

# Extraordinary life spans of naked mole-rats (*Heterocephalus glaber*)

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## Abstract

Senescence is the internal physiological deterioration that accompanies advancing age. Evolutionary hypotheses predict that rates of senescence should vary directly with extrinsic mortality and inversely with fecundity. If so, naked mole-rats (*Heterocephalus glaber*) should live a long time (senesce slowly) because in nature they inhabit heavily protected burrows, and large, old breeding females make disproportionate reproductive contributions. In addition *H. glaber* has an exceptionally low metabolic rate, which may reduce oxidative stress. We have maintained naked mole-rats in captivity since 1974. Here we report that individuals can live a very long time: many are alive after more than 20 years and some are 26 years old (and counting). Although we do not yet know how long naked mole-rats can live, they already are older than the maximum longevity of all but one of 156 rodent species that have been maintained in captivity from birth to death.

**Key words:** life span, longevity, senescence, naked mole-rat, *Heterocephalus glaber*

## INTRODUCTION

Senescence is 'a persistent decline in age-specific fitness components of an organism due to internal physiological deterioration' (Rose, 1991). Natural selection should consistently oppose expression of traits that reduce fitness, so the ubiquity of senescence is an evolutionary puzzle (Williams, 1957, 1999; Hamilton, 1966). To resolve it, several proximate (immediate cause) and ultimate (evolutionary cause) hypotheses have been proposed (reviewed by Finch, 1990; Austad, 1997a; Kirkwood & Austad, 2000).

Evolutionary hypotheses treat senescence as a non-adaptive consequence of the diminishing efficacy of selection on older age cohorts, whereas proximate hypotheses implicate somatic wear and tear (e.g. oxidative damage to DNA and cells because of high metabolic rates: Finkel & Holbrook, 2000). Proximate and ultimate explanations are complementary, not alternative: the former identify the specific physiological mechanisms the breakdown of which results in senescence, and the latter explain how natural selection has acted to maintain those mechanisms (Keller & Genoud, 1997; Kirkwood & Austad, 2000).

Evolutionary hypotheses predict that rates of senescence should correlate positively with extrinsic mortality and negatively with fecundity (Williams, 1957; Ricklefs, 1998). When mortality is high there will be few old survivors, so selection to maintain their somatic functions will be weak, resulting in shorter life spans. Conversely, when extrinsic mortality is lower, selection is stronger to maintain somatic functions among old individuals, resulting in longer life spans. In support, life spans of flies can be reduced or extended by experimentally manipulating extrinsic mortality (Reed & Bryant, 2000; Stearns *et al.*, 2000). Fecundity also is important because the efficacy of selection in maintaining somatic functions depends not only on how frequently it acts, but also on the significance of its effects on reproduction.

Naked mole-rats *Heterocephalus glaber* are small (mean mass = 35 g), colonial (up to 300 individuals), eusocial rodents (Jarvis, 1981; Sherman, Jarvis & Alexander, 1991; Sherman, Jarvis & Braude, 1992). Within a colony, one female and one to three males usually reproduce. For three reasons evolutionary hypotheses predict that naked mole-rats should be able to live a long time. First, they inhabit subterranean burrows in extremely hard soils; protection is enhanced by cooperative defence against predators. In nature, individuals can live at least 10 years (Braude, 2000).

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Fig. 1. Ages of all 86 naked mole-rats *Heterocephalus glaber* that lived  $\geq 15$  years in captivity as of 1 January, 2001. Ages of breeders are from birth or capture, not onset of reproduction. Deceased individuals are indicated.

Second, breeding females can produce very large litters (up to 28 pups; Jarvis, 1991a; Sherman, Braude & Jarvis, 1999) and larger, older breeding females bear significantly more pups per litter and per year than smaller, younger breeders (O'Riain *et al.*, 2000). Established breeders can produce 80–100 pups in a year, and one female bore >900 pups over 11 years (Jarvis & Sherman, in press). Third, naked mole-rats have an exceptionally low basal metabolic rate (Buffenstein, 2000), which should reduce oxidative stress per unit time.

