).

The relative plasticity hypothesis predicts that plastic tactics are regulated by activational hormonal effects, meaning that changes in hormone levels cause a switch in tactic (Moore et al., 1998). In many species with male ARTs, individuals using different tactics differ in their hormone levels. For example, bourgeois males often have higher androgen levels, which might be an important proximate mechanism leading to their high dominance status (Oliveira et al., 2008). Differences between males of different tactics have also been observed for glucocorticoids (Oliveira et al., 2008), which are important to cope with stress and regulate metabolism (Reeder and Kramer, 2005). However, for glucocorticoids the pattern is less clear. In some species bourgeois males have higher glucocorticoid levels than males of a subdominant tactic, while in other species bourgeois males have lower levels. This difference might depend on whether it is more stressful to occupy a dominant or a subordinate rank (Creel, 2001). Differences between males of alternative tactics have also been reported for the protein hormone prolactin (Schradin, 2008a). Prolactin is a hormone important for the regulation of paternal (and maternal) care (Schradin and Anzenberger, 1999; Wynne-Edwards and Reburn, 2000) and if tactics differ in the amount of paternal care shown, prolactin levels might be higher in the paternal than the non-paternal tactic.

Hormone levels have been studied in more than fifty vertebrate species with plastic male ARTs, including fish, amphibians, reptiles, birds and mammals (reviewed in Oliveira et al.(2008)). However, to

* Corresponding author at: Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland. Fax: +41 44 635 5490.
E-mail address: carsten.schradin@ieu.uzh.ch (C. Schradin).

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our knowledge, all these studies compared between males of two different tactics (unpaired data of two categories). So far no investigators have measured hormone levels of the same individuals, before and after they changed their tactic. There is high variation in hormone levels between individuals of one population, even for individuals that belong to the same social category (e.g. breeding males; Kempenaers et al., 2008), but this phenomenon is ignored in studies using unpaired data (Eikenaar et al., 2011). However, this variation can have important consequences, and if studies (or theories) want to conclude that animals change their hormone profile from one life history stage to another, it is important to prove that this change occurs in individuals. For example the challenge hypothesis predicts a decrease in testosterone levels in parental male birds from the period of egg laying to the period of parental care (Wingfield et al., 1990) and this hypothesis has been supported in numerous studies using unpaired data (Hirschenhauser and Oliveira, 2006). In contrast, the first study using paired data failed to demonstrate a decrease in testosterone levels in individual males (Eikenaar et al., 2011). In field studies, it is much easier to sample several males of two different tactics, than to follow individual males and sample them before and after tactic change. For this, long-term field studies would be beneficial to demonstrate that tactic change is associated with a change in hormone levels.

In the present study, we compared hormone levels in individual males before and after they changed their reproductive tactic. Over 6 years we studied male striped mice (*Rhabdomys pumilio*) that can switch between three ARTs (Schradin et al., 2009a). In previous studies using unpaired data it was found that males using the three tactics differ in hormone levels (Schradin, 2008a; Schradin et al., 2009a): 1. group-living philopatric males have low testosterone and low prolactin levels, but high basal corticosterone levels; 2. solitary roaming males have high testosterone but low basal corticosterone and low prolactin levels; and 3. group-living territorial breeding males have low basal corticosterone, intermediate testosterone and high prolactin levels. Striped mouse males have plastic tactics and a single individual can engage in all three tactics during different parts of its life, males switching from philopatric to roaming to breeding male (Schradin et al., 2009a), and in very few cases back from breeding to roaming male (Schradin, unpubl. data).

While we know that males using different tactics differ in hormone levels (Schradin et al., 2009a), it remains to be shown that males change their hormonal profile when changing tactics. For example roamers have a higher mean value of testosterone levels than breeders, but there is significant variation of testosterone level in each tactic and overlap between tactics (not all roamers have higher testosterone levels than all breeders; Schradin, 2008a; Schradin et al., 2009a). It is possible that males with higher testosterone levels are more likely to remain roamers instead of roamers decreasing their testosterone levels when becoming breeders. Furthermore, males with lower testosterone levels might remain philopatric longer than males with higher testosterone levels, leading to a lower mean for the philopatric tactic. This would be an alternative hypothesis explaining low mean testosterone levels in philopatric males (alternative to philopatric males increasing their testosterone levels when switching tactics). Similar scenarios might exist for other species in which the hormonal correlates of alternative reproductive tactics have been studied, but these alternative explanations were not considered. In sum, it is important to demonstrate that individual males change their hormonal profile and not only that different classes of male tactics differ in hormone levels (see also Eikenaar et al., 2011).

