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Arginine vasopressin plasma levels change seasonally in African striped mice but do not differ between alternative reproductive tactics

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ABSTRACT

Arginine vasopressin (AVP) is an important hormone for osmoregulation, while as a neuropeptide in the brain it plays an important role in the regulation of social behaviors. Dry habitats are often the home of obligately sociable species such as meerkats and Damaraland mole-rats, leading to the hypothesis that high plasma AVP levels needed for osmoregulation might be associated with the regulation of social behavior. We tested this in a facultative sociable species, the African striped mouse (*Rhabdomys pumilio*). During the moist breeding season, both solitary- and group-living reproductive tactics occur in this species, which is obligatory sociable in the dry season. We collected 196 plasma samples from striped mice following different reproductive tactics both during the moist and the dry season. Solitary mice did not have lower AVP levels than sociable mice, rejecting the hypothesis that peripheral AVP is involved in the regulation of alternative reproductive tactics. However, we found significantly higher AVP levels during the dry season, with AVP levels correlated with the abundance of food plants, the main source of water for striped mice. Plasma AVP levels were not correlated with testosterone or corticosterone levels. Our study underlines the important role that AVP plays in osmoregulation, particularly for a free ranging mammal living under harsh arid conditions.

1. Introduction

Hormones are potent modulators of social behavior but they also have significant physiological functions. Experimental manipulation of testosterone can influence sexual and reproductive behavior as well as reproductive physiology (Wingfield et al., 1990). Glucocorticoids can influence social behavior and also play a key role in metabolism, including emergency-life history stages (Reeder and Kramer, 2005). The peptide hormone prolactin plays a significant role in the regulation of parental care in both sexes, but also influences osmoregulation, growth, immunology and reproductive physiology (Schradin and Anzenberger, 1999). However, while the dual function of hormones in regulating behavior and physiology is well known, studies in behavioral endocrinology often ignore the physiological function of hormones.

The neuropeptide arginine vasopressin is produced in the brain, where its secretion in different brain areas influences several social behaviors like parental care, pair bonding and aggression (Caldwell et al., 2008; Carter, 1998). Produced in the paraventricular nucleus (PVN) and secreted via the pituitary into the blood stream, it plays an important role in osmoregulation (Bourque, 1998). Dehydration increases AVP secretion, which then acts on the kidneys where it triggers the contraction of arterioles in the glomeruli and reabsorption of water from the collecting ducts, decreasing water loss and increasing blood pressure (Bourque, 1998). Traditionally, it has been assumed that AVP secretion in the brain (influencing behavior) is independent from AVP secretion by the pituitary (influencing osmoregulation) (Churchland and Winkielman, 2012). Several studies have suggested that nasally administrated AVP can pass through the blood–brain barrier (Born et al., 2002), leading to significant behavioral effects in humans and animals (Bartz et al., 2010; Born et al., 2002; Topic et al., 2007). However, this has been recently criticized and it has been argued that putting AVP into the nasal cavity is simply a convenient way to get it into the blood supply, indicating that peripheral AVP can cross the blood–brain barrier (Merkus, 2007) and could then influence behavior via actions in the brain. This criticism has been supported by studies showing that peripheral administration of AVP and the closely related

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oxytocin had significant effects on social behavior (Cushing and Carter, 2000; Cushing et al., 2001). This leads to the hypothesis that peripheral levels of neuropeptides might influence social behavior via central effects. Additionally, peripheral levels of AVP could influence behavior via peripheral effects such as changes in blood pressure and heart rate (Lebrun et al., 1985).

The relationships between AVP and steroid hormones are complex (reviewed by Caldwell et al., 2008). The AVP receptor 1b is expressed in cells producing adrenocorticotropin in the anterior pituitary (Antoni, 1984). Further, AVP is produced in the PVN, which also synthesizes corticotrophin releasing hormone (CRH). AVP from the suprachiasmatic nucleus has been reported to regulate CRH and ACTH secretion from the pituitary (Buijs, 2003). Finally, AVP is secreted from the PVN in response to stress (Aguilera and Rabadan-Diehl, 2000; Wotjak et al., 1996). Another steroid hormone that influences AVP is testosterone (Crowley and Amico, 1993). Experimental testosterone administration increases the density of AVP fibers within the lateral septum (Vries et al., 1983), while gonadectomy reduces AVP in brain areas connected to the basal nucleus stria terminalis and the medial amygdala, (Vries et al., 1985, 1984). Based on these studies, peripheral AVP can be expected to correlate with corticosterone while it is at present not clear whether peripheral AVP might also correlated with testosterone.

