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Postnatal development of three sympatric small mammal species of southern Africa

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Abstract

Four species of small mammals occur sympatrically in an arid area of the southwestern Cape Province. Females of all four species produced young after capture during a field excursion in September 1990. Postnatal development of three species, namely *Tatera afra*, *Acomys subspinosus* and *Elephantulus edwardii*, is reported for the first time, and compared with recorded data for the fourth species, *Aethomys namaquensis*.

T. afra produced altricial, nipple-clinging young, while young of *E. edwardii* were precocial and did not nipple-cling. *A. subspinosus* produced semi-precocial young which grew rapidly. Young of *A. namaquensis* are reported to be altricial, but the level of development at birth is more advanced than that of *T. afra*.

Differences in habitat and body size cannot account for the different life-history styles of these four species. Congenerics of each species included in this study exhibit similar life-history styles, with the exception of *Acomys* species, and it is suggested that altriciality/precociality is a phylogenetically conservative character in small mammals.

Introduction

Many theories have attempted to explain differences in life history styles of mammals (Perrin 1989). Adult body size, environment and phylogeny are just three of the factors which have been implicated in the selection of particular life history styles in animals. Western (1979) found that gestation time, growth rates, age at first reproduction, lifespan, birth mass and litter mass are all allometrically scaled to adult mass in mammals. Neal (1990) reviewed pre- and postnatal growth and development of 29 genera of African muroid rodents. He found that adult body mass had a strong influence on birth mass, gestation time, foetal growth rate, postnatal growth rate and litter growth rate. There was little evidence for phylogenetic effects on developmental parameters.

Stearns (1983) and Creighton and Strauss (1986) agree that most parameters of postnatal development of mammals scale to adult body size, but there appear to be phylogenetic constraints on the evolution of life-histories, and these differ from lineage to lineage.

The role of environment in selection of life history styles has been reviewed by Sibly and Calow (1985). Environmental conditions may determine the growth rates of offspring and age-specific survivorship, but internal constraints and trade-offs also influence life history strategies (Sibly and Calow 1985). Burda (1989) found no correlation between length of postnatal development and habitat, diet, social structure, climate, or ability/inability to vary metabolic rate in several rodent taxa.

The present study arose as a result of a field excursion to the Niewoudtville district of the Cape province. This area falls within the Western Mountain Karoo vegetation type (Acocks 1988). Very little soil covers the stony ground, which consists of shale, fine-grained sandstone and granite. Mean annual rainfall is less than 150 mm, most of which

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falls in winter. Vegetation consists of little grass and small, widely-scattered bushes (Acocks 1988).

Three rodent species of the subfamilies Gerbillinae (*Tatera afra*) and Murinae (*Acomys subspinosus, Aethomys namaquensis*) and one macroscelid species, *Elephantulus edwardii,* were trapped on the farm Sewefontein, and females of all species produced young after capture. Postnatal development of three species, *T. afra, A. subspinosus* and *E. edwardii* has not been recorded previously. Thus an opportunity was provided for recording the postnatal development of these species, and for comparing the development of four sympatric species of different genera and different body size.

Materials and methods

Five female *Elephantulus edwardii*; 4 female *Tatera afra*; 3 female *Acomys subspinosus*; and 4 female *Aethomys namaquensis* were live-trapped between 13. and 15. September 1990.

Individuals were caged singly after capture and returned to the animal house at the University of Natal, Pietermaritzburg. *E. edwardii* were housed in 60 × 30 × 30 cm glass terrain; all other species were kept in laboratory rodent cages. Rodent species were fed a mixture of seeds and rat cubes, supplemented with carrots, greens and insects. *E. edwardii* were fed "Pronutro", insects and sunflower seeds.

Young were weighed on a Sartorius U6300 balance, correct to 0.1 g, and hindfoot measurement was taken correct to 0.1 mm as an index of physical growth. Measurements commenced at birth–1 day old, and were taken at intervals of 1–3 days until young were 40–50 days old.

