

Differences in prolactin levels between three alternative male reproductive tactics in striped mice (*Rhabdomys pumilio*)

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In male fishes, birds and mammals, increased prolactin secretion is thought to play a role in species showing paternal behaviours. This hypothesis was investigated in the striped mouse (*Rhabdomys pumilio*). This paper compares serum prolactin levels in 71 free-living male striped mice following three different reproductive tactics: (i) paternal group-living breeders, (ii) alloparental philopatric group-living males, and (iii) roaming non-paternal solitary males. Prolactin levels of breeding males were significantly higher than that of roamers. Alloparental philopatric males had low prolactin levels, which concur with studies of cooperatively breeding mammals, but contrasts with studies of cooperatively breeding birds. Both breeding males and females showed a decrease in prolactin levels after the breeding season, but not alloparental philopatric males. Prolactin levels were correlated with neither corticosterone levels nor age. These results are in agreement with the hypothesis that prolactin is one proximate mechanism of male reproductive tactics, possibly regulating differences in male parental care.

Keywords: paternal care; seasonal; roaming; helper

1. INTRODUCTION

Social flexibility, such as multiple reproductive tactics within one sex and species, is often regarded as an individualized adaptation to specific ecological conditions (Gross 1996). The proximate mechanisms of social flexibility are largely unknown, but hormones are thought to play an important role because their secretion can change within a relatively short period of time. Hormones can modulate behaviour by acting in the brain (Arnold & Breedlove 1985; Buntin 1996) and individuals of the same species and sex can differ remarkably in hormone levels (Moore 1991; Gross 1996). For example, the steroid hormones, progesterone, testosterone and corticosterone, are known to regulate different male reproductive tactics in tree lizards (*Urosaurus ornatus*), especially influencing territorial and aggressive behaviour (Moore *et al.* 1998; Knapp *et al.* 2003). Therefore, hormones that are known to regulate social behaviour might differ between individuals that are of the same sex and species but follow different social and/or reproductive tactics. One such hormone is the pituitary hormone prolactin. Prolactin is a protein hormone that can cross the blood–brain barrier and act directly in the brain (Walsh *et al.* 1990; Pihoker *et al.* 1993). Species differences in paternal care are correlated with differences in prolactin secretion, with non-paternal species showing no increase in prolactin levels while paternal species do (Schradin & Anzenberger 1999). The question arises whether differences in reproductive tactics within a single species including

differences in caring behaviour also correlate with differences in prolactin levels, which might then be one of several mechanisms of social flexibility.

In contrast to birds (Buntin 1996), few studies have measured prolactin in free-ranging mammals, though captive studies demonstrated a correlation between prolactin and paternal care (Wynne-Edwards 2001). In one field study, increased prolactin levels were found in male meerkat (*Suricata suricatta*) helpers that were babysitting (Carlson *et al.* 2006a). In the same study population, male meerkats that were willing to feed pups had higher prolactin levels than males that did not (Carlson *et al.* 2006b). However, meerkats that were feeding pups also had higher glucocorticoid levels, and in a multivariate analysis it became apparent that pup feeding was mainly related to the glucocorticoid cortisol, not to prolactin (Carlson *et al.* 2006b). Prolactin secretion can be stress responsive (e.g. Aidara *et al.* 1981; Ziegler *et al.* 1996) and prolactin levels can correlate positively with glucocorticoid levels (cortisol or corticosterone; Carlson *et al.* 2006b). Thus, it is important to rule out a simple stress response when studying the relationship between prolactin and social behaviour, which is most easily performed by measuring glucocorticoids at the same time (Ziegler *et al.* 1996; Carlson *et al.* 2006b).

While field studies compared prolactin levels between breeders and helpers in social groups (Vleck *et al.* 1991; Schoech *et al.* 1996; Carlson *et al.* 2003), no comparisons are available between sociable group-living and solitary individuals of the same species. This study compares prolactin levels among three different male classes of a socially flexible mammal, the striped mouse (*Rhabdomys pumilio*; diurnal, 30–80 g). In captivity, paternal striped

