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The ecology and reproduction of the Short-snouted Elephant-Shrew, *Elephantulus brachyrhynchus*, in Zimbabwe with a review of the reproductive ecology of the genus *Elephantulus*

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ABSTRACT

The reproductive ecology of *Elephantulus brachyrhynchus* was studied in an area of mixed woodland in the Sengwa Wildlife Research Area, Zimbabwe (18°10'S, 28°10'E). The year may be divided into three seasons: a cool dry season from mid-May to mid-August, a hot dry season from September to November, and a warm wet season from December to April. No seasonal changes were observed in body mass and male reproductive activity. Reproduction occurred throughout the year, but conceptions and litter size were significantly reduced during the cool season. The average litter size of 51 pregnancies was 1.6 (SD 0.49). Adult females had the capacity to produce five to six litters each year for a total annual production of 8.3 young per female.

Information on the ecology and reproductive biology of other members of the genus was reviewed to determine latitudinal trends in various life-history parameters.

The pregnancy rate and litter size are not influenced by rainfall and exhibit no seasonal variation close to the equator. At intermediate latitudes (15–20°) both parameters are reduced during the cooler period of the year, and at higher latitudes breeding ceases during the period of declining photoperiod. Thus, most young are produced during the warm season when insects are likely to be most available. Litter size increases with latitude, particularly above 15°. This increase does not totally compensate for the reduced period of breeding at higher latitudes and so the annual production of young per female is reduced at the northern and southern limits of the range of the genus.

There is a particular need to study the general habits of species living at higher latitudes to assess how they adapt during the cold winter months.

INTRODUCTION

Elephant-shrews (family Macroscelididae) are endemic to Africa. Nine species of *Elephantulus* live in arid and semi-arid habitats in a more or less continuous distribution from approximately 10° N in Somalia in the north-east, through East, Central and South Africa to approximately 34° S, and there is an isolated species in Morocco, Algeria and Tunisia in the north-west, ranging from 32 to 37° N (Corbet & Hanks, 1968).

The reproductive biology of *Elephantulus* has been reviewed by Brown (1964), Tripp (1971, 1972), Rathbun (1979), Neal (1982), and Séguignes (1989). They are monogamous (Rathbun, 1979), and usually produce one or two but sometimes as many as four highly precocial young (Tripp, 1972; Rathbun, 1979; Séguignes, 1989), after a gestation period of from 50 to more than 75 days (Tripp, 1972; Rathbun, Beaman & Maliniak, 1981; Séguignes, 1989). Thus, their reproductive characteristics are unusual for a small mammal.

There are few detailed field studies of their reproductive ecology over the full seasonal cycle of the year. The only studies to date are those of Rathbun (1979) and Neal (1982) on the Rufous Elephant-Shrew, *E. rufescens*, in Kenya, and Leirs *et al.* (1995) on the Short-snouted Elephant-

Shrew, *E. brachyrhynchus*, in northern Tanzania. All these studies show that breeding occurs throughout the year and there are no obvious seasonal changes in reproduction. However, all these studies are in regions where there is little seasonal change in temperature.

This paper describes the reproductive ecology of *E. brachyrhynchus* in Zimbabwe in a region where there is a more pronounced seasonal change in temperature. In addition, the literature is reviewed to assess latitudinal trends in characteristics such as seasonality of breeding, litter size, and diet.

MATERIALS AND METHODS

A total of 156 animals was collected from the Sengwa Wildlife Research Area, Zimbabwe during the periods July 1987 – June 1988 and July and August 1990. Most animals were collected in an area of mixed woodland (18°10'S, 28°10'E) although a few animals were also collected from other habitats located within an 8-km radius of the main study site.

Animals were measured, weighed and dissected soon after collection. An eviscerated mass was obtained by removing the gut, from the lower oesophagus to the rectum, and also the uterus and embryos of pregnant females.

A sperm smear was taken from the epididymides of each male. Individuals were classed as adults if sperm was abundant. The testes were weighed after fixation.

