The mating behaviour of the Silvery mole-rat

(*Heliophobius argenteocinereus*)

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Introduction

Subterranean rodents in general, and solitary subterranean rodents in particular, do not reproduce easily in captivity. Although most of subterranean rodents are solitary, the available data on reproduction and reproductive behaviour refer mostly to social species representing just three genera: *Heterocephalus glaber* (JARVIS, 1991), *Cryptomys damarensis* (BENNETT and JARVIS, 1988b; BENNETT, 1994), *Cryptomys hottentotus* (HICKMAN, 1982; BENNETT, 1989), *Cryptomys anselli* (BURDA, 1989; BEGALL and BURDA, 1998), *Cryptomys darlingi* (BENNETT *et al.*, 1994), *Cryptomys mechowi* (BURDA and KAWALIKA, 1993; BENNETT and AGUILAR, 1995; SCHARFF *et al.*, 1999), *Spalacopus cyanus* (BEGALL *et al.*, 1999). Solitary forms are territorial, xenophobic and aggressive, so that even observations of their mating are rare. There are reports on mating behaviour in *Georychus capensis* (BENNETT and JARVIS, 1988a), *Spalax ehrenbergi* (NEVO, 1969; SHANAS *et al.*, 1995; GAZIT *et al.*, 1996), *Cannomys badius* (EISENBERG and MALINIAK, 1973), *Thomomys talpoides* (ANDERSEN, 1978), and *Ctenomys mendocinus* (CAMÍN, 1999). It is apparent that any further comparative data on mating behaviour in (particularly solitary) subterranean rodents would

be of interest, in order to be able to establish phylogenetically conserved and ecologically adaptive components of relevant behavioural patterns.

The African mole-rats (Bathyergidae) involve two genera of social and three genera of solitary rodents. Although this African endemic family is one of the best examined taxa of subterranean mammals, reproduction and reproductive behaviour of solitary forms remain still largely unknown. In particular the reproductive biology of the monotypic genus *Heliophobius* has been enigmatic, although among all the mole-rat species, *H. argenteocinereus* is the most widely distributed. This paper provides the first description of the mating behaviour in this species.

Materials and methods

Animals and housing

Altogether 17 wild-captured adult silvery mole-rats (*Heliophobius argenteocinereus*, Bathyergidae) were studied. Animals were kept individually in plastic cages (49 × 30 × 20 cm), or in a Plexiglas maze, or in pairs in a glass terrarium, on a shallow litter of horticultural peat. They were fed with carrots, potatoes, lettuce, and other seasonal vegetables. General activity and mating behaviour was monitored and videotaped continuously. Each mating was assessed qualitatively and quantitatively.

Encounter experiments

Two females and three males captured in Zambia (Lubalashi area, 1996) and Malawi (Nyika, Blantyre, Mulanje, 1996-1998) were used in the study. Mate choice was ascertained in an apparatus (constructed according to SHANAS *et al.*, 1995) consisting of four cross-connected Plexiglas tubes. The tubes were connected with the home cages of three males, while a wire barrier prevented the males entering the maze. The fourth tube leading to the female cage was opened, enabling

the female to enter the system. The female and male that spent the most time at partition were considered as being the most interested in each other. These animals were relocated into another system consisting of two interconnected equal-sized cages, divided by a movable wire barrier. During encounters of animals at partition, the barrier was lifted up carefully and this allowed them physical contact. Both animals were given the opportunity to meet each other for several weeks up to three months.

Mating behaviour

Twelve animals captured from February to April 1999 in Mulanje (Malawi) were repeatedly combined into heterosexual pairs. The contact ended either aggressively, and the animals had to be separated, or the animals were amicable to each other and sexual activity could be recorded. Copulation was observed in three pairs, in which the following parameters were recorded: Courtship behaviour (duration and initiator), intromissions and thrusting (duration and frequency), frequency of marking behaviour (number of incidences of urinating on the cage walls during periods of male activity with copulation versus periods of male activity with no copulation).

Results

Encounters experiments

In spite of long-term (over six months) intensive observations no signs of seismic (vibrational, knocking) communication were observed in animals housed individually, separated by a partition or living in pairs, or living in tubes, boxes and open cages.

