

Differential growth patterns between successive litters of the eusocial Damaraland mole-rat, *Cryptomys damarensis*, from Namibia

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(With 4 figures in the text)

Differential mean rates of growth were calculated for successive litters of mole-rats born to genetically unrelated pairs of *C. damarensis*. The Logistic equation provided the closest fit to the growth data.

Both intra- and inter-colonial variation in mean maximum growth rate between successive litters incorporated into the natal colonies were determined.

The mean asymptote (A), growth rate constant (K) and inflection time (I) were modelled for the first five litters of pups born to pairs of mole-rats. Inter-colonial analysis of recruitment to colonies revealed litters 1, 2, and 5 to grow faster than litters 3 and 4. Litters 1 and 2 had significantly higher asymptotes and inflection times than litters 3, 4, and 5 ($P < 0.001$). All litters were assimilated into their natal colonies. There were no significant differences between males and females for the asymptote, growth rate constant, or inflection time ($P > 0.05$).

Intra-colonial variation of litters 1 to 4 born to a single colony revealed comparable results to that obtained for inter-colonial comparisons. Multiple comparisons showed litters 1 and 2 to have a significantly higher absolute growth rate than litters 3 and 4. The lowest rate of growth being for litter 4.

The patterns of mean differential growth are discussed in the light of the social organization of the colony. It is postulated that growth rates in litters 1, 2, and 3 are more rigid since they constitute the main functional unit of colony organization. Litters 4 and 5 show a greater plasticity in growth; it is speculated that these colony members become incorporated into the various worker and defender groupings which are characteristic of *C. damarensis* colonies.

Introduction

The Damaraland mole-rat, *Cryptomys damarensis*, is a eusocial subterranean rodent (Bennett & Jarvis, 1988; Jarvis & Bennett, 1993). Colonies of *C. damarensis* consist of familial groups with reproduction restricted to a single reproductive female. Some division of labour into frequent and infrequent workers occurs within the remaining non-reproductive colony members (Bennett & Jarvis, 1988; Bennett *et al.*, 1994).

Relative age determination using tooth wear and eruption patterns revealed that colonies were composed of a number of cohorts which represent successive litters born to the reproductive female (Bennett, Jarvis & Wallace, 1990). Interestingly, older animals are not necessarily the larger-sized individuals. These findings were later corroborated from a long-term field study (Jarvis & Bennett, 1993).

A preliminary investigation into the growth rates of litters born to pairs of mole-rats and those born to colonies revealed that those of the former grew faster for the first 80 days of growth (Bennett *et al.*, 1991). Bennett & Jarvis, 1988; Bennett *et al.* (1991) showed that pups born to *C. damarensis* have long gestations and very slow growth rates which may be attributed to the relatively low resting metabolic rate characteristic of this mole-rat (Bennett, Clarke & Jarvis, 1992).

In this study, we investigate the maximum growth rate, absolute upper asymptote, and the inflection point of the sigmoid growth curves derived for successive litters born to pairs of mole-rats. The resulting growth trajectories of pups within colonies and between colonies are discussed in the light of the social organization of Damaraland mole-rat colonies.

Material and methods

The mole-rats for these studies were captured with modified Hickman livetraps (Hickman, 1979) in Dordabis (22°58'S, 17°41'E) south-east of Windhoek and Otjiwarongo (20°27'S, 16°42'E) in northern Namibia.

The mole-rats were housed in large terraria or maintained in Perspex burrow systems (65 × 70 mm). Wood shavings were placed in the tanks and chambers. Wood wool and paper towelling served as nesting material (Bennett, 1990). The room temperature for the mole-rats ranged from 26–28 °C in summer and 18–21 °C in winter. These temperatures were comparable to those recorded in the foraging burrows (Bennett, Jarvis & Davies, 1988). These mole-rats were fed on a variety of chopped root and green vegetables, on apples, grapes, and Pronutro, a commercially prepared breakfast cereal.