Postnatal growth rates were calculated for the relatively linear phase of increase in mass and hindfoot length (Case 1978). Growth rate was calculated as $\frac{mE - mB}{t}$ where mE = measurement at end of growth phase; mB = measurement at birth; t = time in days from birth to end of linear growth phase. Average growth curves were constructed by calculating mean mass and hindfoot length of all young in each 2-day age class.

Physical development was assessed on the days of weighing. Developmenal criteria used in assessing the level of physical development were as follows: ear pinnae folded down and attached to the head or folded back and free of attachment, lower or upper incisors erupted, eyes open or closed, degree of hair proliferation (a dark pigmentation of the skin was taken to represent the beginning of hair proliferation), toes fused or separate. The ages at which young were first attached to and spontaneously detached from the nipples were recorded, if nipple-clinging occurred. Weaning was judged to have begun when young were first seen eating solid food, and was complete when young were no longer suckled.

Results

The number of litters for each species, litter sizes, and longest interval between capture and birth of young are shown in Table 1. All females of the species *T. afra, A. subspinosus* and *E. edwardii* were pregnant when captured. In addition, three out of four *Aethomys namaquensis* gave birth to 3, 4 and 4 young within 2 weeks of capture.

Growth curves for mass and hindfoot length of *T. afra, E. edwardii* and *A. subspinosus* are shown in Figs. 1 and 2. The postnatal development of *Aethomys namaquensis* has been described previously (Neal 1990), and is not included in the present study.

Table 1. **Numbers of litters, litter sizes, and longest interval from capture to birth of young of *T. afra, A. subspinosus* and *E. edwardii***

	T. afra	*A. subspinosus*	*E. edwardii*
Number of litters	4	3	5
Litter sizes	3, 4, 4, 5	3, 3, 3	2, 2, 2, 2, 1
Longest capture-Birth interval	18 days	27 days	30 days

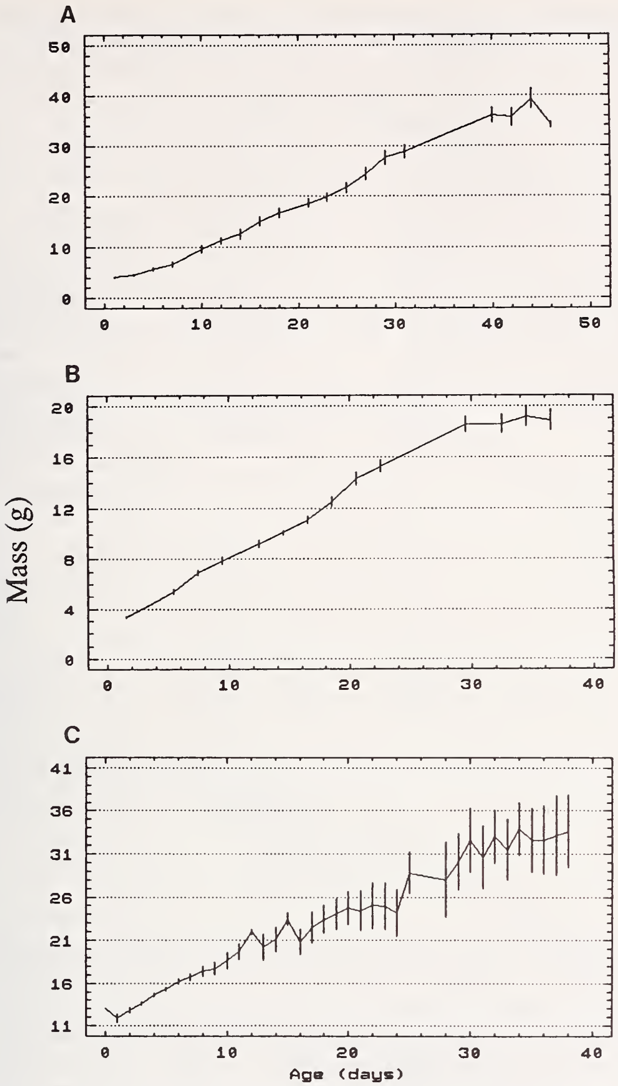

Fig. 1. Mean mass (± s.e.) of A: *Tatera afra*, B: *Acomys subspinosus*, C: *Elephantulus edwardii*

