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Absence of reproductive suppression in young adult female striped mice living in their natal family

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Alternative reproductive tactics of males have been studied in many species, but few studies have focused on females. In many communally breeding mammals, females can be adult nonbreeding helpers, leave the group and breed solitarily, or be a breeder in their natal group, representing three alternative reproductive tactics. The reasons for delayed breeding are not well understood, but in many sociable species both male and female helpers are reproductively suppressed. Male helpers of communally breeding striped mice, *Rhabdomys pumilio*, have increased corticosterone levels and delayed sexual maturation compared with their singly housed brothers. In the present study, we tested whether similar effects occur in female striped mouse helpers. In the field, young adult females typically do not breed in their natal group, indicating that they might be reproductively suppressed. Seventeen sister pairs from 17 family groups were studied. One sister of each pair was kept in the family group, while the other was housed singly at 3 weeks of age. Sisters did not differ in either the age at which they reached puberty (at 6 weeks on average) or in their corticosterone and progesterone levels. However, in neutral encounter tests, singly housed sisters showed more amicable behaviours when presented with unfamiliar striped mice of both sexes. Their high sociable motivation might explain why most females remain philopatric under natural conditions. We conclude that philopatric female striped mice in monogamous family groups are not reproductively suppressed, but reproductive competition might occur in natural communal groups with multiple old breeding females, as observed under high population density.

In many animal species, individuals have the choice between alternative tactics, which are regarded to be the result of adaptive decision processes optimizing individual fitness (Dawkins, 1980; Gross, 1996). For individuals of social species, one such decision could be to choose between remaining philopatric as a helper or dispersing and starting independent breeding (Koenig & Dickinson, 2008). Such alternative reproductive tactics are more common in males than in females (Taborsky, Oliveira, & Brockmann, 2008), perhaps because male reproductive success generally varies more between individuals than does female reproductive success. However, many sociable mammal species have nonbreeding female helpers (Solomon & French, 1997), providing a good opportunity to study the female tactics of helping versus dispersing and solitary breeding. In communally breeding species, more than one female breeds per group, and philopatric nonbreeding female helpers might remain in these groups to start reproduction at a later stage (Hayes, 2000).

This absence of breeding in young adult females could be due to physiological reproductive suppression, defined as highly increased glucocorticoid levels induced by the presence of dominant breeders causing social stress (Creel, 2001; Reyer, Dittami, & Hall, 1986; Wingfield & Sapolsky, 2003). High corticosterone levels lead to suppression of progesterone secretion, thus inhibiting ovulation (Clarke, Miethe, & Bennett, 2001; Saltzman, Ahmed, Fahimi, Wittwer, & Wegner, 2006). Reproductive suppression of subordinate female helpers occurs in several communally breeding species (Brant, Schwab, Vandenbergh, Schaefer, & Solomon, 1998; Getz, Dluzen, & McDermott, 1983; Solomon, Brant, Callahan, & Steinly, 2001).

Alternative reproductive tactics are characterized by behavioural differences between tactics, especially in reproductive and social behaviour. When some individuals disperse while others

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remain philopatric, they follow two alternative tactics that are also characterized by differences in the social environment: living in the natal group, living solitarily, or emigrating into and living in a group of nonkin. Thus, it is not well understood whether behavioural differences between tactics are primarily due to motivational (internal) differences between individuals of the two different tactics, or alternatively simply a consequence of the external differences in social environment: individuals living in groups can show amicable behaviours towards group mates; solitary individuals cannot. Therefore, to understand differences in social behaviour between alternative tactics, it is important to study social behaviour under standardized conditions, for example using a neutral presentation arena.

In African striped mice, *Rhabdomys pumilio*, both sexes have three alternative reproductive tactics (Schradin, Lindholm, et al., 2012): (1) philopatric helper; (2) solitary breeder; or (3) communal breeder. The group-living tactics 1 and 3 occur when population density is very high, the solitary tactic when population density is very low and all tactics under intermediate population densities (Schradin, König, & Pillay, 2010). Under low population density, both males and females can leave their natal group in the season of their birth when they are 4–6 weeks old to start independent breeding (Schoepf & Schradin, 2012a). Dispersing young adults were more aggressive towards individuals of the same sex compared with philopatric individuals and more amicable towards individuals of the opposite sex (Schoepf & Schradin, 2012b). In sum, free-living young adult striped mice can either be group living or solitary living, making this species a prime model to test for reproductive suppression using an experimental approach (Schradin, Eder, & Müller, 2012; Schradin, Schneider, & Yuen, 2009). Philopatric males are known to be reproductively suppressed by the breeding male of the group (Schradin et al., 2009), showing high corticosterone but low testosterone levels, small testes and low, if any, sperm counts (Schradin, Eder, et al., 2012). However, we do not know whether philopatric females are also reproductively suppressed, which could explain why many of them do not breed as young philopatric adults.