When the partition was removed, the animals interacted with each other with open mouths and protruding incisors, and the threat behaviour (fig. 1a) resulted subsequently in sparring. If the animals attacked each other seriously, they were separated. In some cases, a couple spent several hours in interconnected territories without any

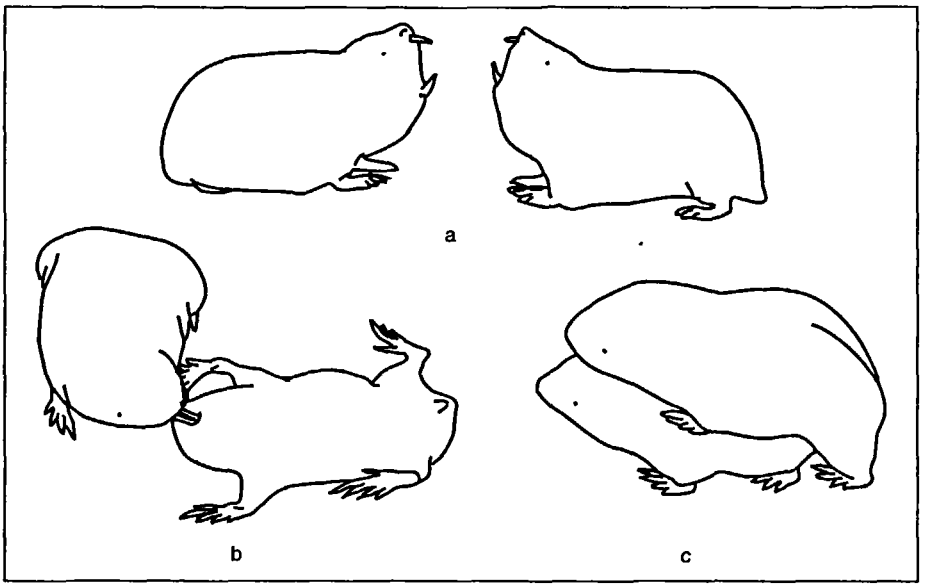

Figure 1
Postures of *Heliophobius argenteocinereus*: (a) agressive encounter, (b) lying on the back during courtship, (c) mounting.

confrontation. Frequent and repeated contacts gradually reduced aggressiveness. Nevertheless, in most cases, the encounters eventually resulted in fighting. During highly aggressive encounters, both partners exhibited (usually simultaneously) short, fast and repeated drumming with the forelimbs.

The females used the opportunity of interconnected territories to steal the food from male boxes (in 62 from 77, i.e., 80.5%, of encounters).

Mating behaviour

Courtship behaviour was initiated by the male which followed the female and sometimes sniffed at her anogenital region. Both partners were vocal, but vocalisation was pronounced in females. Then the animals faced each other frontally, nibbled each other gently, and locked incisors. Alternatively, one of them lied on its back (fig. 1b).

There was no difference between both sexes in the frequency of showing the "back-up" (normal posture) or "belly-up" (supine) position ($\chi^2_{(1)} = 0.391$, $p < 0.531$). Contacts eventually resulting in copulation were mostly initiated by males. However, soliciting behaviour and lordosis posture of a female with no response by the male was frequent. The courtship behaviour of animals lasted for about 2 minutes (ranging 40 to 241 s, n = 11) and resulted in copulation (10 out of 11).

Copulation started when a male mounted a female (fig. 1c). Initial mounting attempts were sometimes interrupted by the female which did not stay still, yet the male continued and remounted the female. Lordosis of a female was a prerequisite for successful intromisions. The male thrusted at a high rate of 7.3 per s (range 4.5-9.5, n = 29 intromissions) for 10-30 s. Copulation ended with deep thrusting during which the female vocalized intensively. First-time copulations and copulations occurring after a longer abstinence culminated, apparently, with ejaculation. The male then fell down from the female, lay on its side or back with his limbs jerking. In the case of more frequent copulations, the ejaculation was less prominent. Nevertheless, sperm found in the female vagina provided evidence that ejaculation still took place. Repeated copulations were very rare. No aggressive behaviour was noted after ejaculation. Males urinated on the vertical walls of the terrarium. The urinating intensified during mating ($U = 27.0$, $p < 0.001$ Mann–Whitney U-test).

Discussion

Encounter experiments

The absence of seismic communication is rather surprising. It has been assumed that this form of communication is widely distributed among solitary subterranean mammals (HETH *et al.*, 1987; RADO *et al.*, 1987; BURDA *et al.*, 1990; NARINS *et al.*, 1992). Seismic communication is relevant not only for mating but also in territorial context, and knocking and drumming (e.g. in *Spalax*) can be recorded and elicited in captive animals outside the reproductive season (cf. HETH *et al.*, 1991). *Georychus*, *Spalax*, and *Bathyergus* drum even in arti-

ficial maze when separated only by a perforated or unperforated partition (HETH *et al.*, 1987; 1991; RADO *et al.*, 1987; BENNETT and JARVIS, 1988a; BENNETT and JARVIS, 1991; NARINS *et al.*, 1992). Seismic communication in *Heliophobius* was not recorded even in cases when both animals were separated by two partitions 40 cm apart. Nevertheless, I have not performed any specific experiment to test for the absence/presence of seismic communication in *H. argenteocinereus*.