Body dimensions, growth rates, and timing of physical developmental parameters are shown in Table 2. Results show a clear difference in level of development at birth among the neonates of the three species. *T. afra* neonates were small relative to adult mass, *A. subspinosus* neonates were larger relative to adult mass than *T. afra*, and *E. edwardii* neonates were the largest relative to adult mass. When mean litter mass relative to adult mass was considered, *T. afra* still had the smallest litter mass (17.3 % of adult mass), while *A. subspinosus* and *E. edwardii* had litter masses of 46.5 % and 42.5 % of adult mass, respectively.

Growth rates in mass and hindfoot length were most rapid for *T. afra*, although at 30 days of age, young of this species had achieved only 30 % of adult mass and 78 % of adult hindfoot length. *A. subspinosus* had reached 87 % of adult mass at 30 days old,and 94 % of

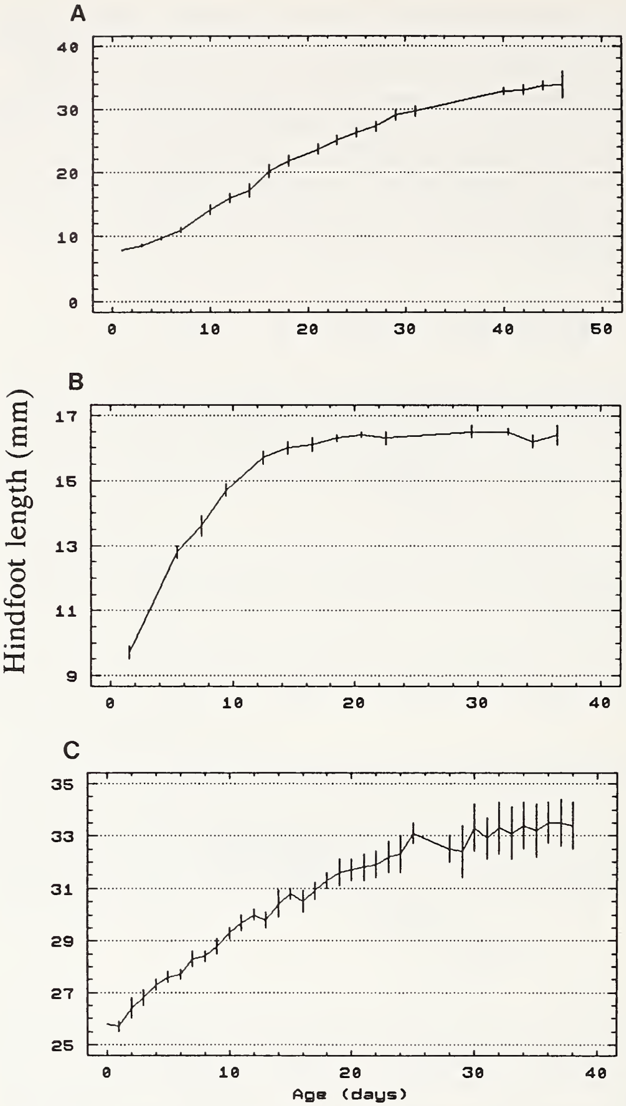

Fig. 2. Mean hindfoot length (± s.e.) of A: *Tatera afra*, B: *Acomys subspinosus*, C: *Elephantulus edwardii*

adult hindfoot length after only 16 days. *E. edwardii* had reached 65 % of adult mass and 95 % of adult hindfoot length by 30 days of age.

