Reproductive ecology of the Rufous elephant-shrew, *Elephantulus rufescens* (Macroscelididae), in Kenya

By B. R. Neal

Department of Biology, University of Saskatchewan, Saskatoon, Canada

Receipt of Ms. 25. 11. 1981

Abstract

The reproductive ecology of *Elephantulus rufescens* was studied in Meru National Park, Kenya during the period August 1974 to June 1975. 174 animals were collected and dissected. The body weights, condition of the reproductive organs, and extent of tooth wear provided information on seasonal changes in breeding activity, litter size, and age structure.

The climate was very seasonal. Rainfall was confined to two periods, from November to December and mid-April to mid-May. Temperature increased during the dry seasons and decreased during the rains. However, no seasonal changes were detected in adult body mass, breeding activity, litter size, or age structure.

Approximately three quarters of the adult females carried implanted embryos. The average interval between litters was estimated to be 62 d, so that adults had the capacity to produce just under 6 litters each year. The average litter size was 1.41 ± 0.07 (range 1–2), and was positively correlated with maternal body mass. The potential annual production of young per adult female was estimated to be 8.3

The reproductive strategy of elephant-shrews is briefly discussed.

Introduction

The specific classification of elephant-shrews can be considered to be nearly definitive (Corbet and Hanks 1968; Corbet 1971). The family Macroscelididae, which includes four genera and fifteen species, is an extremely well defined taxon endemic to Africa. There is general agreement that the elephant-shrews are a monophyletic group not closely related to any other group of living mammals. Their affinity with the Insectivora and Primates is highly debatable (Corbet and Hanks 1968; Rathbun 1979).

The literature on the breeding biology of elephant-shrews has been reviewed by Asdell (1964), Brown (1964), Rathbun (1979), and Tripp (1971, 1972). Elephant-shrews are monogamous (Rathbun 1979) and spontaneous ovulators (Van der Horst 1954). Little is known about the length of the breeding season in most species. Breeding is confined to six months of the year in *Elephantulus myurus* in South Africa, and both males and females are in anoestrus during the remainder of the year (Stoch 1954; Van der Horst 1946, 1954). Breeding occurs throughout the year in *E. rufescens* and *Rhynchocyon chrysopygus* in Kenya (Rathbun 1979), and is thought to be continuous in *E. rupestris* in Namibia (Withers 1979). However, samples were too small to determine seasonal changes in the breeding rate of these species. After a gestation period of 42 to 56 d (Rathbun 1979; Tripp 1972; Van der Horst 1946) females give birth to a litter of 1–2 precocial young (Rathbun 1979). Further development of the young is rapid (Rathbun 1979; Rathbun and Redford 1981) and breeding can occur at an early age in some species (Van der Horst 1946, 1954; Tripp 1972).

This paper describes the breeding biology of a large sample of *E. rufescens* collected in the Meru National Park, Kenya. It complements the work of Rathbun (1979) which was

U.S. Copyright Clearance Center Code Statement: 0044-3468/82/4702-0065 $ 02.50/0
Z. Säugetierkunde 47 (1982) 65–71

ISSN 0044-3468 / InterCode: ZSAEA 7

based on visual observations of a small group of *E. rufescens* in a similar habitat approximately 250 km south of my study area. I investigated seasonal changes in breeding activity and discuss the reproductive strategy of elephant-shrews.

Material and methods

A total of 174 animals were collected from a 2 km² area immediately south of Rainkombe (0° 07′ N, 38° 12′ E) during the period August 1974 to June 1975. Approximately half of the animals were collected using standard trap lines of Reporter break-back traps, and the remainder collected using Sherman live traps.

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

The female reproductive tract was examined macroscopically, with the aid of a dissecting microscope where necessary. Animals were classified as immature if no placental scars or corpora lutea were observed. Corpora lutea are particularly easy to observe in elephant-shrews because they are everted from the surface of the ovary (Tripp 1971). Mature females were classed as either 1. reproductively active, if visibly pregnant (i.e. with implanted embryos) or corpora lutea were observed; or 2. reproductively inactive, if no corpora lutea were visible. Embryos were counted, measured and weighed after fixation. A representative sample was also weighed before fixation to correct for the loss in weight due to the fixation process.

A sperm smear was taken from the epididymides of each male. Individuals were classed as immature if no sperm were present, and as adults if sperm were abundant. The testes were weighed after fixation.

