Comments/Reflections

Anecdotal observation of a sexual encounter between two male naked mole-rats

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Abstract

Same-sex sexual behaviours (SSBs) are widespread across the animal kingdom, yet little consensus exists regarding their potential adaptive functions or evolutionary history. To fully address questions such as why or how a trait has evolved, it is important to first understand its natural history. Here, we present evidence of SSBs in two male naked mole-rats for the first time. Due to extreme natal philopatry, most naked mole-rats never disperse, making encounters with potential mates valuable in fitness terms. However, in captive colonies of naked mole-rats, a rare disperser morph has been described. We speculate that such dispersing individuals may be indiscriminatory in their mating strategy, copulating with conspecifics regardless of sex, to counter the risk of missed reproductive opportunities. This behavioural strategy would contrast with the common characterisation of naked mole-rats, which describes them as fiercely xenophobic and hostile to unfamiliar individuals. Further, the observation of an indiscriminate mating strategy in a species with limited opportunities for dispersal provides interesting context for the study of the evolution of SSBs.

Keywords

same-sex sexual behaviours, mating strategies, naked mole-rats, eusociality, dispersal, sexual evolution.

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1. Introduction

Sexual interactions involving members of the same sex (same-sex sexual behaviours; henceforth referred to as SSBs, following Monk et al., 2019) have been observed in a diverse array of taxa, from bugs to bonobos, worms to whales (Bailey & Zuk, 2009). The extraordinary array of SSBs observed in so many taxa has excited vigorous scientific debate, in no small part due to the ostensible paradox of selection for non-conceptive sexual behaviours. However, the fact that a trait appears to be costly does not mean that it has no adaptive value. Indeed, many traits provide overall fitness benefits despite conferring a cost to their carrier.

Research into SSBs tends to fall into one of two categories, examining either (i) the adaptive significance underlying these behaviours, or (ii) their proximate mechanisms. While non-adaptive explanations posit that SSBs can be a case of mistaken identity, a maladaptation, or an evolutionary by-product (Bailey & Zuk, 2009), adaptive explanations argue that SSBs serve an evolutionary function, such as assisting in the maintenance of social relationships (Mann, 2006; Annicchiarico et al., 2020) or by reducing intersexual conflict (Preston-Mafham, 2006; Grueter & Stoinski, 2016). Research on proximate mechanisms underlying SSBs is also wide-ranging, encompassing genetic (Zhang & Odenwald, 1995; Hoskins et al., 2015), hormonal (Adkins-Regan, 2002), and environmental factors (Adkins-Regan & Krakauer, 2000).

The naked mole-rat, *Heterocephalus glaber*, is a curious subterranean rodent that has received public and scientific interest for a number of unique traits, including its longevity (Buffenstein, 2005, 2008; Kim et al., 2011; Buffenstein & Craft, 2021), cancer resistance (Tian et al., 2013; Keane et al., 2014; Hadi et al., 2021), and extreme sociality (Jarvis, 1981; Jarvis & Bennett, 1993). Naked mole-rat groups display the most extreme reproductive skew seen in any mammal, with up to 99% never reaching full reproductive maturity (Sherman et al., 1992). Instead, they remain as non-breeding workers in their natal group, assisting the reproductive attempts of kin (Jarvis, 1981; Faulkes et al., 1997; O’Riaín & Faulkes, 2008).

The majority of naked mole-rat colonies have one breeding female and one to three breeding males (Jarvis, 1981, 1991; Lacey & Sherman, 1991; Faulkes et al., 1997). All other individuals are physiologically suppressed and do not exhibit any sexual behaviours (Faulkes et al., 1990, 1991; Faulkes & Abbott, 1991), apart from a distinct ‘disperser’ morph. Dispersers were identified as having additional fat reserves, an eagerness to leave the burrow...
system (in captive studies), breeder-levels of luteinising hormones (at least in males), and, unlike other non-breeders, solicit matings when introduced to unfamiliar individuals (O’Riain et al., 1996; Holmes & Goldman, 2021). Encounters between unfamiliar individuals are most likely between two dispersers, or a disperser and a foreign colony, but are thought to occur rarely in wild populations (Braude, 2000; Buffenstein & Craft, 2021).