Females were classed as pregnant if they had implanted embryos and as adults if they were pregnant, had placental scars or a distended uterus; otherwise they were classed as immature. Embryos were counted, and weighed after fixation in Bouin's solution. A representative sample was weighed before fixation to correct for weight changes as a result of the fixation process.

Conception dates were estimated by ageing litters by the method of Huggett & Widdas (1951), assuming a birth mass of 9 g, a gestation period of 50 days, and that embryos attained a measurable body mass on the seventh day of gestation.

The average interval between litters and the potential annual production of young per adult female were estimated by the method described by Neal (1982) and assuming a gestation period of 50 days.

RESULTS

Climate

Rainfall and temperature were monitored at the Sengwa Wildlife Research Institute (18°10'S, 28°13'E). Monthly means were calculated from daily records.

The year may be divided into three main seasons: a cool dry season from mid-May to mid-August when the daily maxima and minima averaged 27–29 °C and 8–11 °C, respectively; a hot dry season from September to November when the daily maxima and minima averaged 34–37 °C and 17–22 °C, respectively; and a warm wet season from December to April when the daily maxima and minima averaged 31–34 °C and 18–21 °C, respectively (Fig. 1). The precise timing of these seasons varies from year to year.

Habitat and habits

The main study area was mixed woodland dominated by *Colophospermum mopane*, *Combretum apiculatum*, *C. zeyheri*, and *Erythroxylum zambesiacum*. Herbs and grasses were abundant and ground cover was reasonably good, even during the dry season.

Elephantulus brachyrhynchus also occurs in a wide range of other habitats including *Brachystegia–Julbernardia* mixed woodland (Miombo), *Combretum–Terminalia–Eragrostis* low woodland on talus slopes, and *Commiphora–Combretum* wooded bushland thicket. They mainly

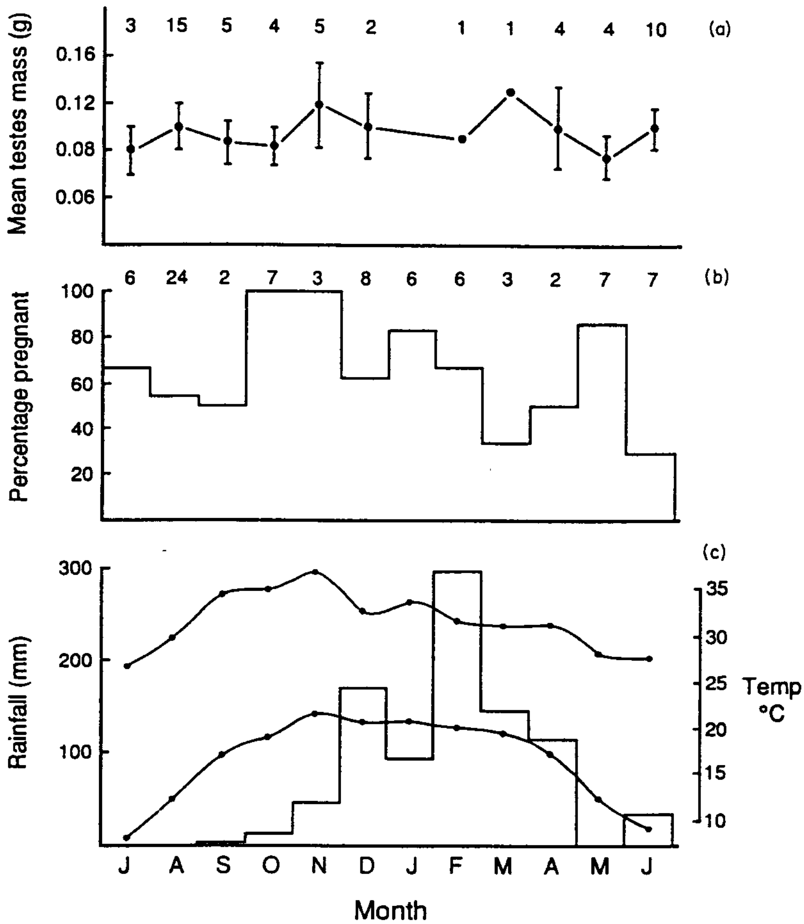

Fig. 1. Seasonal changes in: (a) mean testes mass of adults ± standard deviation; (b) percentage of adult females visibly pregnant (macroscopically); (c) total monthly rainfall histogram) and minimum and maximum temperatures (°C). Numbers are sample sizes.

