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To mate or not to mate? Mate preference and fidelity in monogamous Ansell's mole-rats, *Fukomys anselli*, Bathyergidae

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Abstract. According to a hypothesis addressing the evolution of eusociality in mole-rats, the female (queen) is not able to raise her (first) offspring without a mate and thus to found a family. Therefore, we predict that the reproductive male (king) has to be socially faithful. In this study we tested this prediction and addressed the related question whether or not the presentation of a new female provokes enhanced sexual interest in male Ansell's mole-rats (*Fukomys anselli*).

We performed behavioral partner preference tests in Ansell's mole-rats where two animals of choice were presented to a subject without allowing direct access. The kings spent significantly more time sniffing an unfamiliar queen or female than their own mate. If given the choice between an unfamiliar queen and her respective non-reproductive daughter, however, the tested kings significantly preferred the queen. In contrast, queens did not show a preference for either their own mate, an unrelated unfamiliar king, or a non-reproductive male.

In a second experiment, we allowed the males to access the compartment of an unfamiliar female while their respective family stayed in an adjacent compartment. Only the non-reproductive adult males seized their chances to copulate with the unfamiliar female whereas the kings remained faithful. When reversing the test condition (i.e. females were given access to an unfamiliar male), aggressiveness of the males impeded sexual encounters in most cases. We recorded only three copulations, all of them between queens and non-reproductive males.

We conclude that the reproductive status is crucial for reproductive decisions. Furthermore, the presence of family members influences the kings' behavior. Since in Ansell's mole-rats, repeated copulations over a longer period of cohabitation are necessary for ovulation and fertilization, the kings' sexual fidelity could have been expected. We postulate that the maintenance of Ansell's mole-rats' families depends on the kings' faithfulness.

Key words: monogamy, eusociality, extra-pair copulation, fidelity, mate choice, African mole-rats

Introduction

Monogamy, a pair-bond that is lasting for one breeding period or longer, is a rather uncommon phenomenon in mammals (Kleiman 1977). In fact, the term monogamy has a dual character – it represents both a mating and a social system, and it seems necessary to discriminate between social monogamy (founding a stable pair-bond), and sexual/genetic monogamy (i.e.

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sexual/genetic fidelity) (Reichard 2003). As a mating system, monogamy may constrain fitness of both, males and females. For the male the number of his potential offspring is limited by his commitment to a single female partner, for the female (but so also for the male) choosing "good genes" for instance is restricted to a single reproductive bout per breeding season or even per whole life. Therefore it is not surprising that many bird species formerly regarded as truly monogamous have been found to engage regularly in extra-pair copulations (e.g. Birkhead & Møller 1995, Westneat & Stewart 2003). Although still not studied as well as in birds, extra-pair copulations in mammals are certainly not uncommon, either (e.g. Reichard 1995, Solomon et al. 2004, Cohas et al. 2007). In fact, sexual fidelity seems to be so rare that it is worth noting (Barash & Lipton 2001).

Monogamy is a foundation and prerequisite of two social systems: the family (with or without helpers; Solomon & French 1997) and its extended form, eusociality, which – in mammals – is represented by a multigenerational family, and is defined by three aspects: reproductive division of labor, cooperative care of young, and lifelong philopatry of most offspring (Burda et al. 2000). Thus far, eusociality among mammals has been identified in a few rodent species including Zambian mole-rats of the genus *Fukomys* (e.g. Burda et al. 2000).

Burda (1990) argued that female mole-rats are not capable of raising their offspring alone and are therefore dependent upon the assistance of their partner (or other family members). Furthermore, it was shown that the apparent "sterility" of non-breeders in the family of *Fukomys* mole-rats is due to their "voluntary" sexual abstinence which in turn is due to incest avoidance (Burda 1995). Subsequently, incest avoidance among family members and outbreeding as a system of mating were identified also in other species of *Fukomys* mole-rats (Rickard & Bennett 1997, Herbst & Bennett 2001) as well as in naked mole-rats (Braude 2000, Ciszek 2000). In fact, it has been repeatedly pointed out by students of mole-rat biology that unfamiliar mole-rats of opposite sex, even if classified as "sterile helpers", are prone to mating whenever given the chance, and that the breeding pair is regularly and frequently sexually active (cf. Burda 1995, Dammann & Burda 2006). The encounter of two unfamiliar mole-rats of opposite sex is typically followed up by an extended period of courtship and repeated mating. Apparently a longer cohabitation with regular mating is necessary for inducing ovulation and to guarantee fertilization (Willingstorfer et al. 1998, Burda 1999); and, indeed, females showed a peak in estradiol and progesterone levels 1-4 days after mating (Hagemeyer et al. 2009). This is how a new mole-rat family may be established in the field, e.g. at the periphery of extensive burrow systems. An important prerequisite is however, that both partners are not accompanied by other family members, since unfamiliar mole-rat intruders are immediately attacked by animals of the same sex (own observation in the laboratory).

Nevertheless, in established pairs this readiness to mate with strangers would be fatal, because an abandoned female may not be able to rear her offspring on her own (note long pre- and postnatal developmental times in mole-rats, cf. Burda 1989, Begall & Burda 1998) combined with the females' inability to store effectively body fat (Burda 1999). Therefore, her partner needs to be socially faithful. Sexual infidelity may still occur, although singular copulations are not sufficient to guarantee ovulation and fertilization. Sexual infidelity (extra-pair copulation) would lead to fitness enhancement only if a new partnership was established, which, in turn presumes social infidelity (= abandoning the former partner). On the other hand, sexual fidelity of the breeding female partner is not a prerequisite. Matter of fact, a female should be "interested" in a faithful partner, while she herself may enhance her fitness by copulating with strangers. Under natural conditions she may not have too many chances – at least during lactation she probably stays mostly in the nest, being accompanied and hence being guarded by her mate and adult offspring that are aggressive to intruders.

