Galen B. Rathbun

The Social Structure and Ecology of Elephant-Shrews

Fortschritte der Verhaltensforschung
Beihefte zur Zeitschrift für Tierpsychologie
Advances in Ethology
Supplements to Journal of Comparative Ethology

20

Verlag Paul Parey
Berlin und Hamburg

The Social Structure and Ecology of Elephant-Shrews

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With 48 figures and 10 tables

1979

Verlag Paul Parey · Berlin and Hamburg

Fortschritte der Verhaltensforschung · Heft 20
Advances in Ethology · No. 20

Zugleich Beiheft 20 zur Zeitschrift für Tierpsychologie
Supplement 20 to Journal of Comparative Ethology

Herausgegeben von
Edited by
Prof. Dr. W. Wickler, Seewiesen (Obb.)
Prof. Dr. E. Curio, Bochum-Querenburg

CIP-Kurztitelaufnahme der Deutschen Bibliothek

Rathbun, Galen B.:
The social structure and ecology of elephant-shrews / by Galen B. Rathbun. — Berlin, Hamburg : Parey, 1979.
(Fortschritte der Verhaltensforschung ; H. 20)
ISBN 3-489-60836-4

Cover design: Jochen Goks, Berlin
Cover photograph: Galen B. Rathbun, Gainesville

Addresses: D-1000 Berlin 61, Lindenstraße 44—47, and D-2000 Hamburg 1, Spitalerstraße 12.

Composition: Wilhelm Möller OHG, D-1000 Berlin 28.
Printing: Saladruck, Steinkopf & Sohn, D-1000 Berlin 36.
Binding: Wübben & Co., D-1000 Berlin 42.

ISSN 0301—2808 · ASTM-Coden: AEHYAZ (Fortschritte der Verhaltensforschung / Advances in Ethology)

ISBN 3 489 60836 4 · Printing in Germany

Abstract

Two separate projects on free-living elephant-shrews (Macroscelidea) were undertaken to establish some characteristics of their ecology and behaviour. In Kenya, *Rhynchocyon chrysopygus* was studied in coastal forest during 21 months and *Elephantulus rufescens* was studied in Tsavo bushland for 12 months. Observations of marked individuals were recorded in field notebooks. Stomach contents and food availability data were also collected. Limited information on *Petrodromus tetradactylus* and published accounts on *Macroscelides proboscideus* are used to discuss anti-predator, feeding and reproductive strategies. The life histories of elephant-shrews and other mammals are compared and discussed in terms of the unique phylogeny of the Macroscelidea.

Contents

To the Rhinogradentia
of HARALD STÜMPKE (1967)

I. Introduction

Zoologists have long been fascinated by elephant-shrews and their unique morphology, but unfortunately little more than morphology has been documented for these animals. Since they are small, difficult to maintain in captivity, and may live in habitats and areas in which it is difficult to work, our ignorance of their behaviour and ecology is understandable. A few research projects have been carried out on captive colonies, but none of these have been very successful and, with few exceptions, the only observations of these animals in their natural habitat have been made by collectors, often down the sights of gun barrels.

This monograph includes the results of a comparative study of the ecology and social behaviour of 2 East African species, the Golden-rumped Elephant-shrew, *Rhynchocyon chrysopygus* Günther 1881, and the Rufous Elephant-shrew, *Elephantulus rufescens* Peters 1878. It is based on 33 months of field work on individually known, free-living animals. Limited data on the Four-toed Elephant-shrew, *Petrodromus tetradactylus* Peters 1846, are also presented.

For comparative purposes, information published on other elephant-shrew species, especially the Short-eared Elephant-shrew, *Macroscelides proboscideus,* is also included.

A. Taxonomy and the fossil record

The taxonomy within the elephant-shrew family, Macroscelididae, is fairly straightforward, largely due to the revision by Corbet and Hanks (1968). Two subfamilies are recognized: the Rhynchocyoninae, consisting of a single genus, *Rhynchocyon,* with 3 species; and the Macroscelidinae, consisting of 3 genera: *Macroscelides* (one species), *Petrodromus* (one species), and *Elephantulus* (9 species).

What are elephant-shrews? This has been a controversial question among systematicists for the past 130 years. There are several reviews of the literature (Horst 1950; Tripp 1970; Sauer 1973), so only the highlights are summarized here. The Macroscelididae have been taxonomically associated at one time or another with the primates, various groups of insectivores and the ungulates. They have also been placed in their own taxon and combined with the Tupaiidae to form the Menotyphla. This confusion has been largely due to a reliance on the morphology of extant forms, the poorly understood fossil record and a certain amount of conservative, restricted thinking with regard to mammalian evolution. The generally accepted place for the elephant-shrews has been in the catchall order Insectivora, but since Butler (1956), there has been a growing concensus that they should be referred to their own order.

Patterson's (1965) revision of the fossil elephant-shrews represents an important contribution to the understanding of this group's evolution and systematics. A portion of Patterson's conclusion follows: "The Macroscelididae, a wholly African group so far as known, includes four subfamilies, two of which are extinct. The Macroscelidinae date from the early Oligocene of the Fayum, where they are represented by *Metoldobotes,* a form originally referred to the insectivore family Mixodectidae. *Palaeothentoides* of the early Pleistocene (?), first described as a marsupial, is a valid member of the subfamily. Extinct species of *Elephantulus* are known from the Pleistocene. The early Miocene *Rhynchocyon clarki* provides the only fossil record of the Rhynchocyoninae. The subfamily Mylomygalinae is proposed for the Pleistocene *Mylomygale,* a remarkable form with hypsodont posterior cheek teeth convergent towards those of various rodents. The Myohyracinae, hitherto placed in the Hyrocoidea ... are represented by the early Miocene *Myohyrax* and *Protypotheroides.* Their posterior cheek teeth are decidedly ungulate-like and comparable in complexity and degree of hypsodonty to those of Equinae and hypsodont Noto-ungulata ... The extinct subfamilies were beyond doubt predominately herbivorous ..." A summary of the fossil record is presented in Fig. 1.

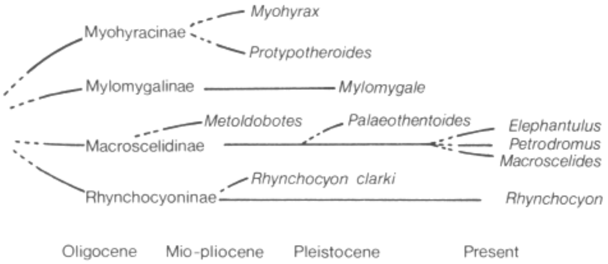

Fig. 1: Dendrogram of Macroscelidea phylogeny with an approximate time scale, based on Patterson (1965)

Patterson (1965) formally referred the elephant-shrews to their own order, the Macroscelidea, but confusion still reigns: in a series of publications on *M. proboscideus* the Sauers claim that some of their behavioural findings support a Macroscelididae-Tupaiidae relationship and they consider both of these groups related to the Insectivora (Sauer and Sauer 1971, 1972; Sauer 1972, 1973). I hope the results and discussion reported here will contribute to a clearer understanding of elephant-shrew relationships with other Mammalia.

Fig. 2: Adult *R. chrysopygus*

Fig. 3: Adult *E. rufescens*

B. Physical description and distribution

All of the elephant-shrews are characterized by long, thin legs, large eyes and external ears, long rat-like tails and, of course, a long flexible proboscis-like nose.

The Rhynchocyoninae are all similar in body shape and size, the main difference being in their colouration (see Kingdon 1974). *R. chrysopygus* is a dark amber colour with black legs and feet and a distinct gold-coloured rump patch (Fig. 2). The mean measurements [1] of 10 adult female and 10 adult male specimens are: total length, 525.6 mm (S.D. = 16.4); tail length, 242.6 mm (S.D. = 11.8); and body weight, 540.3 g (S.D. = 36.9). There is no significant sexual dimorphism except for the longer canines and thicker rump skin of the ♂♂ (Rathbun 1978).

[1] Where a mean is included in the text, it is followed by its standard deviation (S.D.) in parentheses.

The Macroscelidinae are similar in body form to *Rhynchocyon,* but are less colourful, being buff, brown, or grey, and smaller. *E. rufescens,* based on 18 adult specimens (7 ♀♀), has the following mean measurements: total length, 255.3 mm (S.D. = 9.9); tail length, 133.3 mm (S.D. = 8.3); and body weight, 58.0 g (S.D. = 7.3). No sexual dimorphism is evident (Fig. 3). *P. tetradactylus* is the largest member of this subfamily, with mean (n = 34) measurements of 358.5 mm (S.D. = 24.0) for total length and 166.2 mm (S.D. = 7.6) for tail length. The mean (n = 9) weight is 205 g (S.D. = 31.6) (Fig. 4). One of the smallest species is *M. proboscideus* with a mean total length of 235.4 mm (S.D. = 4.7) and a tail length of 122.1 mm (S.D. = 4.9). Its body weight is about 45 g (Fig. 5).

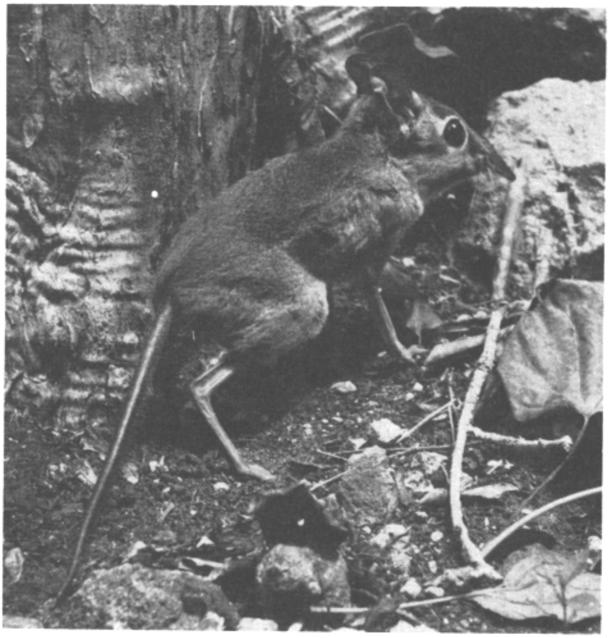

Fig. 4: Adult *P. tetradactylus*

Fig. 5: Adult *M. proboscideus* (photo by M. Rosenthal, Lincoln Park Zoological Garden)

The elephant-shrews are confined to the African continent and in many respects show a peculiar and interesting distribution (Corbet and Hanks 1968) (Fig. 6). The east coast of Africa harbours a number of zoogeographical anomalies, including *Rhynchocyon petersi* south of Mombasa and *R. chrysopygus* north of Mombasa. The distribution of *Rhynchocyon cirnei,* the probable parent species of the coastal forms, seems to support a dispersal route from the central, inland forests, eastward towards Lake Victoria, down the shore of Lake Tanganyika to Lake Malawi, and then towards the coast (Kingdon 1971) (Fig. 6). This is the same dispersal route proposed for butterflies by Carcasson (1964) and for birds by Moreau (1966). On the other hand, in view of the antiquity of the genus *Rhynchocyon* and the relatively recent formation of the Kenya highlands, the coastal *Rhynchocyon* may have been isolated from the main central African population by the formation of the East African highlands and Rift Valley about 16 million years ago, which apparently bisected a continental, continuous east-west belt of lowland forest (Andrews and Couvering 1975).

R. chrysopygus is restricted to a narrow band along the North Kenya coast from the Kombeni River in the hills behind Mombasa (Giriama Tribe Elders, pers. comm.) north to the Boni Forest, just south of the Kenya-Somalia border (Rathbun, pers. obs.; Boni Tribe Elders, pers. comm.) (Fig. 7). Within this area the elephant-shrews inhabit dense bush near the coast and inland the moist, lowland forests and dense woodlands. Over much of this area, including the Boni Forest, *Petrodromus* is sympatric with *Rhynchocyon.*

E. rufescens is confined to eastern Africa, from northern Somalia south to central Tanzania and from northern Uganda and western Tanzania east to the coast (Fig. 6). It occupies dry bushland and woodland and is not sympatric with *Rhynchocyon* or *Petrodromus.* Descriptions and distributions of all the elephant-shrews may be found in CORBET and HANKS (1968).

C. Aims and approach to research

The uniqueness of the elephant-shrews and the paucity of behavioural and ecological data, especially for the Rhynchocyoninae, made them especially attractive for a study of their basic life history traits, particularly their social structure, feeding ecology and reproductive biology. The comparative approach, carried out under natural conditions and on closely related species, is of particular interest because it offers an opportunity to analyze the different environmental and phylogenetic influences on the life histories of the species. This leads to a better understanding of their ecology, behaviour and possibly systematics.

The study of *R. chrysopygus* was conducted between April 1971 and December 1972 and approximately 85 h of actual elephant-shrew observation were accumulated in over 1500 h of searching in the 21 months of field work. Subsequently, the investigations were extended to include *E. rufescens* because it was in a different subfamily and occupied a different habitat than *R. chrysopygus.* Field work was carried out between March 1974 and February 1975

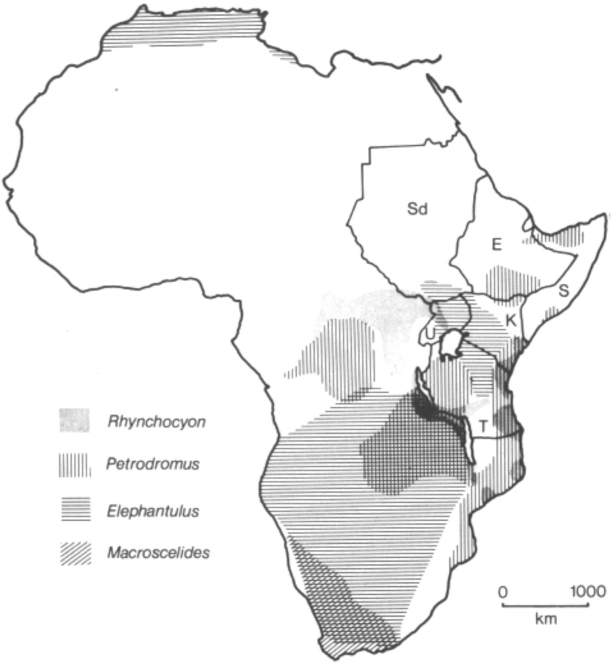

Fig. 6: Distribution of elephant-shrew genera in Africa. E = Ethiopia, K = Kenya, S = Somalia, Sd = Sudan, T = Tanzania, and U = Uganda. The three lakes in eastern Africa are Victoria, Tanganyika and Malawi, from north to south. After CORBET and HANKS (1968)

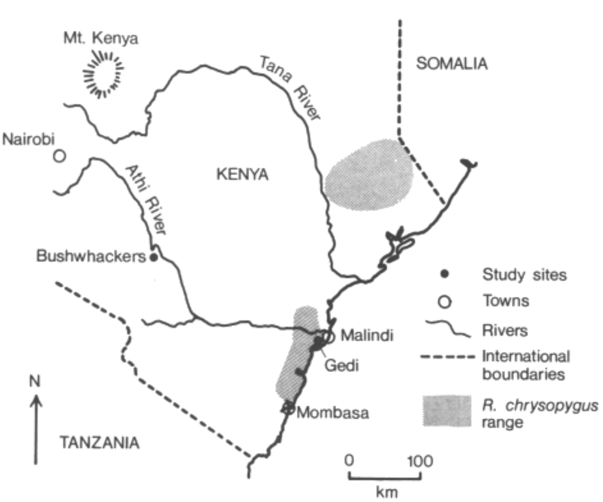

Fig. 7: Study site locations and approximate geographical distribution of *R. chrysopygus*

and in over 560 h of watching for *E. rufescens,* approximately 130 h of observation were accumulated in the 12-month study. Both elephant-shrew populations were periodically monitored until August 1976.

Neither study was efficient in terms of the amount of data gathered per unit time spent in search, but I am convinced that the majority of data could only have been collected by direct observation.

II. Study Areas

A. Gedi Ruins

In the recent past, the north coast of Kenya, between Kilifi and Malindi, was a nearly continuous belt of dense, high bush on coral rag soils near the ocean. Further inland, forests grew on sand soils (MOOMAW 1969). The Gedi Ruins (Fig. 7) are a 44 ha (105 acre) National Historical Monument located 7 km inland from Watamu Beach, within the coral rag habitat. The monument contains a 13th century ruined Swahili city which has become totally overgrown with forest, supported by the civilization-related humic soils deposited on the coral rag. The entire area surrounding the monument is agricultural and the nearest adjacent forest is the structurally similar white sand Sokoke-Arabuko Forest, about 3 km inland. The topography of both forests is slightly undulating and sloping towards the coast.