The data obtained for these analyses were collected between the period 1984 and 1991. The litters were derived from 5 pairs of animals which were maintained in the laboratory. The pairs reared 5, 4, 3, 2, and 2 litters, respectively. The paired animals were derived from geographically distinct colonies, to ensure maximum outbreeding (Rickard & Bennett, *In press*). All mole-rats were fed upon the same diet, maintained at the same temperatures and exposed to natural photoperiod, thus eliminating a large potential source of error. The data were collected from 16 litters comprising a total of 47 animals (25 females and 22 males).

Sigmoid growth curves (sigmoid equations have a lower asymptote of zero and an upper asymptote that is the mass plateau of the growth curve) to growth data using the Derivative-free Nonlinear Regression Program of the BMDP statistical package (Ralston, 1988). The model fitted was:

$$\text{Logistic : } W'(t) = A/(1 + \exp(-k(t - I)))$$

Where $W'(t)$ is the predicted weight (g) at age t , A is the asymptote (g) of the curve, k is the growth-rate constant (day^{-1}), I is the inflection time (days) or the point of maximum absolute rate of increase of the growth curve, and t is the time or age (days) (Ricklefs, 1983). The parameters of the model were used for comparisons of growth performance among litters and sexes using a 2-way analysis of variance (Sokal & Rohlf, 1969).

Comparison of growth parameters between litters within a colony was only possible for colony 1, where sufficient data for 4 litters was gathered. Comparisons were done using a 1-way ANOVA followed by Tukey-Kramer multiple comparisons (Stoline, 1981) at the 5% confidence level. Homogeneity of variances was determined using the F-test.

Results

The Logistic equation reasonably approximated the growth data for most individuals. The data were also fitted by the Gompertz and von Bertalanffy equations (Ricklefs, 1983), but the Logistic equation gave a closer fit to the data in most cases. In spite of the general agreement of

the fitted equations and the growth data, systematic deviations occurred in all individuals during the first two weeks after birth.

Inter-colonial analysis

There were no significant differences between males and females for the asymptote ($F_{\text{sex}[1,38]} = 3.31, P = 0.07$), growth-rate constant ($F_{\text{sex}[1,38]} = 0.04, P = 0.84$) and inflection time ($F_{\text{sex}[1,38]} = 0.16, P = 0.69$). Variation in the parameters of the growth models among litters are illustrated in Fig. 1. All three parameters showed significant differences among litters:

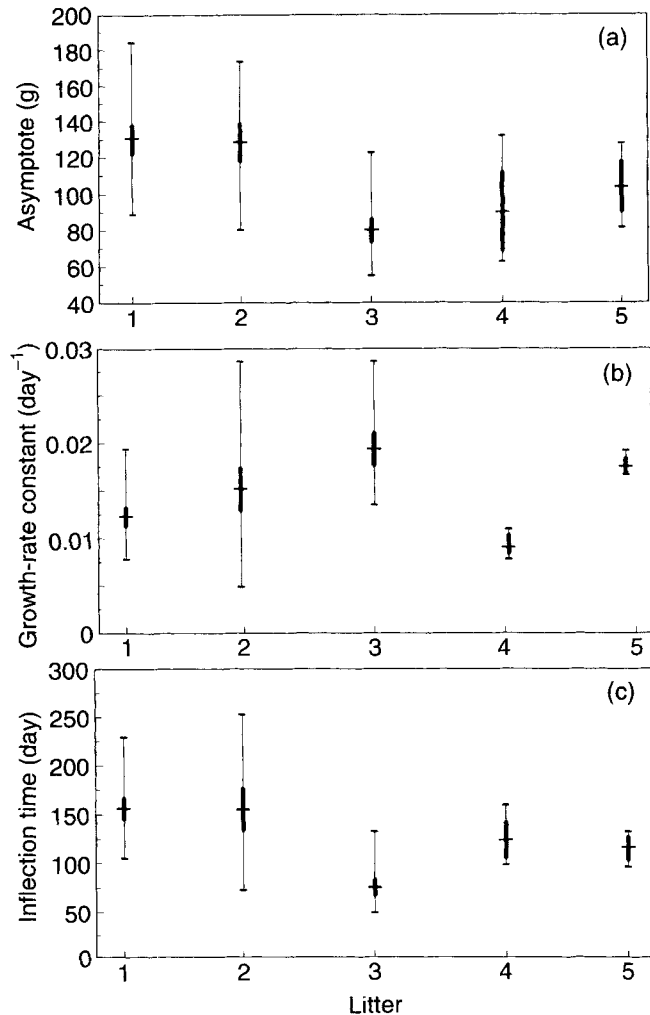


FIG. 1. Parameters of the logistic growth model: (a) asymptote; (b) growth-rate constant; and (c) inflection time. Illustrated are mean (long dash) \pm 1 S.E. (thick line) and range (thin line). Sample sizes are 16, 12, 10, 3, and 3 for litters 1 to 5, respectively.

