

No evidence for multimodal body mass distributions and body mass-related capture order in wild-caught Damaraland mole-rats

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Abstract

Division of labour among workers is a universal property of eusocial insect societies. For Damaraland mole-rats (*Fukomys damarensis*), a eusocial mammal, it was proposed that workers can be divided into morphologically distinct (in terms of body mass) subcastes of frequent and infrequent workers. Here we investigate, by using capture data from a large number of colonies of Damaraland mole-rats, if body mass is multimodally distributed, which may be indicative of worker subcastes and, further, if there is a relationship between body mass and capture order, which may be indicative of morphological specialization for colony defence. Our analysis reveals unimodal body mass distributions for both sexes. Further, there is no evidence for body mass-related differences between individuals in the capture order. These data suggest that body mass is not an indicator of behavioural specialization in Damaraland mole-rats.

Keywords: Bathyergidae; Damaraland mole-rat; body mass; capture order

A universal feature of eusocial insects is the division of labour among workers, which is based on age and/or morphological specialization (Wilson, 1979). In many ants and termites, for example, physical worker subcastes exist, which are specialized for tasks such as foraging or colony defence (Robinson, 1992). The Damaraland mole-rat (*Fukomys damarensis*) is a eusocial subterranean mammal, which occurs in arid regions of southern Africa (red Kalahari sands) in large colonies with a single female (queen) monopolizing reproduction in each colony (Jarvis and Bennett, 1993; Bennett and Faulkes 2000). The subordinate, non-breeding animals are usually the offspring of the breeding pair and constitute the major workforce. The burrows of established colonies consist of a complex network of tunnels and chambers that are almost completely sealed from the surface. Mole-rats are herbivorous and owing to their subterranean lifestyle depend entirely on roots and tubers as food sources, which they locate while excavating foraging tunnels (Bennett and Faulkes, 2000).

Earlier studies on laboratory-maintained Damaraland mole-rats have demonstrated that based on the type and amount of work performed within the burrow system, reproductives differ from non-reproductives, and the latter could further be divided into frequent and infrequent worker subcastes (Bennett and Jarvis, 1988; Bennett 1990; Jacobs et al., 1991). Morphologically, this distinction is thought to be reflected in body mass, with breeders > infrequent workers > frequent workers (Bennett and Jarvis, 1988 Bennett, 1990). Moreover, it was proposed that Damaraland mole-rats exhibit, similar to social insects, a form of age polyethism, where most young animals enter the frequent worker subcaste, with slow-growing animals permanently remaining in this caste while fast-growing animals move to the infrequent worker subcaste (Bennett and Jarvis, 1988; Bennett 1990; Bennett and Faulkes 2000). The age polyethism schedules found in social insects such as honey bees constitute a progression from inside-nest to outside-nest labour, therefore postponing more risky tasks to later in life (Seeley, 1982). When compared to mole-rats, this would suggest that older and presumably heavier animals are involved in defence-related behaviours. Indeed, there is

evidence from a small number of colonies of naked mole-rats (*Heterocephalus glaber*) showing that large animals are captured first, i.e. are the first to be exposed to potential danger (Brett, 1991). A similar report exists from one colony of Damaraland mole-rats, where during repeated trapping sessions the largest males were invariably the first 4 to 5 animals to be caught, suggesting a ‘soldier’ function for this size class (Lovegrove 1988). A subsequent study in the laboratory on five colonies of Damaraland mole-rats could not confirm such a relationship (Jacobs et al., 1991). In order to catch mole-rats, their underground tunnel system needs to be opened up and a baited Hickman live trap is positioned at the opened section. Such an opened tunnel system represents a high risk to the colony as it potentially permits entry to predators. It is therefore assumed that the order by which animals are captured in the traps may reflect the order in which they perform defence-related behaviours.

In the present study, using capture data from 24 completely trapped colonies of Damaraland mole-rats, comprising 244 individuals, we aimed at revisiting some of the earlier findings in Damaraland mole-rats (Lovegrove 1988; Bennett and Jarvis, 1988; Bennett 1990, Jacobs et al. 1991). Specifically, we investigated whether body mass is multimodally distributed in both sexes, which would indicate the existence of physical castes. Further, by analyzing capture order within colonies we aimed to determine if the participation in colony defence is correlated with body mass.

