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Social cues elicit sexual behavior in subordinate Damaraland mole-rats independent of gonadal status

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ABSTRACT

Damaraland mole-rats (*Fukomys damarensis*) are among a small number of eusocial mammals. Eusociality is a social system where only a few individuals within a colony engage in direct reproduction, while remaining subordinate members are non-breeders and support reproductive efforts of breeding individuals. Inbreeding avoidance precludes mating between subordinate siblings and between offspring and parents. Interestingly, non-breeders readily attempt to mate with unrelated opposite-sex individuals. This is unusual since the non-breeding females do not attain puberty while in their natal colony. Based on this finding, the present study investigated the role of the gonads in the regulation of mating behaviors in this species and identified the mechanism of inbreeding avoidance. Gonadal-intact and gonadectomized non-breeders from different colonies were removed from their colonies and tested for the expression of sexual behavior. Results indicated that gonadal status had only minor effects on the expression of sexual behavior in either males or females. In a second experiment, sexual behaviors were absent between opposite-sex siblings so long as they had frequent contact with each other; however, following 5 weeks of separation, sexual behavior between these siblings was robustly expressed. Thus, Damaraland mole-rats avoid establishing mating relationships with familiar individuals but will readily mate with unfamiliar individuals of the opposite sex, with genetic relatedness apparently playing little role. The initiation of sexual behavior in Damaraland mole-rats does not require the presence of the gonads, but does require that the members of the pair have not been in contact with one another for at least several weeks.

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Introduction

Eusociality is a social/reproductive system in which animals form colonies that consist of overlapping generations of adults and where only a few individuals within the colony engage in direct reproduction; the remaining members are non-reproductive and engage in activities that support the reproductive efforts of the breeders. Eusocial systems have been most extensively studied in ants, bees, wasps, and termites and have also been described in certain species of aphids, beetles, gall thrips, and shrimp (Aoki, 1987; Crespi, 1992; Duffy, 1996; Kent and Simpson, 1992). At least two mammalian species meet the criteria for eusociality, naked mole-rats (*Heterocephalus glaber*) and Damaraland mole-rats (*Fukomys damarensis*). Both species are African mole-rats in the family Bathyergidae. Other members of the genus *Fukomys* may also qualify as eusocial, but their colony sizes are smaller than for Damaraland mole-rats, and they have been less studied (Bennett and Faulkes, 2000). Within colonies of Damaraland mole-rats, which can range from 2 to 41 individuals (Bennett et al., 1993), only a single female (often termed the "queen") and her male partner mate and produce offspring. The remaining colony members help raise the offspring and act as workers helping to forage, dig tunnels, and defend the colony (Jarvis and Bennett, 1993). As with other social bathyergids, Damaraland mole-rats are fossorial, and individuals are thought to emerge from their burrows only when dispersing from the colony (Bennett and Faulkes, 2000).

Attempts to characterize the mechanisms underlying reproductive suppression in subordinate female Damaraland mole-rats have yielded somewhat ambiguous results. One study suggested that removal of a non-breeding female from the natal colony results in her reproductive maturation, though with a time lag of several weeks (Molteno and Bennett, 2000). Remarkably, there is also some evidence that suggests that incest-avoidance within colonies may be so strong as to constitute a sufficient mechanism to prevent sexual activation of non-breeding females (Cooney and Bennett, 2000). The mechanism by which Damaraland mole-rats identify colony mates remains unclear. Among mammals different mechanisms can mediate kin recognition, including phenotype matching and prior association (or familiarity) (Mateo, 2003). Belding's ground squirrels (*Spermophilus beldingi*) employ phenotype matching, a system in which individuals identify related conspecifics based on comparing their own phenotypic cues, such as odor, with the cues of other individuals (Mateo, 2003). Prior association

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recognition can be based on familiarity: thus, individuals learn the phenotypes of siblings and parents during early development, and can later distinguish these familiar relatives from unfamiliar animals. Recognition by familiarity does not require that the individuals are genetically related, only that they were raised in close proximity. Kin recognition by prior association may be more likely in cases where relatives interact in environments that exclude non-kin, such as in exclusive burrow systems (Mateo, 2003). If inbreeding avoidance is an important mechanism in preventing the expression of sexual behavior within the natal colony, then the introduction of an unfamiliar individual into a colony should result in the expression of sexual behaviors in subordinate mole-rats. In support of this hypothesis, introduction of a foreign male into a colony of Damaraland mole-rats that had become reproductively quiescent following loss of the breeding female resulted in a renewal of sexual activity in formerly non-breeder females (Rickard and Bennett, 1997). Even more striking, introduction of a single unfamiliar male into a fully functional breeding colony of Damaraland mole-rats resulted in the rapid appearance of soliciting behaviors among non-breeding females, directed in all cases toward the unfamiliar male (Rickard and Bennett, 1997). In five of the 10 colonies so treated, one of the previously non-breeding females was the only female that continued to show sexual activity 3 weeks after introduction of the unfamiliar male (i.e., the status of the breeding queen in these five colonies was usurped; Cooney and Bennett, 2000).