The moist, lowland, semi-deciduous forest at Gedi is multistratal. The trees, from 15—25 m high, are dominated by *Combretum schumannii, Gyrocarpus americana, Adansonia digitata, Ficus bussei* and *Tamarindus indica.* The dominant trees and bushes in the understorey are *Lecaniodiscus fraxinifolius, Fagara chalybea, Grewia* spp. and *Monanthotaxis fornicata* (FADEN and FADEN 1972). In areas where sunlight penetrates the canopy, *Kyllinga cartilaginea,* a sedge, and *Panicum deustrum,* a grass, are common. The forest can be walked through easily with some hindrance from vines, lianes, and understorey vegetation. The forest floor is open and covered with a year round, continuous carpet of dead leaf litter.

The north coast area of Kenya experiences a single rainy season in April—May which slowly tapers off to the dry months of January and February (Fig. 8). The deciduous vegetation at Gedi Ruins loses its leaves when the forest begins to dry out in September and October and does not flush again until April. During the dry months, visibility in the forest is better than in the wet season due to the change in the deciduous component. The temperature at Malindi, 16 km north of Gedi Ruins, is mild throughout the year (mean of 26.5° C). The relatively small seasonal and daily variations are even less pronounced in the buffered environment of the forest (Fig. 9).

Fig. 8 (left): Mean monthly rainfall (circles) and total study period monthly rainfall (bars) at Gede village (n = 30 years). The yearly mean rainfall is 1040.7 mm (S.D. = 348.5)

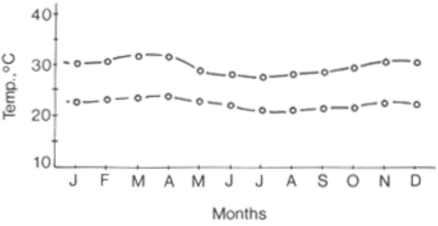

Fig. 9 (above): Mean monthly minimum and maximum air temperature at Malindi, 16 km north of Gedi Ruins (n = 14 years)

The forest at Gedi has been partially cleared in the central area to expose some of the ruins for tourists. A system of 2—3 m wide tourist trails are maintained in the peripheral areas. In addition to these trails, I built a network of small paths in the southern $^{1}/_{3}$ of the forest, which formed the principal study area (Fig. 10).

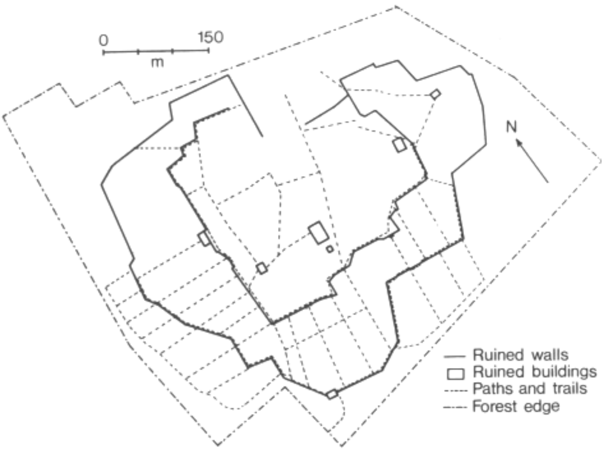

Fig. 10: Gedi Ruins study area map

B. Bushwhackers

Bushwhackers is a 17 ha (42 acre) holiday camp 20 km northeast of Kibwezi town, at the northeast corner of Tsavo East National Park, Kenya (Fig. 7). The area is typical of much of the Park (Greenway 1969), being about 730 m above sea level and flat with occasional seasonal stream beds running towards the river.

The rainfall regime is dramatically bimodal with wet seasons in March—April and November, separated by a very dry period from June through September (Fig. 11). The rainfall pattern results in all the plants being leafless and "dead" looking for much of the year and only becoming lush and green during the 2 wet seasons, when visibility is reduced. The temperature, as measured at Makindu, 32 km west of Bushwhackers, is mild (mean of 22.7° C), although a fairly wide difference occurs between the mid-day highs, often reaching 30° C, and the early morning lows of about 15° C (Fig. 12).

The vegetation is a deciduous, wooded bushland on an orange-brown loam. The principal emergent trees are *Commiphora* spp., *Sterculia* spp., *Acacia tortilis, Terminalia* spp., and *Adansonia digitata.* The bushes, which form dense patches, are dominated by *Combretum exalatum, Premna resinosa, Grewia villosa, Acacia* spp., and *Barleria taitensis.* The vegetation is fenestrated with game trails and open areas supporting numerous grasses and herbs. The main grasses are *Enteropogon macrostachyus, Aristida adscensionis,* and

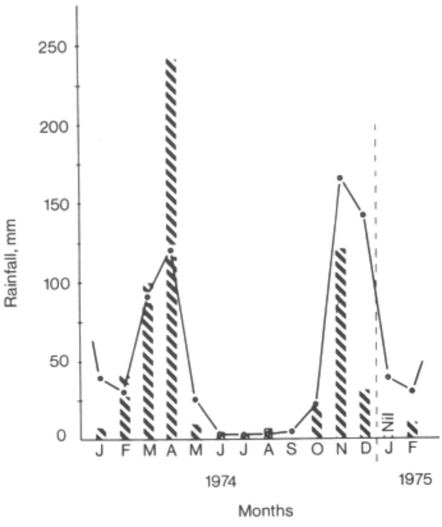

Fig. 11 (left): Mean monthly rainfall (circles) at DWA Plantations, 15 km southwest of Bushwhackers (n = 54 years), and total study period monthly rainfall (bars) at Bushwhackers. Mean yearly rainfall is 640.2 mm (S.D. = 228.6) at DWA Plantations and 461.3 mm (S.D. = 91.6) at Bushwhackers (n = 6 years)

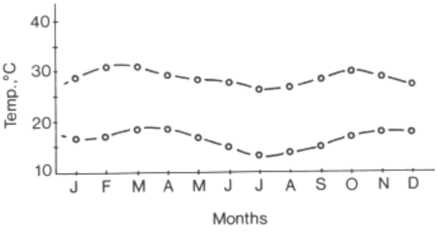

Fig. 12 (above): Mean monthly minimum and maximum air temperature at Makindu, 32 km west of Bushwhackers (n = 25 years)

Fig. 13: Bushwhackers area and study site (BW). See Fig. 33 for detail

Chloris roxburghiana and the dominant herbs include *Ocimum basilicum* and *Neuracanthus ukambensis.* These annually vegetated trails and glades became completely barren during the dry season due to trampling by large mammals and termite activity.

Bushwhackers has a number of roads and paths through it connecting the various buildings. These tracks, together with the game trails, provided easy movement and good visibility in the study area, which included the outlying portions of the camp (Figs. 13, 33).

III. Methods

A. Capturing, marking and observing animals

1. Rhynchocyon chrysopygus

R. chrysopygus was captured in 10 m long, 1 m high, 7 cm mesh brown fishing nets strung vertically and loosely along the trails and paths in the forest. The elephant-shrews tangled themselves in the nets when they tried to get through them or, occasionally, when I chased them into the nets. Captured elephant-shrews were sexed, aged, weighed, and colour-ringed with plastic bird rings (Fig. 14). Both rear legs were given the same one or two-colour combination to facilitate field identification and ensure identity if a ring was lost. A total of 47 individuals were ringed at Gedi during the study. By slowly and silently walking the trail and path network, elephant-shrews were resighted

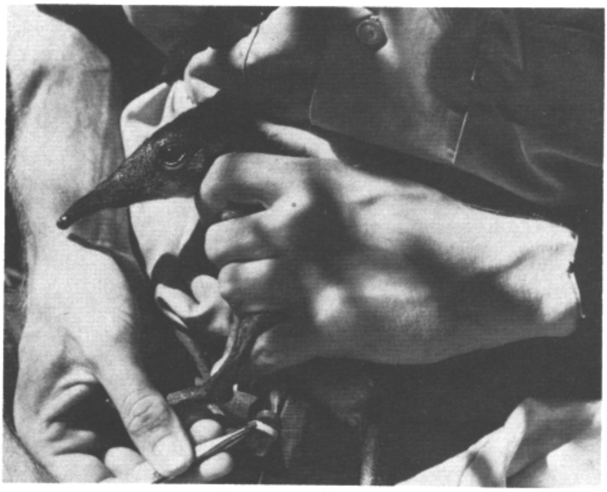

Fig. 14: Fitting coloured rings on the rear leg of an adult *R. chrysopygus*

and, when spotted, were identified and observed with 8 x 40 binoculars. Their location, activity and behaviour were recorded in a field notebook and on a study area map. Identification and observation was usually limited to 10 m because of the dense vegetation.

The study area was usually covered systematically by walking the paths from one end of the area to the other, recording data as elephant-shrews were sighted. In many of the behaviour analyses "first sightings" are used. This refers to the locus and/or behaviour of an animal when it was first spotted and is used instead of subsequent observations because of the possible effect I had on the animal's behaviour. Generally I could expect to spot an animal about every 15 min of searching. *R. chrysopygus* reacted to my approach, if it saw me before I saw it, by freezing or running approximately 10 m away and then freezing. After a few s to a few min, depending on the individual and my proximity and movements, the elephant-shrew continued its activity, either returning to the spot from where it was disturbed or moving on. The animals' habits and behaviour were such that sitting in one spot and waiting for them to appear was highly inefficient.

2. *Elephantulus rufescens*

E. rufescens was captured using a drop trap made of a 20 cm square steel frame with fine mist net stretched across it. The frame was placed over a well-used elephant-shrew trail and one side propped up with a stick. A trigger mechanism was made from a small wood mouse trap which was activated by a trip line across the trail. Captured animals were sexed, aged, weighed, toe-clipped and ear-tagged. The ear was sandwiched between 5 mm diameter coloured "Dymo Embossing Tape" plastic discs and held together with heavy nylon monofilament fishing line strung through the centres of the discs and melted at each end. 21 individuals were marked during the study. Towards the end of the field work, a small self-powered luminous Betalight[2]) was glued with epoxy to the nylon of each new ear tag so that the 1.5 mm x 6 mm glass tube projected perpendicularly from the back of the ear (Fig. 15). These tags permitted observations at night with the unaided eye from 3 m, and with

Fig. 15: Betalight tagged subadult *E. rufescens.* Note brown feet compared to those of an adult, Fig. 3

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[2]) Manufactured by S-R Developments, Ltd., North Hyde Rd., Hayes, Middlesex, UB3 4NB, England.

8 x 40 binoculars from 10 m. Although there was some initial question as to whether the unprotected and unhoused glass Betalight would break or greatly affect the individuals by increased predation or loss of intraspecific compatibility, there was no indication that this occurred. One of the 4 animals tagged still had a perfect Betalight tag after 12 months and successful breeding.

E. rufescens was observed from numerous 3—4 m high tripod towers. Some were used as permanent structures, while others were moved around to areas of temporary interest. For example, 4 permanent towers were placed in a line across 2 territorial-area boundaries (areas A and B, Fig. 33 a). The area of clear vision from these 4 towers varied between 109 m^2 and 278 m^2. The difference in visibility was due to the varying leaf cover of the vegetation. 1 to 3 h per day were spent in towers, mostly during the early morning and late afternoon.

In addition to direct observation, data were collected by tracking *E. rufescens* on sooted or smoked paper cards measuring 12.5 x 7.6 cm (5 x 3"). This technique is similar to that used by JUSTICE (1961) and SHEPPE (1965) (Fig. 16). I placed these cards on the elephant-shrew trails at about 15.30 h and then collected them the next day at approximately 08.30 h. The cards were either placed repeatedly on the same spot, a tracking station, or placed opportunistically on different trails, depending on the type of data I wished to collect. Only one different toe, or part of a toe, was removed from each animal,

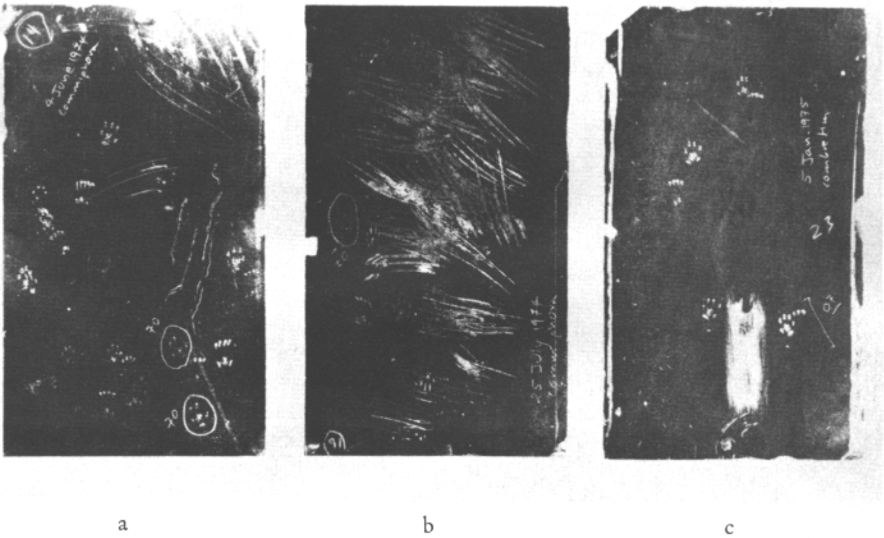

Fig. 16: Sooted cards tracked by *E. rufescens.* a. The 2 circles in the lower right corner of this card encompass the right front foot of Green ♀, who walked from bottom to top and whose fourth digit had been removed. A complete right rear footprint is to the right of the forefoot tracks. b. The elephant-shrews kept their trails clean by brushing off foreign objects, such as leaves, twigs, and sooted cards, with lateral sweeps of the forefeet. This card was swept and scraped many times in attempts to remove it from a trail. c. Both sexes of *E. rufescens* have a well defined sternal gland which they periodically rub on the substrate while traveling along their trails. Occasionally sooted cards were scent marked, which left the distinct bald mark seen at the bottom of this card. The footprints belong to Purple ♀, whose fourth digit on the right rear foot had been removed. She passed from bottom to top, scent marking one of the 2 times she walked on the card

thus increasing track identification success. Approximately 4,000 tracked cards were analyzed during this study and the data, along with that gathered by direct observation, were recorded directly in a field notebook and on study area maps.

For both *R. chrysopygus* and *E. rufescens*, "juvenile" refers to animals between birth and the time they attain adult size, while "subadult" is used to refer to animals that are of adult size, but still retain some juvenile characteristic, such as milk teeth in *R. chrysopygus* and brown feet in *E. rufescens*. Known individuals are referred to by the colour(s) of their ear tag or leg rings and their sex. For example: Gold ♀ and Yellow-purple ♂.

B. Collecting methods

1. Elephant-shrews

Specimens of *R. chrysopygus* and *P. tetradactylus* were collected within 10 km of Gedi Ruins in the white sand Sokoke-Arabuko Forest, between Mida and Msabaha villages.[3] I shot some of the *R. chrysopygus* specimens while others were brought alive by Giriama collectors, who also captured all the *P. tetradactylus* specimens from the Gede[4]) and Msabaha village area.

The *E. rufescens* specimens were all snap-trapped approximately 2 km northwest of Bushwhackers along the Iria Itheethe River (Fig. 13).

All elephant-shrew stomach contents were preserved in 70% alcohol within 1 h of death for later analysis. An individual's stomach content was spread evenly in a Petri dish so that it formed a solid layer of material. A piece of clear plastic with a 100 point grid on its lower surface was then "floated" on top of the stomach content and using a 20x binocular microscope and a strong light source, the first stomach content fragment seen under each grid point was identified and recorded (after M. GWYNNE, pers. comm.). The grid point frequency used for the more voluminous *R. chrysopygus* stomachs was 5 mm and that for *P. tetradactylus* and *E. rufescens* was 3 mm. Each stomach was analyzed once.

2. Leaf litter invertebrates

Diet is more meaningful if it can be compared with some measure of food availability, thus at both study sites leaf litter invertebrates were sampled. Sample points were chosen by pacing, according to a randomly chosen number, from a constant starting point down the same track and then blindly throwing a streamered stone into the vegetation. The spot on the ground where the stone came to rest was sampled. At the coast samples were taken off the Sand Quarry Road, 3 km northwest of Gedi Ruins in the Sokoke-Arabuko Forest. This was the same habitat from which the elephant-shrews were collected. At each sample point 1 m^2 of leaf litter was gathered by hand into a large plastic bag and the upper 5 cm of sand under the leaf sample was gathered into a second bag. One or 2 samples per morning were taken until a total of 10 for the month had accumulated. The faunal components of the leaf samples were chloroformed and then removed by hand. The unchloroformed sand samples were also hand sorted.