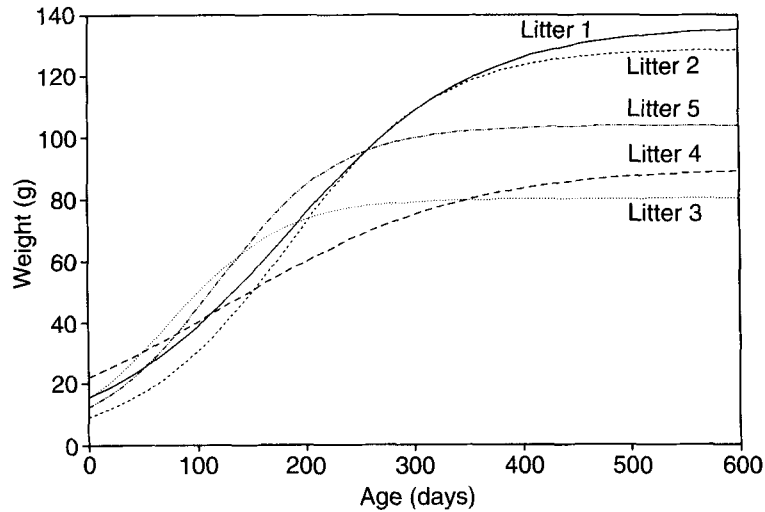


FIG. 2. Logistic growth curves for litters 1 to 5 based on mean values of the parameters.

$F_{\text{litter}[4,38]} = 5.83$, $P < 0.001$; $F_{\text{litter}[4,38]} = 3.13$, $P = 0.018$; and $F_{\text{litter}[4,38]} = 4.06$, $P < 0.005$ for the asymptote, growth-rate constant and inflection time, respectively.

Litters 1 and 2 had significantly higher asymptotes and inflection times than litters 3, 4, and 5 ($P < 0.001$). Litters 1, 2, and 4 had significantly lower growth-rate constants than litters 3 and 5. The overall growth curves for litters 1 to 5 are presented in Fig. 2.

Litters 1, 2, and 5 had the overall fastest rate of growth (Table I). The growth rate of litter 4 was half that of litters 1, 2, and 5. Pups born to litter 1 generally attained the largest body mass of all litters, while pups in litter 2 attained a slightly lower mean asymptote. The pups born to litter 3 had the lowest mean asymptote of all the litters studied (Fig. 1).

Intra-colonial analysis

Growth trajectories were plotted for four successive litters of mole-rats born to a single pair of animals in order to investigate intra-colonial variation. A similar pattern to that obtained for the inter-colonial variation was found. The first two litters grew much more quickly and attained higher asymptotes than the later litters (Table II, Fig. 3). Intra-colonial growth trajectories of the four successive litters illustrates a decline in asymptote with litter position (Fig. 4).

The variance among litters was homogeneous for the asymptote ($F\text{-max}_{[4,1]} = 27.6$, $P > 0.05$), growth-rate constant ($F\text{-max}_{[4,1]} = 8.3$, $P > 0.05$) and inflection time ($F\text{-max}_{[4,1]} = 19.7$, $P > 0.05$).

There was a significant difference among litters for all three parameters of the model: asymptote ($F_{[3,11]} = 7.53$, $P < 0.01$), growth-rate constant ($F_{[3,11]} = 5.94$, $P < 0.05$) and inflection time ($F_{[3,11]} = 6.04$, $P < 0.05$).

