Reproductive characteristics and growth in the eusocial Zambian Common mole-rat (*Cryptomys* sp., Bathyergidae)

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Abstract

A large data set on reproduction, growth, and juvenile mortality in captive eusocial Zambian common mole-rats (*Cryptomys* sp.) has been statistically evaluated. The gestation length was 98 days (range 84–112 days). The mean litter size was 2.4 (SD = 0.9; range 1–5; n = 102). Larger litters (4 and 5) were generally rare but rather frequent in two multiparous females. The mean neonate weight was 7.9 g (ranging from 5.7 g to 10.7 g) and was negatively correlated with the litter size. The neonate and suckling mortality was about 34% and was higher in males; so that the sex ratio (male/female) of sucklings eight weeks after birth was 0.7 : 1 (n = 159). The growth within the first 20 weeks of age was linear (at a rate of about 0.27 g/day) and independent of gender, litter size or family size. The growth constants calculated according to the Gompertz equation were very low (K = 0.006; n = 17). The prediction of the aridity hypothesis of eusociality in mole-rats that the first litters born to pairs should grow faster than litters born to established families was not supported by the evaluation of a larger sample size. Pregnant and at the same time lactating females restricted their investment to embryos and fetuses but not to sucklings. The growth and developmental rate in Zambian mole-rats seems to be a conservative rather than a plastic trait. We may assume (or at least we cannot exclude) that the slow developmental rate is one of the causes rather than a consequence of (eu)sociality.

Key words: Eusociality, mole-rat, growth, reproduction, Bathyergidae

Introduction

Two genera of the African bathyergid mole-rat, the naked mole-rat (*Heterocephalus*) and Gray's mole-rats (*Cryptomys*) are unique among the subterranean rodents in particular and among mammals in general. These mole-rats live in colonies whose structure can be denoted as eusocial: the reproduction is monopolized by a single female and her mate(s), whereas most of their offspring remain within the parental family throughout their lives and do not reproduce (Jarvis 1981; Burda 1990; Burda and Kawalika 1993; Jarvis and Bennett 1993; Jarvis et al. 1994).

Two alternative hypotheses address the ultimate functions of this unique social system. A cooperative (or aridity) hypothesis (e.g., Jarvis and Bennett 1991; Jarvis et al. 1994; Lovegrove 1991) relates sociality in mole-rats to small body size, semi-aridity of the habitat (rainfall less than 350 mm) and prevalent feeding on large but widely spaced geophytes. The scenario assumes that cooperative foraging evolved in semi-arid areas where the risk of dispersal and failure to find enough food is high. The second hypothesis of phylogenetic and developmental constraints (Burda 1990; Burda and Kawalika 1993) argues that sociality of *Heterocephalus* and *Cryptomys* is a conservative trait reflecting sys-

tematic relationships of bathyergids to hystricognath rodents. According to this hypothesis the eusociality in mole-rats is merely a special case of a cooperative breeding system based on monogamy and helpers. The monogamy and helpers are considered to be necessary for successful reproduction since the female mole-rat alone may not be able to rear her offspring competently (Burda 1990; Burda and Kawalika 1993). The point of the dispute between both hypotheses is whether the reason for origin and current function of eusociality are identical.

In any case, even the proponents of the aridity hypothesis speak of eusociality as of a cooperative breeding (and not e.g., a cooperative foraging) system (cf. Jarvis et al. 1994). Hence it is not surprising that considerable attention has been paid to the study of reproductive biology in mole-rats by both research groups. The relatively long gestation periods and slow growth found concordantly in all the social bathyergid mole-rats have been, however, interpreted differently – either as a consequence of sociality (e.g., Bennett et al. 1991) or as one of its causes (Burda 1990). Bennett et al. (1991) and Bennett and Aguilar (1995) pointed out even relatively slight differences in growth rates and litter sizes among different species of *Cryptomys* from different habitats and they looked for adaptive meaning for these differences. However, their data were based on the examination of only very few cases and calculated for incomplete growth periods. Such an analysis can be connected with substantial mathematical errors (Begall 1997).

