Staying put or leaving home: endocrine, neuroendocrine and behavioral consequences in male African striped mice

Carsten Schradin [a,b,c,*], Wiliam Kenkel [d], Sven Krackow [e], C. Sue Carter [d]

[a] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
[b] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa
[c] Université de Strasbourg, IPHC-DEPE, CNRS, UMR7178, 23 rue Becquerel 67087 Strasbourg, France
[d] Research Triangle Institute, RTP, NC 27709, USA
[e] Anatomical Institute, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

ARTICLE INFO

ABSTRACT

Social flexibility occurs when individuals of both sexes can change their social and reproductive tactics, which in turn can influence the social system of an entire population. However, little is known regarding the extent to which individuals of socially flexible species vary in their social behavior and in the underlying physiological mechanisms that support different social tactics. The present study in African striped mice modeled in captivity three male tactics described from the field: (a) philopatric males remaining in the family; (b) solitary roamers; or (c) group-living breeding males. Sixteen pairs and their offspring were kept in captivity, while one male offspring from the family remained as singly housed after he reached 21 days of age. Differences in behavior, morphology, hormone and neuropeptide levels were tested, and physiological measurements were correlated with behavioral measurements. In standardized arena experiments group-living males (philopatrics and breeders) were significantly more aggressive than singly housed males, in agreement with previous data suggesting that group-living, but not roaming males, are territorial. Philopatric males showed signs of reproductive suppression, small testes, lower testosterone and higher corticosterone levels than their singly housed brothers. Higher levels of arginine vasopressin (AVP) were measured in the PVN and BNST of singly housed males compared to group-living males. Based on these findings we hypothesize that roamers are physiologically primed, and capable, if the opportunity to mate arises, to release AVP, form social bonds and become territorial, thus quickly adopting the tactic as breeding male which would yield a higher reproductive success.

© 2012 Elsevier Inc. All rights reserved.

Introduction

Significant within species variations exist in social systems, which in some cases might be due to local adaptation and genetic differences between individuals and populations (Lott, 1991) or due to social flexibility. The term "social flexibility" describes the phenomenon that the social system of a population can be modified if males and females change their social and reproductive tactics (Schradin et al., 2012b). "Tactic" refers here to the behavior shown by an individual which results from the individual decisions rules, which has been called a "strategy" (Gross, 1996). In the case of social flexibility, individuals of a given population may have relatively consistent decisions rules, representing a single strategy with alternative individual tactics (Schradin and Lindholm, 2011). On the population level, such individual strategies can lead to alternative social systems (Schradin et al., 2012b). An example would be living in communal groups, in monogamous pairs, or living solitarily as observed in prairie voles (Microtus

ochrogaster) (Getz and McGuire, 1993, 1997; Solomon et al., 2009). Such plastic tactics can optimize individual fitness under changing environmental conditions (Schradin et al., 2012b).

While social flexibility seems to be regulated by the environment and is likely to lead to fitness benefits, its proximate mechanisms are poorly understood (Lott, 1991; Schradin et al., 2012b). Often the switches in social behavior are dramatic, for example from pair-living to solitary-living as described for invertebrate and vertebrate species (Getz and McGuire, 1993; Müller et al., 2006; Schradin et al., 2010a). Similarly, offspring that reach adulthood may disperse and become solitary or alternatively remain philopatric, eventually living in extended family groups (Emlen, 1995).

The most parsimonious explanation for individual tactic switches would be that the observed change in behavior results from environmental changes constraining individual behavior. For example if population density declines sharply, due to predation or food shortage, previously group-living individuals might be forced to become solitary, as the other group members disappeared. In such cases, changes in social organization might not represent an actual switch in the behavioral tactic of an individual. Thus, to demonstrate true behavioral flexibility it is necessary to demonstrate that individuals actually do

* Corresponding author at: Université de Strasbourg, IPHC-DEPE, CNRS, UMR7178, 23 rue Becquerel 67087 Strasbourg, France. Fax: +33 3 88 10 69 44.
   E-mail address: carsten.schradin@iphc.cnrs.fr (C. Schradin).

change their tactics, i.e. their social behaviors, in the face of a change in environment (Schradin et al., 2012b).

The present experiment examines the hypothesis that environmentally triggered changes in individual social tactics reflect concomitant or antecedent changes in specific physiological mechanisms. For flexible alternative tactics, the relative plasticity hypothesis predicts that changes in steroid hormones, such as testosterone and corticosterone, are components of the mechanisms that allow individuals to change from one tactic to another (Moore et al., 1998). Androgens, and especially testosterone, are powerful mediators of sexual and aggressive behaviors (Wingfield, 2005). In the mammalian brain, testosterone can be converted into estrogen via aromatase, and the estrogen receptor α plays a significant role in the regulation of male social behavior (Cushing and Wynne-Edwards, 2006). Similarly, glucocorticoids such as corticosterone, influence metabolism as well as social behaviors, including pair-bonding and biparental care (Bales et al., 2006; DeVries et al., 1996). Thus, significant changes in steroid hormones are expected to be associated with social flexibility (Schradin et al., 2012b).