occur where there is good ground cover provided by grasses and herbs, low shrubs, or fallen trees and bushes. They avoid open areas and are generally inconspicuous, unlike *E. rufescens* (Rathbun, 1979; Neal, 1982). In some areas they make a few intermittent trails but these are never as obvious or extensive as those made by *E. rufescens*. They appear to make extensive use of small mammal burrows, termite holes, and hollow logs, perhaps requiring more shelter than *E. rufescens*.

Their social structure appears to be similar to that described for *E. rufescens* (Rathbun, 1979). They are highly territorial. The adults typically occur in pairs but very few juveniles were trapped or seen.

Their stomach contents were almost entirely insects, mainly termites and ants, with seeds or leaf material making up less than 2% by volume.

Body size

A female with a litter of two at the most advanced stage of pregnancy had embryos with a mass of 8.7 and 8.3 g. The lightest juvenile trapped had a body mass of 17 g. The body mass of adults was typically 40–60 g (range 31–77 g) for females and 40–50 g (range 37–54 g) for males. There was no seasonal variation in body mass.

Table 1. Seasonal changes in pregnancy rate and mean testes mass of *E. brachyrhynchus* at Sengwa, Zimbabwe

	Season		
	Cool dry	Hot dry	Warm wet
No. adult females	31	18	24
No. pregnant	15	15	17
Percentage pregnant	51	83	71
$R \times C$ test of independence using *G*-test (Sokal & Rohlf, 1981); $G_{adj} = 6.24$; df = 2; $P < 0.05$			
No. adult males	33	11	10
Mean testes mass (SD)	0.10 (0.018)	0.10 (0.03)	0.09 (0.028)

Breeding season

Breeding occurred throughout the year with no obvious seasonal variation (Fig. 1). However, a more careful examination of the seasonal variation in pregnancy rate revealed that a lower proportion of females conceived during the cooler period of the year (late May to mid-August) compared to the warmer period of the year (Table 1). There was little difference in the conception rates of females in the hot dry and warm wet seasons. There was no significant seasonal variation in the testes mass of adults (Fig. 1, Table 1).

Litter size

There were one or two precocial young per litter. Overall, the average number of live embryos of 51 pregnancies was 1.6 (SD = 0.49). Two of these females also carried a second resorbing embryo.

Variation in litter size was also analysed in relation to eviscerated maternal body mass and season of conception by two-way analysis of variance (Table 2). Litter size was significantly reduced during the cool dry season compared with the warmer seasons of the year ($F_{2,43} = 4.3$; $P < 0.025$) and increased significantly with increase in maternal body mass ($F_{1,43} = 11.7$; $P < 0.005$). Rainfall appeared to have no influence on litter size.

Breeding rates and production of young

Both the breeding rate and litter size were at a minimum during the cool dry season. The inferred seasonal variation in the production of young could not be confirmed by direct observation because very few juveniles were collected.

The average interval between litters was calculated to be 90 days during the cool dry season and approximately 60 days during the warmer period of the year. Adult females can produce five–six litters per year, and the calculated potential annual production of young per adult female was approximately 8.3.

Table 2. Mean litter size (SD) of *E. brachyrhynchus* in Sengwa, Zimbabwe in relation to eviscerated body mass and season. Adjusted means were calculated by the method of fitting constants (Steel & Torrie, 1960)

Eviscerated maternal mass	Season: Cool dry	Hot dry	Warm wet	Adjusted means
< 40 g	$n = 8$ 1.1 (0.35)	$n = 8$ 1.5 (0.53)	$n = 6$ 1.7 (0.52)	1.4
> 40 g	$n = 11$ 1.6 (0.50)	$n = 6$ 2.0 (0)	$n = 10$ 1.9 (0.32)	1.8
Adjusted means	1.4	1.74	1.76	1.6

DISCUSSION

Compared with altricial species, precocial mammals have long gestation periods and small litter sizes and, as a consequence, have low birth rates and intrinsic rates of natural increase (Hennemann, 1984; Martin & MacLarnon, 1985; Neal, 1986, 1991a). This implies that for similar sized animals, precocial species will have lower turnover rates (i.e. lower birth and death rates) than altricial species.

