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

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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.

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

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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