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mouse males do not differ in prolactin levels from solitarily kept males (Schradin & Pillay 2004a), but, in this study, males were simply kept under different social conditions but not tested for differences in paternal behaviour. Therefore, it is important to test for differences in hormone levels between males that naturally differ in parental behaviour under natural conditions (Schradin 2007). Male striped mice have a conditional strategy with three different male tactics (defined after Gross 1996): (i) group-living paternal breeders, (ii) group-living alloparental philopatric males, and (iii) solitary roaming non-paternal males (Schradin & Pillay 2004b, 2005). Striped mouse males show behavioural plasticity: a single individual can follow all the three tactics during different parts of its life. Which male tactic is chosen appears to be influenced by population density (Schradin 2005): when population density is very high (30 striped mice ha^{-1} at the start of the breeding season), all males older than 1 year become paternal group-living males and all young adult males remain philopatric; while under low population density (one striped mouse ha^{-1}), all males older than 1 year become roamers, while approximately 50% of the young adult males become roamers and 50% remain philopatric (C. Schradin 2007, unpublished data). This study took place under medium population density, when all the three tactics occurred in the population. Female breeders were included in the study as a control group, which was expected to have the highest prolactin levels due to pregnancy and lactation (Nicoll 1974). It was expected that paternal breeding males would have higher prolactin levels than non-paternal roamers (Schradin & Anzenberger 1999; Wynne-Edwards 2001). While in birds, helpers typically show an increase in prolactin levels, there is little evidence for this effect in mammals (Ziegler *et al.* 1996; Schradin *et al.* 2003; Schradin & Anzenberger 2004; but see Roberts *et al.* 2001b). The prolactin increase in avian helpers might be due to a seasonal, photoperiodically regulated mechanism (Buntin 1996). The same mechanism occurs in several mammal species where prolactin secretion is regulated by photoperiod resulting in high prolactin levels during the breeding season (Curlewis 1992; Donham *et al.* 1994). Thus, this study also compares prolactin levels between the breeding and non-breeding season. Finally, this study tests for a positive correlation between prolactin and glucocorticoid levels as an alternative explanation for differences in prolactin levels among the three male classes (Carlson *et al.* 2006b).

2. MATERIAL AND METHODS

(a) Study area and period

The study was conducted in Goegap Nature Reserve in South Africa (29° 41.56'S, 18° 1.60'E). The area is arid, with an average rainfall of 160 mm per annum, and the vegetation type is classified as Succulent Karoo. The study took place during the 2005 and 2006 breeding seasons (August to October, a photoperiod of 10.0–12.0 hours d^{-1} ; Schradin *et al.* 2007) and the 2007 non-breeding season (March; a photoperiod of 11.5 hours d^{-1}).

(b) Determination of male reproductive tactics

Male strategies were determined by a combination of trapping, behavioural observations and radio-tracking (for a detailed description of methods, see Schradin & Pillay

2004b, 2005). Trapping was done around nesting sites 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. Mice were permanently marked using ear tags (National Band and Tag Co., USA) and, in addition, with hair dye (Rapido, Pinetown, South Africa) for individual recognition during behavioural observations (see pictures on www.stripedmouse.com). Nests were observed in the mornings and afternoons for 45 min. The habituated mice were observed from a distance of 5–10 m (Schradin & Pillay 2004b; Schradin 2006). All individuals present at the nest were recorded. Individuals were equipped with MD-2C radiotransmitters (Holohil, Canada) weighing 2.5–4.5 g, which represented less than 10% of body weight. We radio-tracked males (and radio-collared females) three to five times per week to determine nesting sites.

Fifteen groups were studied. The population has been studied since 2001 such that the natal groups of all mice born in the study area were known and the other striped mice were categorized as immigrants. Each group contained one single breeding male, one to four breeding females and several philopatric adult males and females. Males that were trapped as juveniles (less than 25 g) at a group and consecutively observed there but not at other groups and not trapped more than 100 m away from their natal nest were regarded as philopatric males. Males that were not living in their natal group but had emigrated into a group of females not related to them were regarded as breeding males. These were also always the heaviest males of the group. Males that were living away from their natal nest and did not share nesting sites with any other mice were regarded as roaming males. Roaming males also had significantly larger home ranges than breeding males, and these overlapped the home ranges of the females of several groups (C. Schradin 2007, unpublished data). Females were either philopatric to their natal group or the founders of new groups.