To assess the variation in reproductive parameters (and thus the justification of interpretations based on interspecific comparisons of small samples) we analysed our extensive breeding data in a Zambian species of common *Cryptomys*.

Material and methods

Animals

Gray's common mole-rats (*Cryptomys* sp., karyotype $2n = 68$) originating from the Lusaka area, Zambia, were kept in captivity (at the University of Frankfurt am Main and the University of Essen) since 1986. We denoted these animals *C. hottentotus* in our earlier studies. The Lusaka population is, however, specifically distinct from typical *C. hottentotus* from South Africa and should be considered a new species, not yet formally named (Filippucci et al. 1994).

The animals were kept in pairs and families in plastic or glass cages on horticultural peat. They were fed ad libitum by carrots, potatoes, apples, lettuce, and cereals. For further details on housing conditions, see Burda (1989, 1990). All individuals were weighed at least once a week with an accuracy of 0.01 g.

For the size of the sample examined, see the particular results and tables.

Mathematical analysis

The growth parameters were described using the Gompertz equation:

$$W(t) = A \cdot e^{-e^{-K(t-I)}}$$

where $W(t)$ = weight (g) at time t (days); A = asymptotic value (g); K = growth constant (days^{-1}); I = age at the inflection point (days). All three growth parameters were estimated using the Levenberg-Marquardt-iteration.

The Gompertz model was employed only in those individuals for which the complete data set (from birth to accomplished growth) was available. Maximum growth rates (growth at the inflection point I) were determined by multiplying the growth constant K by $A \cdot e^{-1}$. The slope of the regression line was estimated for each individual separately in order to describe the individual growth rate in the juvenile period of the first 20 weeks after birth.

Table 1. The size of the sample examined for reproductive characteristics in particular species of *Cryptomys* mole-rats.

species	mothers	litters	pups	reference
C. damarensis	5	6	20	Bennett and Jarvis (1988) Bennett et al. (1991)
C. h. hottentotus	2	2	6	Bennett (1989) Bennett et al. (1991)
C. darlingi	2	7	12	Bennett et al. (1994)
C. mechowi	2	5	8	Bennett et al. (1994)
C. mechowi	2	2	3	Burda and Kawalika (1993)
C. sp. (2n = 68)	7	21	45	Burda (1989, 1990)
C. sp. (2n = 68)	18	102	241	present study

Results

Neonates: gestation, litter size, sex ratio and body weight

The previous findings (Burda 1989, 1990) concerning the length of gestation (= 98 days; range 84–112 days) were confirmed. The average litter size was 2.36 (SD = 0.94; range 1–5; n = 102). Litters with twins comprised 40%, litters with triplets 33%, those with single pups 18% of all litters (Tab. 2). The larger litters were rather rare and were delivered by only few mothers. One female produced four litters of four, another female gave birth to one litter of four and three litters of five. It should be noted that the first litters of these females were, however, smaller and larger litters occurred only after at least two years of successful reproduction.

