The reproductive biology of the giant Zambian mole-rat, *Cryptomys mechowi* (Rodentia: Bathyergidae)

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Cryptomys mechowi occurs in the mesic Miombo tropical woodland and savanna of Zambia, Zaïre and Angola. It is a colonial bathyergid in which reproduction is restricted to a single female. Courtship and copulation are initiated by the female. Copulation is brief and does not involve multiple bouts. The gestation length is 97–111 days ($n = 2$). The newborn pups are altricial and the litter sizes small, averaging 1,6 ± 0,5 ($n = 5$). The pups begin to wander out of the nest when 10 days old, begin to eat solids after 20 days and are fully weaned after 35 days. The growth of *C. mechowi* pups is best described by the Gompertz model. The growth rate for the first 80 days of postnatal growth is 0,8 to 0,94 g/day, whereas for the first 275 days this rate is 0,7 to 0,84 g/day. The reproductive biology of the giant Zambian mole-rat is compared with that of other species of southern and central African *Cryptomys*.

Cryptomys mechowi kom voor in die mesiese tropiese woudgebied van Miombo en die savanne van Zambië, Zaïre en Angola. Dit is 'n koloniale spesie van die Bathyergidae, waarin voortplanting beperk word tot een wyfie. Paringsgedrag en kopulasie word deur die wyfie geïnisieer, is kort, en sluit nie veelvuldige kopulasies in nie. Die dratyd is 97–111 dae ($n = 2$). Die nuutgebore welpies is artrisieel, en die werpselgrootte klein, gemiddeld 1,6 ± 0,5 ($n = 5$). Die welpies begin buite die nes beweeg op 'n ouderdom van 10 dae, soliede voedsel eet na 20 dae, en is ten volle gespeen na 35 dae. Die groei van *C. mechowi* welpies word die beste beskryf deur die Gompertz model. Die groeitempo vir die eerste 80 dae van groei na geboorte is 0,8 tot 0,94 g/dag, en vir die eerste 275 dae is die tempo 0,7 tot 0,84 g/dag. Die voortplantingsbiologie van die reuse Zambiese mol word vergelyk met die van ander *Cryptomys* spesies van suidelike en sentraal Afrika.

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The subterranean Afrotropical giant Zambian mole-rat, *Cryptomys mechowi*, is an apparently colonial herbivore feeding upon geophytes, underground swollen tubers and invertebrates (Burda & Kawalika 1993). The mole-rats are found in northern Zambia, southern Zaire and central Angola (Roberts 1951). Details of the life history and reproductive biology are unknown (Skinner & Smithers 1990). In this paper the reproductive biology of the giant mole-rat is presented and compared with other *Cryptomys* species, namely *C. h. hottentotus, C. damarensis* and *C. darlingi.* These three species all live in colonies in which there is a reproductive division of labour.

Materials and methods

The giant mole-rats were collected in July 1992 from Chingola (12°27'S, 27°51'E) in the Copperbelt of northern Zambia. To investigate reproduction and recruitment in the giant mole-rat, a pair of animals and a group comprising one male and three females were maintained in two glass terraria. Wood shavings were placed in the tanks. Wood wool and paper towelling served as nesting material. The room temperature was maintained at 26–28°C, this temperature being comparable to those recorded in foraging burrows (Bennett, Jarvis & Davies 1988). The mole-rats were fed on a variety of chopped root and green vegetables, apples, grapes and Pronutro^{R}, a commercially prepared balanced breakfast cereal. The mole-rats drank no free water.

Growth curves were fitted with procedure AR of BMDP (Biomedical Package) (Ralston 1988), which fits non-linear regression models by an iterative least-square criterion. The growth data were fitted by three different equations: Von Bertalanffy, Gompertz and logistic. The Gompertz model was used because it showed the lesser residual sum of squares in all cases. Since the data represent the early phase of growth and the adult mass is not evident from these data, only two parameters were estimated, leaving the asymptotic value fixed to the body mass at 80 days and 225 days respectively. This was undertaken to allow a meaniful comparison amongst litters to be made at this particular age. Using the Gompertz model, a growth rate and inflection point was obtained.

Growth rate constants (K = days^{-1}) allow comparisons in growth amongst different taxa and these were used to compare growth patterns in the particular *Cryptomys* species (Table 1). Maximum growth rate was determined by multiplying K by $A.e^{-1}$ (where A = the asymptote and e = the exponential).