In small mammals, with a body mass of less than 100 g, the precocial habit is largely confined to lower latitudes. Neal (1986) has suggested that the need to produce several litters, to balance the death rate, may explain this latitudinal trend. In warm, tropical climates animals can breed continuously so that precocial small mammals can produce several litters in a year. However, breeding is more seasonal in temperate regions and it may be possible to produce only one or two litters a year. In this case, breeding may have to be extended for two or more years to balance the death rate. As a consequence, selection will favour either an increase in longevity which tends to be associated with an increase in body size (Bonner, 1965), or an increase in litter size which tends to be associated with the production of altricial young. These selection pressures would explain why small mammals at higher latitudes are predominantly altricial and the smallest precocial species are hares with a body mass of approximately 1 kg.

Thus, an analysis of the latitudinal trends in the life-history parameters of *Elephantulus* species, which bear precocial young, is of interest to determine how they are modified in more seasonal environments. The genus is a particularly appropriate group to investigate in this way because the various species are closely related and appear to be similar in their general ecology. Two aspects of seasonality are investigated. First, responses to seasonal changes in temperature and photoperiod which are predicted to become more pronounced at higher latitudes. Second, responses to seasonal patterns of rainfall which are predicted to show no latitudinal trend because rainfall may be as seasonal on the equator as in temperate regions. The available information is summarized in Table 3.

Table 3. Some life history parameters for various species of *Elephantulus* in relation to latitude. Laboratory (Lab.) studies are indicated where both conceptions and births occur in the laboratory

Species	Locality	Latitude	Matnl. mass (g)	Neonate mass (g)	Breeding season	No. of embryos Mean	(SD)	*n*
E. rufescens	Kenya[1]	0° 07'N	52		12 mths, constant	1.4	(0.50)	46
E. rufescens	Kenya[2]	2° 27'S	52		12 mths, constant			
	Lab.[3]	2° 27'S		10.6		1.4	(0.49)	77
E. brachyrhynchus	Tanzania[4]	7° S			12 mths	1.4	(0.52)	10
E. brachyrhynchus	Zimbabwe[5]	18° S	49		12 mths, min. in cool season	1.6	(0.49)	51
E. brachyrhynchus	Botswana[6]	22° S	43					
E. intufi	Botswana[6]	23° S	57			1.9	(0.60)	9
E. intufi	Lab.[7]	24°30'S	49	10.0		1.3	(0.49)	7
E. myurus	Botswana[6]	23° S	54			1.7	(0.52)	6
E. myurus	S.Africa[7]	26° S	69	8.1	July–March[8]	1.9	(0.30)	21
E. edwardi	S.Africa[9]	31°24'S	50	11.9		1.8	(0.45)	5
E. rozeti	Morocco[10]	32° N	41[7]		January–August	2.4	(0.71)	47
E. rozeti	Algeria[10]	34° N			January–August	2.2	(0.84)	5
E. rozeti	Tunisia[10]	34° N			January–August	2.2	(0.45)	5

[1] Neal (1982); [2] Rathbun (1979); [3] Rathbun *et al.* (1981); [4] Leirs *et al.* (1993); [5] This study; [6] Smithers (1971); [7] Tripp

Breeding season

As expected, breeding appears to become more seasonal at higher latitudes (Table 3). Within a few degrees of the equator *E. rufescens* breeds continuously with no seasonal variation even though the rainfall is highly seasonal (Rathbun, 1979; Neal, 1982). However, there is little seasonal variation in temperature in these localities (mean monthly temperature varied < 4 °C).

Further from the equator, *E. brachyrhynchus* also breeds throughout the year in Tanzania (Leirs *et al.*, 1995) and Zimbabwe (this study). The sample size was too small to assess the seasonal variation in breeding rate in Tanzania, but in Zimbabwe there was a significant reduction in the breeding rate during the cool dry season. Rainfall appeared to have no influence on breeding (see Results).