## METHODS

We have maintained *H. glaber* colonies in captivity since 1974. Original colony members were captured near Tsavo West National Park and the nearby village of Kathekani in southern Kenya (2°45' S, 38°07' E) or around the village of Lerata in northern Kenya (1°30' N, 38°30' E). In captivity, colonies have been maintained under semi-natural conditions, in artificial burrow systems within warm (28–30°C), humid (50–65%), quiet rooms (Jarvis, 1991b; Lacey & Sherman, 1991). They are fed *ad libitum* amounts of a variety of plant materials (especially tubers), with protein and vitamin supplements. Veterinary care is provided as necessary.

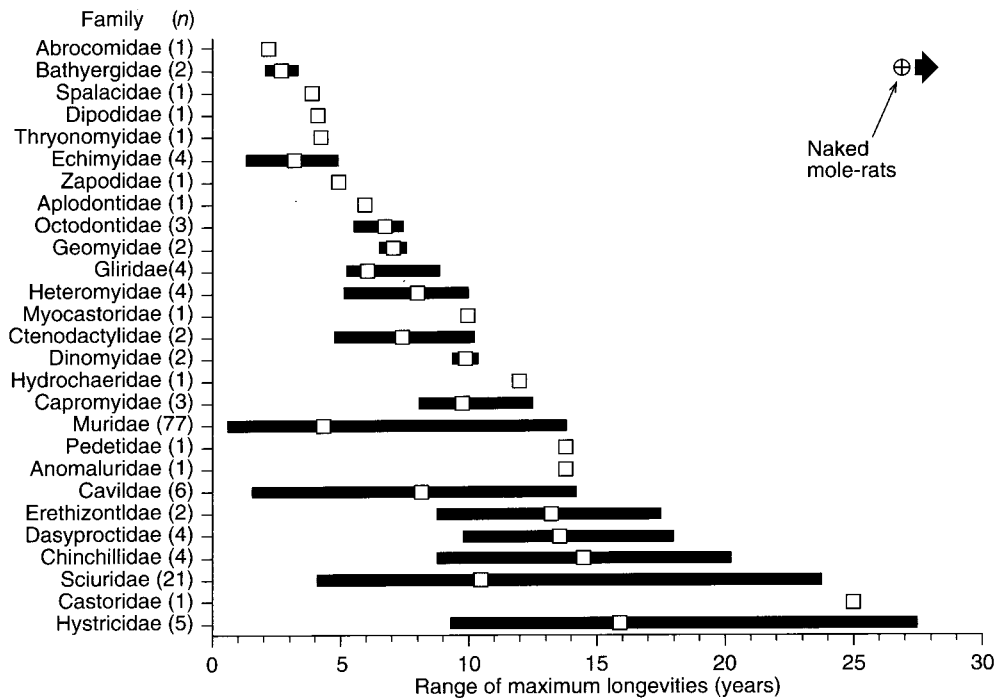
Over the years, mortality among our captive animals has been due to intra-colony fights for reproductive dominance, systemic infections, infectious diseases, and various laboratory accidents that affected entire colonies or specific individuals. Some mole-rats also died of

unidentifiable causes. Because of the obvious artificiality of the laboratory environment and its associated mortality sources, formal demographic analyses of our captive population (e.g. life tables, average life expectancies, population pyramids) is both inappropriate and, quite likely, misleading relative to the situation in nature. However, maximum longevity of males and females and breeders and non-breeders are unbiased and of considerable comparative interest (see Carey & Judge, 2000). Therefore, we focus here on maximum rather than mean life spans.

## RESULTS

Since 1974 data have been gathered on 1140 naked mole-rats in 25 captive colonies. On 1 January 2001 our colonies were censused and records searched to identify individuals, living and deceased, that had survived at least 15 years. There were four cohorts of such individuals: (1) those that were born and had died in captivity (i.e. their life spans were known); (2) those that were born in captivity and were still alive; (3) those that were caught in the wild and had died in captivity (i.e. their minimum life spans were known); (4) those that were caught in the wild and still were alive.