Maximum growth rate was obtained from the Gompertz equation:

$$W = A / \times \exp\left[-\exp\left(-K \times (t - t_i)\right)\right]$$

where W = predicted weight; A = asymptote; exp = exponential function; K growth rate constant; t age and t_i a parameter indicating the inflection time.

Results

Courtship and copulation

In captivity, the vagina of the reproductive female became perforate at the onset of reproductive activity. On encountering the reproductive male, she would raise her tail and thrust her hindquarters into his face emitting a bird-like guttural squeal. The male responded to this solicitation by pursuing her around the cage. During this pre-copulatory activity, both male and female produced a rich repertoire of vocalizations.

The male finally seized her tail with his incisors, mounted, and held her around her shoulders with his forelimbs. The female responded, when receptive, by going into lordosis, whereupon intromission proceeded. Thrusting was slow (1 to 2 thrusts per second) reaching a peak prior to ejaculation. Copulation was terminated by the female emitting a prolonged cry and pulling away from the male. Multiple matings were uncommon. Of the three matings observed to date all were single events, not multiple copulations.

Gestation

The two litters born to one pair of mole-rats were spaced 114 days apart (the first litter died five days after birth). Mating was observed three days post-partum, giving a maximum gestation period of approximately 111 days (Figure 1). In a second pair of mole-rats paired on the 3rd January, 1994, mating occurred on 4th January, 1994 and two pups were born on 11th April, 1994. This gives a gestation of 97 days. In the second pair three litters were spaced 143 and 198 days apart. The increase in body mass during the pregnancy was between 12% (1 pup) or 14% (2 pups). The post-partum body mass of the lactating female dropped to 10% below her non-reproductive level.

Litter size

Of the five litters born to captive *C. mechowi*, three were of two pups and two were of one pup. The sex distribution was three males and five females. The mean litter size in captivity is 1,6 ± 0,5 (n = 5).

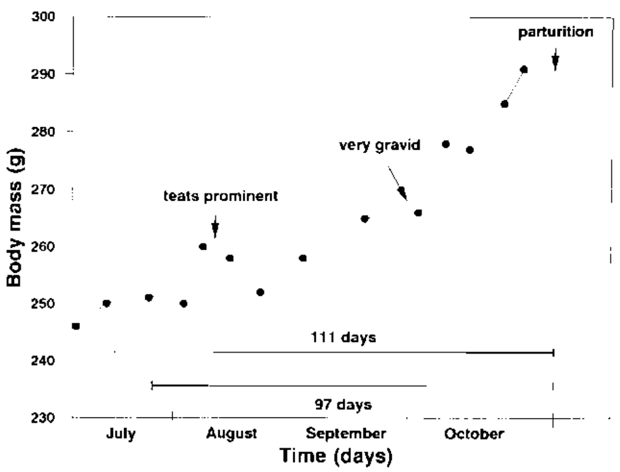

Figure 1 Changes in body mass of a captive female *Cryptomys mechowi* prior to, during and after pregnancy. The maximum gestation length is indicated by a horizontal bar. The lower horizontal bar indicates the minimum gestation period calculated for *C. mechowi* to date.

Development of pups

Newborn pups are between 5–6 cm long, hairless and dark pink, except for purple pigmentation around the head. The eyes and auditory meatus are closed, the digits of the feet are well formed and clawed and the extrabuccal incisors have erupted. The pups produce high frequency squeals, especially prior to sucking. Pups at birth weigh between 15 to 21 g (n = 5).

The pups spend between 30–40% of the time sucking, the rest of the time they sleep. The pups suck from the double row of 12 nipples (six on either side of the midline) which extend along the underside of the body from the pectoral girdle to the abdomen. Sucking bouts occur over extended periods and may occur for at least 20 min at a time.

At day 2, the pups possess a fine chocolate fawn pelage. The pups are remarkably strong and walk with their legs splayed. By day 6 the eyes are open, as is the ear meatus. After 9 days the pup has a thick pelage of brown hair and will bite if picked up. Pups wander freely out of the nest after 10 days. After 20 days, the pups are eating solids, but still infrequently return to suck from the teats. The pups are fully weaned after 5–6 weeks. The pups rarely spar with one another or with their older brothers and sisters.

Growth rate

The mean growth rate for five pups (two male and three female) of *C. mechowi* from birth to 80 days old was 0,8 to 0,94 g/day (Table 1), whereas for the first 275 days the growth rate was 0,7 to 0,84 g/day. The increase in body mass follows the Gompertz model for growth. The growth curves for the first 275 and 500 days of growth are presented for two litters (Figure 2).