However, when absolute growth rate was analysed, the variances were found to be heterogeneous ($F\text{-max}_{[4,1]} = 323$, $P < 0.01$), after removing litter No. 4, homogeneity of variances was attained. Thus for the one-way ANOVA of absolute growth rate litter 4 was excluded. There were significant differences in the growth rate ($F_{[2,10]} = 12.86$, $P < 0.01$) between litters. Multiple

TABLE I

The mean inter-colonial growth rate constant (K), maximum growth rate ($K.A.e^{-1}$), asymptotic weight (A), and inflection time (I) for the logistic model calculated for five successive litters of *C. damarensis*

Litter	A (g)	I (days)	K (days ⁻¹)	K.A.e ⁻¹	n = litters
1	130.6	155	0.012	0.40	5
2	128.5	154	0.015	0.48	5
3	80.0	75	0.019	0.38	3
4	90.0	126	0.009	0.20	2
5	103.8	116	0.017	0.45	1

comparisons showed that litters 1 and 2 have a significantly higher rate of growth than litter 3. The lowest growth rate was for litter 4.

Discussion

The majority of subterranean mammals (both rodents and insectivores) are solitary and highly xenophobic (Nevo, 1979; Bennett *et al.*, 1991). Plural occupancy of burrows is brief and normally results when courtship and copulation are underway or when the female has pups. The young of these solitary subterranean mammals disperse when they are strong enough and establish their own burrow systems (Nevo, 1979). In marked contrast, the young of the social bathyergids become incorporated into the natal colony and, in established colonies, benefit from the co-operative foraging activities of adults in the colony (Bennett *et al.*, 1991). The burrow system is an invaluable asset and represents an enormous investment to the colony; the territory of the burrow system is vigorously defended from other colonies and predators and actively patrolled throughout the 24-hour day (Bennett, 1992; Jarvis *et al.*, 1994). The pups remaining in the colony are essentially delayed dispersers that remain at home until conditions are optimal for them to disperse and establish their own burrows (Jarvis & Bennett, 1993; Jarvis *et al.*, 1994). These individuals increase their inclusive fitness by remaining loyal to the queen.

The selection pressures acting upon successive litters in the social mole-rats are therefore dramatically different from those acting upon solitary mole-rats. Pups born to the first litter reached the largest body mass and had a fast rate of growth. This is logical since the first litter would be important for initially assisting in the excavation of the burrow. As new litters are recruited these larger animals may well take on a defensive role. Indeed, in several of the field captured colonies 'soldier' type behaviour can be observed in one or two of the largest colony

TABLE II

The mean intra-colonial growth rate constant (K), maximum growth rate ($K.A.e^{-1}$), asymptotic weight (A), and inflection time (I) for the logistic model calculated for four successive litters of *C. damarensis*

Litter	A (g)	I (days)	K (days ⁻¹)	K.A.e ⁻¹	n = litters
1	132.8	121.0	0.017	0.570	4
2	115.3	93.8	0.023	0.677	4
3	68.4	66.4	0.019	0.340	5
4	69.0	106.8	0.010	0.170	2