We tested whether hormone levels of individual males changed after they changed their tactics, in the ways as suggested by a previous study using unpaired data (Schradin et al., 2009a). For philopatric males, corticosterone levels were expected to decrease and testosterone levels to increase when becoming roamers. The same changes were expected when philopatric males become breeders, though it was expected that the increase in testosterone would be more moderate. Additionally, an increase in prolactin levels was predicted. For roamers, testosterone levels were predicted to decrease and prolactin levels to increase when becoming breeders.

Methods

Study area and period

The study was conducted in Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60) during the breeding seasons of 6 years (June to December from 2005 to 2010) to collect sufficient blood samples of males that changed tactics. For analysis we defined two breeding stages. Stage 1: onset of breeding in June to September, which also represents the colder and wetter period. Stage 2: period of pup raising from October to December, which also represents the warmer and drier period.

The vegetation type is semi-arid Succulent Karoo with an average rainfall of 160 mm p.a. Animal ethical clearance was provided by the University of the Witwatersrand, Johannesburg, South Africa (no. 2004/87/2A, 2005/82/4, and 2006/3/03).

Study species

Breeding males represent a bourgeois tactic with the highest reproductive success, philopatric males have the lowest reproductive success, while roamers have low success when population density is high, but similar success to territorial breeders when population density is low (Schradin and Lindholm, 2011). In years with high population density, breeders have 10 times higher reproductive success than roamers, and 100 times higher reproductive success than philopatrics (Schradin and Lindholm, 2011). It is important to note that some philopatrics are successful in obtaining reproductive success (Schradin and Lindholm, 2011) as has been reported for helping males in other species (Double and Cockburn, 2003; Young et al., 2007). Helping is typically regarded as an alternative reproductive tactic (Oliveira et al., 2008). Relative body mass appears to determine tactic as philopatric males are small, roaming males are intermediate in mass, and territorial breeders are the heaviest (Schradin et al., 2009a). Males typically remain as adult philopatrics in their natal group in the year they are born (Schradin et al., 2009a). Large philopatric males might take over the breeding position of neighboring groups if this becomes vacant any time of the year. With the onset of the next breeding season, males can either remain philopatric or disperse, becoming roamers. Roamers try to become the breeding male of a group of communally breeding females, if such groups exist (under high population density, while females breed solitarily under low population density; Schradin and Lindholm, 2011).

While it is very difficult to obtain direct measurements of (allo-) parental care from nests in the field (but see pup-retrieval experiments described in Schradin and Pillay(2003)), we know from captive studies that breeding males show similar levels of parental care as females (Schradin and Pillay, 2003; Schubert et al., 2009). Philopatric males show similar levels of alloparental care as breeders show paternal care (Schradin, unpubl. data). In contrast, roamers do not show parental care as they are not associated with breeding females and their pups. Physical contact with pups does not seem to influence prolactin levels in striped mice (Schradin and Pillay, 2004a) nor in other paternal mammal species (Schradin and Anzenberger, 2002).

Trapping, marking and radio-tracking of striped mice

All methods followed standard protocol and have been used successfully since 2001. Trapping was done around nesting sites, at least three days per month, as described elsewhere (Schradin and Pillay, 2004b). Trapped striped mice were weighed, sexed, and permanently marked with numbered ear tags (National Band and Tag

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Co., USA) and temporarily with hair dye (Rapido, Pinetown, South Africa) for individual recognition during behavioral observations (Schradin and Pillay, 2004b). All solitary living individuals and 1 to 4 striped mice from each group were fitted with radio-collars (Holohil, Canada) and were radio-tracked as described elsewhere to determine the sleeping sites and home ranges (Schradin and Pillay, 2006). Carrying a radio-collar does not affect corticosterone levels or behavior (Schradin, 2008b). All nests at the field site were observed for 2 days at least every second week to determine individual group affiliation and first emergence of pups (Schradin and Pillay, 2004b).