The pattern of breeding in South and North Africa is particularly revealing (Table 3). In South Africa, the Rock Elephant-Shrew, *E. myurus,* mates from July to January with births occurring from late August to March, which corresponds mainly to the warmest period of the year (van der Horst, 1946; Tripp, 1972; Woodall & Skinner, 1989). It is possible that the breeding season is extended closer to the equator because one pregnancy has been recorded in April in Botswana (Smithers, 1971). In North Africa, the North African Elephant-Shrew, *E. rozeti,* mates from January to June with births occurring from late March to August which correspond to the period of the year when the temperature is increasing (Séguignes, 1989). One would anticipate that breeding might continue for a longer period in this species because it is still warm in October. However, it may be noted that both *E. myurus* and *E. rozeti* start to breed approximately 1 month after the winter solstice, which suggests that breeding may be under photoperiodic control in these species. Finally, there is no indication that rainfall influences the pattern of breeding. Breeding starts during the dry season and ends during the rains in *E. myurus,* but the opposite is true for *E. rozeti.*

In summary, breeding activity appears to be: continuous with no seasonal variation close to the equator; reduced during the cooler period of the year (which corresponds to the period of minimum photoperiod) at intermediate latitudes (15–20°); and ceases during the period of declining photoperiod at higher latitudes. Rainfall appears to have no influence on breeding activity of *E. rufescens, E. brachyrhynchus, E. myurus,* and *E. rozeti.* It is tempting to speculate that the reduction or cessation of breeding during the cooler months of the year might be related to seasonal changes in insect abundance (see Diet).

Litter size

There is very little information on seasonal changes in litter size. No significant differences in litter size of *E. rufescens* were observed between the wet and dry seasons in Kenya (seasonal changes in photoperiod and temperature were negligible), but litter size increased with increase in maternal body mass (Neal, 1982). Similarly, rainfall appeared to have no effect on litter size of *E. brachyrhynchus* in Zimbabwe, but litter size was positively correlated with maternal body mass (Table 2). However, there was a significant decline in litter size during the cool dry season, but it is not known whether this represents a temperature or a photoperiod effect. The decline in litter size, together with the decline in breeding rate (see Breeding Season), during the cool dry season means that there is considerably less energy invested in reproduction at a time when the availability and abundance of insects is expected to be at a minimum.

Litter size increases with latitude, particularly above 15° (Fig. 2). Similar trends have been reported at higher latitudes (Sadleir, 1969) and the phenomenon has often been explained as a compensation for the reduction in the length of the breeding season at higher latitudes (see below).

It is expected that neonate mass should decrease as the litter size increases (Millar, 1977; Case, 1978) but there is no evidence for this (Table 3). However, most species produce a maximum of two offspring per litter, and there is little difference in the birth mass of singletons or twins in

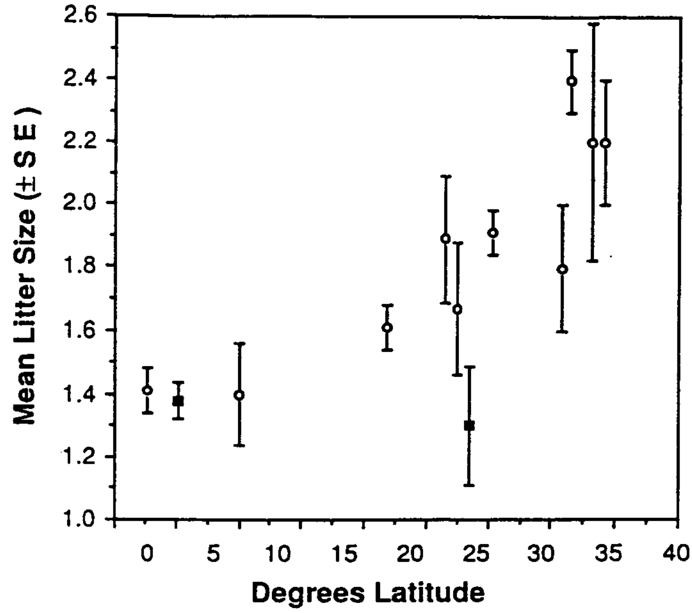

Fig. 2. Mean litter size (± SE) of various species of *Elephantulus* in relation to latitude. Data from Table 3. Solid symbols represent laboratory studies, hollow symbols field studies.