The relative age of individuals was estimated using the eruption and subsequent wear of the upper molars and premolars as a criterion.

Conception dates were estimated by ageing litters by the method of Huggett and Widdas (1951), assuming a birth mass equal to that of the heaviest embryo, a gestation period of 50 d (Rathbun 1979; Rathbun and Redford 1981), and that embryos attained a measurable body mass on the seventh day of gestation.

The average interval between litters, and potential annual production of young per adult female were estimated by the method described by Neal (1981). In this method the ratio of adult females with implanted embryos (N_v) to adult females not visibly pregnant ($N_o + N_I$) is assumed to equal the ratio of the duration of the post-implantation period of gestation (p_v) to the sum of the pre-implantation period (p_I) and the period between pregnancies (p_o). In *E. rufescens* the equation is solved for p_o by assuming that the length of the gestation period ($p_I + p_v$) is 50 d (Rathbun 1979) and the pre-implantation period (p_I) is 4 d. The mean interval between litters ($p_o + p_I + p_v$) can be easily calculated, and the production of young is then estimated using the average litter size.

Results

Habitat and habits

Elephant-shrews were confined to the area of deciduous *Acacia/Commiphora* bushland in the southern half of Meru National Park. The vegetation mainly consisted of a wide variety of tall *Acacia* and *Commiphora* bushes, and in some areas there was a thicker understory of *Bauhinia taitensis, Grewia villosa, Combretum aculeatum* and other species of bushes (Ament 1975). There were a few scattered *Acacia* spp, *Terminalia* app, *Sterculia africana, Delonix elata* and *Adansonia digitata* trees. There was no herbaceous layer for most of the year, and much of the ground was badly eroded. During the dry seasons (i.e. for 8–9 months of the year) the bushes were leafless and the whole area appeared dry and dead. However, during the rains (Fig. 1D) the bushes came into leaf, sparse patches of various annual grasses and dicotyledons appeared, and the whole area looked lush and green.

The presence of *E. rufescens* was obvious because of their network of trails. My observations of their habits are consistent with those of Rathbun (1979). Adults occurred in pairs with either one or two young. They remained above ground and their movements, which were extremely rapid when disturbed, were almost entirely restricted to their trail system. They seemed oblivious to objects placed on their trails, running repeatedly into closed traps before moving off the trail to avoid the obstruction. Only occasionally would they take refuge in a hollow log or hole in the ground. The distribution of territories was very clumped. There were usually three or four families living more or less adjacent to one another, with large gaps of 100 m or more between groups. There seemed to be no association between their distribution and the vegetation, so their absence from most of the available habitat may be due to the presence of spiny mice (*Acomys* spp) which are very abundant in the area (Neal in press). Withers (1979) has shown that *E. rupestris* in Namibia is poorly correlated in distribution with any plant, and appears to avoid *Aethomys namaquensis.*

Body size

The mass of the heaviest embryo of a litter with a single embryo was 10.4 g; that of a litter of two embryos was 7.8 g. The lightest juveniles collected had a body mass of 14–15 g. Delany (1964) records a female carrying a single embryo of 16 g in Uganda, and Walker (1955) records the body mass within 3 d of birth to be just less than 12 g. The birth mass of *E. intufi* is recorded as 10 g (range 8.5–10.5 g) and of *E. myurus* as 8.1 ± 0.6 g (Tripp 1972).

Both sexes matured at a body mass of 32–35 g and apparently at an early age. All animals in which the last upper molar was partly or wholly erupted (age class II or older) were mature, as were 2 of 27 animals in which the last upper molar had still not emerged through the surface of the jaw (age class I). Adult females usually attained a body mass of 45–65 g, and males a body mass of 35–55 g. Adult body mass was similar to that recorded for *E. intufi, E. rozeti* and *E. brachyrhynchus,* and a little less than *E. myurus* (Smithers 1971; Tripp 1972).

Breeding season

E. rufescens bred throughout the year (Fig. 1B), and there was no significant seasonal variation in the testes mass of adults (Fig. 1A). Pregnancy rates in the wet and dry seasons were independent of season ($\chi^2 = 1.11$; $P = 0.3$) when tested by chi-squared analysis of a 2×2 contingency table (Sokal and Rohlf 1969).