Several studies deal with patterns of genetic relatedness in families of (eu)social mole-rats. Burland et al. (2002) showed that, consistently with the previous experience from laboratories, most breeding pairs in wild colonies of *Fukomys damarensis* are indeed unrelated. This finding confirmed the previous theoretical argument by Burda (1999) and Burda et al. (2000) that eusociality represents an extended monogamy and levels of genetic relatedness (coefficient of relationship) of the offspring achieved by means of monogamy are both a required and sufficient precondition of eusociality in mammals. On the other hand, high levels of extra pair paternity (i.e. extra-colony kings/subordinate males being the sires) were found in social *Cryptomys hottentotus* (Bishop et al. 2004) thus challenging the role of kin selection and genetically based altruism in maintaining cooperative societies. The core of the problem here is that the non-reproductive altruistic offspring benefit less than

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expected because the profits for helping to raise half-brothers and half-sisters are comparably low.

The social system of *Fukomys* mole-rats is apparently more cohesive than that of *Cryptomys* (cf. Bennett & Faulkes 2000, Kock et al. 2006), and we predict that the kings have to be faithful. The question arises whether the faithfulness is intrinsically based (evolutionarily fixed) or whether it is just imposed by extrinsic factors, i.e. lack of opportunities for extra-pair copulations (which are expected to be rather rare in xenophobic mole-rats). In other words, does the presentation of a new female provoke enhanced sexual interest in males (also known as "Coolidge effect", described in several species, Brown 1974, Dewsbury 1981)? Specifically, we examined the preferences in mate choice with respect to reproductive status and/or age in Ansell's mole-rats, subterranean rodents of the family Bathyergidae, living in (eusocial) multi-generational family groups (cf. Burda et al. 2000). Furthermore, we tested the fidelity of the reproductive animals and how likely they are to engage in extra-pair copulations and abandon their respective partners. The same experimental set-up was used to investigate the readiness of non-reproductive mole-rats to copulate with unfamiliar animals.

Material and Methods

Animals and housing

Zambian mole-rats of the species *Fukomys anselli* (in previous studies referred to genus *Cryptomys*, cf. Kock et al. 2006) involved in this study were either born in captivity or had been captured in the field and kept in the laboratory for at least two years so that their breeding and family status are well documented. The animals were housed in glass terrariums of various sizes (according to the size of the family) at the animal room of the Department of General Zoology at the University of Duisburg-Essen, Germany under natural day-light conditions. Horticultural peat is used as substrate in the cages and the animals are fed *ad libitum* with carrots, potatoes, cereals, apples and lettuce. Nesting and enrichment material (e.g. tissue paper, tubes, nest boxes) are also provided. All animals are individually marked with subcutaneously implanted micro transponders (Alvic-transponder, ISO-standard 11784, by Alvetra GmbH, Neumuenster, Germany). The tested animals were separated from their respective families only for the duration of the experiments and returned to their home cages immediately after. The animals are accustomed to handling.

All tests were conducted in a separate room, i.e. not inside the animal room, but at the same ambient temperature and light regime.

Experiment 1: preference tests

Test apparatus

The two-choice-labyrinth, made of transparent Perspex®, consisted of the start box (25 cm × 25 cm × 25 cm) in the middle of the labyrinth, which opened to two arms (40 cm × 15 cm × 10 cm) that were terminated at boxes (20 cm × 20 cm × 20 cm) (Fig. 1). Entrance to the arms was controlled by removable sliding doors. The terminal boxes were permanently separated from the arms by perforated metal plates (2.6 apertures of 0.5 cm × 0.5 cm per cm^2). After each trial, the labyrinth was thoroughly washed with a mild detergent and acetic acid (3 %) to remove any odorous traces.

Tested animals and test design

Altogether 68 adult Ansell's mole-rats (12 kings, 12 queens, 20 non-reproductive males, 24 non-reproductive females) from 19 families were

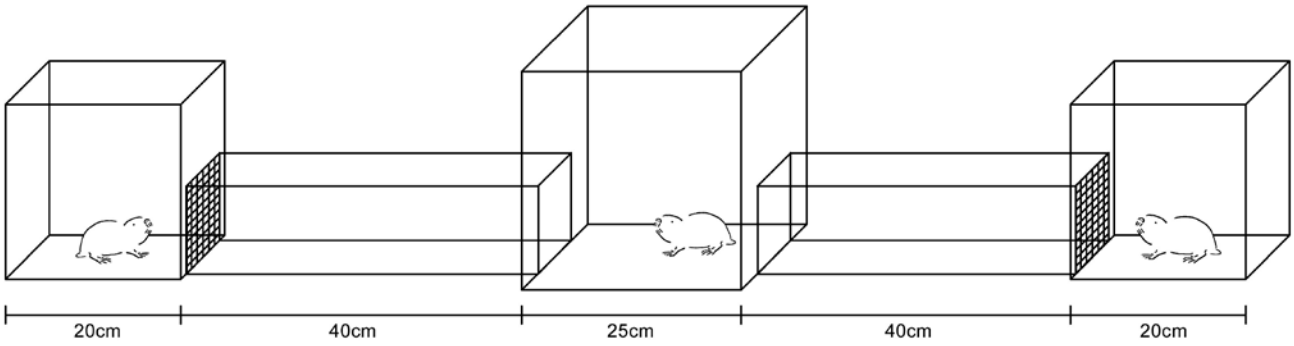


Fig. 1. *Two-choice-labyrinth used in the preference test. The animals of choice stayed in the terminal boxes that were separated by metal grids from the arms of the two-choice-labyrinth. At the beginning of the experiment, the choosing animal was put into the start box (middle) and was allowed to explore both arms, i.e. it could move freely within the arms of the labyrinth.*