AVP is an important modulator of social behavior, but its traditional physiological function is in osmoregulation (Bourque, 1998; Caldwell et al., 2008). Interestingly, arid areas, in which it is necessary to increase AVP secretion to reduce water loss, often are host to especially sociable species such as meerkats, Damaraland mole rats and naked mole rats (Clutton-Brock, 2005; Faulkes and Bennett, 2001). In prairie voles, peripheral AVP injection positively influences the formation of pair bonds only in males from dry areas but not from moist areas (Cushing et al., 2001). This may suggest that the environmental regulation of AVP secretion in response to water shortage could have a positive influence on sociality. In other words, the evolution of group-living in dry habitats might have been associated with environmentally induced AVP secretion.

The African striped mouse (*Rhabdomys pumilio*) in the Succulent Karoo semi-desert of South Africa is obligatory group-living during the dry hot season, which is characterized by both food and water shortage (Schradin and Pillay, 2004). However, this species shows high social flexibility during the moist and cold breeding season in spring (Schradin et al., 2012). Specifically, depending on population density, striped mice can either live solitarily, in small or in extended family groups (Schradin et al., 2010). Individuals of both sexes can adopt three alternative reproductive tactics (Schradin et al., 2012): (1) remain as non-breeding adult philopatric helpers at the nest; (2) disperse and become a solitary breeder (roaming males; solitary breeding females); or (3) communal breeding of females with one group-living breeding male. However, when the breeding season terminates and the hot dry non-breeding season begins, all striped mice become highly sociable and form groups: roamers will join solitary breeding females, while offspring will remain philopatric, staying with their mother long-after reaching adulthood, leading to the formation of family groups. It is therefore possible that an environmentally induced increase in AVP secretion at the end of the breeding season in response to increasing drought is a proximate cause of social change in this species. Laboratory studies have shown that solitarily-kept males do not differ in AVP receptor expression in different brain areas, making it likely that their brains are as responsive to AVP secretion as those of group-living males (Schradin et al., 2014). It has also been shown that solitary kept males have more AVP stored in their PVN than group-living males (Schradin et al., 2013). Thus, solitary males might be able to change their social behavior by increasing their AVP secretion, which could be induced by water scarcity due to increased drought at the beginning of the dry season.

In the present study we compared AVP levels during the breeding season in male and female African striped mice exhibiting alternative reproductive tactics. First, we predicted AVP levels to be higher in the dry season than in the moist breeding season, due to its important effect on osmoregulation. Second, if plasma AVP plays an important role in the regulation of social behavior, we expected significant differences between individuals following different tactics. Specifically we predicted solitary-living roaming males to have significantly lower AVP levels than group-living ones. We focused on males, as during the study few solitary breeding females were present at the field site. Third, as AVP has been reported to be stress reactive and testosterone dependent, we tested for significant correlations between AVP and the steroid hormones corticosterone and testosterone.

2. Materials and methods

2.1. Study species

Striped mice breed in the austral spring (August/September to November/December; (Schradin and Pillay, 2005a) and most individuals born during the breeding season remain philopatric as young adults (>6 weeks old) in their natal group, where they remain for the duration of the entire dry season (December–April) and the cold wet winter (May–July), reaching independent breeding status only the following spring. Typically, males will then disperse and attempt to immigrate into groups of communally breeding females, while females will remain in their group and breed communally. However, both sexes can also breed solitarily and individuals can leave their group at a young age of 4–6 weeks if free territories are available (Schoepf and Schradin, 2012), but often only leave when 1 year old in the next breeding season (Schradin et al., 2010). Group-living breeding males represent the bourgeois tactic with the highest reproductive success, philopatric males have the lowest reproductive success, while solitary-living roamers have low success when population density is high, but similar success to territorial breeders when population density is low (Schradin and Lindholm, 2011). It is important to note that some philopatrics may also be successful in reproducing (Schradin and Lindholm, 2011), a phenomenon that has been also reported for helping males in other species (Double and Cockburn, 2003; Young et al., 2007).

2.2. Study area

The study was conducted in Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60). Goegap lies within the semi-desert biome of the Succulent Karoo, which is characterized by cold and moist winters followed by spring with high food abundance and hot dry summers. In spring, the landscape is dominated by short-living ephemerals, which typically give way to succulent shrubs in summer. Blood samples were collected during the breeding season 2011 (September, October and November) and the following dry season in 2012 (January and February).

2.3. Plant surveys

Striped mice obtain their water from their food plants; in the Succulent Karoo both succulents and ephemerals (wildflowers) are important sources of water. Plant surveys were carried out on the 15th of each month on monitoring plots located within the home-ranges of eight different groups. Each plot covered an