Rathbun (1979) also found that *E. rufescens* bred throughout the year in Kenya, and Van der Horst (1954) reports that Hoogstraal found this species breeding throughout the year in the southern Sudan. The suggestion by Brown (1964) and Kingdon (1974) that breeding is seasonal in *E. rufescens* is based on inadequate data. *E. myurus* breeds during a six month period, from August to January, in the Transvaal (Van der Horst 1946, 1954). Its breeding season appears to be extended in Botswana because pregnancies have been recorded in September, March and April (Smithers 1971). Smithers (1971) also suggests that *E. intufi* breeds during the warmer, wetter months of the year, from August to February, in Botswana; and *E. rupestris* is thought to breed throughout the year in Namibia (Withers 1979).

Litter size

The mean number of embryos of 46 pregnancies was 1.41 ± 0.07 (range 1–2). Two of these females also appeared to have a second resorbing embryo at an early stage of gestation. Variation in litter size was analysed in relation to the evicerated maternal body mass and season of conception by analysis of covariance (Snedecor and Cochran 1967). The sample was divided into those litters conceived during the rains and immediately after (November to early January, mid-April to early June), and those litters conceived during the dry seasons. Litter size was not significantly different in the wet and dry seasons ($F_{1,43} = 0.0002$; $P > 0.75$), but increased significantly with increase in maternal body mass ($F_{1,43} = 7.34$; $P = 0.01$). Females with an evicerated body mass of less than 40 g all carried

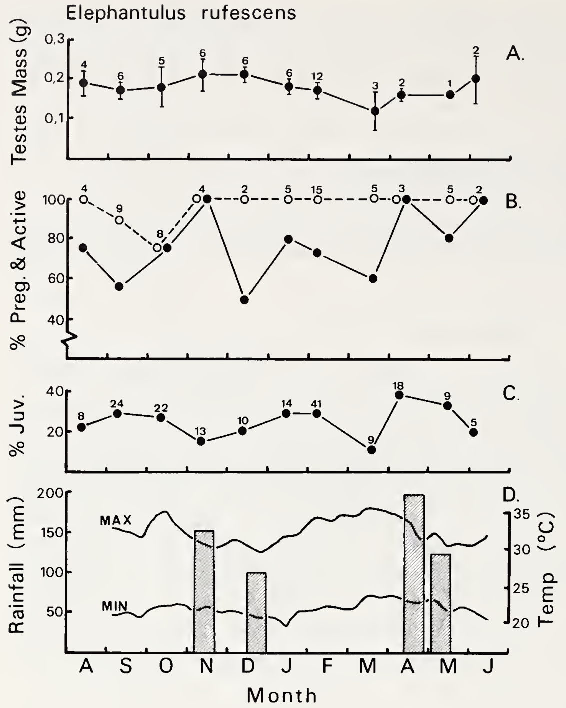

Fig. 1. Seasonal changes in reproductive activity of *E. rufescens.* Numbers in Figs. A–C indicate sample sizes. A: Testes mass of males in age class V or older. Data points represent means ± 2 × S.E. B: Percentage of adult females reproductively active (○– – ○), and visibly pregnant (●——●). C: Percentage of animals in first age class. D: Maximum and minimum daily temperature, and rainfall (histogram)

single embryos (n = 9), whereas those over 40 g had a mean litter size of 1.51 ± 0.08 (n = 37).

Estimates of the mean litter size of *E. rufescens,* based on small samples, range from 1.0 to 1.5 (Brown 1964; Delany 1964; Rathbun 1979; Rathbun and Redford 1981; Tripp 1971), and give a combined estimate of 1.35 ± 0.08 (n = 34). Rathbun (1979) also noted that litter size increased as the mothers increased in age. The mean numbers of embryos in various species for which large samples are available are as follows: In 36 *E. rozeti* from northwest Africa, 2.42 ± 0.11, range 1–4 (Tripp 1971); in 26 *E. intufi* from the Transvaal, Botswana and Namibia, 1.62 ± 0.11, range 1–3 (Shortridge 1934; Smithers 1971; Tripp 1971, 1972); in 20 *E. brachyrhynchus* from East Africa, Zambia and Botswana, 1.60 ± 0.11, range 1–2 (Brown 1964; Shortridge 1934; Smithers 1971; Tripp 1971); and in 27 *E. myurus* from the Transvaal and Botswana, 1.85 ± 0.07, range 1–2 (Smithers 1971; Tripp 1971, 1972). Van der Horst (1944) reports that only 1 percent of *E. myurus* from the Transvaal carried single embryos. The maximum litter size appears to be restricted to two young in most species because implantation is restricted to a single implantation site in each horn of the uterus (Tripp 1971).