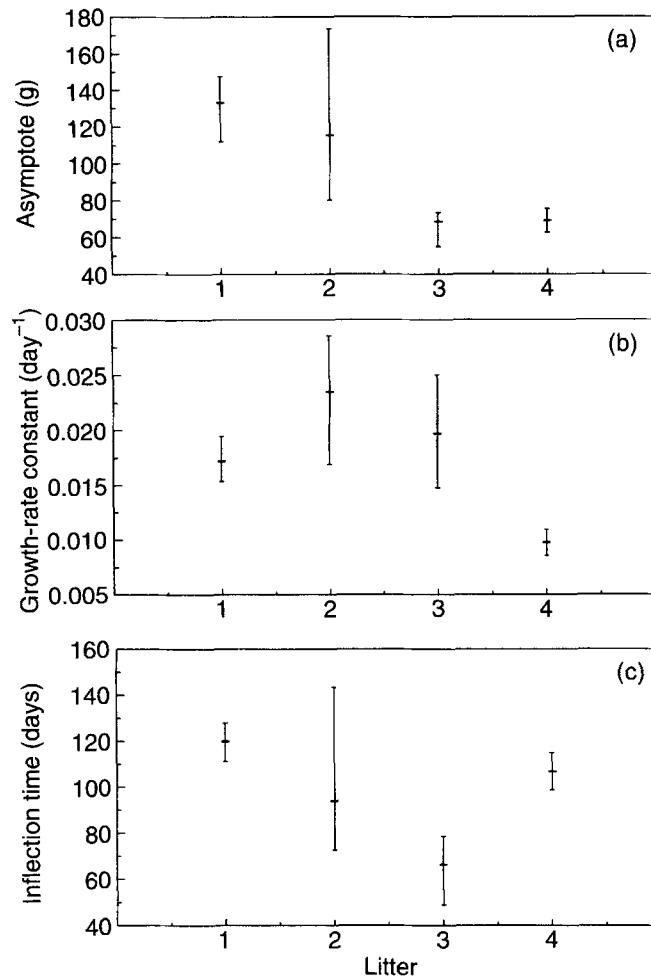


FIG. 3. Parameters of the logistic growth model: (a) asymptote; (b) growth-rate constant; and (c) inflection time. Illustrated are mean and range. Sample sizes are 4, 4, 5, and 2 for litters 1 to 4, respectively.

members (N. C. Bennett & J. U. M. Jarvis, unpubl.). The pups of the second litter, although also attaining a larger critical body mass, tended to grow slightly faster than the first litter. This is of interest, since in the field, the first litters born to the colony tend to grow more slowly in the initial phases of growth (J. U. M. Jarvis & N. C. Bennett, unpubl.), whilst the pups born to litter 3 were generally the slower growing of all litters and attained the lowest asymptote. Bennett & Jarvis (1988) and Jacobs *et al.* (1991) found that non-reproductive colony members could essentially be divided into two subjectively allotted working groups based on the relationship between the amount of work performed and body mass (namely infrequent workers and frequent workers). The smaller animals tended to perform a greater proportion of the burrow maintenance activities. It is plausible that the mole-rats born to litters 1 and 2 are originally frequent workers but with the subsequent recruitment of successive litters attain infrequent worker or defender status. This movement of animals from one worker group to another has been loosely termed

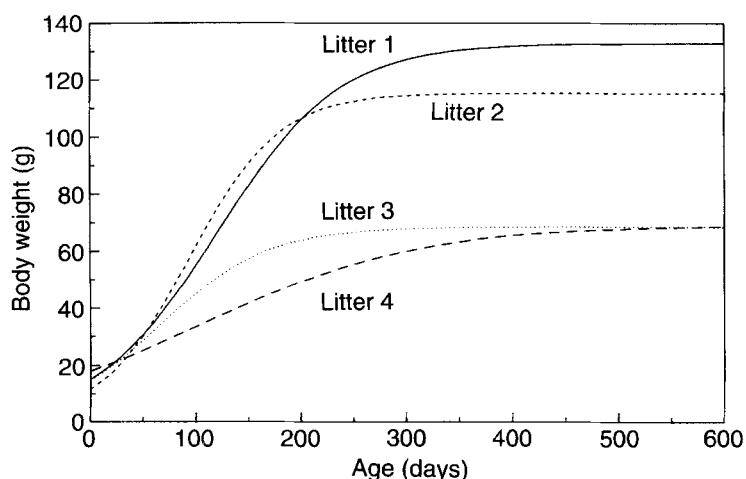


FIG. 4. Logistic growth curves for litters 1 to 4 of a single colony based on mean values of the parameters.

selective role determination (Bennett & Jarvis, 1988; Bennett, 1990; Jacobs *et al.*, 1991). The mole-rats born to litters 4 and 5 generally show no trend in growth or absolute body mass. It is postulated that, once a colony has successfully reared enough litters for the basic functional unit of the colony, subsequent growth in successive litters takes on a different perspective in which dominance position in the colony may become important. The subsequent recruitment of litters 4 and 5 may reveal no definite pattern because these pups become assimilated into the different defensive and work groupings now established. This explanation is supported by the range of relative ages which can constitute the two different worker groups (Bennett, Jarvis & Wallace, 1990). In this scenario, we suggest that in litters 4 and 5, individuals that change their roles are ones which grow faster and become larger than ones which remain as frequent workers. From these studies and from the data on body mass and relative age class (Bennett, Jarvis & Wallace, 1990), it appears that some faster growing individuals within *C. damarensis* colonies show selective role determination, while other individuals (slower growing) do not. In mature colonies, containing up to six successive litters, except for the reproductive pair, adult body mass appears to be independent of age, but is moreover linked to the social status of the animal within the colony.