Table 2. Numbers, neonate weight, and mortality rate in dependence on the litter size in captive Zambian common mole-rats.
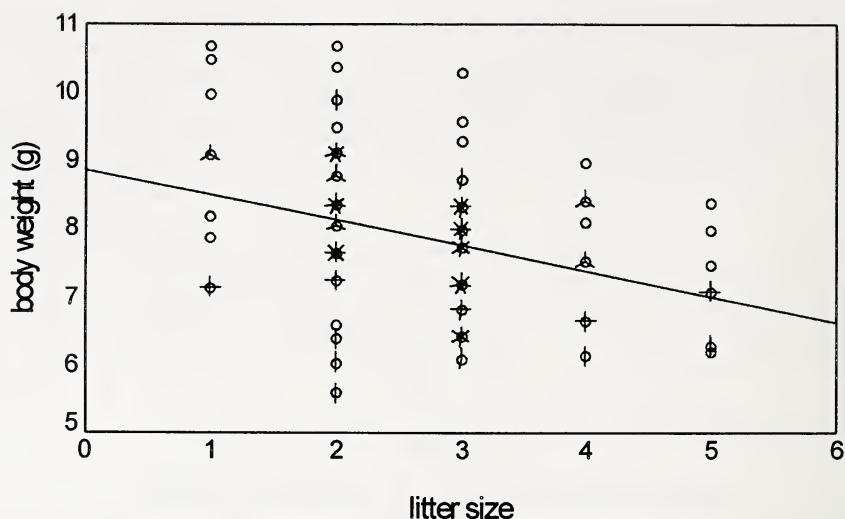
litter size	number of litters	weight of neonates mean (SD, n)	mortality rate (%)
1	18	8.6 (1.3, 13)	16.7
2	41	8.1 (1.2, 47)	39.0
3	34	7.7 (0.9, 48)	40.2
4	6	7.4 (0.9, 14)	16.7
5	3	7.1 (0.7, 10)	13.3

The sex (male/female) ratio of neonates was 0.85 : 1 (98 males : 115 females). The sex in additional 28 newborn pups could not be determined, mostly because these pups have died or been killed and eaten by their respective mothers before being sexed.

The average body weight of neonates was 7.90 g (n = 132). Males were slightly heavier (7.99 g, SD = 1.16, n = 59) than females (7.82 g; SD = 1.12; n = 73), the difference being, however, not significant (t-test; P = 0.406). The weight ranged between 5.7 g and 10.7 g and was negatively correlated with the litter size (Pearson; r = –0.35; P < 0.001) (Tab. 2, Fig. 1).

Mortality of neonates and sucklings

While the mortality in grown-up mole-rats is negligible, it was rather high among neonates and sucklings. Zambian common mole-rats are suckled for at least eight weeks (mostly longer, cf., Burda 1989, 1990), therefore the age of eight weeks was set as a limit for this analysis.

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Fig. 1. Correlation between the weight of neonates and the litter size in Zambian common mole-rats.

Table 3. Numbers of survived and died pups (within first eight weeks of age) in captive Zambian common mole-rats.

litter size	survived		died			total
	males	females	males	females	unidentif.	
1	4	11	2	1	0	18
2	23	27	12	9	11	82
3	26	35	14	10	17	102
4	8	12	3	1	0	24
5	6	7	0	2	0	15
total	67	92	31	23	28	241

The mortality rate of neonates and sucklings within the first eight weeks of age was 34% (including pups of unidentified sex). The mortality rate was significantly higher in males (32%) than in females (20%) ($\chi^2 = 6.92$; 5% level) (Tab. 3).

Mortality rate could be related to the neonate weight: 32.6% of a total of 49 pups with a neonate weight under or equal to 7.0 g died within the first eight weeks of age, while only 15.7% of a total of 83 pups with a neonate weight more than 7 g did not survive ($\chi^2 = 5.19$; 5% level). There was no apparent correlation between the survival (mortality) rate and the litter size (cf., Tab. 2): mortality rates were very low in large litters (4 and 5). Since these large litters were delivered only by a few mothers, the mortality rate seems to depend on the mother rather than on a litter size. There was a positive correlation between the normal (i.e., non-pregnant) body weight of the mother and the survival rate of the pups (Pearson; $r = 0.5$; $P < 0.001$) (Fig. 2). We also found an indication of a positive effect of helpers (or a larger group size) on the survival of pups. However, the correlation was weak ($r = 0.3$; $P = 0.038$).

