Individual recognition and incest avoidance in eusocial common mole-rats rather than reproductive suppression by parents

H. Burda*

Department of Morphology, J. W. Goethe University, Theodor-Stern-Kai 7, D-60590 Frankfurt am Main (Germany)
Received 24 June 1994; received after revision 11 November 1994; accepted 5 January 1995

Abstract. Non-reproductive females in families of eusocial common mole-rats (*Cryptomys* sp., Rodentia) are not suppressed by their mother, (either behaviourally or pheromonally) as is generally assumed. They do not mate with their father and brothers simply because they are not sexually attractive for them (and vice versa). The incest avoidance is based on the capability to recognize (and keep in memory for up to three weeks) each family member individually. A 'sterile' daughter may conceive and deliver young in her parental family if given the opportunity to mate with an unfamiliar mate in a separate cage. In this way, two females may breed side by side in one family.
Key words. Eusociality; reproductive suppression; incest avoidance; individual recognition; monogamy; memory; subterranean rodent; mole-rat; *Cryptomys*; *Heterocephalus*.

During the last decade, following the demonstration that naked mole-rats (*Heterocephalus glaber*)[1] and common mole-rats (*Cryptomys* sp.)[2,3] are eusocial, considerable attention and publicity have been given to these endemic African blind subterranean rodents of the family Bathyergidae[4–7]. Mole-rats of both genera live in colonies whose social system resembles that of the eusocial insects: a single breeding female (queen) and her one to three mates produce all the young. Most of the offspring remain with their parents throughout their lives, and become the work-force for foraging, and for extending, maintaining and defending the burrow system. A non-reproductive mole-rat may, however, become a breeder if separated from its parental family and paired with an appropriate mate.

While the evolution of this unique social system is a subject for speculation[3,10], the mechanisms by which it is maintained are open to experimental study. According to the current state of knowledge, the methods by which the breeders suppress reproduction in other colony members are different in the two genera. While in *Heterocephalus* the queen suppresses reproduction in subordinate females through behaviourally-mediated stress[4,11,12], there are no signs of aggressive behaviour in breeding *Cryptomys* females[3,7,8,10,13,14]. It has been suggested that non-reproductive *Cryptomys* females are reproductively suppressed, most probably by semiochemical mechanisms orchestrated by the reproductive female[13].

The actual mechanism of suppression is, however, far from being clear. While in *Heterocephalus* another female assumes the reproductive role within a short time after the queen has died or been removed[4], this is not the case in families of *Cryptomys*[3,7,8,10,14,15]. In fact, a colony from which the breeding female or the breeding pair has been removed remains sterile. A removed breeding male can be substituted for, however, by some of the elder sons[8,14]. Captured incomplete colonies (without the breeding female) transferred to captivity are cohesive but do not reproduce. The successful breeding of *Cryptomys* in captivity occurred only after a) a complete colony had been captured[2], or b) mates from different colonies had been paired together[10,15].

Frequency of copulation is very high in a newly-formed *Cryptomys* pair, but it may decline after a social bond has been established[3,15]. Nevertheless, even an old breeding pair is engaged in frequent mating, which may be solicited by any of the partners, and which occurs daily, independently of estrus, even during pregnancy (which lasts about 15 weeks) and shortly before, during and after parturition[3,15]. On the other hand, within a family, copulation between siblings has never been observed. Similarly, a father has never been observed to mate with his daughter, even if she has been (for years) his only partner after removal of the breeding female.

These findings on captive mole-rats are corroborated by the results of field studies. While in *Heterocephalus* new colonies are founded through fissioning[4,6], in *Cryptomys* they are apparently founded by pairs composed of mates originating from different colonies[7,8].

The above experience, and a long period of observation of *Cryptomys*, led me to suggest that 'voluntary' incest avoidance may explain the apparent sterility of female offspring better than reproductive suppression imposed by breeders. Here I bring experimental evidence for my hypothesis that 1) daughters/sisters do not reproduce, not because they are suppressed by the breeding female, as suggested in the literature[13], but primarily because they are not mated; 2) they are not mated because they

* Current address: Chair of General Zoology, Faculty of Biology (FB 9), University of Essen, Universitätsstr. 5, D-45117 Essen (Germany).

are sexually unattractive for the male family members (and vice versa); 3) the lack of attraction, resulting in incest avoidance, is based on the ability to recognize each family member individually.