We identified 86 mole-rats that survived  $\geq 15$  years in captivity (Fig. 1). Of these, 43 (20 males, 23 females) were born in the laboratory and 43 (24 males, 19 females) were wild-caught. Most (75/86 = 87%) were still alive on 1 January, and their ages ranged from 15 to  $\geq 26$  years. The living, wild-caught mole-rats were slightly older than individuals born in the laboratory



**Fig. 2.** Ranges of maximum life spans in captivity (birth to death) for 27 families ( $n = 157$  species) of rodents. Boxes, mean (or only) maximum life span in captivity for the family; black bars, total range in maximum life spans. Sample sizes (number of species/family) in parentheses. Data for all species except naked mole-rats from Carey & Judge (2000). Arrow, maximum longevity is not yet known.

(Fig. 1). This is probably because the oldest colonies were caught in the field, rather than that individuals born in the laboratory were less viable. There were no significant differences between ages of living, captive-born females *vs* males or breeders *vs* non-breeders of either sex (all  $P > 0.10$ , Mann–Whitney tests).

Of the 27 breeders alive on 1 January 2001, 18 (67%) were  $> 20$  years old; and of the 48 living non-breeders, 34 (71%) were  $> 20$  years old. The oldest laboratory-born female lived 23 years 8 months, and she bore a litter of 21 pups a month before she died; her wild-caught mate was  $> 26$  years old at that time. The oldest wild-caught female to become a breeder was  $> 26$  years when she died (she had ceased reproducing 3 years previously). The oldest age at which individuals began breeding was 16 years for females and 17 years for males.

## DISCUSSION

Evolutionary hypotheses for senescence are supported by the long life spans of creatures that have low rates of predation, e.g. as a result of large body size (e.g. elephants, bears, and some primates; Austad, 1997a) or unique predator-avoidance mechanisms (e.g. shells of turtles: Gibbons, 1987; flight in birds and bats: Calder, 1990; Austad & Fischer, 1991). Long life also characterizes organisms in which older individuals can make disproportionate reproductive contributions, such as some fishes, amphibians, reptiles (Carey & Judge, 2000) and coniferous trees (Finch, 1998).

A recent compilation of maximum life lengths among mammals (i.e. individuals that were born and died in captivity) by Carey & Judge (2000) lists information for 156 species of rodents (Fig. 2). Although this is a relatively small sample of the Rodentia ( $< 10\%$  of all species) and most families except Muridae and Sciuridae are poorly represented, it is apparent that maximum longevity of naked mole-rats are indeed extraordinary, even relative to other hystricognaths (e.g. Caviidae, Hydrochaeridae, Myocastoridae, Capromyidae, Dinomyidae, Dasyproctidae, Echimyidae, Chinchillidae, Octodontidae, Ctenomyidae, Thryonomyidae and Hystricidae). Naked mole-rats also are an 'outlier' ( $> 2$  SD) to a regression of maximum life lengths on adult body mass for 29 species of Rodentia (Prothero & Jürgens, 1987). And, we do not yet know how long naked mole-rats can live because most of our  $> 15$  year old animals still are alive (Fig. 1).

Based on evolutionary hypotheses, and on our observations, we predict that reduced rates of senescence should characterize other rodents that have relatively low rates of extrinsic mortality (e.g. due to predation). Interestingly, there is one other extremely long-lived rodent (27 years 4 months) in Carey & Judge's (2000) database: the African porcupine *Hystrix brachyura*. These are large-bodied animals that also possess a special anti-predator mechanism: quills.

Long life spans also should characterize subterranean rodents, especially the social species. Thus, longevity of African mole-rats (genus *Cryptomys*: Bennett & Faulkes, 2000) and South American coruros and tuco-

tucos (*Spalacopus* and *Ctenomys*: Lacey, 2000) should be greater than surface-dwelling and solitary relatives. Unfortunately, information in Jones's (1979) and Carey & Judge's (2000) databases are insufficient to quantitatively test this prediction. However, preliminary data seem to be consistent with it: wild-caught *Cryptomys mechowii*, *C. darlingi*, *C. damarensis*, all of which are social, have lived >10 years in captivity, and wild-caught *Georychus capensis* and *Bathyergus suillus*, both of which are solitary, have lived >8 and >6 years in captivity, respectively (N. C. Bennett & J. U. M. Jarvis, pers. obs.).