The same technique was used at Bushwhackers, but only leaf litter was collected because *E. rufescens* was not feeding in the soil layer. Near Bush-

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3) The collecting sites were to be clear-cut and burned for exotic plantations.

4) Gedi Ruins, Gedi Forest and Gedi all refer to the Gedi Historical Monument. Gede is the small village 1 km from the Ged*i* Ruins.

whackers the samples were gathered between 15.30 h and dark, which included the period when the elephant-shrews were most active. The leaf litter samples were put into Tullgren funnels for 24 h before being hand sorted. The size of each sample was 500 cm^2 and 5 samples were simultaneously taken per day. Eight days were sampled in each of the dry (August 1974) and wet (November 1974) seasons. The sampling regime at Bushwhackers was not as intense as for the coast.

The invertebrates were later counted and tabulated. The biomasses were determined after air drying the specimens on filter paper for 3—5 min. They were not oven dried because they were to be used in another study.

The coastal leaf litter and soil samples data were combined before the analyses. The data for the 5 daily samples at Bushwhackers were, in some instances, combined to form a ¼ m^2 sample area and then multiplied by 4, thus making a square metre sample area which is more comparable to the square metre samples taken at the coast.

Feeding studies are among the most difficult to control and compare, for there are innumerable variables associated with every aspect, from the behaviours of the predators and prey to the procedural problems associated with sampling and analysis. Despite such variables, I believe that this preliminary, quantitative assessment reasonably approximates elephant-shrew feeding ecology.

IV. Activity Patterns, Sheltering, and Maintenance Behaviours

A. Circadian activity

1. *Rhynchocyon chrysopygus*

All the evidence indicated that *R. chrysopygus* was diurnal. Extensive netting was done between 21 July and 16 September 1971 at Gedi. In the 102 net days and 87 net nights during this period (a net day is a single net set from dawn to dusk, a net night from dusk to dawn), 31 elephant-shrew captures were made during the day and none during the night. When the nets were set during the night, they were checked after dark between 19.00 and 20.00 h. While making these rounds I never saw or heard an elephant-shrew.

In order to determine whether *R. chrysopygus* had an activity peak during the daylight hours, 1,589 sightings of 7 individuals, from January through November 1972, were tabulated according to the daylight quarter in which they were seen (Tab. 1). Although there is no definite activity peak, it does appear that the elephant-shrews were more active during the middle of the day than expected.

An indirect estimate of the daylight activity budget for *R. chrysopygus* was made by using the total study area sightings made between 1 October and 13 November 1976. Each sighting was tabulated according to the animal's activity when first seen (Fig. 17). The most commonly seen activity was

Table 1: First sightings of *R. chrysopygus* at Gedi Ruins in 1972. ($p < 0.05$, χ^2-test)

Sightings	Time			
	Dawn to 09.00 h	09.00 to 12.00 h	12.00 to 15.00 h	15.00 h to dark
Actual	223	459	379	528
Expected*	267	448	353	521

* Calculated from proportion of time spent searching in each time period

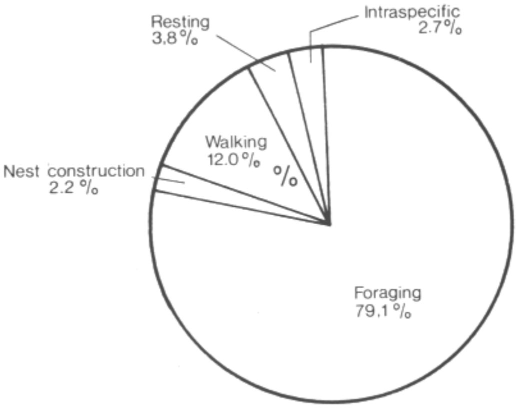

Fig. 17: Activity budget estimate for *R. chrysopygus* during daylight hours at Gedi Ruins during Oct. and Nov. 1971

foraging, which was considered distinct from walking, where the animal moved along with an apparent goal and did not forage. In a few sightings, the animals were resting in the open on the leaf litter, either lying down or dozing, or calmly sitting with no indication of being alert or upset. The duration of these rest periods was variable, lasting anywhere from ½—30 min. Sightings of intraspecific behaviour included both sexual and agonistic encounters. The most infrequent activity tabulated was nest building, and this was also the only behaviour which was related to a particular period of the day (see Section IV, B, 1). In collecting these data I spent 70.2 h in the study area and made 239 sightings. The proportion of searching time for each daylight quarter was 32.7 %, 27.6 %, 20.8 %, and 18.9 %, respectively. Thus, observer bias, in respect to the period of the day, probably did not influence the activity budget estimate greatly.

I estimate *R. chrysopygus* was inactive about 55 % of a 24-h day, nearly all of this time presumably being spent in a nest during the night (see Section IV, B, 1).

2. *Elephantulus rufescens*

One treadle-activated events recorder was used to accumulate 24-h records of trail use activity by the elephant-shrews at Bushwhackers. To ensure that only *E. rufescens* was activating the treadle, care was taken in its placement, and periodic checks with sooted cards were made. In the months of May, June, July, September, and October 1974, on 2 different territorial areas, 55 usable days were recorded. These data show that *E. rufescens* was active 24 h a day with peaks at dawn and dusk and minimal activity around mid-day (Fig. 18). Direct observation of marked individuals both during the day and night supported the treadle data, but in addition indicated that the individuals were polycyclic, alternating rest or sleep with bouts of activity.

From 9 September through 13 October 1974, the pair Red ♀ and Yellow ♂ were sighted 650 times (♀ n = 209) in 68-½ h of observation from a tower. Most observations were during the activity peaks, 48.3 % between 06.00 and 09.00 h and 51.5 % between 16.00 and 19.00 h. Of 7 activities recorded, the ♂ frequency was greater than the ♀ in 3 cases: foraging, trail cleaning and interspecific aggression. The other categories (locomotion, grooming, intraspecific aggression and combined activities) were similar for the ♂ and ♀, and together represented 47.0 % and 43.0 % of the respective first sightings (Fig.

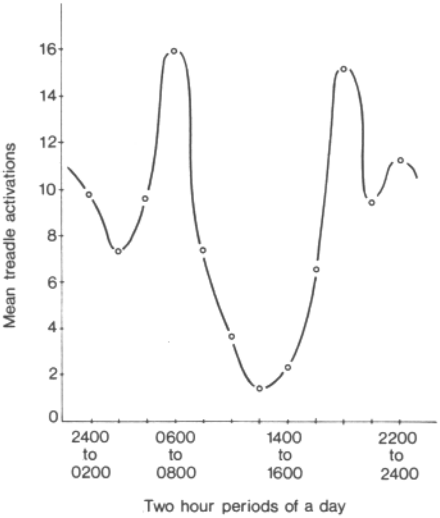

Fig. 18: Mean daily trail use activity for *E. rufescens* at Bushwhackers, as determined with an events recorder activated by a trail-treadle

19). Using the nonparametric Spearman rank correlation coefficient test (Siegel 1956), the activity budgets were significantly different ($p < .05$). Although this may be just an individual difference, my subjective impression of other pairs supports the activity budget estimate.

The elephant-shrews were not easily sighted when resting or sleeping and their polycyclic activity and tendency to use different resting spots all made it difficult to determine the proportion of time they were inactive.

If the average number of first sightings of resting or sleeping by the pair are calculated into a combined-sex activity budget, then these two activities accounted for 17.8 % of the sightings (731). This activity budget only represents an estimate for approximately a quarter of a 24-h day, including the early morning and late afternoon. The mid-day period was mainly, but not entirely, spent in sleep or rest, as shown by the pattern of trail use (Fig. 18) and direct observation. For example on 3 consecutive afternoons (c. 14.00 h) Dark-blue ♀ was disturbed from the same rest spot. On the fourth afternoon she spent 100 % of her time in rest and sleep on the same rest spot between 14.00 and 16.40 h, when she finally ran down a trail and disappeared from sight. She was not seen on this spot on subsequent days. It is estimated that *E. rufescens* spent more than half of its daylight hours in rest and sleep.

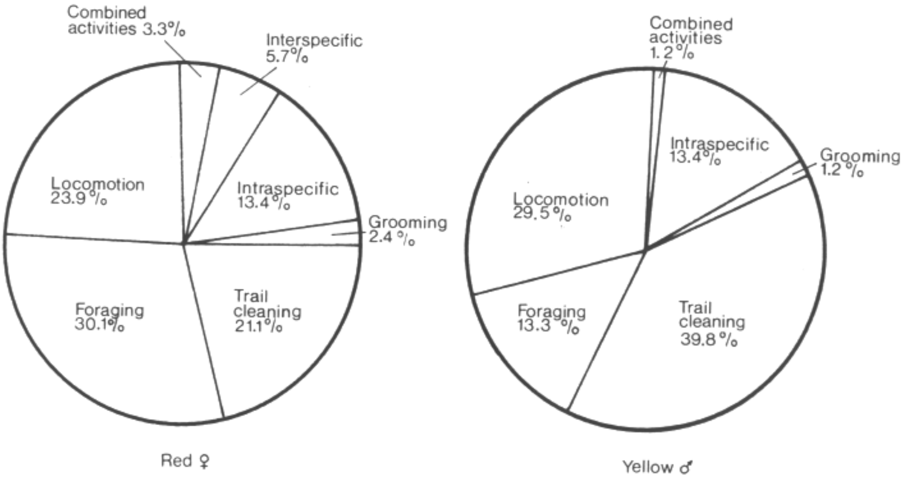

Fig. 19: Activity budget estimate for a pair of *E. rufescens* at Bushwhackers during postdawn and predusk periods in Sept. and Oct. 1974

During the remaining 12 dark h of a day, I estimate the elephant-shrews spent less than half in resting or sleeping. This is based on the trail activity records and supported by direct observation. For example in 260 min of observation on 3 consecutive nights (c. 20.30 h), Betalight tagged Purple ♀ was observed resting or sleeping only about 100 min or 38.5 % of the observation period. I estimate *E. rufescens* was inactive for about half of a 24-h day.

The trail cleaning activity of *E. rufescens* was observed only during the early morning and late afternoon periods and never during the night and occupied about an eighth of the elephant-shrews' active hours.

B. Nest and trail use

1. The nest of Rhynchocyon chrysopygus

The nests at Gedi were comprised of an oval depression in the soil approximately 8 cm deep and wide, which the elephant-shrews excavated with long scraping sweeps of a forefoot. Dead leaves were dragged into this bowl from the surrounding area which were then arranged into a layered lining by rapidly vibrating both front feet on the leaves' surface. Sticks and rootlets were arranged with the mouth. When the lining was completed, additional leaf litter was dragged and piled onto the top of the nest. To drag the leaves an elephant-shrew stretched out its front legs stiffly and then, by jerking its body backwards towards the nest, accumulated a pile of litter under its chest and abdomen. A newly completed nest looked like a 15 cm high pile of leaves about 50 cm in diameter with a ½ m barren area around it where the leaves had been gathered. There was no visible entrance to the nests and within 2 weeks they weathered and became extremely difficult to spot. The entire building sequence took approximately 2 h and was either done all at once or in sessions over 1—2 days. I never saw an elephant-shrew enter a newly completed nest to "try it out."

When the 26 nest building observations for the entire study period and study area are tabulated with respect to the daylight quarter they were seen in, and these are compared with the expected sightings calculated from the proportion of searching time in each quarter (Tab. 2), it is clear that nest building was an early morning activity. A monthly tabulation of the 18 nest build-

Table 2: Nest building observations per daylight quarter of *R. chrysopygus* at Gedi Ruins ($p < 0.01$, Kolmogorov-Smirnov test)

Sightings	Time			
	Dawn to 09.00 h	09.00 to 12.00 h	12.00 to 15.00 h	15.00 h to dark
Actual	17	7	2	0
Expected*	2.9	7.3	5.8	8.5

* Calculated from proportion of time spent searching in each time period

Table 3: Nest building observations per month of *R. chrysopygus* at Gedi Ruins in 1972 ($p < 0.01$, Kolmogorov-Smirnov test)

Sightings	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Actual	0	1	1	1	0	0	2	0	8	4	0	1
Expected*	2.4	2.0	1.8	1.2	1.8	.9	2.0	.5	2.2	1.2	1.3	.5

* Calculated from proportion of time spent searching in each time period

Fig. 20: Territorial areas A, B and C at Gedi Ruins (see Fig. 25). Solid circles show locations of visible nests on territorial area A in Jan. 1972. Arrows illustrate sighting loci of Yellow-red ♀ during Sept. 1975, all within her original territorial area (B). Open circles show locations of scent marking by White-dark blue ♂ on his territorial area (C) during the study period

ing observations in 1972 (Tab. 3) shows a peak of activity in September and October, the same months when the deciduous trees lost their leaves.

In January 1972 a nest count was made on the territorial area of Red-purple ♀ and White ♂. The area was covered by walking parallel transects which were within sight of each other. 12 nests were found (Fig. 20), but these represent something less than the total as only relatively new nests were visible. In addition to the dispersed nests on territorial areas, some were found in loose clusters. One such nest cluster was periodically checked for new activity over one year and it was found that most of the nests were in disrepair, i.e., the cavity collapsed, but there was always one fresh nest in evidence. These clusters represented traditional sites of an individual elephant-shrew and new nests were built or old nests rebuilt as others were abandoned.

Two watches on nests were carried out to determine how frequently they were used. On 12 evenings between 17.30 h and dark, from 14 through 28 May 1971, I sat high in a tree overlooking a nest. A single elephant-shrew entered the nest on 2 evenings and approached, but did not enter, on 2 other evenings. A similar watch was carried out on another nest, from 6 through 13 January 1972, and here a single elephant-shrew entered the nest on 2 evenings. Six instances of solitary elephant-shrews entering nests in the evenings were seen and all occurred between 1 min before and 16 min after sunset. When approaching a nest, the elephant-shrews were extremely cautious. They frequently paused to sniff the air and leaf litter before reaching the site and then sniffed the nest itself before finally slipping into it from a side. I never saw animals emerging from their nests at dawn. There is some indication that they were not fully active in the early morning (Tab. 1), so perhaps they emerged well after dawn.

On 3 occasions *R. chrysopygus* was observed using nests during the day, suggesting that *R. chrysopygus* may occasionally retire to a nest during the day. Green-orange ♀ entered a nest at 12.45 h and then emerged and began foraging at 14.16 h. On another occasion the same ♀ emerged from a nest at 15.33 h, while her mate, White-dark blue ♂, stood on the nest's edge. An unidentified elephant-shrew ran out of a nest at 09.30 h when I scared it by walking past at 1 m distance.

R. chrysopygus did not normally build or use trails. However, one young animal at Gedi, which was using a densely vegetated portion of its parents' home range, repeatedly used a short, very indistinct trail through a thicket.

2. *The trails of Elephantulus rufescens*

E. rufescens built and used trails which were either uninterrupted, clean tracks or patch tracks, each clean patch being where an elephant-shrew landed when running along the trail (Fig. 38). One 5 m section of trail had a mean patch-to-patch distance of 36.3 cm and a mean patch length of 12.6 cm.

The entire trail systems of paired Red ♀ and Yellow ♂, mapped between 27 and 30 June 1974 (Fig. 21), was characteristic of all trail networks at Bushwhackers, in that it was denser towards the middle, and where it was contiguous with another pair's network it joined in only 2—3 places. *E. rufescens* spent a large proportion of its daylight hours cleaning trails (Fig. 19). Cleaning behaviour most commonly observed was a laterally directed forefoot sweep, used to clear leaves, as well as sooted cards, from the trails (Fig. 16). Grass and small twigs were bitten in two and then swept off, while larger twigs and low bush branches were pushed out of the way with both forefeet or the forehead.