Discussion

Within the family Bathyergidae, there are two social genera (*Cryptomys* and *Heterocephalus*). These are characterized by a reproductive pair and helpers at the nest. The restriction of reproduction to a single female in a colony is a feature common to all *Cryptomys* studied to date (Jarvis 1981; Bennett & Jarvis 1988; Bennett 1989; Bennett 1990; Bennett, Jarvis & Cotterill 1994; Burda 1989). In species breeding seasonally (*C. h. hottentotus* and *C. h. natalensis* the male initiates courtship (Hickman 1982; Bennett 1989), whereas in aseasonal

Table 1 The mean growth rate constant (K), maximum growth rate ($K.A.e^{-1}$), asymptotic weight (A) and inflection time (t_i) for the Gompertz model calculated for four species of *Cryptomys*

	A	$t_{(i)}$	K	$K.A.e^{-1}$	
Mashona mole-rat *C. darlingi*	92,6	94,1	0,008	0,272	Bennett, Jarvis & Cotterill 1994
Common mole-rat *C. h. hottentotus*	42,0	12,6	0,015	0,229	Bennett, Jarvis, Aguilar & McDaid 1991
Damaraland mole-rat *C.damarensis*	42,5	15,6	0,015	0,233	Bennett, Jarvis, Aguilar & McDaid 1991
Giant mole-rat *C. mechowi* Litter 1	148,7	52,4	0,017	0,936	Bennett & Aguilar, this study
Giant mole-rat *C. mechowi* Litter 2	242,8	122,2	0,0089	0,798	Bennett & Aguilar, this study
Giant mole-rat *C. mechowi* Litter 3	90,9	26,7	0,0253	0,847	Bennett & Aguilar, this study

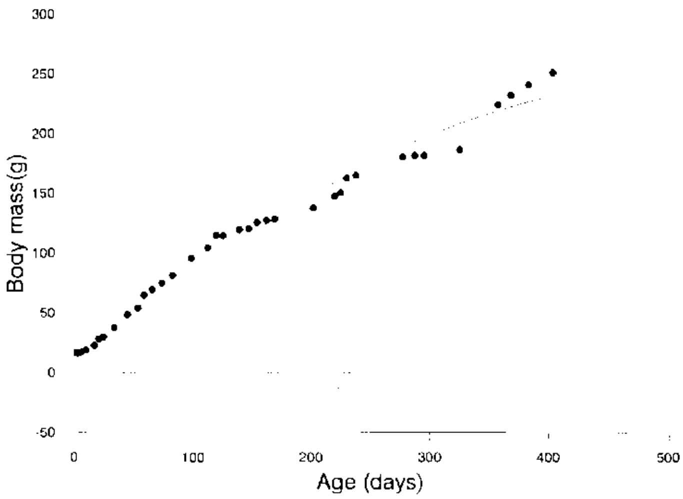

Figure 2a Generated Gompertz plot for postnatal body mass (g) against age (days) for Litter 1 (n = 1 animal) of *C. mechowi* for the first 500 days of growth. Actual data points are presented by (•). A plot of calculated residuals for the Gompertz equation generated (o).

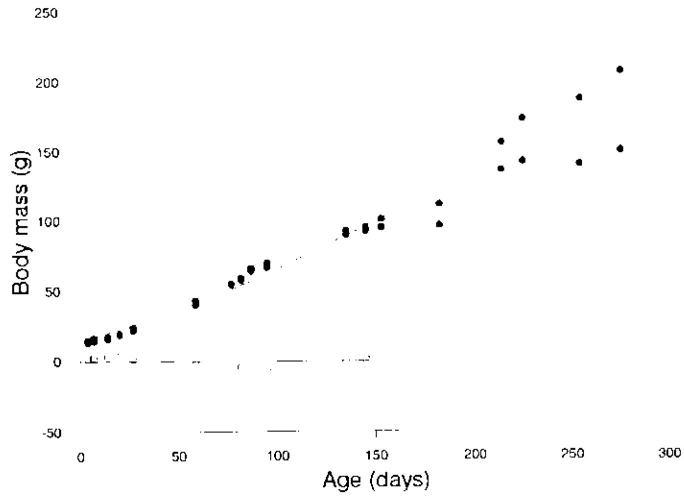

Figure 2c Generated Gompertz plot for postnatal body mass (g) against age (days) for Litter 2 (n = 2 animals) of *C. mechowi* for the first 275 days of growth. Actual data points are presented by (•). A plot of calculated residuals for the Gompertz equation generated (o).