In social insects such as ants and termites, breeding females typically can live many times longer than workers (Keller & Genoud, 1997; Keller, 1998). As yet there is no indication of similar differences in longevity of breeding and non-breeding naked mole-rats. This may be because we have not kept the mole-rats long enough to see any differences that may develop. Alternatively, there may not be life-history differences between breeders and non-breeders because, in contrast to most social insects, non-breeding *H. glaber* retain reproductive competence. When a breeding vacancy occurs in a mole-rat colony it is typically filled by one of the old, dominant non-breeders in the colony (O'Riain, 1996; Clarke & Faulkes, 1997; Van der Westhuizen, 1997).

Our data (Fig. 1) are intriguing not only in light of evolutionary hypotheses for senescence but also because they suggest a new 'model system' for studying the aging process in mammals (e.g. Austad, 1997b). Physiological and metabolic studies of very old *H. glaber* are just beginning (e.g. O'Connor *et al.*, in press). Detailed investigations of naked mole-rats and other long-lived rodent species (Fig. 2) will undoubtedly reveal some unique cellular, molecular, and metabolic mechanisms that minimize oxidative stress and delay the ageing process.

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### REFERENCES

- Austad, S. N. (1997a). *Why we age*. New York: Wiley.
- Austad, S. N. (1997b). Comparative aging and life histories in mammals. *Exp. Gerontol.* **32**: 23–38.
- Austad, S. N. & Fischer, K. E. (1991). Mammalian aging, metabolism, and ecology: evidence from bats and marsupials. *J. Gerontol.* **46**: B47–53.
- Bennett, N. C. & Faulkes, C. G. (2000). *African mole-rats: ecology and eusociality*. Cambridge: Cambridge University Press.
- Braude, S. (2000). Dispersal and new colony formation in wild naked mole-rats: evidence against inbreeding as the system of mating. *Behav. Ecol.* **11**: 7–12.
- Buffenstein, R. (2000). Ecophysiological responses of subterranean rodents to underground habitats. In *Life underground: the biology of subterranean rodents*: 62–110. Lacey, E. A., Patton, J. L. & Cameron, G. N. (Eds). Chicago: University of Chicago Press.
- Calder, W. A. III (1990). Avian longevity and aging. In *Genetic effects on aging II*: 185–204. Harrison, D. E. (Ed.). Caldwell, NJ: Telford Press.
- Carey, J. R. & Judge, D. S. (2000). Longevity records: life spans of mammals, birds, amphibians, reptiles, and fish. *Odense Univ. Monogr. Population Aging* **8**: 1–241.
- Clarke, F. M. & Faulkes, C. G. (1997). Dominance and queen succession in captive colonies of the eusocial naked mole-rat, *Heterocephalus glaber*. *Proc. R. Soc. Lond. Biol. Sci.* **264**: 993–1000.
- Finch, C. E. (1990). *Longevity, senescence, and the genome*. Chicago: University of Chicago Press.
- Finch, C. E. (1998). Variations in senescence and longevity include the possibility of negligible senescence. *J. Gerontol.* **53**: B235–B239.
- Finkel, T. & Holbrook, N. J. (2000). Oxidants, oxidative stress and the biology of ageing. *Nature (Lond.)* **408**: 239–247.
- Gibbons, J. W. (1987). Why do turtles live so long? *BioScience* **37**: 262–269.
- Hamilton, W. D. (1966). The moulding of senescence by natural selection. *J. theor. Biol.* **12**: 1–45.
- Jarvis, J. U. M. (1981). Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* **212**: 571–573.
- Jarvis, J. U. M. (1991a). Reproduction of naked mole-rats. In *The biology of the naked mole-rat*: 384–425. Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D. (Eds). Princeton, NJ: Princeton University Press.
- Jarvis, J. U. M. (1991b). Methods for capturing, transporting, and maintaining naked mole-rats in captivity. In *The biology of the naked mole-rat*: 467–483. Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D. (Eds). Princeton, NJ: Princeton University Press.
- Jarvis, J. U. M. & Sherman, P. W. (In press). *Heterocephalus glaber*. *Mamm. Species*.
- Jones, M. L. (1979). Longevity of mammals in captivity. *Int. Zoo News* **1979**(3): 16–26.
- Keller, L. (1998). Queen lifespan and colony characteristics in ants and termites. *Insectes Soc.* **45**: 235–246.
- Keller, L. & Genoud, M. (1997). Extraordinary life spans in ants: a test of evolutionary theories of aging. *Nature (Lond.)* **389**: 958–960.
- Kirkwood, T. B. L. & Austad, S. N. (2000). Why do we age? *Nature (Lond.)* **408**: 233–238.
- Lacey, E. A. (2000). Spatial and social systems of subterranean rodents. In *Life underground: the biology of subterranean rodents*: 257–296. Lacey, E. A., Patton, J. L. & Cameron, G. N. (Eds). Chicago: University of Chicago Press.
- Lacey, E. A. & Sherman, P. W. (1991). Social organization of naked mole-rat colonies: evidence for divisions of labor. In