Materials and methods

The subjects of my study were several captive colonies of Zambian common mole-rats, *Cryptomys* species (karyotype $2n = 68$, population Lusaka). (We called these animals *C. hottentotus* in our earlier studies. The Lusaka population, is, however, specifically distinct from typical *C. hottentotus* from South Africa and should be considered a new species, not yet formally named[17].) The housing conditions, etc. are described in detail elsewhere[15].

The following experiments were repeatedly performed to test the hypothesis. (Animals and families involved in pilot experiments are not considered here.)

A) Four non-reproductive females, aged one to three years, were selected from three families (with 17, 12, and 9 members), (two females being selected from the largest family), and mated in a separate cage with a non-reproductive male from a foreign family. After 6 to 48 h a female and a male were returned to their respective parental families. The mating sessions were repeated, always after a pause of 6 to 48 h, for altogether 7 to 15 weeks until pregnancy was determined. (The embryos can be palpated as early as 4 weeks after conception[15].)

B) In two larger families, selected siblings (one and three non-reproductive females, and one and two non-reproductive males) were alternately isolated for 1–2 days from their parental families and thus continuously separated from each other. In this way, the contact between the two tested siblings was prevented, yet the relationship of each of them to its respective parental family was not disrupted by the relatively short periods of separation. The two siblings were then put together and their behaviour was recorded when they were in a separate cage, as well as within the parental family, after 3, 7, 10, 12, 14, 16, 18, and 20 days of separation from each other (and after a longer period in some pilot studies done with other animals). Before testing the next step, i.e. a longer isolation period, the siblings were left together within their respective parental families for at least 3 days.

Results

The experiments gave the following results:

A) In agreement with the previous observations[3, 15], animals which were not familiar with each other copulated immediately after being put together. In this particular experiment, however, not all the mating sessions were equally successful, since the available subordinate males were rather inexperienced. Usually, the female was sexually more aroused and more active than the male, with the result that she mounted him. Dominant breeding males (kings) living as one of an established pair attack every unfamiliar female and cannot be used for mating sessions.

After each mating session, the returning animals were sniffed and greeted by other family members. The intensity of this behaviour depended on the length of separation. The breeding male and some of the siblings were more interested in the home-comers than the breeding female was (and sometimes also harassed them). Interest in the home-comers usually ceased within a few minutes. Even after multiple mating outside the parental family, the animals remained sexually unattractive for their own family members of the opposite sex (and vice versa). Three of the four tested females conceived within 3 weeks to 3 months of continuing mating sessions. Pregnant females were not harassed by the breeding female or any other family members, and remained sexually unattractive for their brothers and their father. In fact, these pregnant females spent most of their time in the nest in the close vicinity of the breeding female.

There was no obvious difference in the intensity of care (cleaning, retrieving) dedicated by other family members to the pups of the two mothers. Similarly, the mothers did not obviously differentiate between the two litters. Pups of both litters were nursed by both mothers.

B) The second experiment showed that after more than 14–16 days of separation, the males apparently did not recognize their sisters. They sniffed them and were interested in them for a long time, as if contacting unfamiliar females. Eventually they tried to mate with them. The females allowed mating (and/or exhibited similar behaviour to that shown when they were confronted with unfamiliar males) after about 16–18 days. In control experiments, the isolated males were confronted – in their temporary cage – with their mothers, or with sisters not involved in the experiment. These females were immediately recognized and ignored, and were not mated, indicating that it was not the possession of his own territory and the absence of the father, but the presence of an unknown female that elicited sexual behaviour in the male. Mating with an unrecognized sister took place even in the cage of the parental family, but the intensity of mating attempts declined soon. A sporadically open vagina, indicating that mating (and/or estrus) had taken place, was observed in two experimental females even two months after the separation experiment had been stopped and the contact between the two siblings renewed.