Pups conceived in a postpartum estrus and/or during lactation and born before or when the elder siblings (pups of the previous litter) reached a critical weight of 35 g (weaning weight, cf., BURDA 1989) had significantly (t-test; $P = 0.038$) lower birth weights
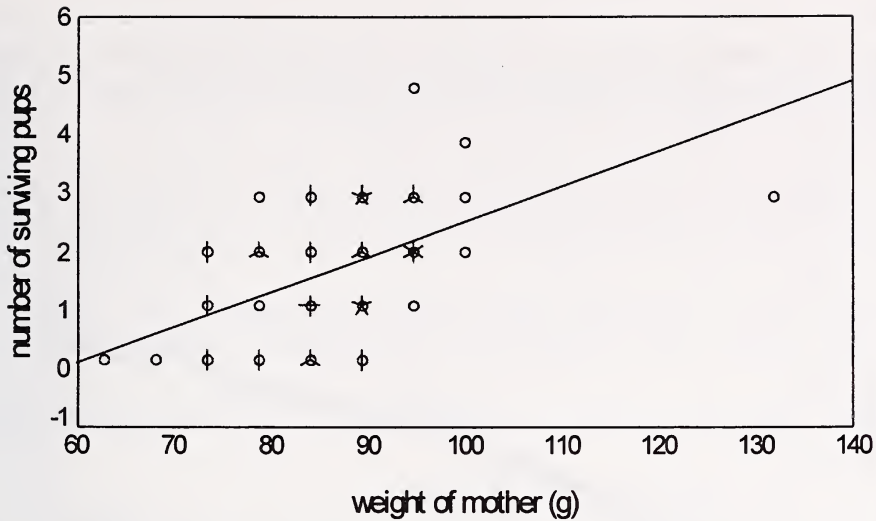
Fig. 2. Correlation between the number of survived pups and the weight of the non-pregnant mother.

(mean 7.59 g; SD = 0.98; n = 21) than pups born after their elder pups had been weaned (mean 8.16 g; SD = 1.16; n = 54). Consequently, there was a higher probability of survival in pups born after their elder siblings were fully weaned (χ^2 = 5.87; P = 0.0154). This effect is obvious when the critical weaning weight but not the age of the elder siblings is considered (Tab. 4).

Table 4. Correlation of mortality of pups with critical parameters (weight of 35 g and age of 20 weeks) of elder siblings at time of birth in Zambian common mole-rats.

	weight of elder siblings		age of elder siblings	
	< 35 g	≥ 35 g	< 20 weeks	≥ 20 weeks
survived pups	22	61	42	40
died pups	19	20	21	19
total	41	81	63	59

Growth
Gompertz modell

The growth data of grown-up animals aged at least 75 weeks (females) or 90 weeks (males) were analysed using the Gompertz equation (Tab. 4). The asymptotic values (A) and the maximum growth rates ($K \cdot A \cdot e^{-1}$) were significantly higher for males than for females (t-test; P < 0.001 and P < 0.01) although the growth constants K did not differ significantly (t-test; P=0.783).

Factors affecting growth
Gender

During the first 18 to 20 weeks after birth there was practically no weight difference between males and females and the growth was almost linear (Fig. 3). The growth equations for this juvenile phase: y = 1.83 x + 7.6 (females) and y = 1.99 x + 6.7 (males) gave the following growth rates: 0.26 g/day (females) and 0.28 g/day (males).