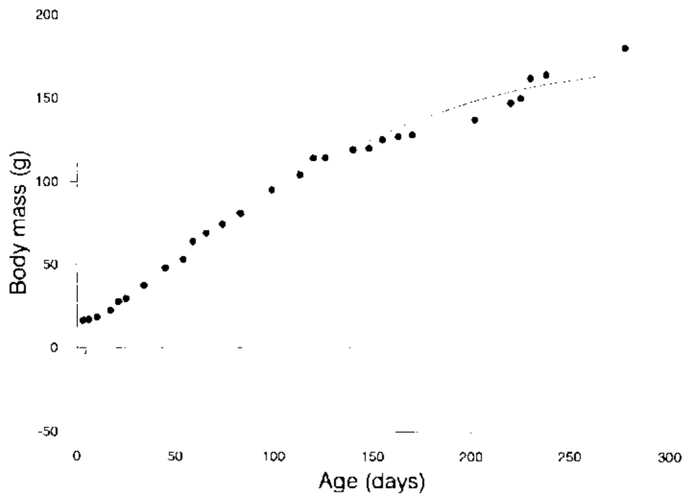

Figure 2b Generated Gompertz plot for postnatal body mass (g) against age (days) for Litter 1 (n = 1 animal) of *C. mechowi* for the first 275 days of growth. Actual data points are presented by (•). A plot of calculated residuals for the Gompertz equation generated (o).

breeders (*C. darlingi, C. damarensis* and *C. amatus)* it is the female (Bennett & Jarvis 1988; Burda 1989; Bennett, Jarvis & Cotterill 1994). Restriction of reproduction to a single female promotes a division of labour within the colony and essentially increases the efficiency of foraging for food, extending and maintaining the burrow system in the non-reproductive members. Indeed, this reproductive division of labour has enabled the genus *Cryptomys* to exploit a range of habitats and yet maintain the conservative nature of its ecotope.

Most *Cryptomys* species have small litters (2 to 6 pups) (Bennett, Jarvis, Aguilar & McDaid 1991), *C. mechowi*, together with *C. darlingi* and *C. amatus* produce the smallest litters (1 to 2 pups). This may account for the relatively small increase in the pregnant female body mass (12 to 31%) when compared with that of the subtropical species *C. h. hottentotus* (21 to 42%) whose mean litter size is 3 (Bennett 1989). It is of interest that the species producing the smallest litters are found in tropical central Africa where temperatures are equable and rainfall is predictable. These two factors would not limit the amount of burrowing performed by the mole-rats to search for their food which comprises the bulbs, corms and tubers of geophytes. These optimally favourable conditions in turn would not lead to selection for large sized colonies.

The relatively long gestation period of *C. mechowi* (97–111 days) is comparable to the other Zambian mole-rat *C. amatus* (90–100 days; Burda 1989) and that of most of the other southern African bathyergids (Bennett *et al.* 1991; Bennett, Jarvis & Cotterill 1994). The extended gestation periods recorded in *Cryptomys* support the notion that they have close affinities with the hystricomorphs. However, unlike those of the hystricomorphs, the young bathyergid pups are born altricial and relatively helpless. Despite the long gestation, *C. hottentotus, C. darlingi* and *C. damarensis* produce relatively altricial young whose mean maximum rate of growth and growth constants (K) are similar (n = 3 species, Table 1). The nidicolous conditions of the pups in the family Bathyergidae could in part be related to the thermally stable and relatively secure environment of the burrow system.

The social *Cryptomys* species are characterized by extremely low mean maximum rates of growth when compared to other solitary bathyergid subterranean rodents (Bennett *et al.* 1991). The low rates of growth may be attributed to a number of complex sociobiological factors acting upon them (these include incorporation of pups into established hierarchies, overlap of litters, co-operative care of young and the strict socially-induced sterility imposed upon individuals in the colonies). *Cryptomys mechowi* grow slightly faster than other members of the genus *Cryptomys* (0,8–0,94 g/day), the growth trajectories of *C. mechowi* being more reminiscent of the solitary *G. capensis* and *B. janetta*. The giant mole-rat is of interest in that it grows at a different rate to that of all other southern African *Cryptomys* studied to date.

Further studies investigating the colony structure and social organization, as well as colony formation in the field are required, since recruitment to the colonies is unusually low, assuming a maximum litter size of two and three litters produced annually. Colony formation would take place over an extended period and theoretically colony sizes are predicted to be small.

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