Male reproductive tactics and change in tactics

Male tactics were determined by a combination of trapping, behavioral observations and radio-tracking (Schradin and Lindholm, 2011; Schradin et al., 2009a). Young adult males that were trapped as juveniles (<30 g) at a nest and continuously observed there (more than 70% of observations) but not at other nests were regarded as philopatric males. Adult males that were associated with a group of females that was not their natal group were regarded as breeding males. There was always only a single breeding male per group. Males that were living away from their natal nest and did not share nesting sites with any other mice (determined by radio-tracking) were regarded as roaming males. When a philopatric male left his natal group, he was either categorized as a solitary living roaming male or as a breeding male once he had joined another group. When a roaming male joined a group of females, he was regarded as the new breeding male of this group.

Blood collection

Blood samples were collected at nests during the morning within 45 min after the mice became active, to control for possible circadian rhythms of hormone excretion. Traps were observed from a distance of 10 m. As soon as a mouse was trapped, it was removed, anaesthetized and a sample was taken within 3 min from the sub-lingual vein (Heimann et al., 2009), which is the preferred method of blood sampling in small mammals from the Swiss National Veterinarian Department. Striped mice recovered soon after the sampling, but were kept for 15–40 min in a trap with food, before being released at the place of capture. This was also done to avoid striped mice re-entering the traps. Blood samples were allowed to clot for 1 h, centrifuged, and the resulting serum was frozen in aliquots.

Hormone assays

All samples were analyzed in our EIA laboratory at the University of Zurich. Prolactin was measured using a kit from SPIbio, testosterone and corticosterone with kits from IBL Hamburg. Procedures were as stated in the kit manuals. However, due to very high corticosterone levels, samples were diluted 1:50. Serial dilution of striped mouse sample pools (2 for each hormone) paralleled the standard curve and the slopes were not different (see Schradin, 2008a, 2008b). Intra-assay variability was determined with serum pools from wild striped mice. Coefficient for intra-assay variation for prolactin was 10.4%, for testosterone 3.3% and for corticosterone 6.0%.

Statistical analysis

Data are presented as mean ± standard deviations. Paired comparisons were done using the Wilcoxon test (T) and p-values were one-tailed, as from previous studies we had one-sided predictions for the expected effects. Since not enough serum was available for all males for all hormone measurements, sample sizes differ between comparisons. Altogether we analyzed 73 samples from 28 males. Thirty-two samples were measured for prolactin, 65 samples for corticosterone, and 69 samples for testosterone. Twenty-six samples were from philopatric males, 23 from roamers, and 27 from breeding males. If a male was sampled more than once during the same tactic, the mean value was used.

Results

Breeding stage when males were sampled

The ratio of samples collected during breeding stage 1 *vs.* breeding stage 2 was 11:14 for philopatric males, 16: 6 for roaming males and 16:10 for breeding males. The ratio of samples collected during breeding stage 1 to breeding stage 2 did not differ between any of the three tactics (Fisher's Exact test; philopatrics: breeders, $p = 0.27$; philopatrics: roamers, $p = 0.08$; roamers: breeders, $p = 0.54$).

Philopatric males that became roamers

Prolactin levels did not change (7.0 ± 8.6 ng/ml *vs.* 7.0 ± 10.4 ng/ml; $p = 0.50$, $T = 7$, $N = 5$). Corticosterone levels decreased significantly (629.7 ± 379.1 ng/ml *vs.* 335.1 ± 108.6 ng/ml; $p = 0.004$, $T = 1$, $N = 9$). Testosterone levels increased significantly (0.6 ± 0.3 ng/ml *vs.* 2.70 ± 2.4 ng/ml; $p = 0.001$, $T = 0$, $N = 10$) (Fig. 1).

Philopatric males that became breeders

Prolactin levels increased significantly (8.9 ± 7.2 ng/ml *vs.* 26.1 ± 19.9 ng/ml; $p = 0.0005$, $T = 0$, $N = 11$). Corticosterone levels decreased significantly (1127.3 ± 794.2 ng/ml *vs.* 357.0 ± 235.6 ng/ml; $p = 0.002$, $T = 7$, $N = 13$). Testosterone levels increased significantly (0.4 ± 0.3 ng/ml *vs.* 1.4 ± 0.8 ng/ml; $p = 0.002$, $T = 6$, $N = 13$) (Fig. 2).