Physical development proceeded at different rates in the three species. *T. afra* neonates were hairless, unable to crawl effectively, blind, and had toes fused and ear pinnae fused to the head. Hair began to emerge from approximately 7 days of age, at which time the ear pinnae became detached from the skin of the head. Young were firmly attached to the nipples and were dragged with the mother when she moved. Incisors emerged at about 10 days and a groove was noticed between the two lower incisors. Eye-opening was recorded at 18–21 days, and shortly after this, young were seen detached from the nipples, eating solid food, and moving freely away from the nest.

A. subspinosus neonates were also naked and blind at birth, but hair was visible 1–2 days after birth, ear pinnae were free, and toes were separated within 2 days of birth. Nipple-clinging was not observed in *A. subspinosus.* Incisors erupted at approximately 7 days, and eyes opened at 9–10 days, at which time young were able to walk efficiently.

E. edwardii neonates were fully furred at birth, with eyes open, incisors erupted, ear pinnae free and toes separated. They were first observed eating solid food at 12–16 days. Nipple-clinging did not occur in this species, and neonates were fully mobile from birth.

Table 2. **Summary of body dimensions, litter, size, growth rates, and timing of certain developmental features in *T. afra, A. subspinosus* and *E. edwardii***

Characteristic	*T. afra*	*A. subspinosus*	*E. edwardii*
Adult body mass[a] (g) $\bar{x}$	95.0 (n = 15)	21.3 (n = 26)	50.4 (n = 16)
Range	78–113	17–25	36–65
Birth mass ± s.e.	4.1 ± 0.1 (n = 13)	3.3 ± 0.1 (n = 6)	11.9 ± 0.5 (n = 5)
Birth mass % adult mass	4.3 %	15.5 %	23.6 %
Litter size	4.0 (n = 4)	3.0 (n = 3)	1.8 (n = 5)
Litter mass % adult mass	17.3 %	46.5 %	42.5 %
Growth rate (g/day)	0.82	0.55	0.59
Linear growth phase	0–43 days	0–28 days	0–38 days
Adult hindfoot (mm) $\bar{x}$	37.7 (n = 15)	17.0 (n = 26)	34.6 (n = 16)
Range	28–40	13–19	33–36
Birth hindfoot ± s.e.	7.9 ± 0.1	9.7 ± 0.2	25.7 ± 0.2
Birth % adult hindfoot	21.0 %	57.0 %	74.3 %
Growth rate (mm/day)	0.64	0.55	0.30
Linear growth phase	0–39 days	2–13 days	1–25 days
Age (days) at development			
Ear pinnae free	6–7	0–1	0
Dorsal hair	6–8	1	0
Ventral hair	12	1	0
Toes separated	10–16	0	0
Incisors erupt	10	7	0
Eyes open	20	9–10	0
Attached to nipples	1–3	–	–
First unattached	22–24	–	–
Efficient walking	24	9–10	0
Eat solid food	22–23	?	12–16

[a] Data from Skinner and Smithers (1990).

Discussion

The distinction between altricial and precocial young has been applied to many bird and mammal species. Precocial mammals are fully furred, have their eyes open, and are fully mobile shortly after birth. By contrast, altricial young are naked, blind, helpless, and unable to maintain their body temperature. Of the species included in the present study, *E. edwardii* is clearly precocial, while *T. afra* bears altricial young. *A. subspinosus* neonates fall between the two extremes, and are classified here as semi-precocial.

Differences in the mass of individual neonates at birth are related to the length of the gestation period in precocial and altricial species (Neal 1990). The gestation period for the species reported here is not precisely known; however, all pregnant *T. afra* gave birth within 18 days of capture, while *A. subspinosus* and *E. edwardii* produced young at intervals up to 30 days from capture. This corresponds with observations of a short gestation period for *T. brantsii* (22 days) and *T. leucogaster* (28 days) (Scott 1979), longer gestation period (45 days) in *A. dimidiatus* (Al-Khalili and Delany 1986), and a gestation period longer than 50 days in *E. rufescens* (Neal 1982; Rathbun et al. 1981), *E. intufi* (Tripp 1972) and *Macroscelides proboscideus* (Rathbun 1979). Litter sizes were smaller for the semi-precocial *A. subspinosus* and precocial *E. edwardii* than for the altricial *T. afra*, and individual mass and litter mass relative to adult mass were more than two times greater in the semi-precocial and precocial species than in *T. afra*. These results agree with the general trends for precocial and altricial species of African rodents (Neal 1990).