Mole-rats were trapped between 2013 and 2016 near the village of Black Rock, Northern Cape, South Africa (27°7'S, 22°50'E) with Hickman live-traps under permission from Northern Cape Nature Conservation authorities. Burrow systems were opened along a foraging tunnel and typically, all colony members were caught from a single trap. For each colony, capture order and body mass of all individuals was recorded. All colonies that were captured were complete. The reproductive female (queen) of a colony was determined by the presence of a perforate vagina and prominent teats (Bennett and Jarvis, 1988). Each colony only contained one queen. The identification of breeding males in the field is less

unambiguous. In the laboratory, up to 3 breeding males per colony have been identified (Jarvis and Bennett, 1993). Thus, we did not attempt to divide the males in breeder and non-breeder. Animals with a body mass ≤ 50 g were considered juveniles.

Statistical analyses were carried out using JMP 12 software. Data are presented as means \pm SE. Differences in body mass were analysed by t-tests. Bimodality of the body mass distributions was tested with the R package implementing Hartigan's dip test (diptest; Maechler, 2016). The relationship between body mass and capture order was analysed for each colony by Spearman rank correlation.

Colony size ranged from 2-29 individuals with a mean size of 10.2 ± 1.3 individuals. Body mass of adult females ($N = 96$) ranged from 52-155 g and that of adult males ($N = 108$) from 53-179 g. Males were on average heavier than females (106.7 ± 3.1 g vs. 94.7 ± 2.3 g; $t = 3.05$, $df = 202$, $p < 0.01$). Among females, queens were significantly heavier than non-reproductives (118.6 ± 3.1 g vs. 86.8 ± 2.2 g; $t = 7.64$, $df = 94$, $p < 0.001$). The overall sex ratio of all animals captured including juveniles did not deviate from parity (108M:96F; $\chi^2 = 0.71$, $p = 0.40$). Only for animals > 110 g the sex ratio became male-biased (48M:25F, $\chi^2 = 7.21$, $p < 0.01$). Average sex ratio (proportion males) within colonies was 0.56, ranging from 0.23-0.86. To determine whether the behavioural division of labour previously described for colonies of Damaraland mole-rats can be identified based on a morphological distinction, we calculated for each sex the Hartigan's dip test. The analysis revealed no evidence for a multimodal distribution of body mass in males (Fig. 1A; Hartigan's dip test, $D = 0.034788$, $p = 0.47$) or in females (Fig. 1B; Hartigan's dip test, $D = 0.027778$, $p = 0.90$). Also, multimodality was not significant among non-breeding females (Fig. 1C; $D = 0.024691$, $p = 0.99$) and among queens (Fig. 1D; $D = 0.065972$, $p = 0.55$). The first animals caught in the traps might be those actively involved in defence and repair of the tunnel system. We found in two out of 24 colonies a significantly negative correlation between capture order and body mass. No significant positive correlation was found in any colony (Table 1). The queen was

found to be among the last 30% of individuals captured in eight colonies. In four colonies, the queen was captured during late pregnancy. In three of these colonies it was either the last to be captured or among the last 20% of the individuals captured.