Mutual attacking after removal of the partition indicates that the animals were not motivated to mate, although at the same time some were sexually active. The reasons for this remains unknown. Solitary subterranean rodents studied so far (*Spalax, Bathyergus, Georychus, Thomomys, Geomys*) are seasonal breeders (NEVO, 1979; JARVIS and BENNETT, 1991). Seasonality of reproduction guarantees synchronised reduction of aggressiveness and territoriality of putative partners. There is indication that reproduction in *H. argenteocinereus* may also be season-dependent (JARVIS and BENNETT, 1991; BURDA and CHITAUKALI, pers. comm.). If so, it may be that some (so far unidentified) environmental stimulus triggering sexual activity was missing in our experimental setting. The nature of such a putative stimulus is, however, unknown for any seasonally breeding mammal with long pregnancy living in the tropics (GOODMAN, 1998). It can be only speculated that some factors linked to changes in precipitation which represent the most fundamental seasonal change may play a role.

Mating behaviour

Mating behaviour in diverse subterranean rodents of solitary habits *Spalax ehrenbergi* (NEVO, 1969; SHANAS *et al.*, 1995; GAZIT *et al.*, 1996), *Cannomys badius* (EISENBERG and MALINIAK, 1973), *Thomomys talpoides* (ANDERSEN, 1978), and *Georychus capensis* (BENNETT and JARVIS, 1988a) is similar in several aspects. The male initiates courtship and/or is the more active partner, or both partners are equally active like in *Spalax* (NEVO, 1969; SHANAS *et al.*, 1995) and *Ctenomys* (CAMÍN, 1999). In social species, mating is usually initiated by a female and female appeal is considered a characteristic

mating pattern of social species (BENNETT and JARVIS, 1988b). In *Cryptomys anselli* and *C. mechowi* female soliciting is common in non-familiar pairs, whereas in established pairs it is usually the male who starts mating (BURDA, 1989; SCHARFF *et al.*, 1999). Initiation by male was also recorded in *Cryptomys h. hottentotus* (BENNETT, 1989). The alternative lying on the back observed in partners of silvery mole-rat can be considered a ritualised form of agonistic behaviour. The same behaviour was observed during aggressive encounters when the animals attacked from supine position. Posting on the back during mating was observed also in female *Spalax* (NEVO, 1969) and both partners in *Ctenomys* (CAMÍN, 1999).

Copulation in solitary subterranean rodents involves pelvic thrusting and multiple intromissions, during which the female adopts lordosis posture, and deep thrusts before withdrawal. Apart from few exceptions, *H. argenteocinereus* appears to conform to this pattern. Short average duration of courtship may be due to the habituation involving familiarity between partners. Repeated intromissions in *H. argenteocinereus* (10-30 s) resemble the situation in *C. badius* (< 22 s, EISENBERG and MALINIAK, 1973), and are longer than in the social common mole-rat *C. hottentotus* (5 s, HICKMAN, 1982), *H. glaber* (< 15 s, LACEY *et al.*, 1991), *S. cyanus* (< 15 s, BEGALL *et al.*, 1999), yet they are shorter than in solitary *C. mendocinus* (up to 5.5 min, CAMÍN, 1999), *S. ehrenbergi* (up to several min, Nevo 1969), or *T. talpoides* (up to 15 min, ANDERSEN, 1978). *Heliophobius* is unique among all subterranean rodents studied to date in the high frequency of thrusting: 7.3 per s in *Heliophobius*, 2-4 in *C. h. hottentotus* (BENNETT, 1989), 3-4 in *C. damarensis* (BENNETT and JARVIS, 1988b), 1-2 in *C. mechowi* (BENNETT and AGUILAR, 1995), 2-3 in *G. capensis* (BENNETT and JARVIS, 1988b), 0-1 in *T. talpoides* (ANDERSEN, 1978) and 1-5 in *C. mendocinus* (CAMÍN, 1999). However, it is difficult to interpret these phenomena.

Urinating on vertical surfaces (both in own or female's territory) was common in mating males. Similar behaviour was noted in *Spalacopus cyanus* (KLEIMAN, 1974) and *Ctenomys mendocinus* (CAMÍN, 1999). One possible assumption is that urine provides the female with some information on male's reproductive state (KLEIMAN, 1974).