A second plausible scenario to explain the differential growth rates could arise from the strict social suppression imposed upon these non-reproductive mole-rats. It is possible that as pups become incorporated into the dominance hierarchy, their lower position results in a slight retardation of growth (Jacobs *et al.*, 1991). The earlier litters (1st and 2nd) may grow at a faster rate because they are less exposed to dominance interactions than the later litters. It is obvious that, with an increasing number of animals in the colony, there will be an increase in the permutations and combinations of interactive behaviours among these animals.

The social *Cryptomys* are characterized by extremely low mean maximum rates of growth when compared to other solitary bathyergid and non-bathyergid subterranean and fossorial rodents (Bennett *et al.*, 1991; Bennett, Jarvis & Cotterill, 1994; Bennett & Aguilar, 1995). These slow rates of growth may be attributed to a number of complex sociobiological forces which act upon the mole-rats. The incorporation of pups into an established colony hierarchy, overlap of

litters, co-operative care of the young, selective role determination, and perhaps even the strict social contraception exhibited by non-reproductive colony members, may all contribute to the slower rates of growth observed in these social Bathyergidae.

The naked mole-rat, *Heterocephalus glaber* exhibits a similar social system with a sole reproductive female responsible for recruitment to the colony (Jarvis, 1981). The colony structure in *H. glaber* is similar to that of the Damaraland mole-rat, in that growth polyethism has been demonstrated in colonies that essentially comprise a breeding pair, non-workers, infrequent workers, and frequent workers (Jarvis, 1981). However, to date there is no published data on the growth trajectories of successive litters of pups born to the breeding female, but it would seem logical to assume that a similar situation arises in this second eusocial bathyergid.

This study has enabled the measurement of growth rates in founding colonies of the Damaraland mole-rat, an otherwise secretive and totally subterranean rodent to be monitored in a controlled environment. The regular measurement of growth undertaken in the field is made impossible because of the subterranean nature of the study animals.

Growth in many organisms is very plastic and can be affected by a multitude of parameters (Fleming, 1977). In subterranean mammals, growth and development, among other things, are subject to constraints stemming from burrowing energetics, the size of the pregnant female, the food availability, the quality of the territory, and the position within the colony (Andersen, 1978; Bennett & Jarvis, 1988; Burda, 1989).

Only when the growth rates of successive litters are analysed in context with the degree of social organization in colonies of *C. damarensis* and the respective dominance positions can one propose possible explanations for the disparate mean maximum growth rates. Thus this laboratory study of growth rates in Damaraland mole-rat colonies, provided with an *ad libitum* food supply and similar temperature regimes, has enabled us to show that growth in colonial mole-rats is controlled, and influenced by, many internal and external variables.

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REFERENCES

- Andersen, D. C. (1978). Observations on reproduction, growth, and behavior of the northern pocket gopher (*Thomomys talpoides*). *J. Mammal.* **59**: 418–422.
- Bennett, N. C. (1990). Behaviour and social organization in a colony of the Damaraland mole-rat *Cryptomys damarensis*. *J. Zool. (Lond.)* **220**: 225–248.
- Bennett, N. C. (1992). The locomotory activity patterns of a functionally complete colony of *Cryptomys hottentotus hottentotus* (Rodentia: Bathyergidae). *J. Zool. (Lond.)* **228**: 435–443.
- Bennett, N. C. & Aguilar, G. H. (1995). The reproductive biology of the Giant Zambian mole-rat, *Cryptomys mechowii*. *S. Afr. J. Zool.* **30**: 1–4.
- Bennett, N. C., Clarke, B. C. & Jarvis, J. U. M. (1992). A comparison of metabolic acclimation in two species of social mole-rats (Rodentia: Bathyergidae) in southern Africa. *J. Arid Environ.* **22**: 189–198.
- Bennett, N. C. & Jarvis, J. U. M. (1988). The social structure and reproductive biology of colonies of the mole-rat *Cryptomys damarensis* (Rodentia Bathyergidae). *J. Mammal.* **69**: 293–302.
- Bennett, N. C., Jarvis, J. U. M., Aguilar, G. H. & McDaid, E. J. (1991). Growth and development in six species of African mole-rats (Rodentia: Bathyergidae). *J. Zool. (Lond.)* **225**: 13–26.
- Bennett, N. C., Jarvis, J. U. M. & Cotterill, F. P. D. (1994). The colony structure and reproductive biology of the afro-tropical Mashona mole-rat, *Cryptomys darlingi*. *J. Zool. (Lond.)* **234**: 477–487.