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confronted with two animals of opposite sex differing either in the level of familiarity, the reproductive status, or age. None of the tested subjects had been used in partner preference tests before, they were not related to the animals of choice, and each animal was tested only once per condition. When animals were used as subjects in different conditions (cf. Table 1; mean number of tests per subject 1.4 ± 0.6), testing conditions were randomized and trials were separated by intervals of at least four weeks, i.e. a sufficient time to forget even genetically related and familiar individuals (cf. Burda 1995). At the beginning of each preference test, two same-sex animals of choice were randomly assigned to the terminal boxes (one animal per box), while the subject (the "choosing" animal) was placed in the start box. The three animals were allowed to acclimate for two minutes inside their respective boxes before the two sliding doors of the start box were removed simultaneously and the subject could move freely in both arms (pilot studies revealed that a longer acclimatization time in the small box resulted in stress). The animals of choice inside the terminal boxes could be perceived (via smell, acoustic communication) but direct encounter was impossible due to the grid partition. (Previous studies using habituation-discrimination tests showed that Ansell's mole-rats are able to discriminate members of their own family from same sex strangers on the basis of anogenital odors – Heth et al. 2002, Hagemeyer et al. 2004). During every 30 min test session the sniffing time, defined as the time the subject spent near the terminal boxes of each animal of choice (with its nose being within a distance of 1.5 cm from the grid), was measured with two stop watches. Furthermore, the number of positive responses of the subject towards each animal of choice was noted per minute. As positive behavioral responses we counted approaching, twitter vocalizations, i.e. typical contact calls especially in sexual aroused mole-rats (Credner et al. 1997, Schleich et al. 2007), and agitated quivering which is often combined with the pattering of the hind feet and also displayed in the context of sexual arousal (personal observation).

We tested the animals under several conditions (Table 1). In condition 1 we tested whether the subjects (10 kings, 10 queens) spend more time near an unfamiliar reproductive animal of opposite sex than near its own mate. We used reproductively active animals as subjects in condition 2 as well (8 kings, 8 queens): this time the animals had the choice between their own mate and an unfamiliar opposite-sex non-reproductive animal. Condition 3 was designed to test whether mole-rats differentiate between unfamiliar breeders and non-breeders (both unfamiliar animals being members of one family, i.e. a parent and her/his offspring). We tested 8 kings, 8 queens, 10 non-reproductive males and 10 non-reproductive females as subjects. Using condition 4 we wanted to test whether the age of the animals of choice had an effect on the decision of the subjects (8 non-reproductive males, 7 non-reproductive females). The animals of choice were unfamiliar non-reproductive siblings with a mean age difference of 28.5 ± 9 months SD (range of age difference: 21-57 months). Control experiments (condition 5) have been conducted to exclude position effects (i.e. labyrinth side preferences independent of the type of stimulus animal that was placed there). For the control experiments, we used same-sex twins as animals of choice and 8 non-reproductive males and 8 non-reproductive females as subjects.

Statistical analysis

Since all data sets were normally distributed (Kolmogorov-Smirnov with Lilliefors correction; $p > 0.05$), paired t-tests have been applied to detect significant differences between the times the subjects spent near the grids of the two animals of choice. To compare the mean number of positive responses the tested animal displayed toward the two animals of choice, we used the Wilcoxon matched pairs test. All means are given as $\bar{x}$ ± SD. All statistical analyses were conducted with PASW (version 18).

Experiment 2: fidelity tests

Test apparatus

Condition 1: The tests with a complete family and a female as lure were carried out in a standard plastic

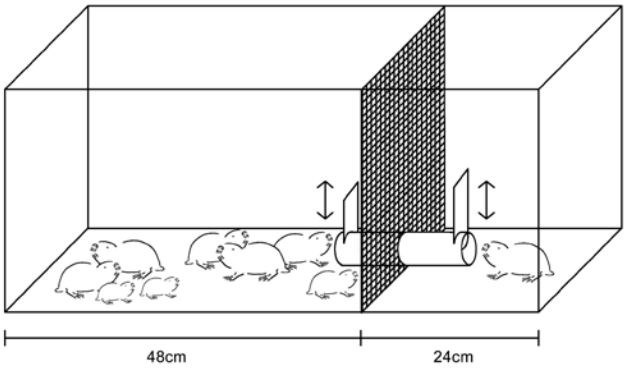


Fig. 2a. *Test apparatus used for testing the fidelity of Ansell's mole-rats. The complete family was put into the bigger compartment whereas a separate extra-colony female used as lure stayed in the smaller compartment.*

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laboratory rat cage (72 cm × 46 cm × 30 cm) that had been divided into two compartments of 2/3 and 1/3 by means of a perforated metal plate (2.6 apertures of 0.5 × 0.5 cm per cm^2). A plastic tube (4.6 cm diameter, 16 cm length) with sliding doors at each end was inserted into the middle of the perforated metal plate level with the cage floor, half of the tube reaching into the bigger and half into the smaller part of the cage (Fig. 2a).

Condition 2: The tests with a complete family and a male as lure were carried out in two standard plastic cages (72 cm × 46 cm × 30 cm) that had been connected by three plastic tubes (4.6 cm diameter, 35 cm length) with sliding doors at each end (Fig. 2b). The test design was changed to this arrangement because of a high level of stress and aggressiveness of the males during pilot studies when a cage as is shown in Fig. 2a was used. All cages were supplied with a layer of horticultural peat, food, and nesting material.

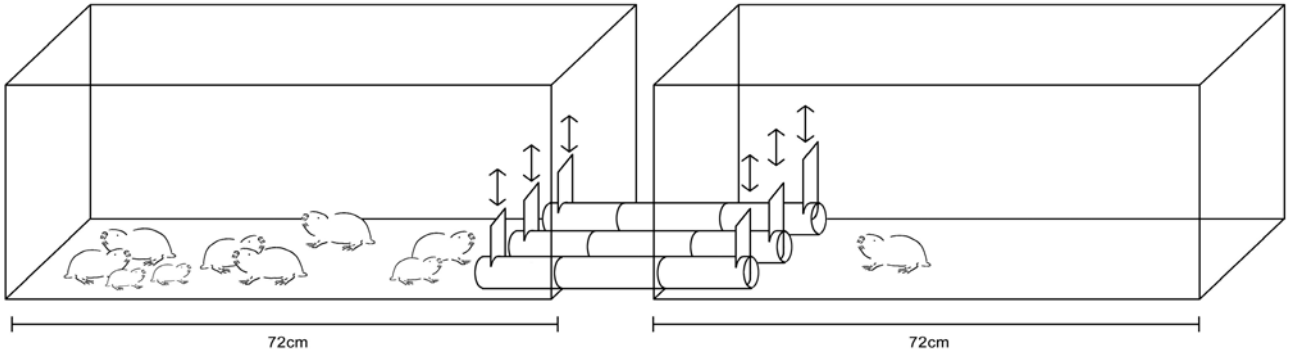


Fig. 2b. *Test apparatus used for testing the fidelity of Ansell's mole-rats. In this test setting only males were allowed to enter the extra-colony females' compartments via manually operated sluice tubes. When males were used as lure, aggressiveness of all animals was rather high. We therefore constructed a different apparatus with two equally sized cages.*