Litter size

Since there were not enough data for larger litter sizes, only the litters with single, twins, and triplets were assessed. There was no obvious effect of the litter size upon the growth rate: $y_1 = 2.1\,x + 8.7$; $y_2 = 2.2\,x + 7.2$; $y_3 = 2.1 + 6.0$ (Fig. 4).
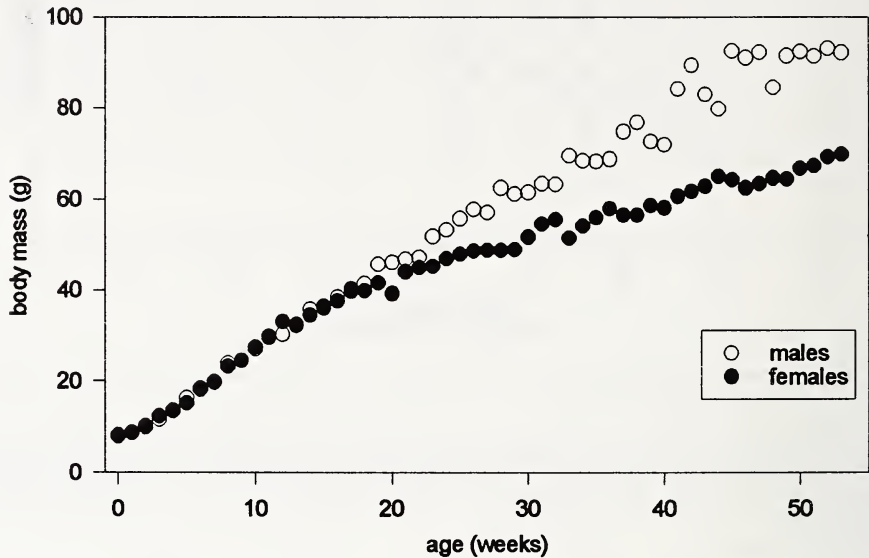
Fig. 3. Growth trajectories for males and females of Zambian common mole-rats within the first year of life.
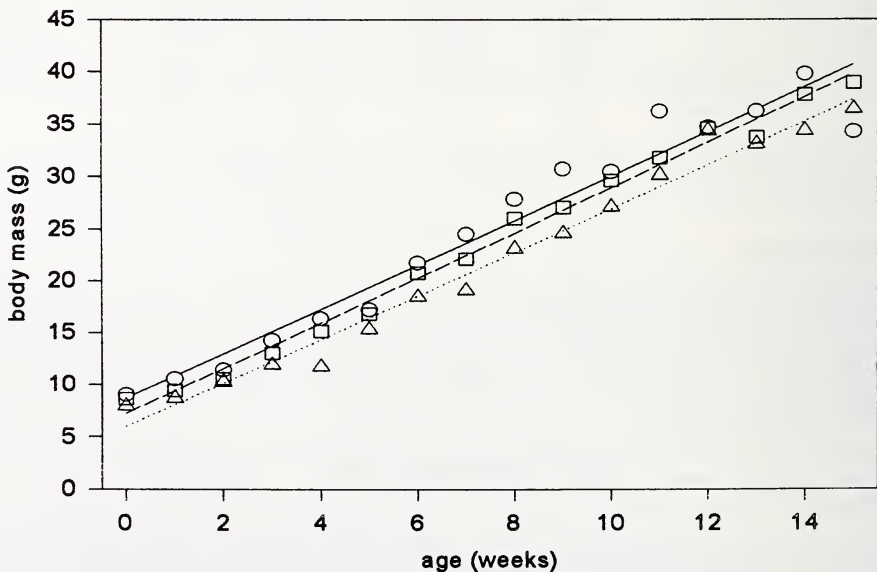
Fig. 4. Growth curves for the linear phase of growth in juvenile Zambian common mole-rats plotted for different litter sizes (circles: litter size 1; squares: litter size 2; triangles: litter size 3).

Age and size of the family

Offspring of fledgling colonies (founder pairs) required on average 53 weeks (SD = 11.4; n = 12) to reach their adult weights, while the offspring born to established families reached their adult weights in 48 weeks (SD = 12.2; n = 12). This difference was, however, not significant (two-tailed t-test; P = 0.302). The analysis of weight data for the linear (juvenile) phase of growth showed no significant differences in growth rates of pups born to pairs and offspring born to families (parents plus elder siblings). In the same way, there were no correlations between the growth rate in the juvenile phase, on the one hand, and order of litter (r = 0.0176; P = 0.868; n = 92) or age of mother (r = 0.298; P = 0.784; n = 43) on the other hand.

Sucklings whose mothers became pregnant during (early phase of) lactation grew at the same rate as those whose mothers were non-pregnant (two-tailed t-test, P = 0.138).