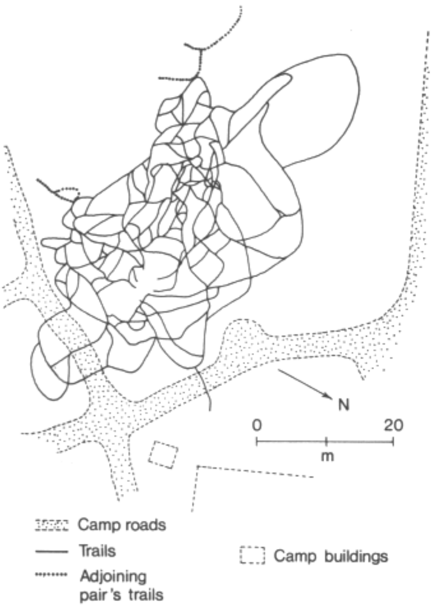

Fig. 21: The trail system of *E. rufescens* pair Yellow ♂ and Red ♀ at Bushwhackers in June 1974 (See Figs. 32 and 33, territorial area A)

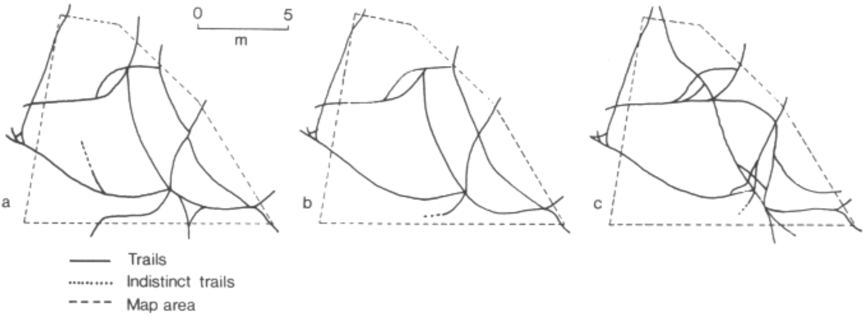

Fig. 22 (bottom): Temporal and spatial changes in a portion of an *E. rufescens* trail network (see text). a. 20 July 1974. b. 5 Nov. 1974. c. 7 Jan. 1975. Rains occurred in Nov.—Dec. 1974

Soon after the first rains of the wet season, a flush of small seedlings occurred and these were removed from the trails by turning the head to one side and biting the shoots off at their bases. Despite these attempts to keep the trails clean, the new vegetation resulted in some trails being abandoned or realigned. A 95.1 m² area in the central portion of Blue ♂'s trail network was mapped on 20 July 1974 (Fig. 22). The trails showed little change when again mapped on 5 November 1974, despite a change in the ♂'s mate in mid-August. When mapped again on 7 January 1975, at the end of the rains, considerable change in trail alignment had occurred due to the rapid increase in vegetation (Fig. 11).

Fig. 23: a. A typical *E. rufescens* rest site (arrow), at the base of a *Combretum* bush (see text).
b. Resting *E. rufescens*, photographed on the rest spot illustrated in Fig. 23 a. Note the posture and half closed eye. A Betalight tag is visible on its right ear (Dark-blue ♀)

I never saw or heard trail cleaning during the night, but only in the late afternoon and early morning.

Except for some foraging, all of the animals' activities were confined to their trails or the paths made by large mammals. When resting or sleeping, the elephant-shrews used a 1 m long section of trail that was in fairly open vegetation, but with a dense canopy, and a variety of exposures to the sun (Fig. 23). This configuration allowed inactive animals a clear view of approaching terrestrial predators, protection from aerial attack, and the ability to thermoregulate using solar radiation (see below). The short lengths of trail that had these "rest spot“ characteristics were slightly wider and more worn because of the more intense use they received.

Several widely spaced rest spots were used alternately by different individual elephant-shrews for a few days or weeks and then abandoned. An example of this pattern was the consecutive afternoon sightings of Dark-blue ♀ at one site (see Section IV, A, 2 above).

The elephant-shrews rarely, and then for only 2—3 min, lay on their sides. In resting or sleeping the feet were kept under the body, a position enabling a quick escape down a trail (Fig. 23). I never saw *E. rufescens* completely close its eyes, even when all other indications were that it was sleeping. On several occasions, I elicited a sudden "awakening" and alertness in "sleeping" animals by silently waving a shirt in the air. Judging from this behaviour, I suspect elephant-shrews can be awakened by motion alone, a highly adaptive behaviour considering their exposed sheltering habits.

During heavy rain *E. rufescens* took shelter on a trail passing under very dense tangles of vegetation or under fallen tree trunks. Captives kept in large outdoor pens measuring 10 m in diameter were provided with a variety of artificial burrows and stone shelters, but they were not used. I never saw captive or free-living animals use burrows or nests.

C. Grooming

Both *R. chrysopygus* and *E. rufescens* yawned and stretched after resting or sleeping in typical mammalian fashion. They frequently scratched themselves with a rear foot while standing on the other 3 feet. They could reach any part of their bodies in this peculiar stance. The hind feet were groomed with the mouth, biting being employed only rarely by *R. chrysopygus,* while *E. rufescens* often licked and nibbled. *E. rufescens* washed its face by repeatedly and rapidly licking its forefeet and then wiping the face and nose. This sequence was often followed by a licking of the rear feet and then the tail (Fig. 24).

At Bushwhackers, animals sandbathed in open sandy areas, such as on their favoured rest spots and in the middle of large mammal paths, by rolling onto their sides. Sometimes only one side was rubbed while at other times a number of alternate side rolls were made. There was no ventral or dorsal rubbing during the rolls and the sandbathing was not site-specific.

E. rufescens often sunbathed; one animal starting at 16.12 h was seen to shift its position in and out of the sun 5 times in 30 min. The polycyclic activity of the elephant-shrews was especially pronounced in the early mornings and late afternoons when they alternated sunbathing with bouts of trail cleaning and foraging.

Fig. 24: E. rufescens neonate (c. 48 h old) face-washing. The stance is also typical of adults

I never saw *R. chrysopygus* face-wash or sunbathe and there was no indication that it used specific rest spots. It is difficult to explain the near absence of grooming behaviour (besides scratching) in this species, although the fine, silky, sparse fur may not require as much grooming attention as the dense, thick fur of *E. rufescens*. In captivity the latter developed oily and bunched fur if not provided with sand, while *R. chrysopygus* did not. Another factor related to the near absence of grooming may be that the relatively specialized forefeet (reduced digits and long claws) were unsuitable for face-washing. Eisenberg and Gould (1966) similarly explain the absence of face-washing in the solenodon *(Solenodon paradoxus)*.

V. Social Structure

A. Rhynchocyon chrysopygus

1. Territory

When all the locations of first sightings for known individual elephant-shrews are cumulatively plotted on a study area map, a mosaic of discrete home ranges is immediately evident. In order to analyze and compare the individual home ranges, boundaries were calculated using the "convex polygon" method as described by Jennrich and Turner (1969). The peripheral observations of an individual were connected to construct a convex polygon. Two exceptions were made: First, I excluded those loci which were due to temporary shifts in an animal's home range (described later in this section) and secondly, I altered the boundaries to conform to the areas where intraspecific aggression indicated a boundary existed (see example in Section V, A, 3 of this chapter).

The calculated boundaries for 8 individuals (Fig. 25) illustrate that a single ♂ and ♀ occupied an almost completely overlapping and congruent home range. Because only the areas that pairs occupied satisfied the definition of a territory,[5]) I will refer to individuals' home ranges, but pairs' territories. Each pair's territory was contiguous and similar in area to its neighbours' territories.

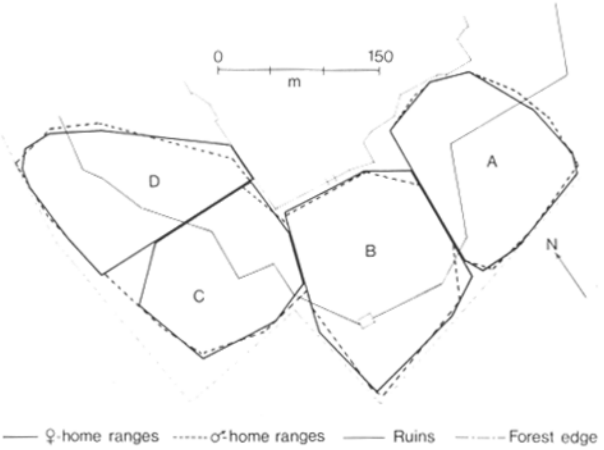

Fig. 25: Territorial areas of 4 pairs of *R. chrysopygus* at Gedi Ruins (see study area map, Fig. 10). Area A, Red-purple ♀ and White ♂; area B, Yellow-red ♀ and Yellow-blue ♂; area C, Green-orange ♀ and White-dark blue ♂; area D, Ragged-ear ♀ and White-red ♂. (See Fig. 26 and Table 4)

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[5]) I define "territoriality" as BROWN and ORIANS (1970): "In brief, the characteristics of a territory are (1) a fixed area, which may change slightly over time, (2) acts of territorial defence by the possessor which evoke escape and avoidance in rivals so that (3) the area becomes an exclusive area with respect to rivals."

The mean home range area for 11 individuals that occupied the 4 territorial areas (Fig. 25) during much of the study period was 1.7 ha, with a range of 1.4—2.0 ha (Tab. 4). The calculated territory of Yellow-purple ♂ and Green-orange ♀, and subsequent occupants of this area (Fig. 26), were underestimates because of my inability to see animals along the very densely vegetated edge of the forest in this region. If the animals' activity is considered to extend to the forest edge, as it probably did, all the home range areas would be in closer agreement. Observations for other portions of Gedi Ruins indicate that the entire forest was occupied with elephant-shrews on similar home ranges. The estimate of the elephant-shrews' mean monthly density of 1.6 animals/ha (including young and subadults) based on the 4 well known territorial areas is probably representative of the entire Gedi Forest.

Considering the same 11 animals, a mean of 8.3 % of their total sighting loci were outside of their calculated home range boundaries; these are defined as home range "violations" (Tab. 4).

Even though White-red ♂ was known for a long time, I only managed to sight him 77 times and a relatively large proportion of these sightings were violations (36.4 %), which may have been related to the frequent changes in individuals on the adjacent territory area (C). If each individual's violations are used to calculate its mean shortest distance to a boundary, then the average for the 11 elephant-shrews was 10.8 m (9.5 m without White-red ♂) (Tab. 4).

Table 4: Home range areas and violations for *R. chrysopygus* at Gedi Ruins

Adult animal	Dates	Loci records	Home range area		Violations	Mean shortest distance for violations
			ha	acres		
Red-purple ♀	18 October 1971 - 13 December 1972	349	1.8	4.4	3.4 %	8.0 M
White ♂	11 December 1971 - 14 December 1972	241	1.8	4.4	1.1 %	11.7 M
Yellow-red ♀	16 September 1971 - 14 December 1972	480	2.0	4.9	1.5 %	19.3 M
Yellow-blue ♂	23 December 1971 - 10 April 1972	131	1.9	4.7	2.3 %	21.0 M
Blue-purple ♂	23 July 1972 - 20 October 1972	44	1.6	4.0	6.8 %	3.5 M
Green-orange ♀	4 January 1972 - 29 June 1972	100	1.5	3.7	6.0 %	6.0 M
Orange-yellow ♀	11 July 1972 - 13 December 1972	42	1.4	3.6	0	0
Yellow-purple ♂	10 November 1971 - 2 March 1972	73	1.5	3.7	16.4 %	8.8 M
White-dark blue ♂	3 March 1972 - 15 December 1972	255	1.6	4.0	11.0 %	4.2 M
Ragged-ear ♀	14 January 1972 - 7 December 1972	154	1.7	4.2	6.5 %	12.0 M
White-red ♂	9 November 1972 - 13 December 1972	77	1.7	4.2	36.4 %	24.5 M
	Mean	176.9	1.7	4.2	8.3 %	10.8 M
	S. D.	140.3	0.18	0.42	10.49	7.84

This demonstrates the proximity of the violations to the boundary areas, since the territories were all about 120 m across.

During the study 5 known, stable, adults completely disappeared from the ruins and their vacant home ranges were all eventually reoccupied by subadult animals with no distinguishable boundary changes. No instances of an animal being driven away and displaced from its home range were observed. On 3 occasions home range vacancies were not immediately filled and an adjacent animal temporarily expanded its home range to include the vacant one. Only ♂♂ were observed to do this, as demonstrated by White ♂ moving onto Yellow-blue ♂'s home range when the latter disappeared on about 10 April 1972. An unringed ♂ elephant-shrew appeared on Yellow-blue ♂'s old home range on 12 June 1972 and White ♂ then moved back onto his own home range and the old boundary was re-established. The ♀♀ did not alter their home ranges during these temporary ♂ shifts.

Yellow-red ♀ was ringed as an adult on 15 September 1971 and during the study she maintained the same home range boundaries. During subsequent visits to Gedi in October 1973, June 1974, and March 1975, she was still within her old home range. During an intensive search of the Gedi Forest study area from 21 through 24 August 1975, Yellow-red ♀ was seen 5 times in widely separated locations, all within her original home range (Fig. 20). She was last seen in April 1976. This, along with data from other individuals (Fig. 26), suggests long term home range stability, even when the surrounding home range occupants all changed at least once. It also indicates a relatively long life span.

The elephant-shrews probably covered their entire home ranges daily, since individuals were sighted at widely distributed loci during the same day. Over periods of 2—3 weeks, individuals seemed to use portions of their home ranges more intensely than others. This was demonstrated for longer periods by using a trend surface analysis (DAVIS 1973; NORTON-GRIFFITHS 1975) on the total distribution of first sighting loci for the pair Red-purple ♀ and White ♂ (excluding ♂ temporary home range shifts). The technique involves constructing a grid of squares on a home range map and tabulating the total number of individual sightings per grid square. Polynomial equations and a computer programme (NORTON-GRIFFITHS and PENNYCUICK 1974) are then used to produce relative figures for all of the grid squares, even those without original data. Successively higher order polynomial equations are used until a set of grid square figures (a trend) is obtained which "best fits" the original data. This may be thought of as a 3-dimensional multiple regression. The best fit trend can then be represented as a contour map, the highest grid square figures representing peaks and the lowest valleys. The pair's contour maps (Fig. 27) illustrate that the sightings for both elephant-shrews were distributed similarly, there being 2 areas of concentrated use. Examination of other pairs' distribution maps also show that certain areas are more intensively used.

It may be that the use pattern was produced by sampling from a trail grid network. A characteristic of trend surface analysis is to reduce this effect and thus it is not surprising that the 2 contour maps do not show a relationship between the trail pattern and the home range use pattern.