- The biology of the naked mole-rat*: 275–336. Sherman, P. W., Jarvis, J. U. M. & Alexander, R. D. (Eds). Princeton, NJ: Princeton University Press.
- O'Connor, T. P., Lee, A., Jarvis, J. U. M. & Buffenstein, R. (In press). Prolonged longevity in naked mole-rats: age-related changes in metabolism, body composition, and gastrointestinal function. *Comp. Biochem. Physiol. A*.
- O'Riain, M. J. (1996). *Pup ontogeny and factors influencing behavioral and morphological variation in naked mole-rats, Heterocephalus glaber* (Rodentia, Bathyergidae). Unpubl. PhD thesis, University of Cape Town.
- O'Riain, M. J., Jarvis, J. U. M., Alexander, R., Buffenstein, R. & Peeters, C. (2000). Morphological castes in a vertebrate. *Proc. Natl. Acad. Sci. U. S. A.* **97**: 13194–13197.
- Prothero, J. & Jürgens, K. D. (1987). Scaling of maximal life span in mammals: a review. In *Evolution of longevity in animals: a comparative approach*: 49–74. Woodhead, A. D. & Thompson, K. H. (Eds). New York: Plenum Press.
- Reed, D. H. & Bryant, E. H. (2000). The evolution of senescence under curtailed life span in laboratory populations of *Musca domestica* (the housefly). *Heredity* **85**: 115–121.
- Ricklefs, R. E. (1998). Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am. Nat.* **152**: 24–44.
- Rose, M. R. (1991). *Evolutionary biology of aging*. Oxford: Oxford University Press.
- Sherman, P. W., Braude, S. H. & Jarvis, J. U. M. (1999). Litter sizes and mammary numbers of naked mole-rats: breaking the one-half rule. *J. Mammal.* **80**: 720–733.
- Sherman, P. W., Jarvis, J. U. M. & Alexander R. D. (Eds). (1991). *The biology of the naked mole-rat*. Princeton, NJ: Princeton University Press.
- Sherman, P. W., Jarvis, J. U. M. & Braude, S. H. (1992). Naked mole-rats. *Sci. Am.* **267**: 72–78.
- Stearns, S. C., Ackermann, M., Doebeli, M. & Kaiser, M. (2000). Experimental evolution of aging, growth, and reproduction in fruitflies. *Proc. Natl. Acad. Sci. U.S.A.* **97**: 3309–3313.
- Van der Westhuizen, L. A. (1997). *Social suppression of reproduction in the naked mole-rat, Heterocephalus glaber: plasma LH concentrations and differential pituitary responsiveness to exogenous GnRH*. Unpubl. MSc thesis, University of Cape Town.
- Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**: 398–411.
- Williams, G. C. (1999). The Tithonus error in modern gerontology. *Q. Rev. Biol.* **74**: 405–415.