Table 5. Growth parameters of Zambian common mole-rats estimated according to the Gompertz equation.

	females (n = 10) mean (SD)	males (n = 7) mean (SD)
asymptotic value (A) (g)	80.2 (13.3)	131.7 (18.2)
growth constant (K) (days^{-1})	0.0065 (0.0023)	0.0061 (0.0015)
age at the inflection point (I) (days)	81.0 (18.7)	148.1 (14.3)
maximum growth rate (K A e^{-1}) (g/day)	0.182 (0.041)	0.292 (0.079)
determination coefficient (r^2)	0.95 (0.02)	0.96 (0.03)

Discussion

The data analysed in this study have not been collected with the intention to address and assess all the possible effects upon reproduction and development. In fact, the study can be considered a by-product of other studies. Due to manipulations of the family size (removal of animals for morphological studies or in order to found new families) there was never a new litter born to a family consisting of more than 14 grown-up animals. Because of these reasons some variables (like the age of the mother, its reproductive experience, and the size of the colony) cannot be separated from each other, and their effect on growth cannot be tested.

Of course, we cannot exclude that reproductive and growth characteristics of captive *Cryptomys* differ from those of wild animals. Since, however, virtually all the published data on reproductive biology in bathyergids were obtained on captive individuals, our results can be compared with those of other authors on other species. The uniformity of growth in the linear juvenile phase (irrespective of the litter size and gender) indicates that at least this parameter is, however, very conservative, species-specific and independent of animal maintenance conditions.

Litter size

It is apparent that any analysis of a small sample may not reveal the maximum possible litter size. Similarly, if we had studied only two particular multiparous females, the mean

litter size for the Zambian mole-rat would have appeared to be higher. Our data set does not allow to distinguish whether the observed tendency for increase of the litter size in some females was an effect of their multiparity or the effect of a larger family size with more helpers. (Of course, all animals were fed ad libitum, so the effect of helpers would be only indirect).

Our experience indicates that statements like the following are not tenable if based on a small study sample. "It is of interest that the species producing the smallest litters (e. g., Zambian common *Cryptomys* or *C. mechowi*) are found in tropical central Africa where temperatures are equable and rainfall is predictable. ... These optimally favourable conditions in turn would not lead to selection for large sized colonies" (Bennett and Aguilar 1995). Additionally, it should be noted that, contrary to this statement, optimally favourable and predictable conditions lead, at least in short terms, to selection for large sized colonies both in captivity and in the field. Note, e. g., that the largest colony sizes of naked mole-rats (about 300 animals) have been found in cultivated sweet potato fields and not in semideserts with widely spaced geophytes (cf., Brett 1991).

Sex ratio

The sex ratio of neonates was skewed in favour of females (M : F = 0.85). Since the mortality of male neonates (31.6%) was higher than in females (20%), it is highly probable that the neonates which died or were killed and eaten by the mother before being sexed, were largely males. If so, the sex ratio of neonates would be more balanced, yet the postnatal mortality of males would still be larger than established here. Assuming that the sex ratio at conception and that of unidentified neonates was about equal, the findings would imply a high male prenatal mortality which continues after birth. This conclusion seems to be corroborated by our records on the sex ratio (80 M : 104 F = 0.77) of subadult and adult Zambian common *Cryptomys* of the same species captured in the field (Burda 1989 plus unpublished data of Scharff 1996).

Growth rate

Bennett et al. (1991, 1994), Bennett and Aguilar (1995) paid particular attention to the value of the growth constant (K) and related it with sociality. The authors found higher K (0.04–0.05/day) in solitary mole-rats, lower K (0.01/day) in social mole-rats. Following their argument, we conclude that very low growth constants (0.006/day) as established here for Zambian common mole-rats would give evidence of high sociality in this species. Bennett et al. (1991) also provided the mean growth rates (actually the authors should speak of maximum instead of mean growth rates) of 1.2–3.3 g/day in solitary and about 0.2 g/day in social bathyergids. Again, the values counted in the present study for Zambian common mole-rats (0.2–0.3 g/day) would rank these animals to highly social species. However, we hasten to add that employing the Gompertz equation and computing growth parameters from data that do not take the complete growth period into account leads to errors (for mathematical reasoning and experimental evidence, see Begall 1997).