E. rufescens (G.B. Rathbun, personal communication). It would be interesting to know how the birth mass varies with litter size in *E. rozeti* because this species has a litter size of up to four young (Séguignes, 1989).

Annual production of young

The production of young is a function of the duration of the breeding season, the intensity of breeding (pregnancy rate), the gestation period, and litter size. Unfortunately, few studies provide an indication of the intensity of breeding to allow for the calculation of the annual production of young. I have estimated annual production of young to be 8.3 per female for *E. rufescens* in Kenya (Neal, 1982) and for *E. brachyrhynchus* in Zimbabwe (this study). Thus, the decline in breeding activity of *E. brachyrhynchus* during the dry season was compensated for by the increased litter size relative to *E. rufescens*. A population study of *E. myurus* in the Bloemfontein and Fauresmith area of South Africa by Du Toit (personal communication) suggests an annual production of young per female to be approximately 4.5 for this species.

Other estimates are much cruder. Van der Horst (1954) estimated that *E. myurus* has three litters each breeding season in South Africa, which would result in 5.7 young per female per year. In North Africa, *E. rozeti* could have a maximum of two litters a year which would result in 4.4–4.8 young per female per year.

These results suggest that the annual production of young per female is reduced at the northern and southern limits of the range of this genus. However, it is not the annual production of young that is important but the lifetime production of young in relation to age-specific mortality rates. Unfortunately, there is almost no information on survivorship of these animals in the wild. The only information is for *E. rufescens* in Kenya (Rathbun, 1979). Approximately 40% of newborn animals survived for 100 days. The survivorship of territorial adults appeared to be high because some individuals marked as adults were still known to be alive 18–21 months later. Similar studies are required on other species to see if these trends are consistent within the genus and to see if longevity is increased at higher latitudes.

Diet

Elephant-shrews are generally considered to be insectivorous, although small amounts of plant material may be eaten, but the presence of a functional caecum indicates that insectivory is a secondary trait (Rathbun, 1979; Woodall, 1987; Woodall & Mackie, 1987). An insectivorous diet has been observed in *E. rufescens* in Kenya (Rathbun, 1979; Neal, 1982) and in *E. brachyrhynchus* in Zimbabwe (this study). However, it can be questioned whether insects are always so available, particularly during the winter at higher latitudes. Do species living in these regions exhibit a seasonal change in diet and consume more plant material during the winter? Such a seasonal change in diet has been observed in the closely related Round-eared Elephant-Shrew, *Macroscelides proboscideus*, living in the Karoo region of South Africa (Kerley, 1992). In this species, insects comprised up to 77% of the diet during the summer but only 42.5% during the winter, whereas herbage made up approximately 58% of the diet during the winter. Again, studies of the feeding habits of the various species at the northern and southern limits of the range of the genus are required to shed light on this question. Such studies may also help us to understand the seasonal breeding patterns of these species.

Body size and habits

There is no latitudinal trend in adult body mass within the genus *Elephantulus* (Table 3). Most species are similar in size with a mass of 40–60 g. Their small body size allows them to use natural crevices in the ground and the burrows of other small animals (they do not appear to construct their own burrows) to exploit a more moderate microclimate. The latter is not created by nestbuilding because nests are unknown in this genus.

In Kenya, *E. rufescens* stays above ground and uses an elaborate network of trails to escape predation by running away. The young are left in an above-ground refuge (Rathbun, 1979; Neal, 1982). In Zimbabwe, *E. brachyrhynchus* appears to spend less time on the surface, particularly during the cool season. It frequently uses burrows and termite holes for shelter. It would be interesting to know if this represents a latitudinal trend, with species at higher latitudes making more use of underground shelter for both adults and young. Obviously, a study of the habits of the various species at the northern and southern limits of the range of the genus would be of interest.

