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Alternative reproductive tactics in female striped mice: Solitary breeders have lower corticosterone levels than communal breeders



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ABSTRACT

Alternative reproductive tactics (ARTs), where members of the same sex and population show distinct reproductive phenotypes governed by decision-rules, have been well-documented in males of many species, but are less well understood in females. The relative plasticity hypothesis (RPH) predicts that switches between plastic ARTs are mediated by changes in steroid hormones. This has received much support in males, but little is known about the endocrine control of female ARTs. Here, using a free-living population of African striped mice (*Rhabdomys pumilio*) over five breeding seasons, we tested whether females following different tactics differed in corticosterone and testosterone levels, as reported for male striped mice using ARTs, and in progesterone and oestrogen, which are important in female reproduction. Female striped mice employ three ARTs: communal breeders give birth in a shared nest and provide alloparental care, returners leave the group temporarily to give birth, and solitary breeders leave to give birth and do not return. We expected communal breeders and returners to have higher corticosterone, owing to the social stress of group-living, and lower testosterone than solitary breeders, which must defend territories alone. Solitary breeders had lower corticosterone than returners and communal breeders, as predicted, but testosterone and progesterone did not differ between ARTs. Oestrogen levels were higher in returners (measured before leaving the group) than in communal and solitary breeders, consistent with a modulatory role. Our study demonstrates hormonal differences between females following (or about to follow) different tactics, and provides the first support for the RPH in females.

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Introduction

Alternative reproductive tactics (ARTs) are discrete reproductive phenotypes selected to maximise fitness in two or more distinct ways in the same sex and population (Gross, 1996). They can be plastic, whereby an individual is able to switch from one ART to another, or they can be fixed for life (Taborsky, 1998). The differentiation and maintenance of ARTs are mediated by changes in the secretion of steroid hormones (reviewed in Oliveira et al., 2008). This idea was first conceptualised in the relative plasticity hypothesis (RPH), which predicts that fixed tactics are regulated by organisational endocrine effects in early development, whereas switches between plastic tactics are regulated by activational endocrine effects in sexually mature individuals (Moore, 1991; Moore et al., 1998). Alternative adult phenotypes of species with fixed ARTs should therefore have similar steroid profiles provided that they experience the same social environment, while

steroid levels are predicted to differ between alternative adult phenotypes in species with plastic ARTs (Moore, 1991).

ARTs are expected to evolve when there is pronounced variance in reproductive success within a sex, leading to reproductive competition (Taborsky et al., 2008). Competition for mates is usually more intense in males than in females (Trivers, 1972), which probably explains why ARTs occur more frequently in males (Alonzo, 2008). Nevertheless, females of many species experience intense reproductive competition (Stockley and Bro-Jørgensen, 2011), and an increasing number of female ARTs has been described in recent years. Examples include brood parasitism versus maternal care in ruddy ducks (*Oxyura jamaicensis*) (Reichart et al., 2010) and monandry versus polyandry in horseshoe crabs (*Limulus polyphemus*) (Johnson and Brockmann, 2012). Little, however, is known about the role of hormones in mediating female ARTs (Oliveira et al., 2008).

Glucocorticoids (GCCs) regulate basal metabolism and facilitate appropriate responses to stress (Reeder and Kramer, 2005; Sapolsky et al., 2000). In species with plastic ARTs, bourgeois (dominant) males sometimes have higher GCC levels than males of subordinate tactics (satellite, roamer, sneaker), while in other species the pattern is reversed (Oliveira et al., 2008). This difference might depend on whether

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it is more energetically demanding to occupy a dominant or a subordinate rank (Creel, 2001). Experimental manipulations of GCC levels in species with plastic ARTs can induce males to switch tactics. For example, bourgeois male Great Plains toads (*Bufo cognatus*) and Woodhouse's toads (*Bufo woodhousii*) with experimentally-elevated corticosterone levels were more likely than controls to switch to a satellite tactic (Leary et al., 2006). Given their role in mediating ARTs in males (Oliveira et al., 2008) and transitions between life history stages in both sexes (Crespi et al., 2013; Wada, 2008), GCCs are a promising candidate for regulating female ARTs.

In species with plastic ARTs, bourgeois males typically have higher androgen levels than subordinates, and experimentally increasing androgen levels in subordinate males can induce a switch to the bourgeois tactic (Oliveira et al., 2008). Marine iguanas (*Amblyrhynchus cristatus*), for example, employ three plastic ARTs, with satellite and sneaker males having lower androgen levels than territorial males (Wikelski et al., 2005). Experimentally increasing androgen levels in satellites and decreasing androgens in territorial males can bring about non-adaptive tactic switches (Wikelski et al., 2005). Bourgeois males are more aggressive than subordinates in many species (e.g. Corlatti et al., 2013; Schutz et al., 2010), and the role of androgens in mediating male aggression is well-established (Wingfield et al., 1987). Fewer studies have tested for an association between aggression and androgen levels in females, but most work suggests that female testosterone levels vary in response to intra-sexual competition and are under direct sex-specific selection (Rosvall, 2013). This raises the possibility that testosterone could facilitate responses to intra-sexual competition in females following different tactics.