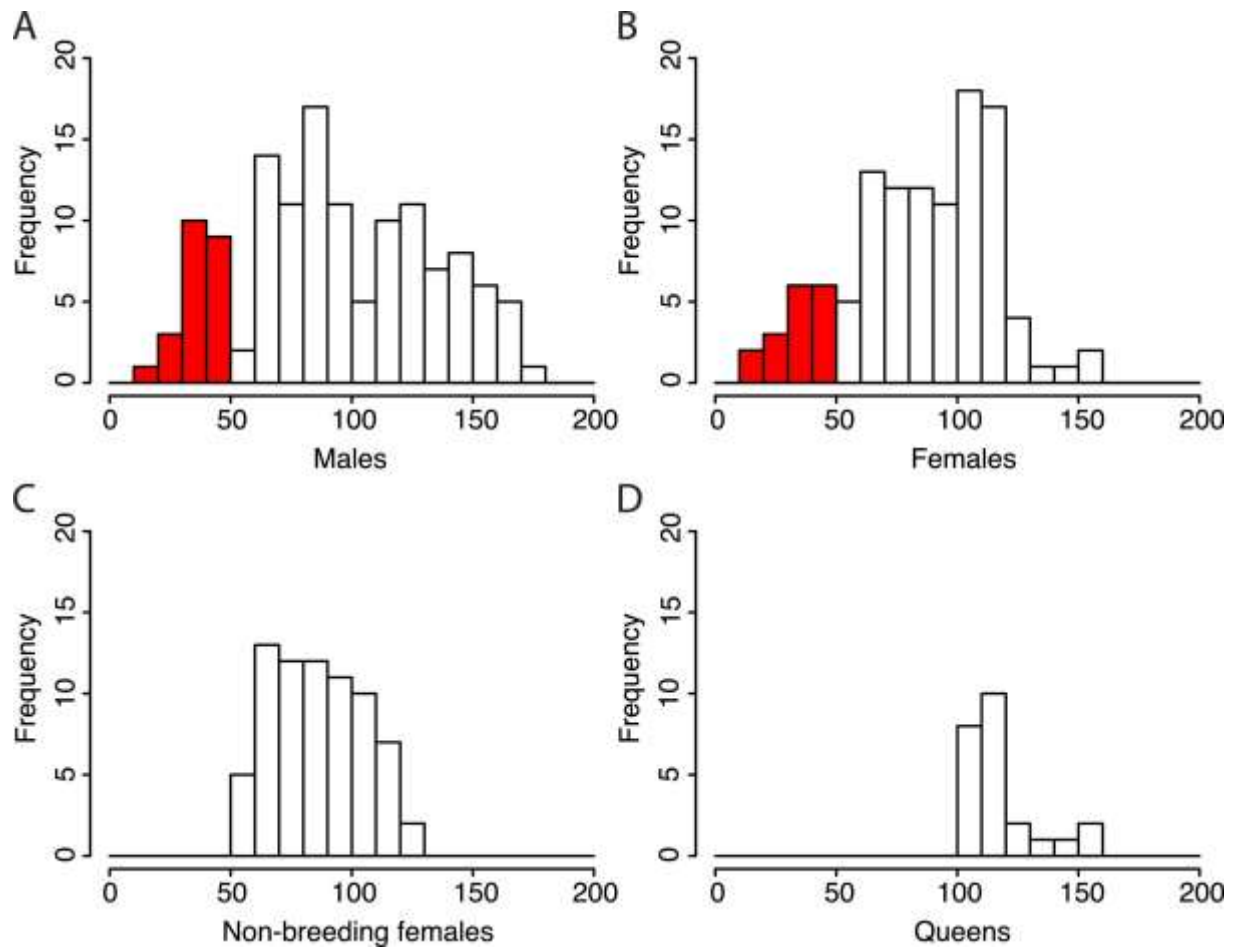


Figure 1: Histograms showing the distribution of body mass in the different categories of mole-rats. The distributions were tested for bimodality using Hartigan's dip test (see text). No distribution was found significantly bimodal. Juveniles are indicated in red.

Table 1: Results of Spearman’s rank correlation analysis of the relationship between capture order and body mass for individuals from 24 complete colonies of wild-caught Damaraland mole-rats

Colony No.	Colony size	Spearman’s Rho	<i>P</i>
1	7	0.00	1.04
2	8	-0.57	0.14
3	2	N/A	N/A
4	11	-0.30	0.37
5	13	-0.13	0.68
6	4	0.63	0.50
7	7	-0.68	0.11
8	29	-0.22	0.26
9	15	-0.12	0.67
10	6	0.06	0.93
11	9	-0.70	0.04
12	9	-0.37	0.34
13	8	-0.57	0.15
14	12	0.26	0.41
15	5	0.90	0.08
16	10	-0.44	0.20
17	6	-0.03	1.00
18	8	0.05	0.94
19	5	-0.50	0.45
20	14	-0.40	0.16
21	15	-0.11	0.71
22	25	-0.57	0.003
23	10	-0.44	0.20
24	6	-0.46	0.39