2. *Adult association*

R. chrysopygus was spatially paired, but the individuals were infrequently associated in time. Three stable ♀♀, Yellow-red, Red-purple, and Ragged-ear, were seen associated with their ♂♂ 17.7 %, 25.0 %, and 20.0 % (mean =

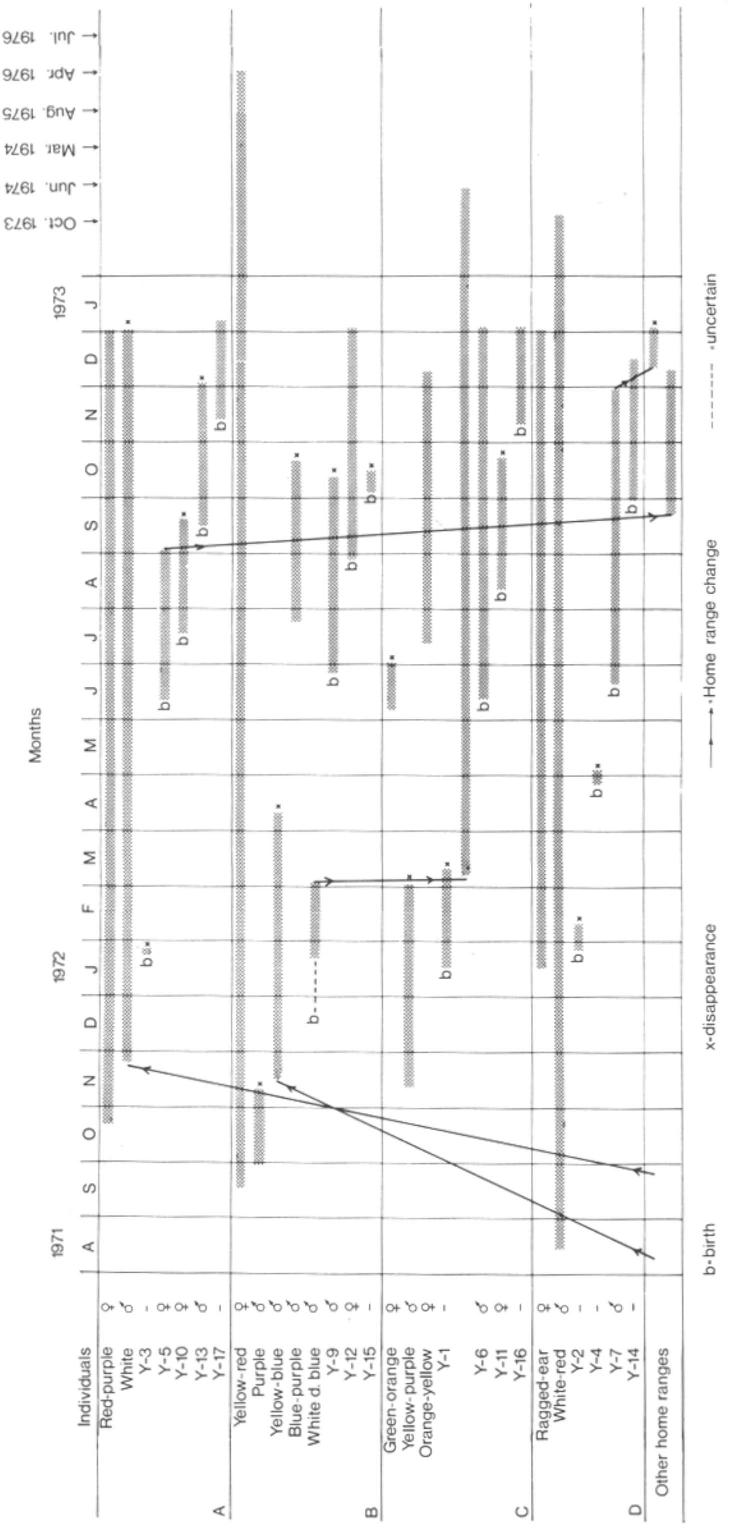


Fig. 26: Summary of spatial and temporal relationships of *R. chrysopygus* individuals (horizontal bars) at Gedi Ruins. Individuals are grouped into the territorial areas (A, B, C and D) they occupied (see Fig. 25). Juveniles are designated by the letter 'Y', e.g. Y-3

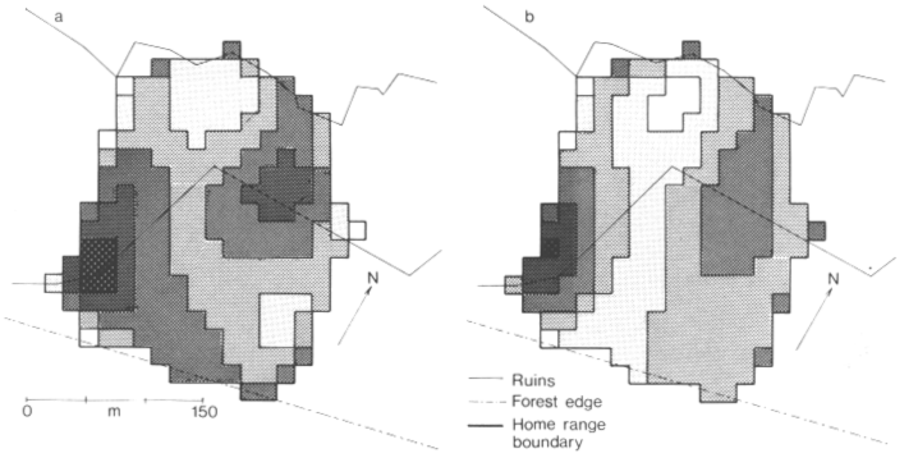


Fig. 27: Trend surface analysis contour maps (see text) showing home range use by *R. chrysopygus* Red-purple ♀ (a) and White ♂ (b) at Gedi Ruins during the entire study period. Shading intensity within each figure indicates use on a proportional gradient. Darker shading represents more intensive use. Shading does not represent equal usage by each animal

20.7 %) of the total combined sightings of 1040. During associations the ♂♂ always followed the ♀♀, sometimes never letting them get more than a m ahead. During these intense associations the ♂ often made nose-rump contact and sometimes attempted to mount, indicating the ♀ may have been near estrus during these 1 or 2 day periods. The nose-rump contacts did not appear to be a case of the ♂ smelling a ♀, but the ♂ resting his nose and chin on the rump as a prelude to mounting or attempting to mount. The reaction of the ♀♀ to the nose-rump contacts and mountings was always the same, they would jerk forward a few steps and continue foraging. No agonistic behaviour was observed in a total of 13 nose-rump contacts and 6 mounting attempts.

More often the ♂ of the pair would follow more leisurely at 3—20 m, which meant that the 2 animals typically were not in visual contact. The ♂ appeared to be following a scent trail, for he would take the exact path of the ♀, even when she was visible to him and a short-cut would have been more appropriate for an approach. While following the ♀'s path, the ♂ would wander back and forth with his nose continually sniffing the leaf litter surface, as though trying to stay on the strongest part of a scent gradient.

Only 9 times were pairs seen to come together and greet with a very brief nose-nose contact, sometimes followed by the ♀ moving to the side of the ♂ and nudging his side with her nose. In some of these encounters the ♀ rolled against the side of the ♂ and once a ♀ crouched down onto her belly in front of the ♂ in, I assume, a submissive posture. An entire greeting lasted only 4—5 s and the 2 animals would then resume foraging, the ♂ following the ♀. I never observed allogrooming between individuals.

R. chrysopygus was potentially promiscuous, for when nonresident animals of the opposite sex wandered onto a territory, the ♂ followed the ♀. On 2 occasions mounting attempts were seen.

The only complete mating sequence was observed 3 weeks after my arrival at Gedi. It was preceded by a fast running chase, presumably by the ♂. The ♂ mounted and copulated with the ♀ 5 times in quick succession for about 2 s each time and then while one of the pair sat and licked its genitals (? ♂), the other moved away foraging.

All of the pairs I observed persisted until one of the members presumably died (Fig. 26).

Although aggressive behaviour was never observed within a pair, considerable aggression occurred between pairs, often near the periphery of the territories. During the study period 38 aggressive chases were seen and 16 of these were between identified individuals (Tab. 5).

Table 5: Interpair encounters for *R. chrysopygus* at Gedi Ruins

	Aggression			Tolerance	
	Female	Male		Female	Male
Female	6	1	Female	0	10
Male	0	9	Male	4	0

(p = 0.0009, Fisher test) (p = 0.009, Fisher test)

Of 14 observations where 2 animals from different territorial areas were seen together and were tolerant (Tab. 5), all involved opposite sexes.

The single instance of a ♂ chasing a ♀ occurred when a resident ♂ was intensely following a presumed estrous ♀ and they came upon an intruding ♀ from the adjacent territorial area. She was chased back to her area and the ♂ immediately returned his attention to the resident ♀, which included nose-rump contacts and attempted mounts. It was this highly protective behaviour towards estrous ♀♀ by the ♂♂ that seemed to prevent promiscuity and resulted in the only observed case of inter-sexual aggression.

A typical intrasexual aggressive encounter started with a resident animal detecting an intruder and cautiously approaching it in a low, crouched position with its nose waving about and its ears turned forward. Every 2—3 s the resident loudly slapped the leaf litter with its tail. If the intruder did not retreat, then a fast, running chase in zig-zags and wide circles occurred. As soon as the intruder crossed out of the resident's territory, the chase abruptly stopped and the pursuer continued foraging. Once, when the distance between 2 unidentified chasing animals closed, they tumbled to the ground in a flurry of leaves. Seconds later they were up and out of sight.

3. *Scent marking*

R. chrysopygus scent-marked with a subcaudal gland located just posterior to the anus at the tail insertion (Fig. 28), by periodically lowering the rump and rubbing the gland on the substrate while walking along, their movement and foraging activity hardly being interrupted by the action. This scent-marking was not confined to any particular loci or even to the peripheral areas of the territory (Fig. 20), but was done continually as the animals moved about foraging. Some of the scent-marks were very exaggerated, suggesting that the perineal region was also dragged on the substrate. Of the 1857 observations of 8 known individuals, 118 (6.3 %) included scent marking behaviour. Occasionally I saw a ♀ scent-mark and when the following ♂ passed over the spot he also scent-marked.

Captive and freshly captured elephant-shrews always smelled strongly and the oily secretion from the subcaudal gland was always visible. The tail of *R. chrysopygus* dragged on the leaf litter as it walked along and it is likely

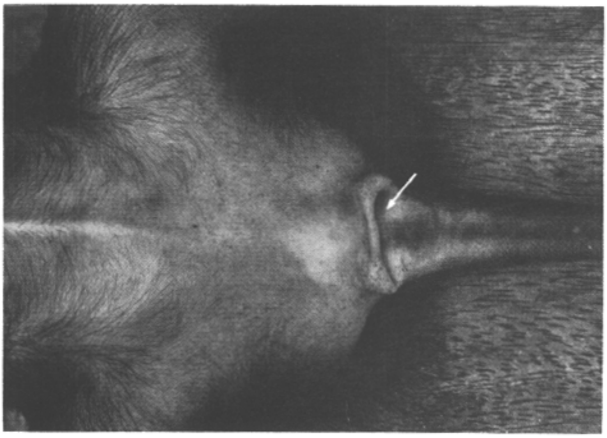


Fig. 28: Subcaudal scent gland of a *R. chrysopygus* (arrow). The anus is located on the anterior edge of the skin fold forming the gland. The penal sheath is on the left margin of the photograph, in the middle of the animal's abdomen

that small amounts of secretion from the subcaudal gland were continually deposited as the animals moved about. This may explain how ♂♂ followed nonvisible ♀♀.

Once I came upon a ♂ foraging 3—4 m inside his neighbours' territory; after about a min the resident pair appeared. The intruding ♂ had moved out of sight when the pair reached the spot where I first sighted him. The pair reacted to a very small area on the leaf litter by immediately halting, becoming very alert and tense and slapping their tails on the leaf litter every 1—2 s. For a ½ min the pair nervously slapped and sniffed around the spot, until the ♂, with obvious intent, walked away in the direction of the intruding ♂, while the ♀ continued to forage. One min later a fast chase commenced from where the 2 ♂♂ had disappeared. The intruding ♂ was driven right to the boundary, a tourist path in this case, where the resident ♂ stopped abruptly, turned around and returned foraging to the ♀, who was 3 m away and within sight. The initial behaviour in this sequence was probably in response to a scent mark left by the intruding ♂.

No boundary related static-optic scent-marking (dung piles, scent posts, etc.) was observed.

4. Gestation, litter size and inter-birth interval

R. chrysopygus breeds throughout the year (Fig. 26). One of the more obscure aspects of its life history was the location of the birth site and the duration of the young's residence at this site. With one exception (see Section V, A, 5 below), I saw juveniles only after they had emerged from hiding. In addition, only one copulation was observed, so that estimates of gestation and therefore age of juveniles are necessarily rather speculative.

The dates of nest emergence and last sightings of 16 young were made on 4 well known territorial areas. Eleven of these animals were presumed to be consecutive births of the same ♀♀. The mean interval was 82 days (S.D. = 36.55) with a maximum of 142 days, which may have been due to a birth in the interim. The minimum interval of 36 days between emergences probably represents a birth from a postpartum conception and thus may be very close to the gestation period. Since all intervals are based on first sightings of young, as opposed to copulation and birth dates, there may be an error of several days due to consecutive young remaining hidden for different periods of time. Thus, a more realistic estimate of the gestation period is about 42 days.

The litter size was always one, based on the Gedi Forest animals and 10 pregnant specimens from the Sokoke-Arabuko Forest.

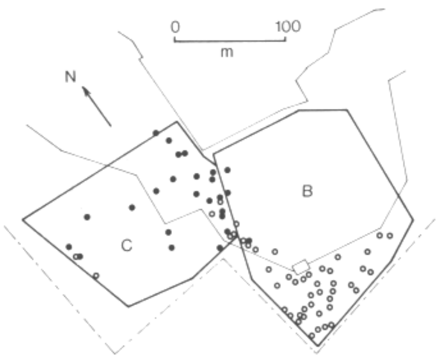
5. *Ontogeny*

The single neonate, weighing an estimated 80 g, is probably deposited in its own leaf nest, separate from the nest of the ♀. Presumably the ♀ visits it briefly a number of times a day until it starts accompanying her at about 2 weeks of age.

I once observed a very young *R. chrysopygus* walking unsteadily on the forest floor and squealing in a high pitched voice. The ♀ appeared and the 2 exchanged nose-nose greetings, the ♀ softly chattering and pushing her nose against the side of the juvenile. The 2 then walked away in the direction from which the ♀ had come. About 4 min later the lone juvenile returned, still walking unsteadily and about 5 m from where I was standing slipped into an absolutely invisible nest. It was never seen again. I estimate that it was about 7 days old and, judging from its behaviour, size and unsteady gait, was not yet old enough to accompany the mother. On examination of the nest the juvenile had entered, a few days later, it was revealed that it was empty and large enough for only one occupant.

I never saw any of the newly emergent juveniles nurse, so they were probably weaned. Based on the above observation, on fetuses from the pregnant ♀♀ collected in the Sokoke-Arabuko Forest, and 3 live juveniles brought to me by collectors, newborn *R. chrysopygus* were barely able to walk, only just had their eyes open, and their fur was not fully grown.

Newly emergent juveniles were fully haired, very mobile, about half as tall as their mothers and weighed an estimated 180 g. They accompanied their mothers for 2—3 days, gradually becoming more and more independent until by the fifth day they were rarely seen with the ♀, although they still occupied the parental territory. While accompanying the mother, the juveniles



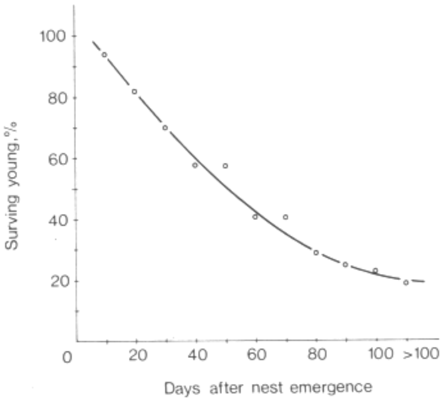


Fig. 29: Loci of first sightings of *R. chrysopygus* subadult White-dark blue ♂ between 20 Jan. — 3 March 1972 (open circles) while it occupied its parental territory (B). Loci of sightings between 5—24 March 1972 (closed circles) show it had dispersed to the adjacent territorial area (C), when the latter's ♂ disappeared on 2 March 1972

Fig. 30: Survivorship curve for 17 juvenile *R. chrysopygus* at Gedi Ruins

would occasionally greet the ♀ with a nose-nose contact and rub and roll against her side. No male-young interactions were seen nor was any parental-offspring aggression observed, even when the juveniles were subadult and approaching adult condition. During a short period (c. 10 days) on the territory of Yellow-red ♀, the adult pair and 3 consecutive young, ranging in age from 11—108 days after nest emergence, were all coexisting without aggression (Fig. 26).

There was no particular pattern of home range use by the juveniles; some ranged over the whole parental territory while others only used a portion of the area (Fig. 29).

During the study 17 known juveniles were born. One of these successfully took up a vacant home range 32 days after nest emergence, while another was still on its parents' territory 193 days after nest emergence, when field work was terminated. Offspring were tolerated on the parental territory indefinitely and, during their residence, they were prone to wander onto other territorial areas. Presumably they eventually found a vacant territory and occupied it, or were taken by predators. Older juveniles and subadults were not tolerated on non-parental territories. For example, White-dark blue ♂ was using a corner of its presumed parental territory (Fig. 29) and was completely tolerated by the pair, despite the fact he was a subadult estimated at over 150 days from nest emergence. On 2 March 1972 adjacent territory resident Yellow-purple ♂ disappeared and within 3 days White-dark blue ♂ had moved onto his vacant home range. Twice he had been sighted deep in this adjacent area prior to Yellow-purple ♂'s disappearance.

During the study on the 4 territorial areas, 6 non-resident, subadult elephant-shrews were netted, ringed and released. Only 2 were briefly seen again on different territories from their original capture sites. All 6 animals completely disappeared from the forest; they were probably dispersing juveniles "looking" for vacant home ranges and were preyed upon.

A survivorship curve, based on 17 known juveniles (Fig. 30), shows that there was nearly steady mortality of young from nest emergence to about day 60, when the mortality started to level off. Of these 17 animals, 2 successfully dispersed (12.5 %) and the remainder disappeared from the ruins.

Based on known-age skulls from Gedi Ruins, tooth wear and the longevity of Yellow-red ♀ (see Section V, A, 1), adults probably live for 3—4 years once established on a territory (Fig. 26).