The tested families were placed in the bigger compartment of the test cage (or in one of the connected cages respectively) for at least 24 h before the test trial started, to allow the family to settle down. After each trial, the test cages were thoroughly washed with a mild detergent and acetic acid (3 %).

Tested animals and test design

Condition 1: Nine entire families (with an average of 8 ± 4 family members; range: 3–13) of Ansell's mole-rats were indirectly confronted with an unfamiliar adult female (n = 16) of a different family as lure. Half of these females were queens (n = 8), the other half non-breeders (n = 8), and their order was randomized. Every family was tested 2-3 times (making a total of 23 experiments), each time with a different unfamiliar female. The males were categorized by age and reproductive status: non-reproductive young (12-18 months of age; n = 18), non-reproductive adult (> 18 months of age; n = 13) and reproductively active (the king being the only reproductive male of the family; n = 9). None of the tested animals had been exposed to each other before (i.e. in experiment 1).

At the beginning of the experiment, an unfamiliar female was placed into the smaller compartment of the test cage and allowed to acclimate for 15 minutes. Then, the males of the tested family (all being at least 12 months old) were allowed to access the unfamiliar female via the sluice tube. To prevent females from accessing the compartment with the unfamiliar mole-rat, the sliding doors of the sluice tube were operated manually – opening and closing only for males. The males were thus allowed to travel back and forth between the compartments. Two or more visits of an individual during the same trial have been counted as one event (longer encounters would be underestimated if all events (short visits) were counted within a single trial and besides it would result in the same constellations being counted repeatedly). Only one male at a time was allowed to access the unfamiliar female. The order of the males' entry into the female's compartment after habituation was randomized. The unfamiliar female was not allowed to access the family compartment. The operation of the gates was silent and moving animals did not show any reaction to the gate operation.

During each trial, the behavior of the visiting male was recorded and categorized as either sexual (pre-copulatory behaviors like sniffing the other animal's anogenital region, agitated quivering, vocalizations, lordosis, mounting, and copulations), agonistic, or neutral behavior (like digging or resting). In the case of serious aggression between two mole-rats, the animals were separated to avoid injuries, and the male

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was returned to the cage compartment of the family. Each trial was finished after 120 minutes and all animals were returned to their respective home cages. Condition 2: Five complete families (with an average of 10 ± 4 SD family members; range: 7-13) of Ansell's mole-rats were indirectly confronted with an unfamiliar adult male of a different family as lure. Here, every family was tested 3-6 times (25 trials in total), each time with a different unfamiliar male (n = 18, 7 of these were kings, 11 non-breeders, and the order was randomized). Six trials were interrupted before the regular time ended, because the males (seldom the females) were highly aggressive. The second set of experiments followed the protocol for condition 1, except that we used a different test apparatus (Fig. 2b), and that only females were allowed to visit unfamiliar males via sluice tubes. The females were categorized by age and reproductive status (cf. condition 1). None of the tested animals had been exposed to each other before (i.e. in experiment 1).

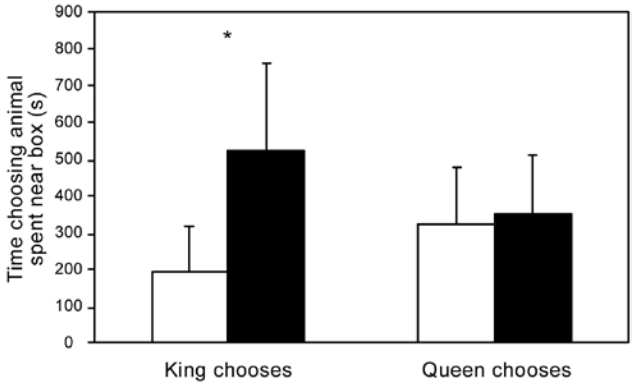


Fig. 3. *Condition 1 (preference test): King chooses: Mean times ($\bar{x}$ ± SD) kings spent near the terminal boxes of the two-choice-labyrinth containing their own mate (white bar) and an unfamiliar queen (black bar). Queen chooses: Same condition with queens as subjects (= choosing animals) and own mate (white bar) versus unfamiliar kings (black bar) as animals of choice. Asterisk indicates a significant difference.*

Statistical analysis

Differences between the mean times the male mole-rats spent in the unfamiliar female's compartment have been analyzed with the Kruskal-Wallis-test (comparison between the three groups: adult and reproductively active, > 18 months and reproductively non-active, < 18 months and reproductively non-active). The Fisher's exact test was used to compare the number of reproductive and non-reproductive males that were engaged in copulations during the visits. Means are given as $\bar{x}$ ± SD, and all statistical analyses were conducted with PASW (Version 18). For condition 2 of the fidelity tests this analysis was not possible because too many trials had to be interrupted. The Fisher's exact test was used in condition 2 to compare the number of older and younger females that were aggressive towards the unfamiliar males.