A population-specific growth curve has been obtained from individuals trapped when weighing less than 20 g (being two to four weeks old; Brooks 1982), which were repeatedly trapped afterwards (C. Schradin 2007, unpublished data). Birth dates were estimated for each individual when trapped for the first time by using this growth curve and the individual's body weight. These estimated birth dates were used to estimate the age of males, in steps of half months.

(c) Blood collection

Altogether 106 samples from 97 individuals were collected. 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 collected during this morning period 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 and anaesthetized with diethyl ether and a blood sample of approximately 300 μl was taken from the retro-orbital sinus within 3 min. Blood samples were brought to the research station shortly after being collected. Here, they were left at room temperature to clot for 1.5 hours (breeding season, indoor morning temperatures below 15°C) or 1.0 hours (non-breeding season, indoor morning temperatures approx. 20°C) before being centrifuged for 10 min. The resulting serum was frozen in aliquots. Seventy-seven samples were collected by watching

the traps. An additional 29 samples were collected from traps that were checked 45 min after they had been set.

(i) *Hormone assays*

Prolactin levels were measured for 14 roamers, 23 breeding males, 34 philopatric males and 29 breeding females. Corticosterone was measured in 83 out of the 106 samples in which prolactin was measured. Of these, from three individuals, two samples were measured and the mean value was taken (both for prolactin and corticosterone). Thus, the effective sample size was 80 for correlations between prolactin and corticosterone.

Prolactin was measured using a kit from SPIbio (A05101, rat prolactin) and corticosterone with a kit from IBL Hamburg (RE52211). For prolactin, volumes of samples and all other reagents were halved to 25 µl instead of 50 µl (as stated in the kit instructions). For corticosterone, samples were diluted 1 : 100. All measurements were within the standard curve of the assay except for five prolactin samples, which were regarded as zero. All samples were run in duplicates.

For both hormones, serial dilution of two striped mouse sample pools paralleled the standard curve. Intra- and inter-assay coefficients of variation for a pool of medium and low concentration were 11.1%/16.1% and 15.0%/15.2% for prolactin, and 8.3%/10.0% and 6.4%/2.3% for corticosterone. Recovery of samples added to the prolactin standards curve was 106.3 and 96.9%, for corticosterone 95.9%.

(d) *Statistics*

The software packages INSTAT v. 3.05 and SAS v. 9.1.3 were used. Correlations were done in INSTAT as Spearman correlations (r_s). Age of males between social classes and across seasons was compared by ANOVA followed by the Tukey–Kramer multiple comparisons test (q). To test for the effects of social category (roamer, philopatric male, breeding male or breeding female), season (breeding or non-breeding) and trap handling method (whether traps were watched or checked after 45 min) on prolactin levels, generalized linear mixed models were fitted to normal data using REML (SAS, proc MIXED). Social category, season and trapping method were entered as fixed categorical effects into the model, while individual identity was introduced as a random effect on the intercept because animals were measured repeatedly (see above). Residuals were accepted as being normally distributed when Shapiro–Wilk statistics yielded $p > 0.05$. Error degrees of freedom (d.f.) were calculated using the Satterthwaite method. Effects were tested using type III (simultaneous) modelling; that is, in multiple fixed-effects models, parameters for each independent variable are corrected for all other fixed effects in the model. Since roamers were only present during the breeding season (they had either disappeared during the non-breeding season or became permanent members of social groups), hormone levels of roamers were compared with the other three social groups in a separate model including only data from the breeding season. Differences between the least-square means (function LSMEANS in SAS) of multiple categories were compared *post hoc* using a t -test.

3. RESULTS

Males differed in age among classes and seasons ($F_{4,66} = 36.64, p < 0.0001$). Roamers and breeding males were of similar age ($q = 0.1, p > 0.05$) but significantly older than

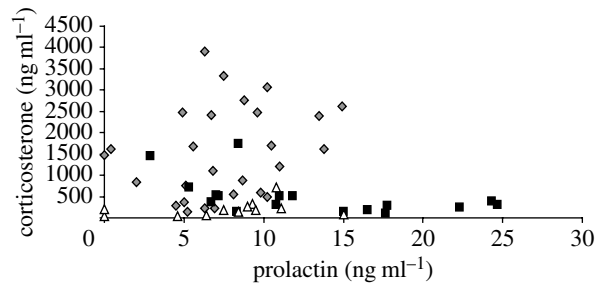


Figure 1. Correlation between prolactin and corticosterone for the three different male reproductive tactics (diamonds, philopatric males; squares, breeding males; triangles, roamers). Only the correlation for breeding males was significant (see text).