The observations cited above indicate the importance of incest-avoidance as a determinant of sexual behaviors in Damaraland mole-rats (Jacobs et al., 1998). Taken together, these findings suggest that multiple mechanisms may act to keep females from breeding while in their natal colony. Regardless of the mechanism, female non-breeders, even after attaining a mature body size, fail to undergo puberty and exhibit unstimulated uteri and ovaries (Holmes et al., 2009). These females exhibit lower basal concentrations of luteinizing hormone and progesterone when compared to breeding females. Non-breeding females also fail to ovulate and do not exhibit sexual behavior while living within their natal colony (Bennett et al., 1993).

In order to maintain a supply of breeding animals, some non-breeding Damaraland mole-rats must be capable of becoming breeders. This is thought to be accomplished primarily via dispersal of non-breeders of both sexes from their natal colonies (Hazell et al., 2000) and the success of some of these dispersers in becoming breeders and establishing new colonies. When non-breeders are paired with opposite-sex conspecifics taken from a foreign colony, they usually exhibit mating behavior (Cooney and Bennett, 2000; B. Goldman and S. Goldman, unpublished data; Nice et al., 2010). It is remarkable that these females often mate within minutes following exposure to a foreign male since the unstimulated uteri of non-breeding females are indicative of very low levels of estrogen secretion. Female rodents typically require elevated estrogen for at least 18–24 h to permit the expression of mating behaviors (Pfaff and Schwartz-Giblin, 1988).

During development, differential exposure to sex steroid hormones in males and females results in the organization of certain neural tissues in a sex-specific manner (Cooke et al., 1998; Phoenix et al., 1959). Later in development these same sex steroid hormones activate the previously organized neural tissues resulting in sex-specific behaviors (Cooke et al., 1998; Phoenix et al., 1959). Given that non-breeding female Damaraland mole-rats are physiologically prepubescent yet do express sexual behaviors under certain social conditions, we hypothesized that an activational role of gonadal steroids in the expression of these behaviors may not be essential as it is in most mammals. It is well established that for most mammals testosterone is important for the stimulation of male sexual behaviors (Sachs and Meisel, 1988), whereas estrogen and progesterone are important for female sexual behaviors (Pfaff and Schwartz-Giblin, 1988). Thus, males and females of most mammals exhibit significantly reduced (or absent) sexual behaviors when sex steroid hormones are removed via gonadectomy (GDX), and treatment with exogenous sex steroids generally results in the return of sexual behaviors (Beach, 1976; Nelson, 2005; Pfaff and Schwartz-Giblin, 1988).

Two aspects of Damaraland mole-rat sexual activity were explored in the present study: First, since non-breeding females appear to secrete little estrogen yet were reported to exhibit sexual behavior when exposed to a male from another colony (Cooney and Bennett, 2000; B. Goldman and S. Goldman, unpublished data), we tested the hypothesis that the expression of sexual behaviors in Damaraland mole-rats is independent of the gonads. The role of the gonads in the regulation of reproductive behaviors in non-breeders remains unclear; however, inbreeding avoidance has been hypothesized to be sufficiently strong in DMR so as to contribute to the lack of reproductive behavior in non-breeding individuals. Second, we explored the mechanism underlying incest-avoidance by testing whether it was more dependent on genetic relatedness or on social familiarity.

Methods

Animals

Male and female Damaraland mole-rats from colonies at the University of Memphis (animals originally provided by Dr. Bruce Goldman at the University of Connecticut), approximately 2 to 3 years of age were used in the behavior tests (these rodents can live up to 15 years (Holmes et al., 2009)). Their diet consists of ad libitum sweet potatoes (EasyWay Produce) with dry rodent pellets (Harlan 2019, 19% protein diet) provided as a supplement. Colonies were maintained in caging systems that consisted of two different sized (60 × 40 × 20 cm) and (48 × 25 × 20 cm) polypropylene tubs with Plexiglas™ lids. The tubs for each colony were connected by lengths of extruded polycarbonate tubing. Cages contained a 1:1 mixture of corncob and pine bedding. All experimental procedures and husbandry were approved by the University of Memphis Animal Care and Use Committee and comply with the criteria established by the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

Role of the gonads in sexual behavior

Surgeries

Sixteen adult mole-rats (comprised of eight opposite-sex sibling pairs) from seven different colonies were anesthetized with an intraperitoneal injection of Ketamine/Xylazine/Acepromazine “cocktail” (0.0017 ml/g). An abdominal incision was made in the males to remove their testes. Bilateral dorsal incisions were made to remove the ovaries from the females. Incisions were sutured with surgical thread following the removal of the gonads. Lidocaine cream (4%) was applied topically to the incision site to ameliorate discomfort. After removal, the gonads were weighed to the nearest 0.1 mg. An additional 16 mole-rats (comprised of eight opposite-sex sibling pairs) from multiple colonies served as sham-operated controls; thus they were treated identically to the GDX group but the incisions were sutured without removing the gonads.

Sexual behavior

GDX animals were housed in isolation for 5 to 7 days following surgery to allow for recovery. During this time, we exposed siblings to each other for 10–20 min on alternate days, to maintain familiarity. After the animals had recovered from surgery, testing began. Animals were housed individually except during behavioral tests and during exposure to siblings every other day. Gonad-intact controls were also housed individually when not being tested, with the exception that intact animals that were siblings were housed together for 20 min on alternate days to maintain familiarity. This was done in preparation for the second experiment (below). We tested pairs of mole-rats by placing one GDX male and an unrelated (non-sibling) GDX female in a large arena (60 × 40 × 20 cm) for 20 min. This was done twice a week until all

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