O’Riain et al. (1996) noted that captive dispersers preferred to spend time with unfamiliar conspecifics of either sex, perhaps indicating that familiarity is more important than sex in determining social behaviour between dispersers. The descriptions of sexual behaviours in the naked mole-rat ethogram (Lacey et al., 1991) refer exclusively to interactions between different-sex individuals. Opportunities for SSBs in naked mole-rats are limited and, as far as we are aware, have never been reported. While SSBs have received relatively little scientific interest in general (Roughgarden, 2013), it is possible that previous observations of SSBs were not recorded because they did not match any of the behaviours described in the ethogram. Here, we report the first observations of same-sex sexual behaviours in captive naked mole-rats, and discuss the implications for our understanding of dispersal behaviour in this species.

2. Study site and subjects

2.1. Animals observed

The animals in this report are maintained in captivity at Queen Mary University of London. Institutional guidelines were followed throughout. The animal husbandry and behavioural observation methods used in this study are described in Gilbert et al. (2020). Briefly, the animals are descendants of individuals wild-caught in Kenya during the 1980s. All colonies are kept in separate networks of acrylic tunnels and boxes in a single room maintained between 26–34°C. Light and noise levels vary with human activity in the surrounding rooms and corridors, and animals are fed ad libitum every day.

Animal 1 (i.d. 052-370-362), a previously non-breeding male, 5 years-old at time of observation, was paired with a previously non-breeding female (i.d. 025-030-049, 17 years old) to form colony 20A on 6th February 2020 because the female had been fighting in her former colony. Animal 2 (i.d. 109-256-061), a 13-year-old non-breeding male, was removed from his colony and housed singly on May 7, 2021 after receiving aggression from
others in the social group. Naked mole-rat non-breeders quickly show signs of reproductive activation on removal from their natal group (Faulkes & Abbott, 1993; Smith et al., 1997; Swift-Gallant et al., 2015). Although neither animal had previously been identified as breeders or dispersers, it is likely that by the time we observed the behaviours reported here, Animal 1 had reached sexual maturity, while Animal 2’s reproductive status was unknown. Both animals subsequently lived in a new colony with the aforementioned female (025-030-049) until December 2021, with no aggression or pregnancies recorded during their co-habitation.

2.2. Filming protocol

On May 12, 2021, we introduced Animal 2 to Animal 1 by removing Animal 1 from colony 20A and placing him in the temporary housing box of Animal 2. We recorded five videos of the interaction on a Huawei P20 (EML-L09) mobile smart phone that occurred over a period of approximately 20 min. Videos of the interaction are available in the supplementary material at 10.6084/m9.figshare.19376090.

2.3. Behavioural analysis

Sexual behaviours were identified using descriptions from a classic ethogram of naked mole-rat behaviours (Lacey et al., 1991). Specifically, we noted instances of the male-male equivalent of three behaviours: mounting, copulating, and ano-genital nuzzling (Table 1).

3. Observations

3.1. Ano-genital nuzzling

Ano-genital nuzzling (Figure 1) is the most common behaviour we recorded between the two males. In Video 1, the animals lie head-to-tail for 30 s, sniffing and nuzzling each other’s genitals throughout. Head-to-tail mutual ano-genital nuzzling can also be seen in Videos 2, 3 and 5 at 10.6084/m9.figshare.19376090.