In the present study, we set up 17 family groups to mimic the philopatric and the solitary female tactic. From each family, two same-litter sisters were used, one of which remained philopatric with the family, while the other was housed singly after reaching 3 weeks of age, the earliest age at which dispersal occurs (Schoepf & Schradin, 2012a). This experimental design has been used previously and successfully mimics the philopatric and solitary tactics in male striped mice, inducing increased testosterone and decreased corticosterone levels in singly housed males (Schradin et al., 2009), increased levels of stored arginine vasopressin in the brain (Schradin, William, Krackow, & Carter, 2013) and enhanced testes development (Schradin, Eder, et al., 2012).

The present study had three aims.

(1) We tested whether reproductive suppression occurs in philopatric females by investigating whether they show delayed onset of puberty (measured as age of first perforation of the vagina, indicating their readiness to mate), higher corticosterone levels and lower progesterone levels. Such reproductive suppression would explain why most young philopatric females do not breed in nature.

(2) We determined whether living alone or in the family group was associated with differences in response to unfamiliar conspecifics. If the solitary tactic were due to an internal motivation to avoid the company of conspecifics, we would expect solitary females to be more aggressive, less amicable and more explorative than philopatric females.

(3) We further predicted that solitary females would show higher levels of amicable behaviour towards males, as solitary females would be more ready to mate while philopatric females would defend their family territories even against strange males.

METHODS

Study Species

The African striped mouse is a communal breeder with nonbreeding helpers at the nest (Schradin, Lindholm, et al., 2012). Groups consist of one breeding male (immigrated from another group), up to four closely related communally breeding females and up to 25 adult young male and female philopatric individuals that act as helpers at the nest (Schradin, Lindholm, et al., 2012). Striped mice breed in spring (August/September to November/December) and most individuals born during the breeding season remain philopatric as young adults (>6 weeks old) in their natal group, where they stay for the entire dry season (December–April) and the cold wet winter (May–July). Some of the young adult philopatric individuals are able to reproduce successfully in the season of their birth by mating with partners from outside the extended family group (males: Schradin & Lindholm, 2011; females: Schradin, Schneider, & Lindholm, 2010), but the vast majority of young adults that remain as philopatric individuals do not reproduce until the next breeding season when they are 1 year old (Schradin, Schneider, & Lindholm, 2010). At this age, males disperse and attempt to immigrate into groups of communally breeding females, whereas females remain philopatric in their group and breed communally. In both sexes, solitary breeding also occurs as an alternative tactic, and individuals can leave their group as young as 4–6 weeks of age when free territories are available (Schoepf & Schradin, 2012a). Fewer than 1% of striped mice survive for a second breeding season. Thus, most females breed only during one breeding season when they are 1 year old, and produce two to three litters during this breeding season.

Sexual Maturity

We conducted an experiment to confirm whether a perforate vagina was indicative of sexual maturity in our study species. At the University of the Witwatersrand, South Africa, we assessed the mating behaviour of 32 young females that had a perforate vagina for the first time by pairing them individually with sexually mature and experienced males. These females were housed in their family groups before pairing, and vaginal smears were examined daily from the day they were first perforate for a maximum of 4 days or unless they displayed oestrus.

For the smears, we used the pipette lavage method, which was minimally stressful and did not cause vaginal trauma in any of the females. The female was restrained with a glove and a small plastic pipette with a rounded tip containing a few drops of isotonic saline was inserted approximately 5 mm into the vagina. The fluid was expelled and immediately sucked up. The cell contents in the saline were transferred onto a clean microscopic glass slide. The procedure was repeated three times to ensure adequate numbers of cells. The procedure from restraining to release of the female was about 90 s. The slides were air dried and stained with Crystal Violet stain. The cell composition of the smears was evaluated by light microscopy for the relative abundance of cornified epithelial cells, leucocytes and macrophages. Smears were obtained in the morning before 0900 hours and females in oestrus (superabundant cornified epithelial cells; Byers, Wiles, Dunn, & Taft, 2012) were placed in a neutral tank with a mature male for 30 min at 1100 hours, and the occurrence of lordosis (female), mounting and intromission was recorded.