B. *Elephantulus rufescens*

1. *Territory*

Observations of individual *E. rufescens* indicated that animals rarely wandered further than one metre from trails; thus, the trail network was a good indicator of a pair's presence and afforded a rapid means of measuring home range. By tracking, especially on the peripheral trails and in areas where 2 trail networks joined, I could quickly determine the areas used by individual elephant-shrews.

Home ranges were computed by taking all of the sooted card tracking records and observations for an individual and cumulatively plotting them on a study area map. I then connected the peripheral loci so as to form a "minimum polygon" (Jennrich and Turner 1969) that most closely fitted the trail system and habitat. The only exception to this procedure was that I did not include those loci where an individual was tracked or sighted 5 m beyond the centre of the area where its trail network met an adjacent animal's trail network (Fig. 31). These excluded loci were considered to be home range "violations".

E. rufescens was spatially distributed similarly to *R. chrysopygus;* 2 individuals of opposite sex occupied home ranges that almost completely overlapped and that were congruent. Each pair's home range functioned as a territory, which was often contiguous with at least one other pair's territory. The habitat was not saturated with territories (Figs. 31 and 33).

The mean home range area for 10 stable individuals was 0.34 ha with a variation from 0.16—0.52 ha (Tab. 6). Contiguous territories which were joined by means of trails (Fig. 21) were usually located in a 2—3 m wide clearing or sparsely vegetated area, which included a pile of elephant-shrew dung. These areas were used by all resident individuals and thus represented an overlap area in the contiguous territories. Three stable adult individuals were noted (by tracking or sighting) to "violate" their territories on 5 occasions by being at least 5 m beyond the centre of these overlap areas (0.16 % of total records) (Tab. 7). Individuals from contiguous territories were observed to meet (all on overlap areas) 6 times and each time it resulted in a violent, aggressive encounter (see Section V, B, 2 below).

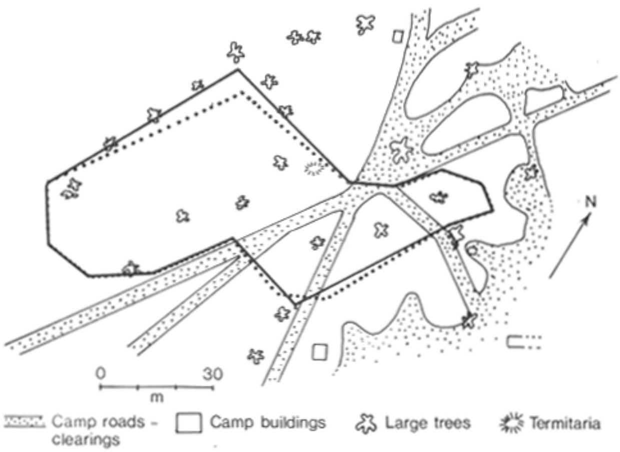


Fig. 31: Home range areas for paired *E. rufescens* Orange ♀ (solid line) and Light-green ♂ (dotted line) at Bushwhackers (see Figs. 32 and 33, territorial area D, and Tab. 6)

Table 6: Home range areas for *E. rufescens* at Bushwhackers

Adult individual	Date	Loci records	Area		
			acres	ha	m²
Red ♀	21 April 1974 - 25 November 1974	900	.40	.16	1602.8
Yellow ♂	6 April 1974 - 25 November 1974	1088	.42	.17	1677.8
Green ♀	22 April 1974 - 18 August 1974	249	.89	.36	3600.2
Blue ♂	22 April 1974 - 19 August 1974	256	.96	.39	3884.7
Purple ♀	1 November 1974 - 26 February 1975	404	.54	.22	2183.0
1/2 yellow ♂	25 July 1974 - 9 February 1975	107	1.3	.52	5248.0
1/2 red ♀	7 July 1974 - 16 August 1974	46	.99	.40	3952.0
Orange ♀	6 July 1974 - 17 February 1975	105	.91	.37	3726.8
Light green ♂	2 May 1974 - 17 February 1975	131	.86	.35	3471.8
Gold ♀	1 October 1974 - 17 February 1975	365	1.14	.46	4583.6
	Mean	365.1	.84	.34	3393.1
	S. D.	353.8	.30	.12	1210.33

Table 7: Home range violations of *E. rufescens* at Bushwhackers

Individual		Loci records	Violations	%
Adults	Red ♀	900	0	0
	Yellow ♂	1088	1	.09
	Blue ♂	256	0	0
	Green ♀	249	0	0
	Grey ♂	212	2	.9
	Purple ♀	404	2	.5
	Total	3109	5	.16
	Mean	518	.8	.16
	S. D.	379.07	.98	
Juvenile	Grey ♂	246	14	5.7
	Purple ♀	275	11	4.0
	Brown ♀	513	14	2.7
	Refl. green ♂	366	47	12.8
	Total	1400	86	6.14
	Mean	350	21.5	6.14
	S. D.	120.09	17.06	

The territorial areas were not temporally stable, but varied when the occupants or the environment changed. For example, paired Green ♀ and Blue ♂ withdrew from about 1,450 m^2 of their territory when their offspring, Gold ♀, dispersed into the adjacent uninhabited area and set up a contiguous territory that included the area the parents had withdrawn from.

A major change in individuals and their home ranges occurred towards the end of the study (Fig. 32). During this period Yellow ♂ disappeared, which resulted in Grey ♂ occupying 2 female home ranges for about 42 days. There was no indication of any aggression between Grey ♂ and Yellow ♂'s mate, Red ♀, during this time. The situation returned to normal when Red ♀ also disappeared from the study area and Grey ♂ and his original mate, Purple ♀, established a territory that covered portions of the 2 original territorial areas (Figs. 32 and 33; see Section V, B, 2).

During the rains the vegetation flushed and resulted in some trail changes (as already described), which caused minor and periodic changes in the peripheral areas of territories.

An analysis of tracking results for 2 pairs over approximately 2 months showed that a paired ♂ and ♀ used their territory areas about equally with no exclusive use of particular lengths of trail.

During the study one set of twins, which were born about 23 July 1974, survived to be subadults. These twins, Brown ♀ and Reflective Green ♂, often played, rested and nursed together as juveniles, but at about 40 days of age, they began to experience considerable parental aggression, as well as fighting with each other (8 aggressive chases between them were seen). An analysis of their tracking cards between 10 September and 1 October 1974 suggests that they were using different portions of the parental territory and all of the observed aggression between the twins occurred in the region between their respective areas, thus indicating they were attempting to maintain exclusive areas (Fig. 34).

Excluding the area of concentrated camp buildings at Bushwhackers, the mean monthly density of *E. rufescens* was about 2.0 animals/ha, including juveniles and subadults.

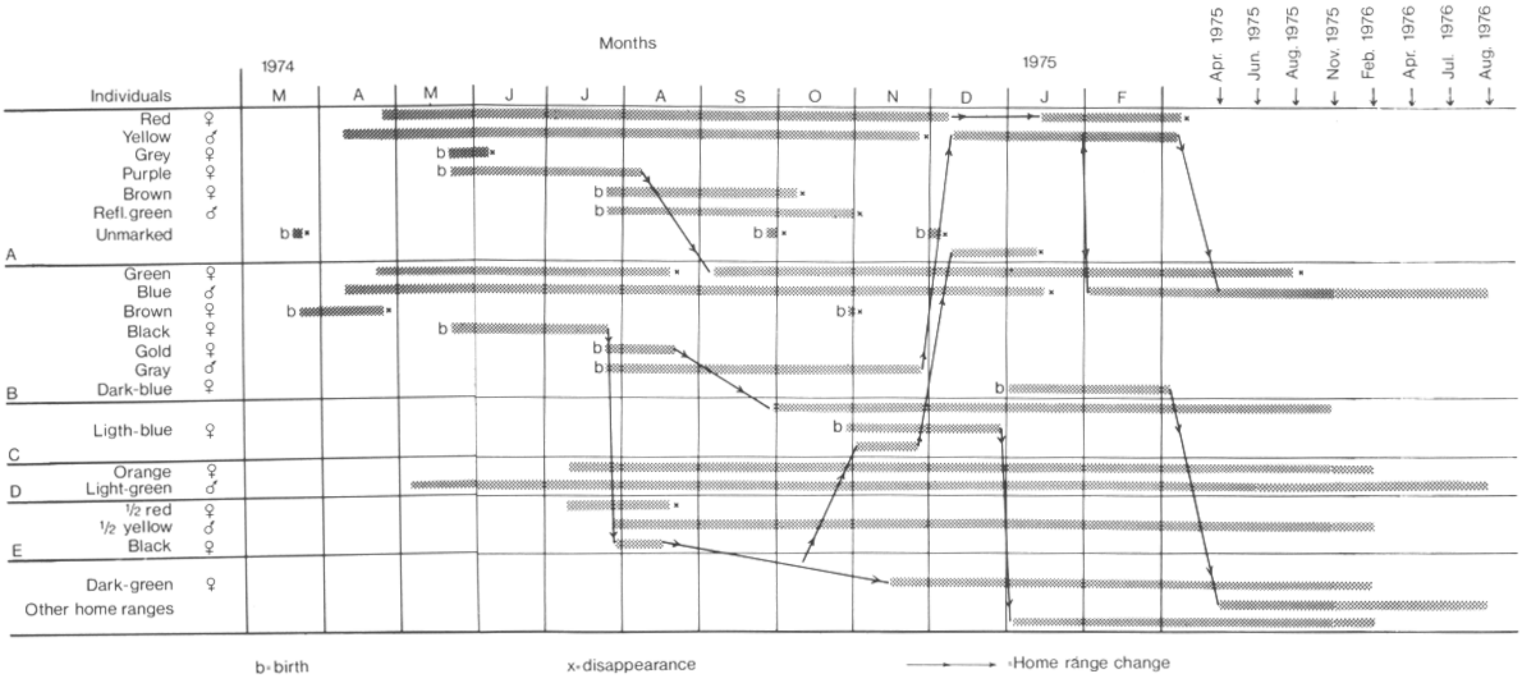


Fig. 32: Summary of spatial and temporal relationships of *E. rufescens* individuals (horizontal bars) at Bushwhackers. Individuals are grouped into the territorial areas (A, B, C, D and E) they occupied (see Fig. 33)

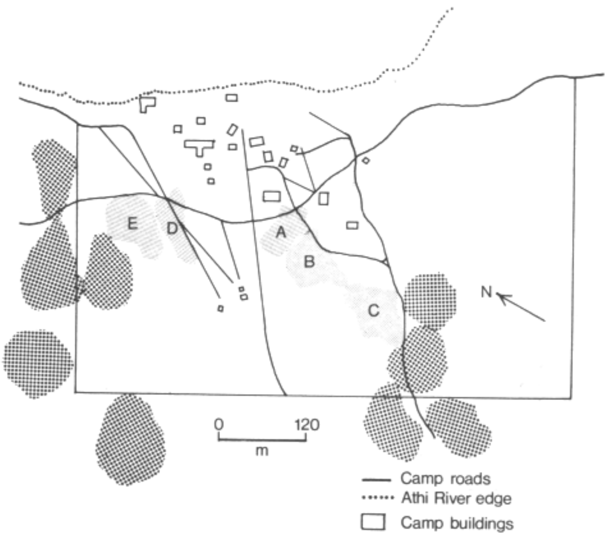
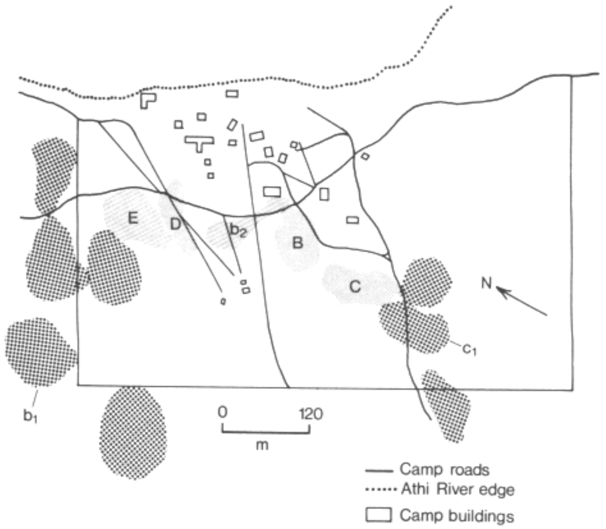


Fig. 33: Territorial areas of *E. rufescens* pairs at Bushwhackers (see study area map, Fig. 13). The darker toned areas are approximations.

a. Territories in Sept. 1974. Area A, Red ♀ + Yellow ♂; area B, Purple ♀ + Blue ♂; area C, Gold ♀ + unmarked; area D, Orange ♀ + Light-green ♂; area E, 1/2 yellow ♂ + unmarked.



b. Territories in April 1975. Area B, Purple ♀ + Grey ♂; area C, Gold ♀ + unmarked; area D, Orange ♀ + Light-green ♂; area E, 1/2 yellow ♂ + unmarked. The lower case letters represent dispersed offspring: Area b1, Black ♀; area b2, Dark-blue ♀; area c1, Light-blue ♀ (see Fig. 32)

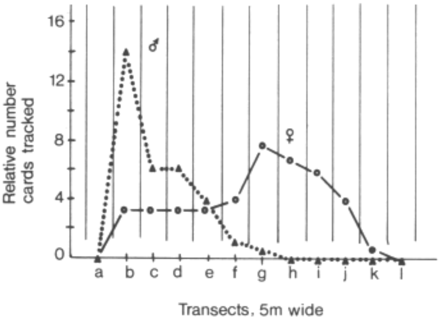


Fig. 34: Sooted card tracking results for *E. rufescens* twins (Reflective Green ♂ and Brown ♀) at Bushwhackers in Sept. 1974. The relative number of cards tracked per 5 m wide transect across their parental territory (area A) shows the twins were using different portions of the area. Eight aggressive chases occurred between the twins in transects d, e and f

2. *Adult association*

The spatial pairing of *E. rufescens* was persistent, with a change only occurring at death. An exception was the appearance of an immigrant subadult in the study area, Dark-green ♀, who was seen being chased off of the various territories by the female occupants. Yellow ♂, the mate of Red ♀, suddenly disappeared, after which the immigrant ♀ occupied Red ♀'s home range and Red ♀ was relegated to a small corner of her former area. Three fierce aggressive encounters were observed between the 2 ♀♀ on the new boundary (Fig. 35). The subadult ♀, after 23 days of occupancy, suddenly disappeared and Red ♀ immediately moved back onto her entire home range.

Although the elephant-shrews were spatially paired, their pair association was infrequent. Only 34 cases of non-food or non-sexual pair interactions were observed. In 9 of these (26.5 %) there was neutral tolerance between the pair, in 2 (5.9 %) the pair nose-nose greeted, in 20 cases (58.8 %) the ♀ dominated the ♂, and in the remaining 3 sightings (8.8 %) the ♂ dominated the ♀ (dominance figures, $p < .001$, χ^2-test). Of the 20 sightings where the ♀♀ dominated, 15 included an actual aggressive approach by the ♀, while

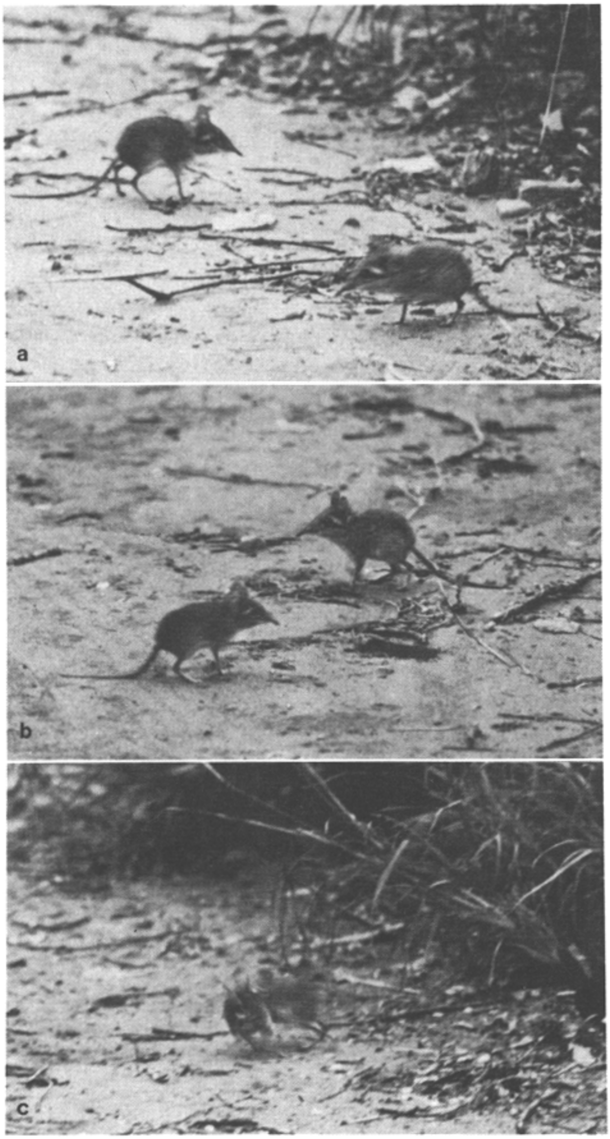


Fig. 35: An adult pair of *E. rufescens* (Immigrant Dark-green ♀ and Red ♀) in an aggressive encounter on a territorial boundary, a camp road in this case (see text). a. and b. The animals "mechanical walk" while circling one another. c. The ♀ on the right lunges at the neck of the other, which is running away from the camera's position

in the remaining 5 cases the ♂ either avoided the ♀ by moving out of her way before she approached him or he stopped and returned when a ♀ was sighted on a trail in front of him.