Discussion

The results of both experiments fully support the hypothesis proposed in the introduction, and allow a new interpretation of the previously-available histological and endocrinological findings. The ovaries of non-reproductive *Cryptomys* females show normal follicular development[8,13,16]. The follicles fail to ovulate, however, and luteinize instead. It has been suggested that progesterone produced by the corpora lutea may feed back to the neuroendocrine system, to maintain a form of pseudopregnancy and thus prevent ovulation[8,13]. The unusual luteinization of unovulated follicles and/or failure of ovulation has been attributed to pheromonal suppression by the queen[13]. However, (pseudo)pregnancy itself cannot be a primary reason for suppression of sexual behaviour, as even pregnant females are mated. Since corpora lutea developing from unovulated follicles are a common feature in hystricomorph rodents[18], this form of pseudopregnancy is probably not a particular 'invention' of eusocial common mole-rats. It is possible that all (i.e. even dominant) *Cryptomys* females are primarily pseudopregnant. It is possible that pseudopregnancy can be interrupted by frequent multiple mating, for example as a result of the luteolytic effect of oxytocin[19], which is normally released during coitus. Even if this is not the case, frequent mating in *Cryptomys* may serve not only to establish and reinforce the pair bond as previously suggested[3,15], but may also be necessary for provoking ovulation.

Since no special pheromones are necessary for reproductive suppression in common mole-rats, which would be missing in naked mole-rats, it is also not necessary to assume[8] that the mechanisms of suppression and eusociality in the two genera have evolved independently. The behavioural suppression in naked mole-rats may have evolved from a *Cryptomys*-like system, when individual recognition failed in larger families with too many individuals and/or when a breeding female and not a male became the most dominant animal in a family. Incest avoidance, considered here to be a mechanism responsible for the 'sterility' of offspring, may have evolved not only for its genetic benefits but also as an evolutionarily stable strategy ensuring that a family would not grow too big. Intrinsic or extrinsic (i.e. imposed by breeders) control of the breeding of offspring, particularly of females, may be necessary as long as the offspring stay in their parental families. By such control, uncontrollable growth of the family and the resulting competition for resources is prevented. From this point of view, the question about the eusociality of mole-rats is not 'Why do the offspring not reproduce?' but 'Why do they not disperse in order to reproduce?'.

Acknowledgements. I thank J. Winckler for his support, and G. Klauer and E. Nevo as well as the anonymous reviewers for comments on the manuscript.

1 Jarvis, J. U. M., Science *212* (1981) 571.
2 Bennett, N. C., and Jarvis, J. U. M., J. Mammal. *69* (1988) 293.
3 Burda, H., Z. Zool. Syst. Evol.-forsch. *28* (1990) 26.
4 Sherman, P. W., Jarvis, J. U. M., and Alexander, R. D. (eds), The Biology of the Naked Mole-Rat. Princeton University Press, Princeton 1991.
5 Honeycutt, R. L., Am. Scient. *80* (1992) 43.
6 Sherman, P. W., Jarvis, J. U. M., and Braude, S. H., Scient. Am. *267* (1992) 72.
7 Jarvis, J. U. M., O'Riain, M. J., Bennett, N. C., and Sherman, P. W., Trends Ecol. Evol. (TREE) *9* (1994) 47.
8 Jarvis, J. U. M., and Bennett, N. C., Behav. Ecol. Sociobiol. *33* (1993) 253.
9 Lovegrove, B. G., Behav. Ecol. Sociobiol. *28* (1991) 26.
10 Burda, H., and Kawalika, M., Naturwissenschaften *80* (1993) 235.
11 Faulkes, C. G., Abbott, D. H., and Jarvis, J. U. M., J. Reprod. Fert. *88* (1990) 559.
12 Faulkes, C. G., and Abbott, D. H., J. Reprod. Fert. *99* (1993) 225.
13 Bennett, N. C., Jarvis, J. U. M., Faulkes, C. G., and Millar, R. P., J. Reprod. Fert. *99* (1993) 81.
14 Arndt, H., and Burda, H., Z. Säugetierk. Suppl. *57* (1992) 6.
15 Burda, H., Z. Säugetierk. *54* (1989) 360.
16 Willingstorfer, W., MD-Thesis, School of Medicine, J. W. Goethe Univ., Frankfurt am Main (1994).
17 Filippucci, M. G., Burda, H., Nevo, E., and Kocka, J., Z. Säugetierk. *59* (1994) 42.
18 Weir, B. J., and Rowlands, I. W., Symp. Zool. Soc. Lond. *34* (1974) 303.
19 Cao, L., and Chan, W. Y., J. Reprod. Fert. *99* (1993) 181.