Neal (1990) reported that postnatal growth rates of altricial and precocial rodent species were positively correlated with birth mass, i.e. larger neonates grew faster than smaller neonates. This was the case in the present study, in which young of the larger rodent neonate, *T. afra*, grew at a faster rate than the smaller rodent neonate, *A. subspinosus. E. edwardii* young had a faster growth rate in mass than *A. subspinosus*, but the hindfeet of *E. edwardii* grew more slowly than either of the rodent species.

The present study describes postnatal development in three small mammal species which inhabit the same macro-environment, but employ different reproductive strategies. A fourth species, *Aethomys namaquensis,* occurs in the same habitat, and bears small altricial young which nipple-cling for the first 2–3 weeks of life (Neal 1990). The synchrony of reproduction in the four species trapped in the area was remarkable; 15 of the 16 females trapped were pregnant. Environmental differences and differences in body mass cannot explain the range of reproductive strategies exhibited by these species.

Reference to postnatal development of other *Tatera* species, *Acomys* species, *Elephantulus* species, and *Aethomys* species reveals that many of the patterns observed in this study are shared by other species of each genus. Reproductive parameters are summarized in Table 3. Three southern African *Tatera* species, *T. afra*, *T. brantsii* and *T. leucogaster* have a short gestation period, altricial young, low birth mass relative to adult mass, litter mass approximately 17 % of adult mass, and hindfoot length 21–25 % of adult size (Scott 1979). *T. brantsii* is a partial nipple-clinger, while *T. leucogaster* does not nipple-cling (Scott 1979; Neal 1990). Age at eye-opening is approximately 20 days in all three species. Mean litter size is 2.95 for *T. brantsii,* 3.22 for *T. leucogaster* (Scott 1979) and 4.0 for *T. afra*. Postnatal growth rate in mass is 1 g/day for *T. leucogaster* and *T. brantsii.*

Three *Acomys* species are non-nipple-clingers, with gestation periods longer than 4 weeks (Neal 1983; Al-Khalili and Delany 1986). Individual neonates weigh 13–18 % of adult mass, and litter mass is 31–47 % of adult mass. *A. dimidiatus* (Al-Khalili and Delany 1986) and *A. wilsoni* (Hubbard 1972) neonates are fully furred and have their eyes open at birth, while *A. subspinosus* and *A. hystrella* (Hubbard 1972) develop these characters a few days after birth. Litter size of 1–3 neonates is characteristic of four *Acomys* species for which information is available (Neal 1990), and postnatal growth rates in two species are lower than growth rates of *Tatera* species (Al-Khalili and Delany 1986).

Three *Aethomys* species are nipple-clingers, bearing small altricial young in litters of 3–4 young. Birth mass is 3–6 % of adult mass in all 3 species, and litter mass 13–25 % of adult mass. Eyes open at 8–14 days of age, and incisors are present at birth in all three species. Growth rates vary from 0.45 g/day for *A. namaquensis* (Neal 1990) to 1.6 g/day for *A. kaiseri* (Cheeseman 1981).

E. edwardii, E. rufescens (Neal 1982; Rathbun et al. 1981) and *E. intufi* (Trip 1972) bear litters of 1–2 precocial neonates which do not nipple-cling. Litters of 1–4 young, with a mean litter size of 2.2, have been recorded for *E. rozeti* (Séguignes 1989). Litter mass varies from 28 % of adult mass in *E. rufescens* (Neal 1982) to 42.5 % of adult mass in *E. edwardii*. Gestation periods of 51 days for *E. intufi,* 57 days for *E. rufescens* and at least 75 days for *E. rozeti* have been recorded (Tripp 1972; Rathbun et al. 1981; Séguignes 1989). Growth rate in mass varied from 0.59 g/day for *E. edwardii* to 1.0 g/day in *E. intufi* (Tripp 1972).