Results

Experiment 1: preference test

During each 30-min trial, all subjects entered both arms of the labyrinth, generally changing sides several times (the subjects visited each arm at least five times). Mole-rats approaching conspecifics in the terminal boxes displayed either affirmative behaviors (e.g. sniffing, twitter vocalizations, quivering), defensive (e.g. fast retreat, teeth chattering), neutral behaviors (e.g. "digging", resting, gnawing, autogrooming), or even aggressive behavior (e.g. fiercely biting the metal grid). Agonistic behavior that might occur when animals are in direct contact with each other was not shown inside the test apparatus.

Condition 1: Kings spent more time near the box with the unfamiliar queen than near the box with their own mate, the differences being significant (Table 1, Fig. 3). Kings also showed significantly more positive responses towards the strange queens than towards their own mates ($Z = -2.43$, $p = 0.015$, $n = 10$). In contrast, the queens displayed no preference for their own mates compared to unfamiliar kings (Table 1, Fig. 3), the number of positive responses were not significantly different ($Z = -0.141$, $p = 0.888$, $n = 10$). Condition 2: Kings showed significantly more interest in the unfamiliar non-reproductive females than in their own mates (Table 1). The number of positive responses towards the unfamiliar non-reproductive females was also significantly higher than towards their own queens ($Z = -2.527$, $p = 0.012$, $n = 8$). Queens did not reveal any preference (Table 1, Fig. 4). Condition 3: Ansell's mole-rats having the choice between an unfamiliar queen and her adult non-reproductive daughter, or between a king and his son, showed a differential pattern: whereas kings preferred the unknown queens over their daughters, queens showed slightly less interest in unfamiliar kings than in their respective non-breeding sons although this difference was not statistically significant. The non-reproductive animals neither preferred the reproductive animals of a different family nor their non-reproductive same-sex offspring (Table 1, Fig. 5). In condition 3, the number of positive responses towards unfamiliar reproductive animals and their offspring, respectively, differed only for the kings ($Z = -1.973$, $p = 0.049$, $n = 8$). Condition 4: Neither males (n = 8) nor females (n = 7)

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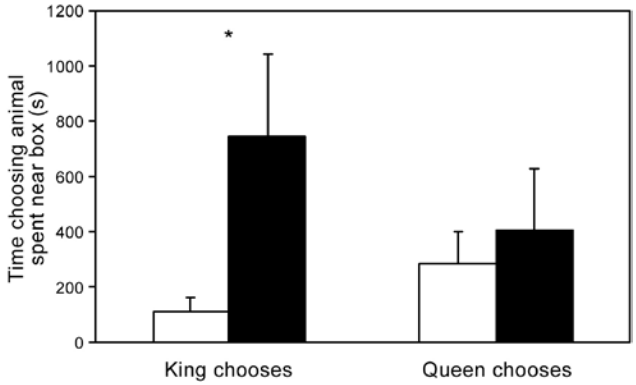


Fig. 4. *Condition 2 (preference test): King chooses: Mean times ($\bar{x}$ ± SD) kings spent near the terminal boxes of the two-choice-labyrinth containing their own mate (white bar) and an unfamiliar non-reproductive female (black bar). Queen chooses: Same condition with queens as subjects (= choosing animals) and own mate (white bar) versus unfamiliar non-reproductive male (black bar) as animals of choice. Asterisk indicates a significant difference.*

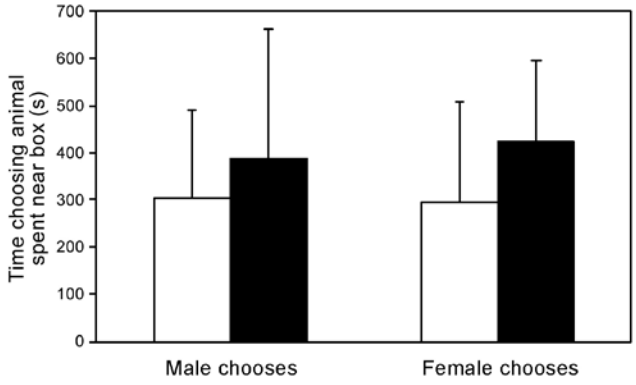


Fig. 6. *Condition 4 (preference test): Male chooses: Mean times ($\bar{x}$ ± SD) non-reproductive males spent near the terminal boxes of the two-choice labyrinth containing an old female of an unfamiliar colony (white bar) and the female's younger sister (black bar). Female chooses: Same condition with non-reproductive females as subjects (= choosing animals) and unfamiliar old male (white bar) versus the male's younger brother (black bar) as animals of choice.*