The ecological aridity hypothesis predicts that the first litters born to pairs would be larger and would grow faster than subsequent litters, as there is a necessity for fast recruitment of a large work force in fledgling colonies. Indeed, Jarvis et al. (1991) found evidence for a faster growth rate in the first litters born to pairs in *H. glaber*. Bennett et al. (1991) reported the same phenomenon for *C. damarensis*. Our data, demonstrate, however, that one should be very cautious to make similar conclusions when based on small sample sizes. In any case, the data for the Zambian common mole-rat are in contrast with the prediction or, at least, they do not support it.

The independence of the developmental rate on the litter size, family size, age or reproductive history of the mother gives evidence for a conservative rather than plastic (and hence adaptive) nature of this trait. Consequently, we may assume (or at least we cannot exclude) that the slow developmental rate is one of the causes rather than a consequence of (eu)social way of life in some bathyergids.

Maternal investment

Two results obtained in this study are of special interest: Firstly, pups conceived during lactation had significantly lower birth weights than others; secondly, sucklings of pregnant mothers grew at the same rate as those of non-pregnant mothers. This indicates that pregnant mothers which were (still) suckling the pups of the previous litter invest less in their yet unborn pups. This finding is in concordance with theoretical prediction that mothers should invest more into those offspring, in which larger investments have been made already.

Zusammenfassung

Reproduktive Charakteristika und Wachstum bei eusozialen Kleingraumullen aus Sambia (Cryptomys sp., Bathyergidae)

Reproduktion, Wachstum und Mortalität wurden an in Gefangenschaft gehaltenen sambischen Kleingraumullen (*Cryptomys* sp.) statistisch untersucht. Die Tragzeit betrug 98 Tage (von 84 bis 112 Tagen). Die durchschnittliche Wurfgröße lag bei 2,4 (SD = 0,9; n = 102), wobei zwischen 1 und 5 Junge geworfen wurden. Große Würfe waren selten, kamen aber bei zwei multiparen Weibchen recht häufig vor. Das Gewicht der Neugeborenen lag zwischen 5,7 g und 10,7 g – im Durchschnitt bei 7,9 g – und war negativ mit der Wurfgröße korreliert. Die Sterblichkeitsrate der Neugeborenen betrug ca. 34% und war bei den Männchen höher als bei den Weibchen; dadurch ergab sich 8 Wochen nach der Geburt ein Geschlechterverhältnis von 0,73 : 1 (n = 159). Innerhalb der ersten 20 Wochen war das Wachstum nahezu linear (mit einer durchschnittlichen Wachstumsrate von 0,27 g/Tag) und unabhängig von Geschlecht, Wurf- und Familiengröße. Die nach der Gompertz-Gleichung berechneten Wachstumskonstanten waren sehr niedrig (K = 0,006; n = 17). Durch die vorliegende Untersuchung konnte die Vorhersage der Ariditäts-Hypothese („die ersten Würfe eines Paares wachsen schneller als Junge, die in etablierten Familien geboren werden") zur Begründung der Eusozialität bei Graumullen nicht bestätigt werden. Trächtige und gleichzeitig laktierende Muttertiere investieren offensichtlich mehr Energie in die Säuglinge als in die Embryonen. Das Wachstum und die Entwicklungsrate der sambischen Graumulle sind eher als konservative und nicht als apomorphe Merkmale zu interpretieren. Wir können annehmen (oder zumindest nicht ausschließen), daß die langsame Entwicklungsrate eine der Ursachen und nicht eine Folge der (Eu)Sozialität ist.

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