Mating behaviour in different rodent taxa

Sciurognatha versus Hystricognatha

DEWSBURY (1972) classified copulatory behaviour in mammals into 16 categories according to the absence or presence of four traits: lock during copulation, pelvic thrusting during insertion, multiple intromissions with no sperm transfer, and multiple ejaculation within an hour of the first ejaculation. Based on these categories there are conspicuous differences between sciurognath and hystricognath rodents (YOUNG and GRUNT, 1951; BIGNAMI and BEACH, 1968; KLEIMAN, 1974), although they are not absolute (DEWSBURY, 1975). Two patterns are typical for the Hystricognatha: no lock, thrusting during intromission, few intromissions, single (pattern 10) or multiple ejaculations (pattern 9) (KLEIMAN, 1974). Single intromission and one ejaculation (pattern 12) was reported for *Cavia porcellus* (YOUNG and GRUNT, 1951), *Ctenomys mendocinus* (CAMÍN, 1999), and *Spalacopus cyanus* (Begall *et al.*, 1999). Sciurognatha display a much more variable copulatory behaviour. The typical pattern (pattern 13) for most sciurognaths involves multiple intromission with multiple ejaculations, and no lock or thrusting after penetration (DEWSBURY, 1972). Thrusting is a trait typical for hystricognaths (KLEIMAN, 1974) and atypical for most sciurognaths (DEWSBURY, 1972). Copulation in *H. argenteocinereus* is characterised by intravaginal thrusts, multiple intromissions, and absence of any lock. The next copulation and ejaculation follows after a long interval, so that *Heliophobius* conforms to basic hystricognath pattern (pattern 10). The same pattern can be ascribed also to *Cryptomys hottentotus* (HICKMANN, 1982; BENNETT, 1989). The descriptions for other bathyergids are not complete with missing data on the number of intromissions and ejaculations. As typical representatives of hystricognath rodents they display thrusting and it can be assumed that their pattern is not basically different from the hystricognath patterns.

Subterranean versus supraterranean rodents

Supraterranean rodents display short precopulatory interval (incl. courtship) and very short intromissions (i.a. YOUNG and GRUNT, 1951;

BEACH and RABEDAEU, 1959; BIGNAMI and BEACH, 1968; KUEHN and ZUCKER, 1968; DEWSBURY, 1972; GRAY and DEWSBURY, 1973; KLEIMAN, 1974; DEWSBURY and HODGES, 1987). The copulation of subterranean sciurognath rodents markedly resembles those of the especially solitary bathyergids through their longer precopulatory interval, prolonged intromissions lasting up to several minutes, and thrusting (Nevo, 1969; EISENBERG and MALINIAK, 1973; ANDERSEN, 1978; GAZIT *et al.*, 1996). Following DEWSBURY (1975) the displayed pattern is 10 (*Spalax, Cannomys*), or, in the case of multiple ejaculations, pattern 9 (*Thomomys*). Detection of ejaculation is difficult, however. Longer mating sequence may reflect higher safety of the subterranean ecotope (ANDERSEN, 1978; BENNETT and JARVIS, 1988a).

Social versus solitary subterranean rodents

Courtship of solitary species *Ctenomys* (1-65 min, CAMÍN, 1999), *Spalax* (8-55 min, NEVO, 1969) *Cannomys* (EISENBERG and MALINIAK, 1973) and *Thomomys* (ANDERSEN, 1978) is much longer than in the social mole-rat *C. hottentotus* (max 3 min, BENNETT, 1989). Solitary territorial rodents have first to reduce aggression of any intruders, irrespective of sex (NEVO, 1969; BENNETT *et al.*, 1991; *Shanas et al.*, 1995; GAZIT *et al.*, 1996). The other characteristic feature, short intromissions in social subterranean rodents, has been attributed to disturbance by other inhabitants of the burrow system (HICKMANN, 1982; JARVIS, 1991). The difference is conspicuous in species with the same copulation pattern, like in solitary *Ctenomys mendocinus* and social *Spalacopus cyanus*, both representatives of the same family, Octodontidae. Whereas the intromission in *C. mendocinus* can last up to six minutes (CAMÍN, 1999), it takes no more than 15 s in *S. cyanus* (BEGALL *et al.*, 1999).

In conclusion, the mating pattern of solitary subterranean silvery mole-rats (recorded here for the first time) reflects both their subterranean way of life and their hystricognath affinities.

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