In addition to steroid hormones, the neuropeptides oxytocin (OT) and arginine vasopressin (AVP), which are produced and secreted in the brain, have been causally implicated in social behaviors (Bales et al., 2006; Carter, 1998). While OT may be of particular importance to female reproduction and some features of behavior (Lee et al., 2009), the evolutionary closely related AVP plays an central role in male social behavior, especially social bonding, paternal care, and defensive aggression (Carter, 2007). Functional connections among brain regions of the social behavior network (SBN) are assumed to regulate phenotypic variation in behavior. AVP and OT are produced and secreted by neurons in several areas of the SBN including the medial bed nucleus of the stria terminalis (BNST), the supra-optic nucleus (SON) and the paraventricular nucleus (PVN), with well-documented effects on social behaviors (Caldwell et al., 2008; DeVries et al., 1981; Goodson and Kabelik, 2009). AVP contains processes from BNST project into the lateral septum, a brain region which is rich in AVP receptors. AVP has been specifically implicated in male–male aggression (Ferris et al., 1986), social recognition (Dantzer et al., 1988) and social bonding (Winslow et al., 1993). The SON is involved in the regulation of emotional reactivity and mobilization to a variety of stressors (Landgraf et al., 1998). The PVN is of particular importance in the synthesis and release into the brain of neuropeptides implicated in behavior and stress reactivity. For example, neurons containing peptides project from the PVN into both the basal forebrain and brainstem (Sawchenko and Swanson, 1982). AVP from the PVN has been associated with increased anxiety, and in response to stressors, can act as a secretagogue for ACTH release. These neuropeptides and associated changes in their receptors also have been associated with species, population and individual differences in social behavior (Cushing et al., 2001; Heckel and Fink, 2008; Solomon et al., 2009). If OT and AVP play a mechanistic role in social flexibility, we hypothesized that these peptides would differ as a function of different social tactics, possibly regulating the differential expression of social behaviors that form a specific tactic.

One mammalian species that shows high social flexibility is the African striped mouse (*Rhabdomys pumilio*; Schradin et al., 2012b). In this species, both sexes can express alternative reproductive tactics: (a) remaining as a non-breeding philopatric helper at the nest, (b) leaving the natal group and initiating solitary breeding, or (c) group-living as a communally breeding female or as the dominant breeding male within a social group. The present study models in a laboratory setting these conditions for males. In the field under high population density, males typically remain philopatric in their natal group long after reaching sexual maturity (Schradin and Pillay, 2004). Under low population density, males may leave their natal group when they are 3–4 weeks old, living as solitary roaming males (Schoepf and Schradin, 2012), or if a group of communally breeding females becomes available they switch to be territorial breeders (Schradin et al., 2009a). Solitary males have higher testosterone but lower corticosterone levels than philopatric males, which

seem to be reproductively suppressed by the breeding male of their group (Schradin et al., 2009a,b). In sum, striped mouse males may either grow up in extended family groups of up to 30 adult mice or leave their natal group and become solitary when they are only a few weeks old (Schradin, 2005).

In the present study we examined patterns of change in behavior, as well as steroid and neuropeptide hormones in male striped mice, originating from the same population, but subsequently randomly assigned in the laboratory to live either alone or remain as a philopatric member of the natal family. The breeder male from each family was also studied. We hypothesized that different living conditions would be associated with changes in social behavior, indicating that the tactic is expressed as an individual trait, rather than a simple consequence of environmental conditions experienced in nature. Specifically, we predicted that solitary males would mature more quickly, with higher testosterone, but lower corticosterone levels. Using immunhistochemistry we also indexed tissue levels of AVP and OT in brain areas of the SBN, testing the prediction that AVP, which has often been implicated in male social behavior and territoriality would be particularly likely to differ as a function of living conditions (Caldwell et al., 2008; Carter, 2007). Finally, we examined correlations among the observed behavioral and physiological changes to test the hypothesis that individual differences in social behavior would be related to patterns of change in the neuropeptides and steroid hormones measured here.

Methods

Housing conditions

The captive colony used in the experiments consisted of descendants from animals originally trapped in 2002 in the Succulent Karoo in South Africa. Animals were kept at the University of Zurich under a 12:12-h light regime. Wild rodents kept in captivity are prone to develop stereotypic behavior (for striped mice see Jones et al., 2010) which is known to affect both social behavior as well as physiology and brain structure (Würbel, 2001). Thus, all animals were kept under environmentally enriched conditions, which were successful in avoiding the development of stereotypic behaviors (Schradin, unpublished data) and may help to reduce weight gain. Families were kept in two glass tanks $50 \times 30 \times 30$ cm, connected to one another by a flexible plastic tube ($n = 16$ families). Additionally, one plastic cage $20 \times 13 \times 15$ cm was connected by another tube, and a water bottle was provided in this cage. Single individuals were kept in a single glass tank connected to two plastic cages. All tanks and cages had 5-cm deep wood shavings for bedding. The tanks contained natural branches and each family and singly kept mouse had one running wheel. Mice were supplied with water ad libitum. Striped mice in the Succulent Karoo display significant weight fluctuations, gaining weight during spring and losing more than 10% during the following dry season (Schradin and Pillay, 2005a), which may explain why this species is prone to extreme obesity in captivity. To further avoid obesity and as a means of behavioral enrichment, striped mice were not fed ad libitum, but rather three times a day: in the morning they received a seed mix of 4.0 g/individual (guinea pig and hamster food, Haefliger AG, Herzogenbuchsee, Switzerland), at noon one piece (approx. 1.0 g) of fruit or vegetable per individual and in the afternoon two mealworms per individual.

Animal ethical clearance was provided by the Kantonale Veterinärmt of the Kanton Zürich in Switzerland (ethical clearance number 91/2006).

Experimental procedure

Three males per family were used for the study: the father (approximately 3 months older than his sons) and two of his sons from the same litter, which were fully developed, scrotal adults (9–10 weeks old) at the end of the experiments. Families were kept together until offspring were three weeks old (weaning is on D16; Brooks,