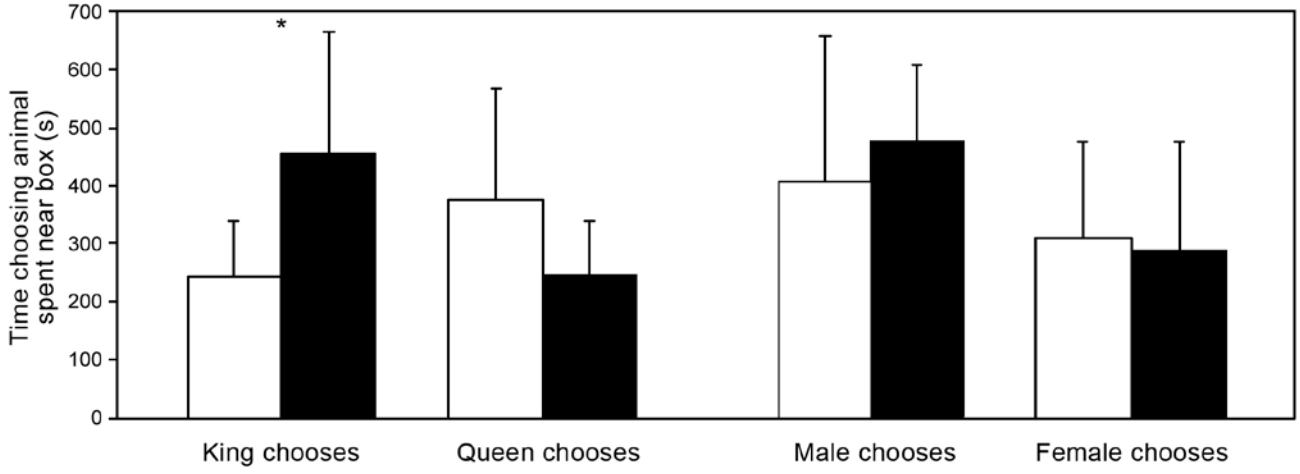


Fig. 5. *Condition 3 (preference test): King chooses: Mean times ($\bar{x}$ ± SD) Ansell's mole-rat kings spent near the terminal boxes of a reproductive female of an unfamiliar colony (black bar) versus the boxes of the reproductive female's daughter (white bar). Queen chooses: Same condition with queens as subjects (= choosing animals) and unfamiliar king (black bar) versus the king's son (white bar) as animals of choice. Male chooses: Same condition with non-reproductive males as subjects (= choosing animals) and unfamiliar queen (black bar) versus the queen's daughter (white bar) as animals of choice. Female chooses: Same condition with non-reproductive females as subjects (= choosing animals) and unfamiliar king (black bar) versus the king's son (white bar) as animals of choice. Asterisk indicates a significant difference.*

showed any age preferences for opposite-sex non-reproductive animals of choice (Table 1, Fig. 6).

Condition 5 (control): Neither females nor males displayed a preference for a certain side of the labyrinth when the same-sex twins were used as animals of choice (Table 1).

For all conditions (but for the kings in condition 1, 2, and 3; see above), the differences in the number of positive responses towards the two animals of choice were not significant (data not shown).

Experiment 2: fidelity tests

Condition 1 (complete family – access of males to an unfamiliar female): The interest of the family members was aroused when the unfamiliar female was put into the small compartment of the test cage, and most animals

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Table 1. *Conditions used in experiment 1 to test preferences of Ansell's mole-rats performed in a two-choice-labyrinth (cf. Fig. 1). Mean times ($\bar{x}$ ± SD) in seconds the choosing animals spent near the terminal boxes containing the animals of choice are given. Each trial lasted 30 minutes.*

	subject (choosing animal)	n	animal of choice A ($\bar{x}$ ± SD)	animal of choice B ($\bar{x}$ ± SD)	statistics
1	king	10	own mate (194.8 ± 123.9)	unfamiliar queen (523.3 ± 240.1)	t = –3.184; p = 0.011
	queen	10	own mate (321.8 ± 158.5)	unfamiliar king (355.3 ± 169.2)	t = –0.413; p = 0.689
2	king	8	own mate (111.1 ± 50.3)	unfamiliar non-reproductive female (742.4 ± 299.8)	t = –5.561; p = 0.001
	queen	8	own mate (282.3 ± 119.2)	unfamiliar non-reproductive male (407.9 ± 218.7)	t = –1.233; p = 0.257
3			unfamiliar queen	unfamiliar non-reproductive female, offspring of A	
	king	8	(454.6 ± 209.5)	(243.6 ± 96.0)	t = 2.894; p = 0.023
	non-rep. male	10	(476.2 ± 128.7)	(406.4 ± 250.2)	t = 0.745; p = 0.475
			unfamiliar king	unfamiliar non-reproductive male, offspring of A	
	queen	8	(246.3 ± 93.5)	(347.5 ± 192.4)	t = –1.876; p = 0.103
	non-rep. female	10	(286.8 ± 186.7)	(308.9 ± 163.6)	t = –0.226; p = 0.827
4			unfamiliar non-reproductive opposite-sex conspecific, sibling of B, but at least 20 months older than B	unfamiliar non-reproductive opposite-sex conspecific, sibling of A, but at least 20 months younger than A	
	non-rep. male	8	(307.1 ± 184.0)	(388.8 ± 276.0)	t = –0.601; p = 0.567
	non-rep. female	7	(297.1 ± 211.9)	(426.4 ± 171.1)	t = –1.11;p = 0.309
5			unfamiliar non-reproductive opposite-sex conspecific, same-sex twin of B	unfamiliar non-reproductive opposite-sex conspecific, same-sex twin of A	
	non-rep. male	8	(517.8 ± 204.6)	(424.4 ± 174.7)	t = 0.757; p = 0.474
	non-rep. female	8	(255.9 ± 122.3)	(240.9 ± 99.4)	t = 0.244; p = 0.814

approached the grid partition or the tube leading to the female's compartment during the habituation phase (15 min). Males having the possibility to access the female's compartment showed a differential pattern depending on their age and reproductive status. Non-reproductive older males (33.6 ± 27.2 min, n = 9 encounters) spent significantly (Kruskal-Wallis $\chi^2 = 8.174$, $p = 0.017$) more time in the unfamiliar female's presence than non-reproductive youngsters (4.9 ± 8.2 min, n = 8 encounters) or kings (13.7 ± 28.5 min, n = 9 encounters in 23 trials). In half of all the potential encounters (8 out of 16 = 50 %) where young males were involved, they did not enter the unfamiliar female's compartment at all (Table 2). Encounters between young males and unfamiliar females were only rarely neutral (2 out of 8) and mostly resulted in mutual aggression, the male attacking the female or vice versa (6 out of 8). In contrast, four out of five older non-reproductive males (> 18 months of age) entered the unfamiliar female's compartment (access in 10 out of 13 cases = 76.9 %). Most of these encounters resulted in attempted or realized copulations (9 out of 10). In one case, the unfamiliar female displayed aggressive behavior (and rejected the male), and the animals had to be separated. In only nine out of 23 (= 39 %) trials, kings sought direct contact to the unfamiliar female. In five of these encounters the animals were aggressive and had to be separated (aggressiveness shown by both animals (n = 4) or the king (n = 1)). In three cases, the king and the unfamiliar female had no interest in each other and the encounter proceeded neutrally. Copulation between a king and the unfamiliar female occurred only once (Table 2). The Fisher-test showed that there was a significant difference in the number of kings (1 out of 9 kings) and non-reproductive adult males (4 out of 5 males) engaged in copulations (p = 0.023).