3.2. Mounting and copulating

We also recorded one male trying to mount the other several times, using his front paws to gain position before pelvic thrusting (Figure 2). In Video 1 at 10.6084/m9.figshare.19376090 (8–10 s), the animal on the left mounts
Table 1.
Description of typical naked mole-rat sexual behaviours.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mounting</td>
<td>Male “exhibits a pedaling motion of the hind legs as he attempts to bring his genitals into contact with those of the female”</td>
<td>Lacey et al. (1991), p. 229</td>
</tr>
<tr>
<td>Copulating</td>
<td>“contact between the genitalia of the male and female. Pelvic thrusting by the male is observed just before and during copulation. Ejaculation is not obvious. Copulations last less than 15 s, after which the male dismounts.”</td>
<td>Lacey et al. (1991), p. 229</td>
</tr>
<tr>
<td>Ano-genital nuzzling</td>
<td>“an animal of one sex sniffs and uses its muzzle to nudge the genitalia of an animal of the other sex. One animal may mount the head of another, so that the genitalia of the animal on top are in contact with the muzzle of the animal on the bottom. More commonly, both animals lie on their sides, head-to-tail, such that the genital area of each is in constant contact with the muzzle of the other” “Unless there is colony strife (…), ano-genital nuzzling and sniffing occurs only occasionally between the breeders and a few other colony members (of both sexes) and among these other colony members (both sexes)”</td>
<td>Lacey et al. (1991), p. 235</td>
</tr>
<tr>
<td>General mating</td>
<td>“Mounting appears clumsy. The male climbs onto the back of the female, grips her flanks with his forefeet, and often kneads her back or sides with his hind feet. His back is strongly arched, and he tucks the posterior part of his body to one side and partly under the female as intromission is attempted. The male does not bite the female’s neck, and he often falls off the female while attempting to mate. It seems likely that mating in the wild occurs in the confines of a narrow, rough-surfaced burrow where the burrow walls would help keep the male atop the female.” “Other colony members are not solicited by the female when she is in estrus and show no apparent reproductive interest in her when they meet in the burrow or nest. Mating occurs primarily in the tunnels and only occasionally in the nest box.”</td>
<td>Jarvis (1991), p. 393</td>
</tr>
</tbody>
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the head of the other and tucks the posterior part of his body to thrust his pelvis, as is typical during copulation (Table 1), before returning to ano-genital nuzzling head-to-tail. In Video 4 at 10.6084/m9.figshare.19376090 (4–8 s), the male in the foreground mounts the shoulder of the other briefly before falling off. This is in-keeping with typical naked mole-rat different-
Figure 1. Ano-genital nuzzling. Animal 1, on the right in these images, is larger and has darker colouration on his back.

sex sexual behaviour, whereby “the male does not bite the female’s neck, and he often falls off the female while attempting to mate” (Jarvis, 1991: p. 393). Somewhat unsurprisingly, this has led naked mole-rat mating behaviour to be characterised as “clumsy” (Jarvis, 1991: p. 393). In Video 4 at 10.6084/m9.figshare.19376090 (19–21 s), the same male tries to mount again, using his forelegs to position himself.

3.3. Erections

Genital mounds are similar in naked mole-rats of both sexes, including breeders (Peroulakis et al., 2002; Seney et al., 2009). However, we observed both individuals had pink, erect penises during the observation period (Fig-

Figure 2. Animal 2 attempts to mount the front of Animal 1 (left, centre panels) and arches his back to thrust his pelvis (right panel).
Figure 3. Naked mole-rat genital mounds are normally the same colour as adjacent skin (top left). During sexual activity, erect penises may appear pink in different-sex (top right) and same-sex (bottom) pairs.

4. Discussion

Here we report the first evidence of SSBs in naked mole-rats. Besides adding to the growing number of species for whom SSBs have been described, this
finding contributes to our understanding of naked mole-rat social and sexual behaviour in a number of interesting ways.