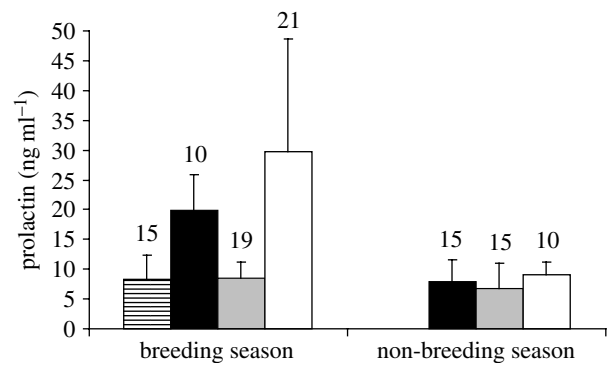


Figure 2. Prolactin levels in striped mice during the breeding and non-breeding season (horizontally striped bar, roamers; black bars, breeding males; grey bars, philopatric males; white bars, breeding females). Roamers were only present during the breeding season. Mean + s.d. is shown and sample sizes are indicated above each bar.

philopatric males (roamers versus philopatrics: $q = 10.8, p < 0.001$; breeding males versus philopatrics: $q = 9.3, p < 0.001$). Both breeders and philopatrics were older during the non-breeding season than the previous breeding season (philopatrics: $q = 4.5, p < 0.05$; breeding males: $q = 4.0, p < 0.05$) and breeders were still older than philopatrics ($q = 10.6, p < 0.001$), while no roamers were present during the non-breeding season (they either had disappeared or became permanent members of a group).

Blood samples were collected significantly later in the morning during the breeding than during the non-breeding season ($t_{104} = 3.693, p = 0.0004$). As mice were trapped at their nest when their natural activity period starts, which is highly correlated with sunrise (Schradin *et al.* 2007), this indicated that striped mice experienced a longer photoperiod during the non-breeding season. Mice were sampled on average at 07.54 hours during the breeding season and at 07.30 hours during the non-breeding season.

Breeding males showed a significant negative correlation between corticosterone and prolactin ($r_s = -0.58, N = 18, p = 0.01$; figure 1). All other correlations were non-significant (all individuals: $r_s = +0.03, N = 80, p > 0.7$; all males: $r_s = -0.09, N = 57, p > 0.5$; roaming males: $r_s = +0.50, N = 12, p = 0.10$; young adult males: $r_s = +0.28, N = 27, p > 0.10$; figure 1; female breeders: $r_s = -0.04, N = 23, p > 0.80$). During the breeding season, prolactin levels were significantly different between social categories ($F_{3,47.99} = 8.52, p = 0.0001$; figure 2), while whether traps were watched or checked after 45 min had no influence ($F_{1,47.8} = 0.10, p = 0.75$). *Post hoc* analyses of

the social factor category revealed that breeding females had significantly higher prolactin levels than roamers ($t_{50.1} = -4.44$, $p < 0.001$) and philopatric males ($t_{49.17} = -4.58$, $p < 0.001$). The difference between breeding females and breeding males was close to significance ($t_{43.6} = -1.97$, $p = 0.0548$). Breeding males had significantly higher prolactin levels than both roamers ($t_{49} = 2.40$, $p = 0.02$) and philopatric males ($t_{48.1} = -2.40$, $p = 0.02$), while there was no significant difference between roamers and philopatrics ($t_{52.2} = 0.15$, $p = 0.88$).

During the non-breeding season, no significant differences in prolactin levels were found between classes ($F_{2,32} = 1.49$, $p = 0.24$; figure 2). For the seasonal comparison, whether traps were watched or checked after 45 min had no influence on prolactin levels ($F_{1,73.3} = 0.01$, $p = 0.91$). However, season ($F_{1,72.9} = 29.99$, $p < 0.0001$), social category ($F_{2,71.3} = 9.40$, $p = 0.0002$) and their interaction ($F_{2,71.3} = 5.57$, $p = 0.006$) were significant. While prolactin levels decreased from the breeding to the non-breeding season in both breeding males ($t_{71.5} = 3.46$, $p = 0.0009$) and breeding females ($t_{69.64} = 5.19$, $p < 0.0001$), no change was observed in philopatric adult males ($t_{72.7} = 0.65$, $p = 0.52$; figure 2). No roamers were present during the non-breeding season.