From our capture data we find no evidence for bimodality or multimodality in the distributions of body mass in either sex as data points did not fall into clearly separable groups. This would have been expected if division of labour in Damaraland mole-rats is based on morphological specialization for particular tasks as found in eusocial insects. There, the variations in adult body size results from differences between growth rates of colony members (Wilson, 1953; Grüter et al., 2017). Recent investigation of the growth trajectories of a large sample of captive-born Damaraland mole-rats shows that the distribution of body

mass among non-breeders is unimodal. Although it was found that growth varied widely between individuals there was no evidence for differentiation into physical castes (Zoetl et al., 2017). Unimodal distributions of body mass also exist in both sexes of the closely related eusocial Ansell's mole-rat (*Fukomys anseli*, Skliba et al., 2012). Further, a radio-telemetry study investigating the space-use patterns found no evidence for the existence of distinct behavioural castes in this species (Skliba et al., 2016). The present findings do not support the results from earlier studies in Damaraland mole-rats, which divided workers into morphologically (in terms of body mass) distinct subcastes, namely frequent and infrequent workers. These studies were performed on a population from a more arid region in central Namibia, which also had a different karyotype to those in the Kalahari (Bennett and Jarvis, 1988; Jacobs et al., 1991). However, the proposed relationship between work and body mass in these studies was based on a low sample size (one and two colonies respectively). Also in naked mole-rats, the existence of physical worker castes, originally proposed by Jarvis (1981), could not be confirmed by later studies (Brett, 1991; Lacey and Sherman, 1991).

On the other hand, reproductive division of labour and the morphological specialization of the female breeder is well documented in Damaraland mole-rats (Bennett and Jarvis, 1988; Young and Bennett, 2010). In relation, our analysis reveals that, overall, reproductive females are of larger body mass than non-reproductives, although this did not result in a bimodal size frequency distribution. The overlap in body mass between queens and non-reproductives probably indicates high plasticity in growth rate of females in response to social and environmental cues.

Field and laboratory studies in naked mole-rats suggest that risky behaviours such as colony defence are primarily performed by large non-reproductive colony members (Brett 1991; Lacey and Sherman, 1991). These behavioural differences among non-breeders are thought to reflect differences in age as it was found that body mass increases as a function of age in naked mole-rats (Lacey and Sherman, 1991). Moreover, in captivity, large non-

breeders were found more often in the position facing out of the nest, a behaviour thought to relate to the defence of the colony, than small individuals. And these large individuals were the first to arrive at the site of disturbance (Lacey and Sherman, 1991). In relation, radio-tracking studies conducted in three species of free-living *Fukomys* revealed that larger individuals including breeding males spend more time close to the nest than smaller individuals, which suggests that they are involved in guarding and protecting the nest (Lovegrove, 1988; Lövy et al., 2013; Skliba et al., 2016).

Capture data from wild-caught naked mole-rats revealed significant negative correlations between capture order and body mass in five out of six colonies captured by Brett (1991) and in four out of 12 colonies captured by others (reviewed by Brett, 1991). Previous findings, obtained from small numbers of colonies in *Cryptomys* and *Fukomys* provide no evidence for such a relationship (reviewed in Bennett and Faulkes, 2000). Similarly, our present finding of significant negative relationships in only two out of 24 colonies of wild-caught Damaraland mole-rats does not suggest that large individuals are more likely to participate in colony defence than smaller individuals. Capture order in our study may have been influenced by the position of the trap in relation to the nest site. Although there are several indications for the position of the nest within a colony, excavation of the tunnel system would be needed to be certain. It was found in Damaraland mole-rats and two other *Fukomys* species, by means of radio-tracking, that breeders and non-breeders differ in the amount of time spend in or close to the nest (Lovegrove, 1988; Lövy et al., 2013; Skliba et al., 2016). For example, breeding female Ansell's mole-rats are more often found close to the nest than non-breeding females, which were often located in the periphery of the burrow system (Skliba et al. 2016). There is also the possibility that the trapping method employed by us was not perceived as a threat by the individuals and thus did not elicit a response. Experimentally induced defence against conspecific intruders in captive Damaraland mole-rats was found to be primarily led by the reproductive individuals of the

colony and this is thought to reflect defence of breeding status rather than defence of the burrow system (Cooney, 2002).

In conclusion, our capture data obtained from a large number of colonies of Damaraland mole-rats shows that body mass is not an indicator of behavioural specialization. More data are needed to substantiate the presence of work-related castes in this species.

Acknowledgements

This study was supported by a fellowship to CV from the University of Pretoria. The DST-NRF SARChI chair of Mammalian Behavioural Ecology and Physiology to NCB. Permits were obtained from the Northern Cape Department of Nature Conservation. The study was approved by the ethics committee of the University of Pretoria (EC003-12, EC103-13, EC117-13). The Family Reynecke is thanked for letting us work on their farm.

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