Breeding rates and production of young

There was no seasonal variation in either the breeding rate (see Breeding season) or litter size (see Litter size). Consequently, it is inferred that there was no seasonal variation in the number of young entering the population. The percentage of animals in age class I varied irregularly (Fig. 1C) and showed no seasonal trend. The proportion of young in the wet and dry seasons was independent of season ($\chi^2 = 0.48$; $P = 0.49$) when tested by chi-squared analysis of a 2 × 2 contingency table (Sokal and Rohlf 1969).

Approximately three quarters (46 of 62) of adult females were visibly pregnant. The average interval between litters was calculated to be approximately 62 d, so that adults had the capacity to produce just under six litters each year. Assuming an average litter size of 1.41 (see Litter size) the potential annual production of young per adult female was approximately 8.3.

RATHBUN (1979) observed a mean interval of 61 ± 1.23 d (range 56–65 d) between 7 consecutive litters of this species in an area 250 km south of my study area. The potential production of young per adult female was very similar to my estimate because the average litter size was not significantly different in the two areas. VAN DER HORST (1954) estimated that *E. myurus* gave birth to three litters during its six month breeding season in South Africa. This translates to an average interval of approximately 61 d between litters and a potential annual production of young per adult female of just under 6. Finally, RATHBUN (1979) observed an average interval of 81 d between 11 consecutive litters of *Rhynchocyon chrysopygus* in Kenya. There was only one offspring per litter, and so the potential annual production of young was 4.5 per adult female.

Table

Comparison of life history characteristics of the four genera of elephant-shrews

(Data summarized from BROWN [1964], CORBET and HANKS [1968], RATHBUN [1979], VAN DER HORST [1954] and this paper)

	Rhynchocyon	*Petrodromus*	*Elephantulus*	*Macroscelides*
Habitat	Lowland/montane forest. Thick riverine bush	Forest, thickets, dense savanna woodland	Open savanna woodland, steppe, subdesert	Subdesert
Climate	Moist ←			→ V. dry
Environmental stability	High ←			→ Low
Body size (mass)	c. 400 g	c. 200 g	35–90 g	< 50 g
Longevity	3–4 yr	?	1–2 yr	?
Age 1st reprod.	Late	Late?	Early	Early?
Breeding season	All year	All year?	6 months – all year	?
Interval between litters	82 d	?	61–62 d	?
Litter size	1–2	usually 1	1–2	1–2
Prod. young/female/year	4.5	?	6–8.3	?

Discussion

The key to understanding the reproductive strategy of *Elephantulus,* and perhaps all elephant-shrews, seems to lie in their ability to give birth to precocial young. This ability appears to be a secondary evolutionary development in mammals (CASE 1978; LILLEGRAVEN 1975), and so it is interesting to speculate on the reasons for this development. Elephant-shrews live above ground and most species do not build nests (RATHBUN 1979). They also avoid predation, in part, by running away (RATHBUN 1979) so that neonates must be well developed. These habits are probably associated with the evolution of precocial young. It is interesting to note that in *Rhynchocyon,* which is the only genus of elephant-shrews that builds nests, the neonates are not as advanced as those of the other three genera (RATHBUN 1979).

The long gestation period of 42–56 d (RATHBUN 1979; TRIPP 1972; VAN DER HORST 1946) and small litter size (usually 1–2) are probably associated with the development of precocial young (SACHER and STAFFELDT 1974). One consequence of this developmental strategy is that the rate of production of young per adult female is very low (less than 10 per year) compared to most other small mammals (FRENCH et al. 1975).

To compensate for this low birth rate elephant-shrews generally breed continuously and have an extended period of reproductive life. The latter is achieved by increasing adult survivorship and decreasing the age of first reproduction (Table). The available evidence suggests there is an interaction of longevity and age of first reproduction with body size.