4. DISCUSSION

Serum prolactin levels differed significantly as a function of reproductive tactics and seasons. Breeders of both sexes had higher prolactin levels than both group-living philopatric males and solitary living roamers. Only breeders showed a decrease in prolactin levels from the breeding to the non-breeding season. High prolactin levels are known to be associated with paternal care (Schradin & Anzenberger 1999) and striped mouse fathers show the same patterns of parental care as mothers (with the obvious exception of nursing) and to the same extent (Schradin & Pillay 2003). In contrast, roaming striped mouse males do not engage in parental care nor are they associated with pups, but search for receptive females (Schradin & Pillay 2005). Prolactin levels did not differ between philopatric and roaming males. Philopatric males act as helpers at the nest, participating in nest defence, nest building (Schradin & Pillay 2004b) and alloparental care such as huddling and licking of pups (C. Schradin 2007, unpublished data). In cooperatively breeding primates, increased prolactin levels have been reported in paternal males but not in alloparental helpers (Ziegler *et al.* 1996; Schradin *et al.* 2003; Schradin & Anzenberger 2004). Thus, the endocrine regulation of paternal care seems to differ from that of alloparental care in mammals, which is in contrast to the situation found in birds where helpers show an increase in prolactin levels (Buntin 1996).

The increase in prolactin levels during the breeding season in avian parents and alloparents can to some extent be explained by a photoperiodically triggered seasonal increase (Buntin 1996). Striped mice showed a seasonal pattern of prolactin secretion too, but only in parents. Breeders had higher prolactin levels during the breeding season, the period of infant care, a pattern described previously for male striped mice (Schradin & Pillay 2004a). In some mammals, prolactin secretion is highest during periods of long photoperiod (Curlewis 1992; Donham *et al.* 1994; Jöchle 1997). In this study, the

photoperiod during the breeding season ranged from 10 hours d^{-1} in August to 12 hours d^{-1} in October, while the photoperiod during the non-breeding season in March was in between with 11.5 hours d^{-1} (Schradin *et al.* 2007). The seasonal increase in prolactin levels in mammals is often discussed in relation to reproduction, which can be regulated by photoperiod (Curlewis 1992; Donham *et al.* 1994; Jöchle 1997). However, reproduction in male striped mice is not regulated by photoperiod (Jackson & Bernard 1999) but by food availability (Jackson & Bernard 2005). For example, the non-breeding season in this study in the Succulent Karoo is part of the breeding season of striped mice in the moist grasslands of South Africa (Brooks 1982; Schradin 2005). Even in this study population, striped mice can breed in March if unexpected summer rainfall occurs, as was the case in 2005 (C. Schradin 2007, unpublished data). Therefore, breeding is not regulated by photoperiod in male striped mice and the seasonal difference in prolactin levels found in this study cannot be explained by differences in photoperiod, though an influence of photoperiod on prolactin levels in striped mice cannot be ruled out.

Prolactin levels did not positively correlate with glucocorticoids, as is the case in meerkats (Carlson *et al.* 2006b). The correlation matrix showed a random pattern, with most correlations being close to zero, others being negative or positive, as would be expected when no relationship exists. The only significant correlation was in breeding males, but here the correlation was even negative. Thus, breeding males did not have high prolactin levels because they were more stressed, as indicated by their low corticosterone levels. If high prolactin levels would be due to stress, a positive correlation with corticosterone would have been expected, with roamers and philopatrics having low levels and breeders having high levels of both hormones. However, for all males combined, the correlation was nearly zero. Therefore, the differences in prolactin levels found in the present study were neither due to a by-product of differences in corticosterone levels nor due to differences in stress.

Age cannot explain the difference in serum prolactin levels among the three male classes either. While philopatric males were younger than the two other categories, they differed only from the older breeders, but not from the older roamers, in serum prolactin levels. Additionally, roamers and breeders were of similar age but differed in prolactin levels. Furthermore, the decrease in prolactin levels in breeding males from the breeding to the dry season four months later, and the fact that prolactin levels did not change seasonally in philopatrics, indicates that prolactin levels do not increase with increasing age. Therefore, as neither age nor stress (corticosterone) can explain differences in prolactin levels among these three male classes, the most parsimonious explanation would be the differences in their reproductive tactics.