Comparison when philopatric males became roamers or breeders

Testosterone levels tended to increase more when philopatric males became roamers than when philopatric males became breeders (increase of 2.1 ± 2.2 ng/ml, $N = 10$ *vs.* 1.0 ± 1.0 ng/ml, $N = 13$; $p = 0.06$, $U = 39.50$, Mann–Whitney U-Test).

Roamers that became breeders

Prolactin levels increased significantly (2.90 ± 2.4 ng/ml *vs.* 29.9 ± 22.5 ng/ml; $p = 0.03$, $T = 0$, $N = 5$). There was no statistical difference for corticosterone levels (276.6 ± 145.5 ng/ml *vs.* 402.2 ± 286.6 ng/ml; $p = 0.23$, $T = 12$, $N = 8$). Testosterone levels decreased significantly (2.9 ± 2.8 ng/ml *vs.* 1.1 ± 0.8 ng/ml; $p = 0.03$, $T = 6$, $N = 9$) (Fig. 3).

Discussion

The relative plasticity hypothesis states that changes of reproductive tactics will be associated with changes in steroid hormone levels (Moore et al., 1998). Numerous previous studies demonstrated that males of alternative reproductive tactics do differ in hormone levels (Moore et al., 1998; Oliveira et al., 2008), but we know of none that showed that hormone levels change in individual males when they change their tactic. Ours is the first study demonstrating that hormone levels changed as individuals changed their reproductive tactic.

When comparing the hormone levels of two different categories, e.g. males of two alternative reproductive tactics or two different life history stages, it is difficult to conclude that the observed differences in hormone levels are directly related to differences in behavior (Eikenaar et al., 2011). This is because of the high variation in endogenous hormone levels between individuals of the same social category within a single population (Kempenaers et al., 2008). For example, striped mouse males show high intra-specific variation in

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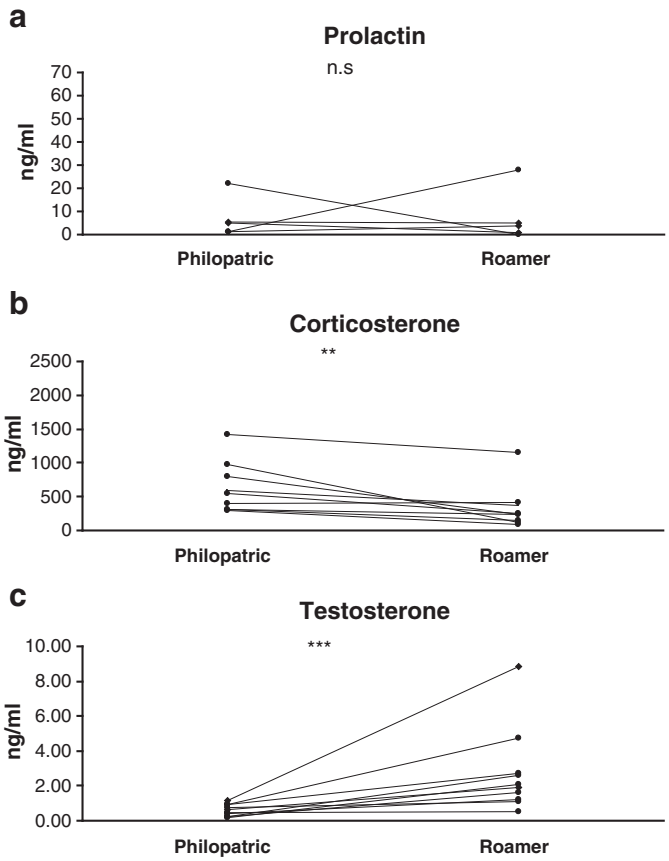

Fig. 1. Changes in hormone levels of philopatric males that became roamers. Data of each male are connected by a line. (a) Prolactin, (b) corticosterone, and (c) testosterone. n.s. not significant; *p<0.05; ** p<0.01; *** p<0.001.