Progesterone and oestrogen control many aspects of female reproduction (Christensen et al., 2012; Hewitt et al., 2005), and are associated with female–female competition in some species (Goymann et al., 2008; Parn et al., 2008; Rubenstein and Wikelski, 2005) but not in others (Elekovich and Wingfield, 2000; Hay and Pankhurst, 2005; Navara et al., 2006). In female house mice (*Mus musculus*), ovariectomy during gestation brought forward the onset of maternal aggression (Ghiraldi et al., 1993), while an experimental increase of oestrogen levels inhibited maternal aggression (Svare and Gandelman, 1975). To our knowledge, no study has yet tested whether females following alternative tactics differ in levels of progesterone and oestrogen, and tests in males with plastic ARTs are limited to a few teleost species. Progesterone levels are either higher in bourgeois than subdominant males (Cheek et al., 2000; Oliveira et al., 1996) or do not differ (Hourigan et al., 1991; Ros et al., 2003). Oestrogen levels are higher in subdominant than bourgeois male stoplight parrotfish (*Sparisoma viride*) (Cardwell and Liley, 1991), but do not differ between ARTs in saddleback wrasse (*Thalassoma duperrey*) (Hourigan et al., 1991). These studies suggest that the role of progesterone and oestrogen in modulating female ARTs is worth exploring.

Here, for the first time, we ask whether the RPH, which predicts differences in steroid hormones in males that follow plastic ARTs (Moore et al., 1998), also applies to females. The striped mouse (*Rhabdomys pumilio*) is an appropriate model in which to test this because plastic ARTs occur in both sexes. Male striped mice have three ARTs that differ in steroid hormone levels (Schradin et al., 2009b, 2013): 1) philopatric males have very high corticosterone and low testosterone levels; 2) solitary-living roamers have low corticosterone and high testosterone levels; and 3) dominant group-living breeding males have low corticosterone and intermediate testosterone levels. Like males, female striped mice can breed in groups or solitarily. Breeding groups usually comprise 2–4 closely related females and one male (Schradin and Pillay, 2004). Communally-breeding females show alloparental care, including allo-nursing (Schradin and Pillay, 2004; Schubert et al., 2009). Nevertheless, reproductive competition between female nestmates is intense, involving aggression and infanticide (Schradin et al., 2010). Females can avoid reproductive competition by leaving the natal group to nest alone, and solitary and communal females usually co-occur during

the breeding season (Schoepf and Schradin, 2012; Schradin et al., 2010). As an alternative to breeding solitarily or communally, gestating females may adopt a third tactic termed 'returner' in which they leave the group to give birth, but later return to it (Hill, D.L., Pillay, N. and Schradin, C., unpublished data). Females can switch between the three phenotypes, which means that tactics are flexible and likely to be regulated by activational endocrine effects.

We tested whether ARTs in free-living female striped mice were associated with differences in baseline levels of steroid hormones. We expected (i) corticosterone levels to be higher in communally-breeding females than in solitary breeders owing to increased social stress and reproductive competition in groups; and (ii) testosterone levels to be higher in solitary breeders than in communal breeders because solitary breeders must defend a territory alone. We focussed on these two hormones because they have been studied in detail in male striped mice (e.g. Schradin et al., 2009b; Schradin and Yuen, 2011). Where additional aliquots of serum were available, we tested for (iii) differences between ARTs in progesterone and oestrogen. The social environment can affect hormone secretion (Wingfield et al., 1990), and so tactic switches that involve a change in social situation (e.g. from communal to solitary breeding) might in turn affect hormone levels. Similarly, returners, which experience a change in social situation from group- to solitary-living and back to group-living within a single tactic, might also show associated changes in hormone levels. These hormonal changes could occur in response to changes in social stress or energetic demands. We therefore tested (iv) whether changes in social situation in solitary breeders and returners were accompanied by changes in hormone levels. Throughout our analyses, we distinguished between females that became solitary while their relatives were still living (and which therefore had the potential to use any tactic) and those that were constrained to live solitarily because their relatives died. Importantly, the two types of solitary breeder experience a similar social environment that is elicited by different mechanisms: solitary breeders with relatives show a true tactic (the outcome of a strategy) that is predicted to be under hormonal control, whereas females without relatives are solitary as a consequence of external stochastic processes. If the decision to follow a solitary tactic is indeed under hormonal control, we would therefore expect (v) solitary breeders with living relatives to differ hormonally from solitary breeders without living kin.

Materials and methods

Fieldwork

We collected data every month during 2006–10 in Goegap Nature Reserve, South Africa (S 29 41.56, E 18 1.60) using methods approved by the Animal Ethics Committee at the University of the Witwatersrand (2004/87/2A, 2005/82/4 and 2007/10/01). The study site receives 180 mm precipitation per annum, mostly falling between April and September (in austral winter and spring; C. Schradin, unpublished data). It is an open habitat of shrubs, in which striped mice nest, and sandy areas.

Striped mice were captured using Sherman-style live-traps (26 × 9 × 9 cm) baited with bran flakes, salt and sunflower oil. Traps were placed in the shade close to a group's nest site in the morning and the late afternoon five days a week, as striped mice are diurnal, and checked 30–45 min after being set. Each group was trapped every two weeks. Females were weighed to the nearest gramme using an electronic balance, and we recorded whether their nipples were pink and elongated (characteristic of lactation), otherwise visible or not visible. Newly-trapped individuals were provided with numbered aluminium ear-tags (National Band and Tag, Newport, KY), and marked with non-toxic hair dye (Inecto, Pinetown, South Africa), so that they could be recognised during behavioural observations at their nest sites (described in Schradin and Pillay, 2004). All adults trapped during

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