- Bennett, N. C., Jarvis, J. U. M. & Davies, K. C. (1988). Daily and seasonal temperatures in the burrows of African rodent moles. *S. Afr. J. Zool.* **23**: 189–195.
- Bennett, N. C., Jarvis, J. U. M., Millar, R. P., Sasano, H. & Ntshinga, K. V. (1994). Reproductive suppression in eusocial *Cryptomys damarensis* colonies: socially-induced infertility in females. *J. Zool. (Lond.)* **233**: 617–630.
- Bennett, N. C., Jarvis, J. U. M. & Wallace, D. B. (1990). The relative age structure and body masses of complete wild-captured colonies of two social mole-rats, the common mole-rat, *Cryptomys hottentotus hottentotus* and the Damaraland mole-rat, *Cryptomys damarensis*. *J. Zool. (Lond.)* **220**: 469–485.
- Burda, H. (1989). Reproductive biology (behaviour, breeding and postnatal development) in subterranean mole-rats, *Cryptomys hottentotus* (Bathyergidae). *Z. Säugetierkd.* **54**: 360–376.
- Fleming, T. H. (1977). Growth and development of two species of tropical heteromyid rodents. *Am. Midl. Nat.* **98**: 109–123.
- Hickman, G. C. (1979). A live-trap and trapping technique for fossorial mammals. *S. Afr. J. Zool.* **14**: 9–12.
- Jacobs, D. S., Bennett, N. C., Jarvis, J. U. M. & Crowe, T. M. (1991). The colony structure and dominance hierarchy of the Damaraland mole-rat, *Cryptomys damarensis* (Rodentia: Bathyergidae), from Namibia. *J. Zool. (Lond.)* **224**: 553–576.
- Jarvis, J. U. M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science (Washington DC)* **212**: 571–573.
- Jarvis, J. U. M. & Bennett, N. C. (1993). Eusociality has evolved independently in two genera of bathyergid mole-rats but occurs in no other subterranean mammal. *Behav. Ecol. Sociobiol.* **33**: 253–260.
- Jarvis, J. U. M., O’Riain, M. J., Bennett, N. C. & Sherman, P. W. (1994). Mammalian eusociality: a family affair. *Trends Ecol. Evol.* **9**: 47–51.
- Nevo, E. (1979). Adaptive convergence and divergence of subterranean mammals. *Annu. Rev. Ecol. Syst.* **10**: 269–308.
- Ralston, M. (1988). Derivative-free nonlinear regression. In *BMDP statistical software manual* **1**: 389–417. Dixon, W. J., Brown, M. B., Engelman, L., Hill, M. A. & Jennrich, R. I. (Eds), Berkeley, L. A.: University of California Press.
- Rickard, C. A. & Bennett, N. C. (1997). Recrudescence of sexual activity in a reproductively quiescent colony of the Damaraland mole-rat (*Cryptomys damarensis*), by the introduction of an unfamiliar and genetically unrelated male—a case of incest avoidance in ‘queenless’ colonies. *J. Zool. (Lond.)* **241**: 185–202.
- Ricklefs, R. E. (1983). Avian postnatal development. In *Avian biology* **7**: 1–83. Farner, D. S., King, J. R. & Parkes, K. C. (Eds). New York: Academic Press.
- Sokal, R. R. & Rohlf, F. J. (1969). *Biometry*. San Francisco: Freeman.
- Stoline, M. R. (1981). The status of multiple comparisons: simultaneous estimation of all pairwise comparisons in one-way anova designs. *Am. Statist.* **35**: 134–141.