Naked mole-rats are considered to be highly xenophobic (Lacey & Sherman, 1991; O’Riain & Jarvis, 1997) and are often aggressive towards unfamiliar conspecifics (Smith & Buffenstein, 2021). This defensive behaviour generally refers to in-colony situations, where aggression is used to defend the burrow from rivals or predators. Field data already show that naked mole-rat colonies can be formed by new pairs (Braude, 2000), so flexibility in responses to unfamiliar individuals must exist. The circumstances of the introduction reported here were completely artificial, but it is still noteworthy that these two individuals greeted each other with clear excitement before engaging in sexual behaviours.

Our evidence shows ano-genital nuzzling between two males along with instances of pelvic thrusting, a behaviour normally only seen during mating (Lacey et al., 1991). The use of the forefeet to gain position and pedalling back feet seen in Videos 1 and 5 strongly suggest the animals were performing SSBs as well as ano-genital nuzzling. Ano-genital nuzzling is thought to assist the recognition of reproductive status rather than to constitute a mating behaviour itself (Holmes & Goldman, 2021), although here it occurred during a period of same-sex sexual activity. Ano-genital nuzzling mostly occurs between queens and reproductive males but can occasionally occur among other colony members (Jarvis, 1991). However, to our knowledge pelvic thrusting and mounting have never been reported between two males. The ano-genital nuzzling and pelvic thrusting between two newly introduced males may demonstrate context-dependent use of these behaviours.

These observations could be an example of indiscriminate SSBs in a species that generally has limited opportunities for mating with individuals from other colonies. In the wild, two reproductively-mature animals encountering one another would need to find a nest and reproduce quickly to establish a viable colony. An indiscriminate mating strategy would reduce the risk of missing a valuable mating opportunity due to incorrectly identifying the sex of a potential partner. This fits with what is known of dispersing naked mole-rats, who prefer to spend time with unfamiliar individuals of either sex, while non-dispersers prefer to spend time with colony-mates (O’Riain et al., 1996). The same study found that dispersers readily copulated with unfamiliar conspecifics and had hormone levels comparable to breeding males, suggesting they were primed for mating opportunities when still living in the
colony. Pups born to small colonies appear to gain weight faster than those born to established colonies (Jarvis et al., 1991), which may reflect the urgent need to establish a workforce of non-breeders. All of these traits may allow dispersers to quickly form new colonies on encountering a conspecific.

Naked mole-rat behaviour has been observed extensively in captive colonies, but little is known of behaviour that occurs outside of the colony, especially in the wild. That SSBs have not been reported indicates that they are rare between colony-mates, but future research may reveal them to be more common among dispersing individuals. In the present study, one animal had been housed singly for several days after receiving aggression in his previous colony, suggesting he may have been experiencing some degree of reproductive activation. The other animal had been housed with a single female for over a year, and while they had not produced any pregnancies, it is possible that he was also reproductively active. It is notable that these two unfamiliar males engaged in SSBs but did not impregnate the female in colony 20A in the 18 months following their introduction. While we do not have the behavioural or physiological data required to confirm whether these males possessed other traits typical of the disperser phenotype, this behaviour is consistent with both males being dispersers that will readily mate with unfamiliar individuals, but would not solicit matings from the reproductive female of their own colony (O’Riain et al., 1996).

Evolution may favour less discriminatory mating strategies when encounters with potential mates are rare (Lerch & Servedio, 2021). Different-sex sexual behaviours may depend on an imperfect ability to determine the sex of any potential partner, meaning some opposite-sex mates will be rejected and some same-sex mates accepted. Crucially, whether the threshold of acceptance for potential mates should be more restrictive or permissive varies according to a number of factors, such as the encounter rates with different partners (Reeve, 1989; Monk et al., 2019). Research suggests that males of certain species engage in more SSBs when the time spent searching for females is higher (Hoving et al., 2012; Engel et al., 2015; Bonnet et al., 2016). Observations of SSBs in a species that has few opportunities for dispersing makes an interesting contribution to this discussion.

References


Smith, T.E., Faulkes, C.G. & Abbott, D.H. (1997). Combined olfactory contact with the parent colony and direct contact with nonbreeding animals does not maintain suppression