The only times ♂♂ were seen to follow ♀♀ were during periods of presumed female estrus. For example, during the night of 21 September 1974, Red ♀ gave birth and the next morning her mate, Yellow ♂, was seen constantly following her closely and at one point he briefly established a nose-rump contact. These encounters included a posture that was characteristic of sexual interactions as well as intraspecific aggressive encounters. In a sexual context the ♂ followed the ♀ until she stopped. He then adopted a slightly stiff, elevated posture while standing high on his legs and walked after the ♀ in a 20 to 30 cm arc. As he followed the ♀, he took short steps and displayed his white feet by swinging them slightly outwards at each step. I call this behaviour a "mechanical walk." If the ♀ did not move away when a ♂ approached, then he would make nose-rump contact and attempt to mount. In all cases the ♀ either turned and approached the ♂ aggressively or just ran away. In the 10 sexual encounters observed, I never saw a successful copulation. Three of these encounters were seen on the evening, or following morning, of the 3 known birthnights, which suggest a postpartum estrus.

Of 105 intraspecific aggressive encounters, 33 (81.4 %) were food related (see Section VI, B, 1), 29 (27.6 %) were parental aggression towards their subadult offspring (see Section V, B, 5 below), 18 (17.1 %) were related to a territorial boundary and the remaining 25 (23.8 %) were undetermined as to context. Of the 18 boundary related encounters, 8 were between the already mentioned juvenile twins and the remaining 10 involved adults and subadults. Nine of the 10 encounters were sex specific ($p = .033$, Fisher test); ♂♂ chased ♂♂ 3 times, ♀♀ chased ♀♀ 6 times and once a near-term pregnant ♀ chased a subadult ♂ from her territory.

Typical boundary related aggression occurred when 2 adjacent resident animals encountered each other and they drummed one or both rear feet on the ground, resulting in a "prrr, prrr, prrr" sound. Each drum lasted about ½ s and was separated from the next by 1—2 s. The 2 elephant-shrews then approached and followed one another on opposite sides of a 1 m diameter circular path (Fig. 35). While thus laterally facing and following each other, one or both of the animals displayed the "mechanical walk." This led to a high speed chase which resulted in either one animal being driven away or sometimes in the 2 animals rolling and tumbling in a kicking and biting bout. These boundary encounters lasted from 5 sec to 3—4 min, after which the animals returned to their respective territories.

If a non-resident was encountered well within a territory, it resulted in a fast, direct chase to a boundary, with no "mechanical walk" display. Direct chases were also observed between parents and their subadult offspring and between twins.

3. Scent marking

♀♀ and ♂♂ have a very prominent sternal gland, located on the chest between the front legs, which was periodically rubbed on the substrate as the animals moved along their trails (Figs. 36 and 37). The action was very cryptic, since forward motion was not interrupted, and thus it took several weeks before I consistently recognized it. Sternal gland scent marking was observed 67 times, half the time (33) on boundary areas and the remainder within the territories. There was no indication of locus-specific scent marking over time, nor was it seen during any sexual encounters.

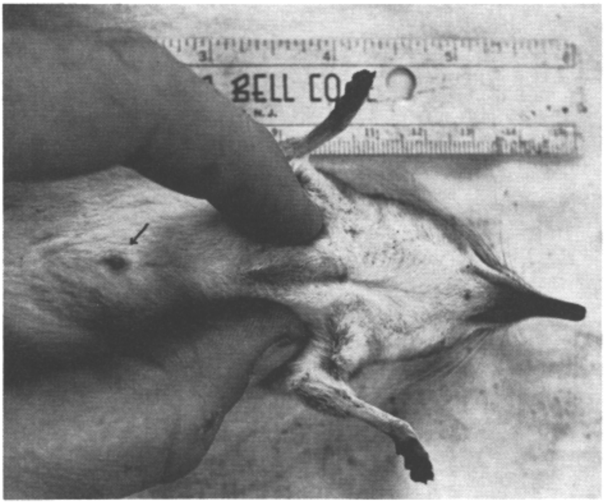


Fig. 36: The sternal gland of an adult *E. rufescens.* Note penal sheath (arrow) posterior to the gland in the middle of the abdomen

Only rarely did animals mark the same spot as they subsequently passed over it. However, in one instance, Purple ♀ scent marked a patch track as she walked over it and 2 min later when her mate, Grey ♂, trail cleaned over the spot, he too scent marked. Seven minutes after the ♂ marked, juvenile Dark-blue ♀ passed over the spot and scent marked. Thus, the whole family had sternal-rubbed the same spot within 9 min. Despite many additional hours watching this area, I never saw them mark the same patch-track again.

During the study 6 instances of perineal drag were observed. Three of these were on boundary areas, one occurred during a boundary area aggressive encounter and the remaining 2 were associated with sexual encounters.

E. rufescens also deposited its dung and urine in a manner which suggested a communicatory function. Dung piles were a very characteristic feature of the animals' territories, always being found where trail networks were contiguous as well as in scattered loci throughout the territory. For example, in June 1974 Red ♀ and Yellow ♂ were using 8 dung piles, 5 of which were on the periphery of their territory. Based on direct observations, there is little doubt that dung piles, which varied from 10 pellets to hundreds, scattered over a 75 cm diameter area, were important static-optic markers (Fig. 38). When an elephant-shrew visited its boundary area, it went to recent dung deposits and carefully smelled each pile before depositing 3—4 pellets as well as urine (Fig. 39).

In late December 1974 a 5 m long portion of camp road was drawn to my attention when small piles of

Fig. 37: An adult *E. rufescens* sternal marking

Fig. 38: Dung pile of *E. rufescens.* Note the trails leading into the area (arrows)

elephant-shrew dung started to appear along both sides of the 4 m wide road. Tracking and later observations indicated that the area was the new home range boundary between immigrant Dark-green ♀ and Red ♀, as already described. For 12 days from 29 December 1974, all scent marking behaviours of the ♂ and 2 ♀♀ at this site were recorded (22.8 h of observation) (Tab. 8). Of all the visits to the boundary by the 2 ♀♀, 50 % involved urination and/or defecation, 37 % involved sternal marking and 26 % did not involve marking at all. The corresponding figures for Grey ♂ were 14 %, 17 % and 76 %.

Fig. 39: Defecating posture of an adult ♀ *E. rufescens*

Table 8: Scent marking activity of *E. rufescens* on a territorial boundary at Bushwhackers

Individual	Visits			
	to boundary	included elimination	included sternal marking	included no marking
Dark green ♀	18	13 (72 %)	5 (28 %)	3 (17 %)
Red ♀	28	10 (36 %)	12 (43 %)	9 (32 %)
Grey ♂	29	4 (14 %)	5 (17 %)	22 (76 %)

4. Gestation, litter size and inter-birth interval

Only indirect estimates of gestation can be made for *E. rufescens* because copulations were never observed and 6 of the birthdates were approximations within 2 days. Seven consecutive births from the same ♀♀ occurred with intervals varying from 56—65 days and having a mean of 61 days (S.D. = 3.26). This suggests a gestation period of approximately 56 days because a postpartum conception is likely. Current studies of captive, breeding animals indicate the gestation may be closer to 50 days (Rathbun, in prep.).

Based on collected specimens, the study area births, and current work with captives at the National Zoological Park, older ♀♀ may have twins while younger ♀♀ may give birth to a single young. Of 11 known births at Bushwhackers, 4 were twins, 4 were suspected single births and the remaining 3 were undetermined. Breeding occurred throughout the year (Fig. 32).

5. Ontogeny

Newborn *E. rufescens* were nidifugous[6]) and kept at the bases of multiple-stemmed bushes, such as *Combretum exalatum* and *Grewia villosa,* or among the litter of fallen and rotting tree trunks. No nests were used; instead a small cavity was cleaned in the litter. Newborn young stayed crouched

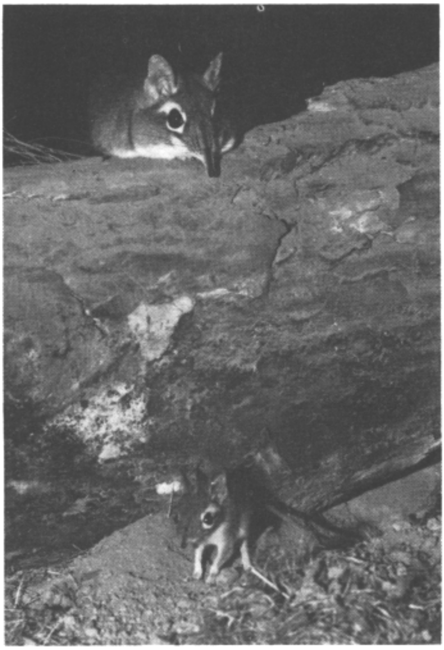


Fig. 40: E. rufescens mother (top) in a typical rest posture, watching one of her precocial neonate twins (bottom), which is about 48 h old and has been fully mobile since 3—4 h postpartum. Also see Fig. 24

Fig. 41: Red ♀ nursing her 25 ± day old twins on a favourite rest spot. The twin on the left is suckling from a pectoral breast, while the other is on an abdominal breast

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[6]) The terms "nidicolous" and "nidifugous" refer to the use or non-use of a nest by neonates, while "precocial" and "altricial" refer to the degree of neonate development.

motionless for the first 1—2 days, but were capable of rapid flight within hours after birth. When disturbed they tended to remain motionless until the very last second, when they would dash away into the undergrowth and again become motionless. I saw a pair of juveniles running, grooming and playing when 24 h old after a nursing bout. During the first 1—2 days young stayed very close to the birth place and were apparently only active at dusk and dawn. They slowly expanded the area of familiarity and hours of activity until by the third week they used the entire parental territory and were active at the same time as the adults.

Mothers spent the day resting and foraging near neonates and visited them at dusk for a 10—20 s session of nursing (Figs. 40 and 41). They might have also visited them periodically during the night. The only male involvement was the protective mobbing of snake predators near juveniles (see Section VII, A, 2). Juveniles were weaned by day 25 and parents began to chase them aggressively when they were about 40 days old. At this time the juveniles' brown feet began to change to white, a characteristic of adults. The intensity of parental aggression steadily increased until juveniles were chased whenever encountered. There was no sex specificity in 29 parent-offspring aggressive encounters that were not food related.

When the offspring reached subadult age, they tended to wander over adjacent territories; of the 1,400 loci records for 4 subadults, 86 (6.1 %) were recorded beyond parental overlap areas (Tab. 7).

Of 16 known births, 6 young successfully dispersed by establishing new, or inheriting old, home ranges. Five were adjacent to the parental territory, while Black ♀ dispersed about 320 m from the parental (Green ♀) territory (Fig. 33). A typical example of dispersal was Reflective Green ♂, born about 23 July 1974, who remained entirely within his parents' territory until 25 September 1974; from 15 to 25 September, 5 chases by his parents were observed. From 26 September to his disappearance on about 29 October 1974, 32 % of his sightings and tracking records were outside of the parental territory and 4 more parental chases were seen. If a vacancy had occurred, he would have probably occupied it. Instead he tried to inhabit the unoccupied area adjacent to the parental territory, which was probably unsuitable habitat since it was largely clear of vegetation due to camp roads and buildings. Before his disappearance Reflective Green ♂ was observed soaking wet after a heavy rain; he probably died of exposure. No other wet elephant-shrews were seen. Generally offspring were driven from the parental territory by the time the next offspring were born (Fig. 32).

The survivorship curve for 16 known juveniles at Bushwhackers shows two dips, the first reflecting neonatal deaths and the second disappearances between day 70 and 80, when juveniles were driven away by their parents (Fig. 42).

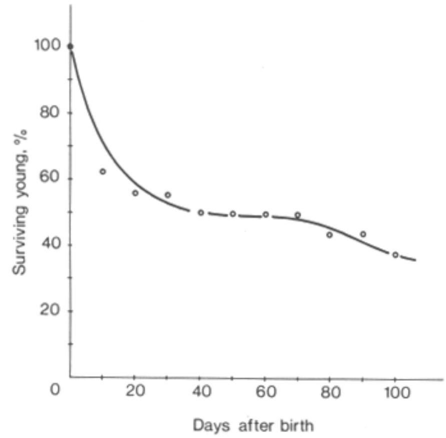

Fig. 42: Survivorship curve for 16 juvenile *E. rufescens* at Bushwhackers

Among the longest lived individuals at Bushwhackers was Black ♀, tagged in May 1974 and still alive in November 1975, nearly 19 months later. Lightgreen ♂ and Orange ♀, a stable pair, were tagged as adults in May and July 1974 and tracked again in February 1976. In April 1976 the ♂ and an unmarked ♀ were tracked in the original territorial area. Apparently Orange ♀ had disappeared and a new ♀ had taken her place. This suggests, along with other individual records (Fig. 32), pair association for life and a relatively long life expectancy.

VI. Feeding Ecology

A. *Rhynchocyon chrysopygus*

1. Foraging behaviour

R. chrysopygus fed on the forest floor mainly in the leaf litter, although some soil excavation was also performed. While foraging, an animal slowly walked along continually poking its long nose in and out of the leaf and branch litter. Occasionally a forefoot was used to sweep away an obstructing object or to create a small opening in the litter into which the nose probed. A forefoot was also used to disturb the leaf litter by vibrating it on the surface while the animal probed under it with its nose. The elephant-shrews often flushed flying or hopping insects, such as cockroaches, but these were only rarely pursued. During a pursuit the elephant-shrews chased with short, quick bounds and frantically attempted to pin the insect with the forefeet. Of the 9 pursuits observed, it is doubtful if more than one resulted in a successful capture. Foraging animals turned the ears forward from the normal laterally facing position, presumably allowing them to localize prey acoustically.

The nearly continuous forward movement while searching for food items was periodically interrupted when an animal started to dig into the soil, which was removed posterior-laterally either with long sweeps of a single forefoot or by simultaneous movement of both forefeet, which was reminiscent of a digging dog. The resulting excavations were conical holes up to 5 cm deep and 2—3 cm across at the top. The elephant-shrews normally foraged while standing on their hind toes, but if more stability was required (as when digging a hole), they dropped down onto their heels.

The majority of food items were small enough to be ingested with a flick of the long tongue, which could be extended at least 5 mm beyond the tip of the nose. However, ingestion was rarely seen as the elephant-shrew's nose and mouth were nearly always hidden in the leaf litter. The only food items that I saw being ingested by free-living animals were 10—15 cm long earthworms, family Lumbricidae (8 cases) and the 6—10 cm long red-legged millipedes, genus *Metiche* (9 cases). This millipede was not recorded in the leaf litter nor in the stomach samples from the Sokoke-Arabuko Forest. After a large prey item was exposed, it was awkwardly taken into the side of the mouth by tilting the head to one side. While being chewed, portions hanging from the mouth were clawed apart with a forefoot. Ingestion of large items was sloppy and some of the small pieces that fell from the mouth were eventually flicked up with the tongue. In only one case did this feeding technique vary, when an earthworm was pinned to the ground using a forefoot and then ripped in two when ingested. The red-legged millipedes were only partially consumed and large pieces were left on the ground. Neither the toss nor the death shake, as described by EISENBERG and LEYHAUSEN (1972) for other mammals, were observed.

Several attempts were made to keep captive *R. chrysopygus*, but the animals did not feed properly and all died after about 2 weeks. Most captives would not eat the living invertebrates I provided, much less any food not characteristic of their diet.