The life history characteristics of the different genera (Table) agree with conventional ideas on r- and K-selection (PIANKA 1970; STEARNS 1976), although the meaning of the concept used here may be more appropriately called birth and death rate selection (PARRY 1981). Species inhabiting moister, less seasonal environments appear to be more K-selected (i.e. have lower birth and death rates) than those inhabiting arid, more seasonal environments. I have noted a similar set of relationships in the unstriped grass rat, *Arvicanthis* (NEAL 1981).

The reproductive characteristics of precocial young, long gestation period, small litter size, continuous breeding, and early maturation are also exhibited by the spiny mice, *Acomys* (NEAL in press), and the laminate-toothed or vlei rats, *Otomys* (DAVIS and MEESTER 1981; PERRIN 1980). These genera either do not build nests, or their nests are very rudimentary (KINGDON 1974). Thus, these species and elephant-shrews may have evolved their reproductive strategy for similar reasons.

Acknowledgements

The field work in Kenya was carried out during a sabbatical leave from the University of Saskatchewan. I wish to thank the former Director and Trustees of the Kenya National Parks (now a subdepartment in the Ministry of Tourism and Wildlife of Kenya) for permission to study in Meru National Park, the Park staff for their help and cooperation, and Prof. F. MUTERE of Kenyatta University College for making my stay in Kenya possible. It is a pleasure to thank the Park Warden, Mr. P. JENKINS, for providing excellent facilities and help for the field and initial laboratory work; the Park Rangers, JOSEPH NAMERIO and THOMAS NTOBURI, for their help with the field work; and my wife, JENNY, for help with the field and laboratory work and critically reading an earlier draft of this paper. Finally, it is a pleasure to thank Drs. C. RALPH and B. WUNDER of the Department of Zoology and Entomology, Colorado State University, for the use of the facilities of the Department during the completion of this work.

Zusammenfassung

Die Fortpflanzungsökologie der Elefantenspitzmaus, Elephantulus rufescens (Macroscelididae), in Kenia

Die Fortpflanzungsökologie von *Elephantulus rufescens* wurde im Meru-Nationalpark in Kenia im Zeitraum von August 1974 bis Juni 1975 untersucht. Insgesamt 174 Tiere wurden gefangen und seziert. Körpergewicht, Status der Fortpflanzungsorgane, und der Grad der Zahnabnutzung lieferten Informationen über Fortpflanzungsaktivität, Wurfgröße und Altersstruktur.

Das Klima schwankte je nach Jahreszeit erheblich. Die Niederschläge beschränkten sich auf 2 Perioden, von November bis Dezember und von Mitte April bis Mitte Mai. Die Umgebungstemperaturen stiegen während der Trockenzeiten an und fielen in den Regenzeiten. Es konnten jedoch keine jahreszeitlichen Veränderungen in bezug auf das Körpergewicht der adulten Tiere, die Fortpflanzungsaktivität, Wurfgröße oder Altersstruktur festgestellt werden.

Annähernd Dreiviertel der adulten Weibchen trugen implantierte Embryonen. Der Zeitraum zwischen den Würfen wurde auf durchschnittlich 62 Tage geschätzt, so daß die adulten Tiere eine Kapazität von knapp 6 Würfen pro Jahr hatten. Die durchschnittliche Wurfgröße war 1,41 ± 0,07 (Bereich 1–2) und korrelierte positiv mit dem Körpergewicht des Muttertieres. Die mögliche jährliche Anzahl von Jungen pro adultem Weibchen wurde auf 8,3 geschätzt.

Die Fortpflanzungsstrategie der Elefantenspitzmaus wird kurz diskutiert.

References

AMENT, J. G. (1975): The vascular plants of Meru National Park, Kenya. J. E. Afr. Nat. Hist. Soc. **154**, 1–33.

ASDELL, S. A. (1964): Patterns of Mammalian Reproduction. 2nd Ed. Ithaca: Cornell University Press.

BROWN, J. C. (1964): Observations on the elephant-shrews (Macroscelididae) of equatorial Africa. Proc. zool. Soc. Lond. **143**, 103–119.

CASE, T. J. (1978): Endothermy and parental care in the terrestrial vertebrates. Am. Nat. **112**, 861–874.