Figure 3 presents the results of weighted pair-group cluster analysis of 11 species, based on eight developmental characters. Characters were selected on the basis of availability of information in the literature and included litter size, litter mass relative to adult mass, gestation period, age at eye opening, age at incisor emergence, age at appearance of fur, nipple-clinging, growth rate in mass. The resulting dendrogram clearly demonstrates the grouping of congenerics in clusters, with the exception of one species of *Acomys*. The differences among species, while not clearly related to habitat or body mass, clearly represent the distinction between altricial, semi-precocial and precocial species.

Table 3. **Some life-history parameters for *Tatera afra, T. brantsii, T. leucogaster, Acomys subspinosus, A. dimidiatus, Aethomys chrysophilus, A. namaquensis, A. kaiseri* and *Elephantulus edwardii, E. rufescens, E. intufi***

		Tatera		*Acomys*			*Aethomys*			*Elephantulus*	
	afra[1]	*bra*[2,3]	*leuc*[2]	*subs*[1]	*dim*[4]	*chry*[5,6]	*nam*[6]	*kais*[7]	*edw*[1]	*ruf*[8,9]	*int*[10]
Litter size	4.0	3.0	3.2	3.0	2.4	3.1	3.4	2.6	1.8	1.4	1.6
Litter mass % Adult mass	17.3	17.1	17.2	46.5	31.5	17.7	19.3	13.4	42.5	28.2	32.4
Individ. mass % Adult mass	4.3	5.8	5.3	15.5	13.0	5.7	5.7	5.2	23.6	20.1	20.2
Gestation	–	22	28	–	44	26	–	27	–	57	51
Eyes open	20	17.5	16	9.5	0	12.5	12	9	0	0	0
Incisors erupt	10	6	5.5	7	2.5	0	0	0	0	0	0
Fur visible	7	4	3.5	1	0	0	0	1	0	0	0
Nipple cling[a]	1	1	0	0	0	2	2	2	0	0	0
Growth rate (g/day)	0.82	1.10	0.90	0.55	0.65	0.90	0.45	1.60	0.59	0.77	1.00
Adult mass	95.0[11]	79.9[11]	69.8[11]	21.3[11]	45.0[4]	72.3[11]	46.1[12]	118.0[7]	50.4[11]	52.0[9]	49.2[11]
n	15	130	696	26	359	675	58	?	16	21	19

1 = this study, 2 = Scott (1979), 3 = Measroch (1953), 4 = Al Khalili and Delany (1986), 5 = Brooks (1972), 6 = Neal (1990), 7 = Cheeseman (1981), 8 = Neal (1982), 9 = Rathbun et al. (1981), 10 = Tripp (1972), 11 = Skinner and Smithers (1990), 12 = De Graaff (1981).

[a] 0 = no nipple-clinging, 1 = nipple-clinging 1–4 days after birth, 2 = nipple-clinging from birth.