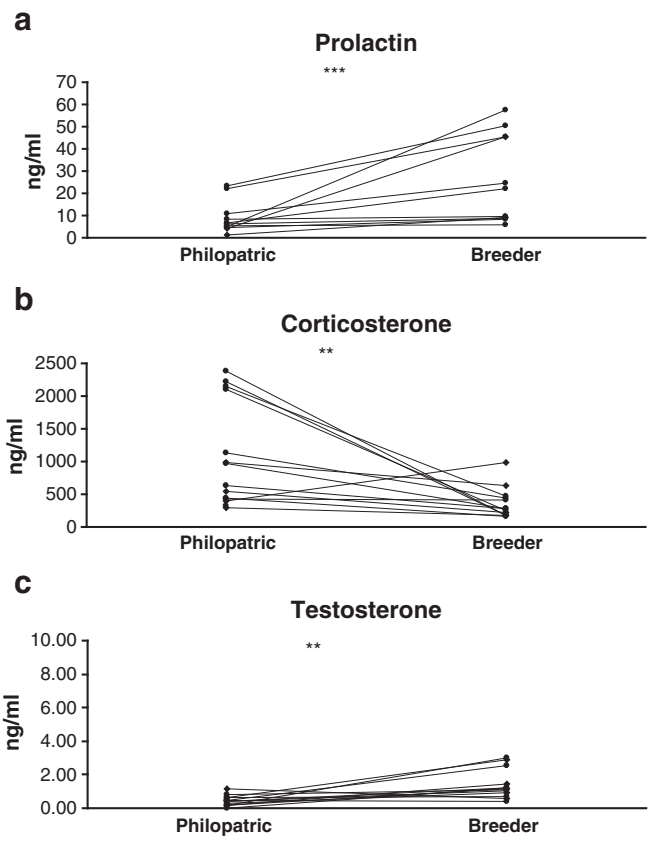

Fig. 2. Changes in hormone levels of philopatric males that became breeders. Data of each male are connected by a line. (a) Prolactin, (b) corticosterone, and (c) testosterone. n.s. not significant; *p<0.05; ** p<0.01; *** p<0.001.

testosterone levels even within the same tactics and the (traditional) conclusion was that males of different tactics differ in hormone levels because hormone secretion changes when males change tactics (see Fig. 5 in Schradin et al.(2009a)). However, alternative explanations are possible: if philopatric males with higher testosterone levels disperse and change their tactic at an earlier age than philopatric males with lower testosterone levels, this alone could explain why philopatric males have lower mean value of testosterone levels than roamers. In this alternative scenario, hormone levels of individual males would not change, and the switch between tactics would not be regulated by an increase of testosterone levels. Instead, the high levels already present in some philopatric males would have led to an earlier switch, such that males with high testosterone levels are overrepresented in the roamer category. This is why it is not sufficient to demonstrate categorical differences in hormone levels between males of ARTs (see also Eikenaar et al., 2011). We additionally need to demonstrate that individual males do in fact change their hormonal profile when changing tactics. Together with studies using experimental hormone manipulations that led to change in tactics (Oliveira et al., 2001; Wikelski et al., 2004) this gives further support to the hypothesis that hormones are the proximate factors regulating the expression of ARTs.

Variation in hormone levels can be due to a wide variety of factors, reproductive tactic being only one of them. In the current study, we could not include these factors as co-variables in the statistical analyses, due to small sample sizes. However, we controlled such factors as much as possible, for example by collecting samples for each of the three tactics both at the start of the breeding season when it is moist and cold and at the end of the breeding season, when it is warm and dry. Further, all samples were collected in the morning at nests soon after mice became active, controlling for a potential circadian rhythm