Only in five trials (kings, n = 2; non-reproductive older males, n = 3), the males remained in the compartment of the unfamiliar female until the end of the experiment. In all other trials, the males returned via the sluice tube to their family before the experiment ended.

There were no differences in the behavior of the tested males with respect to the reproductive status

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Table 2. *Outcome of the 23 trials with 52 possible encounters between males and unfamiliar females.*

	No encounters	Number of encounters with neutral behavior	Number of encounters with agonistic behavior	Number of encounters with sexual behavior
Reproductive males (kings) (n = 9; 23 trials)	14	3	5	1
Non-reproductive males (> 18 months) (n = 5; 10 trials)	3	0	1	9
Non-reproductive young males (< 18 months) (n = 6; 6 trials)	8	2	6	0

of the females they were confronted with (i.e., males copulated with reproductive (n = 4 encounters) as well as non-reproductive females (n = 3 encounters)). Condition 2 (complete family – access of females to an unfamiliar male): Pilot studies showed that in contrast to the females, the males used as lure are highly stressed when being indirectly confronted with an unfamiliar family (separated just by a grid, Fig. 2a) and behave aggressively towards any visiting female. Even though the changed experimental design (Fig. 2b) was used, the level of stress and aggressiveness was still very high during these experiments.

During the habituation phase most animals approached and tried to access the tubes leading to the male's cage. Of the 25 possible encounters where a queen could have visited a single male, meetings were realized in 56 % (total of 14 cases: 6 with kings, 8 with non-reproductive males) (Table 3). One third (five meetings) of these encounters ended in aggressive behaviors, and in four cases the queen was taken out of the male's cage to prevent serious injury. In three cases the queen copulated with a non-reproductive male. None of the kings copulated with any of the visiting females.

In contrast to the queens, reproductively quiescent females seized their chance to enter the cage of the single males more often (68 realized encounters out of 77 possible encounters, in over half of them kings were involved). However, about 60 % (41 out of 68) of all encounters were of aggressive nature (irrespective of the reproductive status of the male), and 33 of these encounters had to be interrupted because the females were being attacked by the male (n = 30) or the females were aggressive towards the males (n = 3). Females often tried to appease the aggressive males by soliciting (presenting their ano-genital region to the male and/or emitting appeasing calls). Not a single copulation occurred when non-reproductive females visited the males (Table 3). There was no difference in the behavior of non-reproductive adult (> 18 months) and younger (12-18 months) females. The number of animals showing aggressive versus non-aggressive behavior was comparable for adult and young non-reproductive animals, respectively (two out of 12 adults were aggressive, one of the seven younger animals showed signs of aggressiveness; Fisher-test, p = 0.704).

Discussion

One of the most surprising findings of our study is that in mole-rats, males seem to be the choosy gender whereas females behave opportunistically in terms

Table 3. *Outcome of the 25 trials with 102 possible encounters between females and unfamiliar males.*

	No encounters	Number of encounters with neutral behavior	Number of encounters with agonistic behavior	Number of encounters with sexual behavior
Reproductive females (queens) (n = 5; 25 trials)	11	6	5	3
Non-reproductive females (> 18 months) (n = 12; 19 trials)	4	21	32	0
Non-reproductive young females (< 18 months) (n = 6; 15 trials)	5	6	9	0

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of mating and mate choice. This is in contrast to the majority of mammal species as postulated by Bateman (1948) and Trivers (1972), since, as generally known, the female invests significantly more into reproduction than males do. The question arises why mole-rats are different in this regard. Since the physiological investment into offspring is comparable to other mammal species the answer must be concealed within other factors such as the social system or ecology. For a detailed examination of these factors a separate discussion of the animals according to gender (and reproductive status) is helpful.

Females

Neither the reproductive nor the non-reproductive females showed any mate-choice in the preference test. The females used as stimulus animals in the second experiment (fidelity test, condition 1) readily copulated with almost any adult non-reproductive male that came for a visit (70 %), rarely initiating aggressive behavior. In fact for reproductively quiescent helpers this is the only way to gain direct fitness. We assume that for these animals the benefits of founding a new family are greater than possible costs (e.g. necessity of establishing an own burrow system and foraging without assistance of a larger workforce). Apparently, the chances to meet a stranger of opposite sex (and not being disturbed by other family members) are so rare under natural conditions, that every chance of this kind will be seized (this is what Burda 1999 called "provoked or induced dispersal"). Established queens may also benefit from extra-pair copulations by increasing the genetic quality and/or diversity of their offspring (Jennions & Petrie 2000). Since there is only a minimal probability that a king is cuckolded, it is also rather improbable that the males would have developed abilities to distinguish between own and conspecific offspring and react with less paternal investment. Furthermore, soliciting (lordosis and typical vocalization, and even allowing mounting) may serve in mole-rats also as a gesture of submission and appeasement (Burda 1989), so that the readiness of females to copulate with unfamiliar males fits in (there is a sexual dimorphism with females being significantly smaller than males, Begall & Burda 1998).

One should also take into account that the females' motivation to reproduce may have been manipulated by removing the animals from their families. The absence of the family may have imposed pressure on both, the queens and non-reproductive females to create a new family resulting in similar behavior. Condition 2 of the second experiment (males used as lure) confirmed the submissive behavior of females, when males were highly aggressive due to stress from isolation and/or being confronted with too many new stimuli (a strange family adjacent to the male's cage).