Habitat

Elephant-Shrews have an interesting distribution. The largest species (body mass approximately 400 g), of the genus *Rhynchocyon*, live in lowland and montane forest and thick riverine bush, and the smallest species (body mass of about 40 g), of the genera *Elephantulus* and *Macroscelides*, live in arid and semi-arid environments. This pattern where the larger species inhabit moister, less seasonal environments and the smaller species inhabit drier, more seasonal environments has been noted by Neal (1982) who explained it in terms of *r*- and *K*-selection theory. An alternative explanation, however, is that body size follows a productivity gradient, with the larger species living in habitats of higher primary productivity than those of the smaller species.

Elephantulus successfully exploits arid and semi-arid environments over a wide range of latitude, but why is it restricted to these habitats where the primary productivity is so low? Why doesn't *Elephantulus* invade wetter, more productive habitats where the small mammal insectivorous feeding niche is filled by similar sized shrews (*Crocidura*) and rodents (e.g. *Deomys*, *Lophuromys*, and *Zelotomys*)? A simple explanation is that *Elephantulus* is physiologically and behaviourally adapted to arid and semi-arid environments and cannot change. However, an additional or alternative explanation is that *Elephantulus* is restricted to habitats of low primary productivity because of its habit of producing precocial young and that it cannot successfully compete against species bearing more altricial young in more productive habitats.

Why should this be so? Precocial species have low population growth rates relative to altricial species (Hennemann, 1984), and this difference is likely to be large in habitats with a high primary productivity because the altricial species may breed for extended periods. However, in habitats with a low primary productivity this price of precociality is likely to be much less. This is because altricial species generally confine their breeding to periods when food is plentiful, such as during and immediately after the rains, but precocial species can have a more protracted breeding season and breed even during periods when food is scarce or of low quality (Perrin, 1980; Neal, 1986). Thus, the annual population growth rates of altricial and precocial species should be more similar in habitats with a low primary productivity compared with habitats with a high primary productivity.

There is some circumstantial evidence to support the suggestion that small mammals producing precocial young may be restricted to habitats of low productivity. Other small precocial mammals with a body mass of less than 150 g also tend to live in habitats with a low primary productivity. For example, the spiny mice (*Acomys*) live in arid and semi-arid environments in Africa and Arabia, and the laminate-toothed or vlei rats (*Otomys*) are particularly common in semi-arid areas and montane forests in Africa.

The available evidence suggests that *Elephantulus* may compete for food with other small mammals. In Kenya, the most common rodents and *E. rufescens* all used insects as their major food resource (Neal, 1984a, b); in Zimbabwe the most common rodent inhabiting the same areas as *E. brachyrhynchus* was the bushveld gerbil, *Tatera leucogaster*, and insects made up 10–40% of its diet (Neal, 1991b). Although there is undoubtedly some partitioning of the insect food resource by the various species it seems improbable that there is a total separation of feeding niches.

From one perspective, the habit of producing precocial young can be seen as a constraint that may partly explain why *Elephantulus* is restricted to arid and semi-arid environments. From another perspective, however, it may be viewed as an adaptation which allows the genus to exploit these environments in ways which are not available to altricial species.

CONCLUSIONS

The reproductive strategy of *Elephantulus*, involving the production of highly precocial neonates, is obviously not only successful at lower latitudes where the temperature is relatively constant but is also successful at higher latitudes where the temperature is much more variable. However, the genus is confined to arid and semi-arid regions of low productivity, and it is suggested that the precocial habit may be one reason why the genus is restricted to such environments. As expected, the breeding season tends to become restricted to the warmer period of the year at higher latitudes and litter size is increased compared to lower latitudes. There are several unanswered questions about the general habits of species living at higher latitudes. Do they make more use of burrows or other crevices in the ground to escape the colder temperatures of the winter months? Do they modify their feeding habits, eating insects when available during the summer months but switching to seeds or herbage during the winter months? Clearly, further field studies of those species at higher latitudes are required.

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