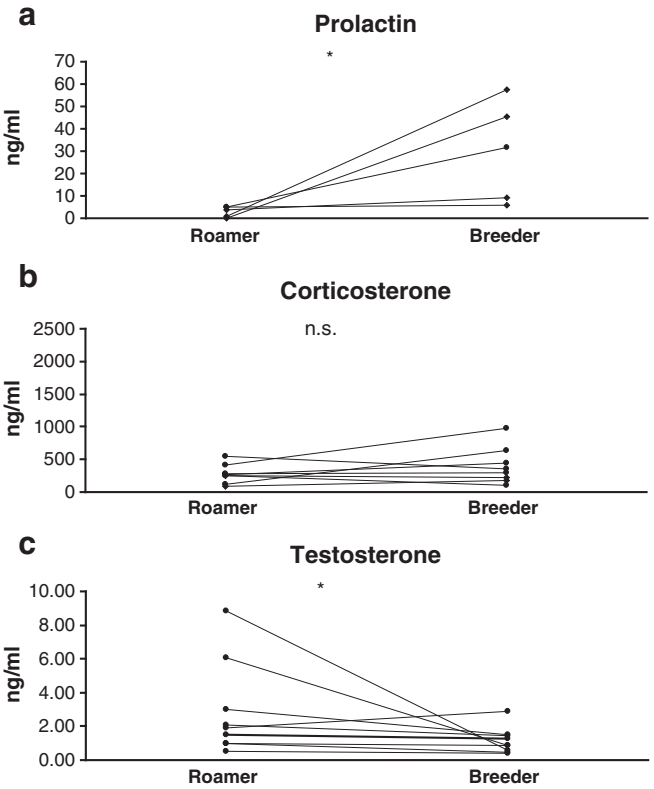

Fig. 3. Changes in hormone levels of roaming males that became breeders. Data of each male are connected by a line. (a) Prolactin, (b) corticosterone, and (c) testosterone. n.s. not significant; *p<0.05; ** p<0.01; *** p<0.001.

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of hormone secretion. In a previous study on the same study population with a sample size much higher than in the present study, we controlled for age and body mass of males, which did not have a significant influence on hormone levels (Schradin, 2008b). As confounding variables would make it rather more difficult than easier to find differences in hormone levels, the most parsimonious explanation for our data is that hormone secretion changed after males changed their tactic.

Androgens, such as testosterone, regulate spermatogenesis and sexual behavior (Wingfield et al., 1990). Philopatric striped mouse males are reproductively suppressed by the breeding male of the group (Schradin et al., 2009b). They have high levels of the stress hormone corticosterone, which might be the proximate mechanisms leading to lower testosterone levels, smaller testes and lower sperm counts when compared to singly housed males (Schradin et al., 2009b). In the present study, we demonstrated that corticosterone levels decreased and testosterone levels increased after philopatric males switched tactic. Interestingly, philopatric males that switched to breeders tended to have a comparatively lower increase in testosterone levels than philopatric males that became roamers, and testosterone levels decreased in males that switched from roamer to breeder. This supports a previous study that roamers have higher testosterone levels than the bourgeois breeders (Schradin et al., 2009a). Our results are in contrast to most other species with male ARTs where the bourgeois males have the highest androgen levels (Moore et al., 1998). There might be a trade-off between testosterone driven aggressive behavior and amicable behavior towards other group members for breeding males that does not exist for roamers (Schradin et al., 2009a). High testosterone levels found in roamers might also promote risky behavior such as invading territories defended by breeders. In stoplight parrotfish, androgen levels of bachelor males increase after they became territorial due to an increase of territorial encounters (Cardwell and Liley, 1991) and high testosterone levels in roaming striped mouse males could be a consequence of frequent encounters with territorial males (Wingfield et al., 1990).

The relative plasticity hypothesis makes predictions only regarding steroid hormones, but protein hormones might also be important. The protein hormone prolactin is known to regulate parental care (Schradin and Anzenberger, 1999), and the three ARTs of male striped mice differ in the amount of paternal care (Schradin and Pillay, 2003), with paternal breeders having higher prolactin levels than non-paternal roamers and alloparental philopatric males (Schradin, 2008a). Accordingly, we found that prolactin levels increased both in philopatric and in roaming males when they became paternal breeders. This is in agreement with other studies on paternal mammals where prolactin levels increased when males became fathers (Wynne-Edwards, 2001).

We demonstrated that males change their hormone levels when switching tactics, which is in agreement with the relative plasticity hypothesis. However, more data are necessary to differentiate between the hypothesis that changes in hormone levels led to change in tactics, and the alternative hypothesis that tactic change influences hormone levels. It is well known that hormones can influence behavior, but behavior also influences hormone levels, and both processes are likely to play a role. It is likely that changes in hormone levels influence the choice of tactics, especially the decision to leave their natal group, disperse and to become a roamer. Our study shows that the entire hormone profile of individual males changes as they change tactics.

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