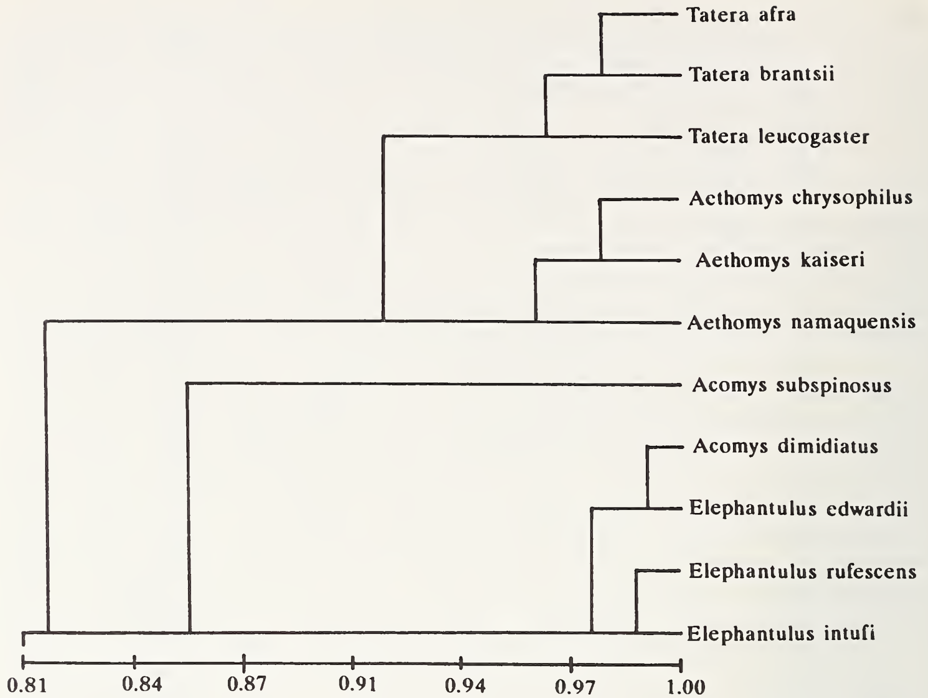

Fig. 3. Dendrogram derived from weighted-pair group cluster analysis based on a correlation matrix of eight developmental characters (listed in text). Values along x-axis are similarities

With the accumulation of information on neonatal development of several species belonging to the same genus, it is apparent that the level of development of young at birth is fixed with a genus. Thus three *Tatera* species, four *Gerbillurus* species (DEMPSTER and PERRIN 1989; DEMPSTER and PERRIN 1991), three *Mus* species (NEAL 1990) all have altricial young. Three *Otomys* species and three *Acomys* species have precocial young (NEAL 1990), with *A. subspinosus* and *A. hystrella* (HUBBARD 1972) bearing semi-precocial young. All elephant-shrew species are reported to bear precocial young (RATHBUN 1979). The designation of "semi-precociality" is unclear: NEAL (1990) classifies *Aethomys* species as altricial despite the fact that all developmental events such as eye opening, incisor eruption, and hair growth occur earlier than in *Tatera* species. Clearly the altricial-precocial distinction represents a continuum, with species exhibiting different levels of altricial or precocial development.

This study has clearly shown that the most important factor influencing the developmental strategies of the species included here is altricial/precocial development, which is a phylogenetically conservative character in small mammals.

Zusammenfassung

Postnatale Entwicklung bei drei sympatrischen Kleinsäugerarten aus Südafrika

Vier Arten kleiner Säuger kommen gemeinsam in einer trockenen Region der südwestlichen Kapprovinz vor. Mehrere Weibchen aller dieser Arten warfen Junge, nachdem sie während einer Feldexkursion im September 1990 gefangen worden waren. Erstmalig wird hier über die Frühentwicklung der drei Arten, *Tatera afra, Acomys subspinosus* und *Elephantulus edwardii* berichtet. Die erhobenen Daten werden ferner mit entsprechenden Ergebnissen der vierten Art, *Aethomys namaquensis,* verglichen.

T. afra brachte pflegebedürftige, an der Brustwarze haftende Junge zur Welt, während die Jungen von *E. edwardii* frühreif waren und nicht an der Brustwarze hafteten. *A. subspinosus* brachte Junge in einem Zwischenstadium hervor, die aber sehr schnell wuchsen. Die Jungtiere von *A. namaquensis* gelten zwar als pflegebedürftig, aber ihr Entwicklungsstadium bei der Geburt ist weiter fortgeschritten als bei *T. afra*.

Verschiedene Habitate und Körpergrößen können diese Unterschiede nicht erklären. Andere Arten der untersuchten Gattungen zeigen ähnliche Entwicklungsabläufe, mit Ausnahme der *Acomys*-Arten. Nesthocker- und Nestflüchter-Ontogenesen werden daher als phylogenetisch konservative Merkmale bei diesen Kleinsäugern bewertet.

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