The differences in prolactin levels found in this study are best explained by the well-established correlation between prolactin and being a parental male (Schradin & Anzenberger 1999). Which stimuli lead to an increase in prolactin levels in striped mouse fathers is so far unknown. In a laboratory study, striped mouse fathers did not have higher prolactin levels than adult males housed singly, but as no comparison was made between paternal motivation between both types of males, it is not possible to conclude

that prolactin is not necessary for paternal motivation (Schradin & Pillay 2004a). This laboratory study did not find indications that pup stimuli led to increased prolactin levels in striped mouse fathers (Schradin & Pillay 2004a). In addition, if stimuli by pups and juveniles are responsible for increased prolactin secretion, similar levels would be expected in alloparental and paternal males, as both male classes sleep in the communal nests. Furthermore, it is unlikely that the event of experiencing birth can explain the increased prolactin levels in this study, as breeding males were sampled throughout the breeding season when pups and juveniles of different ages were present, and philopatric males would have experienced the same events as births occur in the communal nest with all group members present (C. Schradin 2007, unpublished data). Detailed studies on the behaviour of philopatric males are lacking and it is possible that male helpers show significantly less alloparental care than fathers show paternal care, as is the case in cooperatively breeding callitrichid primates (Ziegler *et al.* 1996; Schradin & Anzenberger 1999). Possibly alloparental care is regulated differently from paternal care and breeding males react differently to environmental stimuli than helpers, as is the case in callitrichid primates (Schradin & Anzenberger 2004).

Philopatric males are often sexually suppressed, i.e. they are not scrotal (Schradin & Pillay 2004b), while breeding males and roamers are always scrotal (Schradin & Pillay 2005). These three male classes also differ in testosterone levels, with philopatric males having significantly lower testosterone levels than the other two classes, and roamers having significantly higher levels than breeding males (C. Schradin 2007, unpublished data). Thus, neither testosterone nor the fact whether males are scrotal or not can explain prolactin levels, as the two male classes that are always scrotal (breeders and roamers) differ in prolactin, and breeders have the highest prolactin levels but have intermediate testosterone levels.

Several studies in captivity have demonstrated a positive correlation between paternal care and prolactin (Ziegler *et al.* 1996; Schradin & Anzenberger 1999; Wynne-Edwards 2001), and experiments in ring doves (Buntin *et al.* 1991) and fishes (Blüm 1974; Kindler *et al.* 1991) have demonstrated that prolactin has a causal influence on paternal care. However, whether the correlation between prolactin on paternal care in mammals reflects a causal relationship or whether mammalian paternal males differ from non-paternal ones in other aspects, e.g. metabolism, remains a topic for future research (Schradin 2007; Wynne-Edwards & Timonin 2007). Field studies are important to demonstrate that the correlation found in the laboratory also holds for the natural situation, as captive conditions could have pronounced effects on metabolism and thus could also alter hormone levels. For example, laboratory and field diets often differ dramatically. So far, experimental support for a direct positive influence of prolactin on paternal care in mammals is either weak (Roberts *et al.* 2001a) or lacking (Brooks *et al.* 2005; Almond *et al.* 2006). Laboratory studies mimicking the natural situation more closely (Schradin 2007) and taking the natural pattern of prolactin secretion into account (Schradin & Anzenberger 2004) are needed for testing a causal influence of prolactin on paternal care. This is why field studies are so important. However, so far, very few field studies have

been conducted in mammals and comparisons between single living non-paternal and sociable paternal males of the same species in the same population at the same time are even more scarce. In future, it will be important to determine both the stimuli leading to the reported differences in prolactin among striped mouse males following three different tactics as well as to study the function of increased prolactin levels in paternal males. Future field studies are needed to test for changes in prolactin levels when males change their reproductive tactic to provide further evidence that prolactin is one proximate mechanism of social flexibility. Experimental suppression or experimental increase in prolactin levels combined with behavioural tests and observations could then test for a causal effect of prolactin on male social behaviour.

The study complied with the current laws and regulations in the Republic of South Africa. Animal ethical clearance nos. 2004/87/2A and 2005/82/4, University of the Witwatersrand.

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