Male non-breeders

The fidelity experiments revealed that the motivation to copulate with any unfamiliar female is very high in mature non-breeding male mole-rats (condition 1). As for non-breeding females, the (direct fitness) benefits of breeding undoubtedly outweigh the costs. The outcome of copulation with a stranger however depends on the breeding status of the female partner. Since female *Fukomys* mole-rats are apparently induced ovulators (Willingstorfer et al. 1998, Hagemeyer et al. 2009), repeated frequent copulations may be necessary to conceive (Burda 1999). For non-breeding females, incidental mating is probably not sufficient to induce ovulation even though females are not reproductively suppressed (Burda 1995). The queen of a foreign family, being regularly and frequently (cf. Dammann & Burda 2006) engaged in sexual activity (normally with her partner only) may become pregnant from extra-pair copulation easily and return to her family. Mating with a non-breeding female on the other hand should lead to the foundation of a new family permanently changing the breeding status of the involved pair (from non-breeding helpers to reproductively active king and queen). This scenario is in accordance with the field studies conducted by Bishop et al. (2007) who never found more than one breeding/lactating female per colony in *C. hottentotus*. The same seems to be true for *Fukomys* mole-rats, since previous trappings always revealed only one queen per colony (Burda, Dammann, Kawalika, Scharff, pers. comm.). This might not hold for *Fukomys mechowii* where in rare instances (four out of 32 families) two queens per colony have been found (Sichilima et al. 2008). On the other hand, Šumbera et al. (pers. comm.) found that there was only one reproductive pair in each of two adjacent colonies whose tunnel systems were interconnected but plugged.

The fact that in condition 1 of the fidelity tests younger males (12-18 months) mostly behaved aggressively or neutrally towards the unfamiliar female (if entering her compartment at all) suggests that at this age they (or at least most of them) are still not fully sexually mature.

Even though the experimental setup in condition 2 of the fidelity tests was improved to give the males used as lure more space they were still highly stressed

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when being indirectly confronted with an unfamiliar adjacent family. Therefore the lack of mating behavior and the agonistic behavior shown instead were probably due to the high level of stress. Nevertheless, in three cases non-reproductive males did use the opportunity to copulate – with a queen.

Male breeder (king)

The preference tests revealed that the kings spent significantly more time near the unfamiliar queens or non-reproductive females than near their own mates which might be interpreted as a preference for a strange animal. In previous odor habituation tests it has been demonstrated that novel stimuli often motivated the subjects to spend more time sniffing the novel stimulus in comparison to the "habituation odor" – however, this choice does not necessarily reflect a preference (Todrank & Heth 2003). Keeping this in mind, it may be that the king is interested in the unknown animal just because it represents a novel stimulus. Occasionally, the observed behavior displayed by the males in this context does indicate a clear sexual motivation (typical vocalizations, feet tapping, incidentally an erected penis). On the basis of these tests we expected that kings would seize their chances to copulate with the unfamiliar females when gaining direct physical access to them. However, contrary to our expectations, most kings remained faithful and did not "seize the given chance". This finding is consistent with our primary hypothesis that pair-bond and assistance of the partner is a prerequisite to successful breeding in Ansell's mole-rats. If a king would abandon the queen and her (unborn) offspring each time opportunities for extra-pair copulations with an unfamiliar female occur, the family, and thus the eusocial system, would collapse diminishing the potential direct fitness for the male to zero. This situation however does not explain why the kings should not engage in extra-pair copulations while remaining socially faithful – just as seen in many other monogamous species (Westneat & Stewart 2003). Indeed, there are no apparent costs for a king of extra-pair copulation. It might therefore be speculated that the kings' fidelity is intrinsic, and proximately (most probably hormonally) fixed. Interestingly, the kings preferred unfamiliar queens over non-breeding females, which were daughters of the respective unfamiliar queens during condition 2 of the preference tests indicating that they can recognize the breeding status of females. Note that a single extra-pair copulation with an unfamiliar queen could lead to conception while we could speculate that a single mating event with a "non-breeder" may be unfruitful. In condition 2 of the fidelity tests, the reproductive males showed no attempts to mate with the foreign females but behaved either neutral or even aggressively. In this case the lack of sexual interest may also have been due to the high level of stress in the males used as lure.

In condition 4 of the preference tests animals were confronted with unfamiliar potential mates that were siblings from different litters with an age difference of at least one year. Neither males nor females showed any age preference. This is in accordance with our breeding experiences as animals with several years of age difference may be mated successfully (note that the maximum life-span of reproductive mole-rats is more than 20 years, Dammann & Burda 2006).

General aspects

Based on extensive evidence gained from voles, gerbils, rats etc. (cf., e.g. Brown et al. 1995, Young et al. 1998, Balaban 2004), we may speculate that in mole-rats as well, the breeding status (hormone status) influences the motivation of the animal to engage in mating. It might be presumed that high levels of oxytocin, vasopressin, and prolactin (which may be expected in kings) strengthen the pair-bond and decrease the motivation for extra-pair copulations. It would be of interest to study profiles of the above mentioned hormones and additionally also dopamine levels, to learn, why the Coolidge effect (cf. Brown 1974, Dewsbury 1981, Fiorino et al. 1997) may not apply to mole-rat kings.

When examining the genetic composition of neighboring *C. hottentotus* families, Bishop et al. (2007) found that primarily "non-reproductive" males (and probably not kings) were the sires of "cuckold offspring" in adjacent families. These findings are clearly in accordance with our results and a further support of our hypothesis that the breeding males have a low motivation for extra-pair copulations. Certainly, field and genetic studies are necessary to confirm whether extra-pair copulations actually take place in *Fukomys*, and if so which males and females (kings, queens, or offspring?) are involved in them. Furthermore, it would be of interest to learn whether all encounters of strange mole-rats of opposite sex result in their emancipation from their respective families and founding a new own family, or whether they may return (maybe even after successful fruitful mating to their parental families, where females may become second breeders, next to their mother, the queen (cf. Burda 1995)).

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Conclusion

To sum up, the comparison of the two male groups (kings versus non-reproductive males) shows that the current reproductive status of the male is crucial for its reproductive decisions. In contrast, the females' behavior does not seem to be influenced by their reproductive status. In our study, non-breeding mole-rats of both genders are highly motivated to mate whenever the opportunity occurs. Kings on the other hand are socially and probably also sexually faithful. Our "fidelity tests" reveal that the king's interest in an unfamiliar and inaccessible female does not predict the behavioral response which could be expected, if the subject was given the chance. It appears that the presence of family members influences the behavior of the kings. We postulate that the maintenance of Ansell's mole-rats' families depends strongly on the faithfulness of the kings.

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