CORBET, G. B. (1971): Family Macroscelididae. In: The mammals of Africa: an identification manual. Ed. by J. MEESTER; H. W. SETZER. Washington: Smithsonian Institution.
CORBET, G. B.; HANKS, J. (1968): A revision of the elephant-shrews, family Macroscelididae. Bull. Brit. Mus. Nat. Hist. (Zool.) **16**, 45–111.
DAVIS, R. M.; MEESTER, J. (1981): Reproduction and postnatal development in the Vlei rat, *Otomys irroratus,* on the van Riebeeck Nature Reserve, Pretoria. Mammalia **45**; 99–116.
DELANY, M. J. (1964): A study of the ecology and breeding of small mammals in Uganda. Proc. zool. Soc. Lond. **142**, 347–370.
FRENCH, N. R.; STODDART, D. M.; BOBEK, B. (1975): Patterns of demography in small mammal populations. In: Small mammals: their productivity and population dynamics. Ed. by GOLLEY, F. B.; PETRUSEWICZ, K.; RYSZKOWSKI, L. Cambridge: Cambridge University Press.
HORST, C. J. VAN DER (1944): Remarks on the systematics of *Elephantulus.* J. Mammalogy **25**, 77–92.
— (1946): Some remarks on the biology of reproduction in the female of *Elephantulus,* the holy animal of Set. Trans. Roy. Soc. S. Afr. **31**, 181–199.
— (1954): *Elephantulus* going into anoestrous; menstruation and abortion. Phil. Trans. **238B**, 27–61.
HUGGETT, A. St. G.; WIDDAS, W. F. (1951): The relationship between mammalian foetal weight and conception age. J. Physiol. **114**, 306–317.
KINGDON, J. (1974): East African Mammals: An Atlas of Evolution in Africa. Vol. II, part A: Insectivores and Bats. London: Academic Press.
LILLEGRAVEN, J. A. (1975): Biological considerations of the marsupial-placental dichotomy. Evolution **29**, 707–722.
NEAL, B. R. (1981): Reproductive biology of the unstriped grass rat, *Arvicanthis,* in East Africa. Z. Säugetierkunde **46**, 174–189.
— (1982): The breeding pattern of two species of spiny mice, *Acomys* (Muridae: Rodentia), in central Kenya. Mammalia (in press).
PARRY, G. D. (1981): The Meanings of r- and K-Selection. Oecologia **48**, 260–264.
PERRIN, M. R. (1980): The feeding habits of two coexisting rodents, *Rhabdomys pumilio* and *Otomys irroratus,* in relation to rainfall and reproduction. Acta Oecol. Oecol. Gen. **1**, 71–90.
PIANKA, E. R. (1970): On r- and K-selection. Am. Nat. **104**, 592–597.
RATHBUN, G. B. (1979): The social structure and ecology of elephant-shrews. Z. Tierpsychol. Suppl. **20**, 1–76.
RATHBUN, G. B.; REDFORD, K. (1981): Pedal scent marking in the Rufous Elephant-Shrew, *Elephantulus rufescens.* J. Mammalogy **62**, 635–637.
SACHER, G. A.; STAFFELDT, E. F. (1974): Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. Am. Nat. **108**, 593–615.
SHORTRIDGE, G. C. (1934): The mammals of South West Africa. London: Heinemann.
SMITHERS, H. N. (1971): The mammals of Botswana. Salisbury: Nat. Mus. Rhodesia.
SNEDECOR, G. W.; COCHRAN, W. G. (1967): Statistical Methods. 6th Ed. Ames: Iowa State University Press.
SOKAL, R. R.; ROHLF, F. S. (1969): Biometry. San Francisco: W. H. Freeman & Co.
STEARNS, S. C. (1976): Life history tactics: a review of the ideas. Q. Rev. Biol. **51**, 3–47.
STOCH, Z. G. (1954): The male genital system and reproductive cycle of *Elephantulus myurus jamesoni* (Chubb). Phil. Trans. **238B**, 99–126.
TRIPP, H. R. H. (1971): Reproduction in Elephant-Shrews (Macroscelididae) with special reference to ovulation and implantation. J. Reprod. Fert. **26**, 149–159.
— (1972): Capture, laboratory care and breeding of Elephant-Shrews (Macroscelididae). Lab. Anim. **6**, 213–224.
WALKER, E. P. (1955): African elephant shrews. Nature Magazine **48**, 295–297, 332.
WITHERS, P. C. (1979): Ecology of a small mammal community on a rocky outcrop in the Namib desert, South-West Africa. Madoqua **11**, 229–246.

Author's address: Prof. Dr. B. R. NEAL, Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N OWO