2. *Diet*

21 *R. chrysopygus* stomachs (12 ♀♀, 9 ♂♂) were analyzed (11 in the March 1972 dry season; 10 in the May 1972 wet season). 10 leaf litter samples were collected in each of the 2 months and were used to assess what invertebrates were potentially available to the elephant-shrews. 17 invertebrate groups were found. Of these, 8 groups were represented by less than 1 % of the total invertebrates and were not found in the stomachs (hemipterans, lepidopterans, isopods, mites, antlions, earwigs, embiopterans, and egg cases). Two food items, winged ants and dipteran larvae, together represented less than 1 % of the stomach sample points and were not found in the leaf litter.

When the mean % occurrence of invertebrates in the stomach contents and the mean % leaf litter occurrence of the more common invertebrates were compared, it was found that some invertebrate groups were eaten less than their litter occurrence predicted, while others were eaten more than expected (Fig. 43). In the first instance, the differences were most striking and included orthopterans, spiders, millipedes, ants and centipedes. Invertebrates whose occurrence in the stomachs was greater than expected included termites, coleopteran adults and larvae, earthworms, and pupal cases. The diet and potential availability figures were not correlated ($p > .05$, Spearman rank correlation coefficient test), so that the overall diet was probably different from the food's potential availability.

If one considers the foraging behaviour of *R. chrysopygus* along with the invertebrate size, density, and behaviour (a subjective measure of their *actual* availability), then the differences between litter and diet occurrence for each food item may be explained. The orthopterans were highly mobile, being capable of flight, and were not usually pursued or captured when flushed. The most numerous spiders were small, swift leaf litter dwelling species that were rarely identified in the stomachs. Stomach fragments indicated that *R. chrysopygus* was feeding more on the large, rare, and presumably slower, soil dwelling spiders. Similarly, the smaller and swifter ants and centipedes were

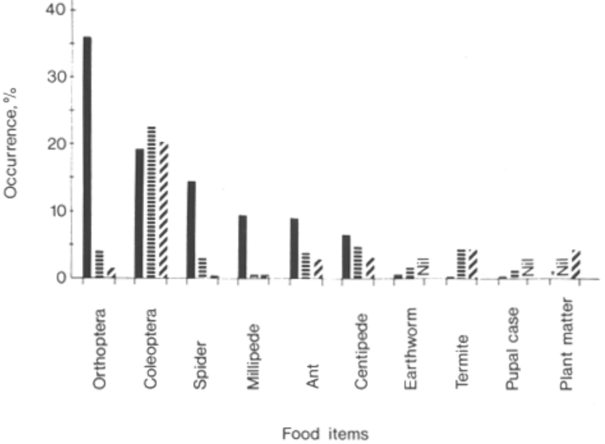

Fig. 43: Potential food availability in the leaf litter and soil (solid bars) and diet of *R. chrysopygus* (broken, horizontal bars) and *P. tetradactylus* (broken, diagonal bars) in the coastal forest. + = undetermined occurrence. Percentages on the graph do not = 100 because only the more plentiful food items are considered and 52.3 % of the *Rhynchocyon* and 58.6 % of the *Petrodromus* stomach sample points were represented by either unidentifiable or no material

not eaten as often as the larger, slower, rarer ones. The relatively slow and/or large food items (earthworms, termites, coleopteran adults and larvae, and pupal cases) were found in the stomachs in greater proportion than their leaf litter occurrence predicted because of their greater *actual* availability. The only exception to this dichotomy was the large, slow millipedes, mainly the 2—5 cm long *Prionopetalum* sp. (Fig. 44).

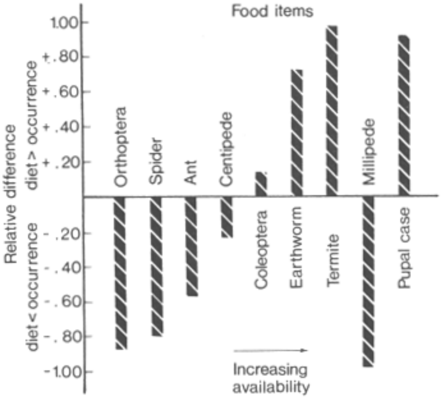

Fig. 44: Relative differences between % invertebrate leaf and soil occurrence and % stomach content occurrence for *R. chrysopygus* in the coastal forest. Negative values indicate the food item contributed a smaller proportion to diet than predicted by its leaf and soil occurrence. The invertebrate groups are subjectively ranked with the least available to the elephant-shrews at the left

Wood (1974) and Wood, et al. (1975) report that the millipedes, *Metiche tanganyicense* and *Prionopetalum frundsbergi,* from the Kenya coast produce "repellant" substances composed of various quinones. The accumulation of these compounds on captured and partially ingested *Metiche* may have eventually made them unpalatable to *R. chrysopygus,* thus explaining the observed partial ingestion of this millipede. *Prionopetalum* may likewise have been unpalatable and thus was not eaten as often as its leaf litter occurrence predicted.

Large quantities of soil, estimated at 5 % by volume, were found in the stomachs, probably a result of the elephant-shrew's feeding in the soil layer and residue from earthworm digestive tracts. No evidence of herbivory was found.

In order to determine whether there were any significant seasonal and sexual differences in diet, a 3 factor (sex, season and food item) analysis of variance was carried out on normalized (arcsine transformation) data (Sokal and Rohlf 1969). None of the factors were found to be different ($p > 0.2$).

B. *Elephantulus rufescens*

1. *Foraging behaviour*

Foraging activity of *E. rufescens* lasted from a few s up to 5 min and was separated by bouts of trail cleaning, scratching, resting, and alert pauses. Some of the foraging was done off the trail system, but normally no further than 1 m. I once saw a ♂ foraging in some dense leaf litter nearly 3 m from a trail, but this was unusual. Most foraging was done along the edges of trails and in the numerous 1—2 m diameter barren areas in the habitat. In leaf litter, which was not continuous, the nose was used as a probe while the forefeet cleared obstructing leaves and twigs. The extremely rapid in-and-out flicking of the tongue was easily observed when animals foraged in the barren areas on small black ants (Formicidae) or on the harvester ants (*Pheidole* sp.) emerging from their volcano-shaped holes in the soil.

Only twice were prey captured that required more than a single bite or tongue flick for ingestion. A subadult once encountered a live scorpion (superfamily Scorpionoidea) on a barren spot and killed it, with difficulty, by making 15—20 quick rushes at the prey, biting it, then retreating some 8 cm and pausing for 2—3 s before repreating the rush-bite sequence. After the scorpion was motionless, the elephant-shrew turned its head to one side and took the prey into the side of its mouth and proceeded to chew it up, ineffectually clawing the pieces hanging from its mouth with a forefoot. A toss or death-shake were never observed in this or any other feeding sequence.

Of 5 cases of chasing flushed prey items (small spiders and flying or hopping insects), 3 were successful. The escaping prey appeared to be caught with a tongue flick or a quick bite, but not pinned with a forefoot.

During the 2 wet seasons at Bushwhackers, the common bush, *Premna resinosa,* fruited for about 2—3 weeks. The fruits, which were dark mauve, round, and about 4 mm in diameter, dropped to the ground when ripe and were eaten by several birds as well as *E. rufescens.* When eating the fruits (drupes), the elephant-shrews could be heard up to 10 m away, loudly chewing up the pips. During the fruiting period the elephant shrews' normally dark grey or black dung became a dark, glossy, mauve colour due to the diet. No other vegetation was seen to be eaten by free-living *E. rufescens.*

The termite genera *Macrotermes* and *Odontotermes* were characterized by periodic, localized surface activity which resulted in large portions of the dead ground litter and dead twigs on low bushes being covered with their earth foraging tunnels. The termites' activity was mainly at night, but often extended into the morning and afternoon, and when overcast, into mid-day. These out-breaks were localized and their boundaries were easily determined by the extent of the earthworks and the sounds of the foraging termites themselves. An estimated $^1/_3$ of the elephant-shrews' foraging time was spent on termites. The earthen tunnels were broken open either with a forefoot or by biting with the front of the mouth. The exposed termites were rapidly flicked up as they came out of their tunnels or were ingested with the long tongue while still inside their tunnels. Large numbers of smaller termites, such as *Microtermes,* also were taken from under leaves and small branches on the ground.

Between 06.17 and 07.35 h and 16.35 and 18.20 h on 17 September 1974, I observed a foraging outbreak of *Odontotermes* which covered an area of 28.1 m^2. Except for 17 min in the morning, Red ♀ was in sight all of the time and was continuously within the boundaries of the *Odontotermes* outbreak. She rested or slept for 10 min between 17.10 and 17.20 h, but otherwise foraged and had aggressive encounters with her young, Brown ♀ (one encounter), and her mate, Yellow ♂ (3 encounters), and 2 bird species; the grey Wren Warbler, *Calamonastes simplex* (3 encounters), and the d'Arnaud's Barbet, *Trachyphonus d'arnaudii* (one encounter). These attacks were precipitated by the attempts of these animals to enter the termite outbreak area and feed. The area which included all of the foraging and aggressive activities of Red ♀ corresponded almost exactly to that of the *Odontotermes* surface activity and there is no doubt that she was defending it. In 6 other cases I clearly observed termite concentrations being temporarily defended within the larger territorial areas of pairs.

Of 33 intraspecific food-related aggressive encounters, 31 involved aggressor ♀♀ and 2 involved aggressor ♂♂, a significant difference ($p < .001$; χ^2

test). Of all the food-related interspecific aggressive encounters involving adult elephant-shrews, 41 were by ♀♀ and 5 by ♂♂ (Tab. 9), also significant ($p < .001$, χ^2 test). Observations of Betalight tagged individuals indicated that defense of termite outbreaks may occur more frequently during the night than the day. This is expected, as the termites were mainly nocturnal.

Table 9: Interspecific aggressive encounters for *E. rufescens* at Bushwhackers

Pursued species	Number of encounters in relation to:			Estimate of density on 1600 m²
	Food	E - shrew young	Shelter	
Grey Wren Warbler *Calamonastes simplex*	30	0	1	3 - 4 pairs
D'Arnaud's Barbet *Trachyphonus darnaudii*	19	1	0	2 pairs
Slate-coloured Boubou *Laniarius funebris*	13	0	0	2 pairs
White-winged Scrub Robin *Erythropygia leucoptera*	1	0	0	1 pair
Sprosser *Luscinia luscinia*	1	0	0	2
Skink Lizard *Mabuya* sp.	0	1	0	2
Speckled Sand Snake *Psammophis punctulatus*	0	3	0	0.25
Total	64	5	1	
Elephant- shrew aggressor				
Adult ♀♀	41	4	0	
Juvenile ♀♀	12	0	0	
Adult ♂♂	5	1	1	
Juvenile ♂♂	6	0	0	
Total	64	5	1	

2. *Diet*

18 *E. rufescens* stomachs were analyzed (8 ♀♀, 10 ♂♂), 8 from the dry season in August 1974 and 10 from the wet season in November 1974. Comparing the stomach contents with the leaf litter fauna shows that 16 invertebrate groups were potentially available to the elephant-shrews and of these, 9 were not found in the stomach contents. 4 of the 9 were each represented by less than 0.5 % of the total invertebrates (isopods, snails, pupal cases and mites), while the remaining 5 represented 20.8 % of the invertebrates (hemipterans, lepidopterans, silverfish, millipedes and false scorpions). Only egg cases, 0.1 % of the stomach sample points, were not found in the leaf litter.

In comparing the mean % occurrence of the more plentiful invertebrate groups in the leaf litter with the mean % occurrence of the invertebrates in the stomachs, some differences are seen, with only the termites being eaten in greater proportion than their leaf litter occurrence would predict. Ants, orthopterans, coleopterans, spiders and silverfish were eaten in smaller proportion than their occurrence predicts (Fig. 45). A Spearman rank correlation

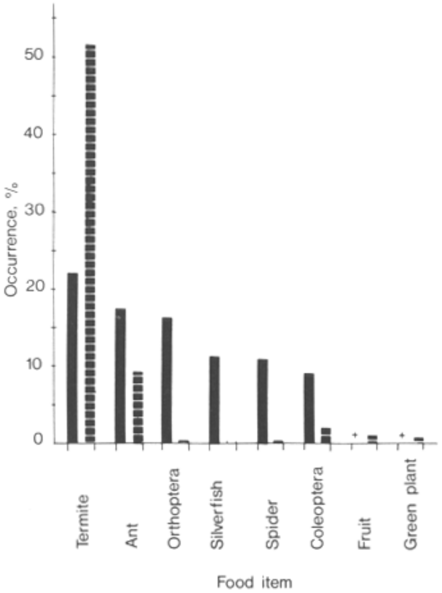

Fig. 45: Potential food availability in the leaf litter (solid bars) and diet of *E. rufescens* (broken bars) at Bushwhackers. + = undetermined occurrence. Percentages on the graph do not = 100 because only the more plentiful invertebrates are considered and 33.7 % of the stomach sample points were represented by either unidentifiable or no material

coefficient test of these two series is insignificant ($p > .05$), indicating that there was no correlation, and therefore some degree of food selection probably occurred. Considering the feeding behavior of *E. rufescens,* termite selection certainly occurred. The other prey items would be expected to be eaten in smaller proportions than their leaf litter densities predict, because they would be ingested only when encountered incidentally, if at all. This may explain the differences between stomach and leaf litter occurrences in ants and coleopterans. As was pointed out for *R. chrysopygus,* orthopterans and spiders are highly mobile and are not as available as their % occurrence indicates, thus the low consumption of these 2 groups. The silverfish, being very swift and delicate, were probably unidentifiable if they were ingested. The other invertebrate groups were either very rare or very small and so unless selected for, they may not have contributed enough to the diet to show up in the analysis.

Green plant tissue and fruits were found in 7 of the stomachs, but in small proportion (1.9 %) compared to the invertebrate material. Non-food items, such as hair, feathers, small stones and twigs, were identified in 0.6 % of the stomach sample points.

In comparing the diet of ♂♂ and ♀♀, the only 2 food items with large differences were beetles; 3.6 % and 0.5 %, respectively, and *Premna* fruit; 2.0 % and 0 %, respectively. Although these differences are not great, they support the observations of female food defense (see above). ♂♂, being deprived of termite sources by the aggressive ♀♀, may have been forced to rely more on other food items.

A comparison of seasonal diets reveals no large differences, although there is an interesting reversal in the termites. During the wet season termites formed a greater proportion of the litter invertebrates than in the dry season, 27.3 % and 10.2 %, respectively, yet their diet figures for the same seasons were 48.0 % and 56.5 % respectively. This may have been due to the greater diversity and availability of other food items during the wet season, such as green plants and fruits, thus reducing the elephant-shrews' reliance on termites. As expected, vegetable matter was eaten in greater quantities during the wet season.

An analysis of variance of these 3 factors (season, sex and food items) was not significant in any combination ($p > 0.2$), thus the differences may be due to normal variation or the small sample sizes.

C. *Petrodromus tetradactylus*

No feeding observations of free-living *Petrodromus* were made, but based on limited observations of captives, they were similar to *E. rufescens.*

27 *Petrodromus* stomachs were collected (12 ♀♀ and 15 ♂♂) from the same habitat at the coast as the *R. chrysopygus* specimens. The invertebrate groups eaten by *Petrodromus* were the same as those consumed by *R. chrysopygus*, except for earthworms, which required soil excavation for which *Petrodromus* was not morphologically equipped. Invertebrate egg cases (only 0.04 % of the *Petrodromus* stomach sample points) made up 0.1 % of the leaf litter invertebrates and were not eaten by *R. chrysopygus.* The remaining invertebrate groups were consumed by the two elephant-shrews similarly, the largest difference being spiders. *Petrodromus* utilized this group much less than *R. chrysopygus* (Fig. 43), perhaps as a result of the already mentioned unavailability of the small, swift, leaf-litter-dwelling spiders compared to the larger, slower soil-dwelling types. *Petrodromus* was not equipped to pursue the latter because of its unspecialized forefeet compared to *R. chrysopygus.*

Petrodromus had a fairly high proportion of plant material in its stomachs (4.6 %), composed about equally of green tissue and seeds. A very small proportion (0.9 %) of the stomach contents was non-food materials, such as twigs, hair, feathers and stones.

D. Invertebrate faunas

For this comparison a full year's monthly sampling was used for the coastal forest and the wet and dry season samples were used for Bushwhackers. In order to reduce the effects of the different sampling techniques used at each study site, the combined Bushwhackers samples were used (see Section III, B, 2).

Comparing the mean densities and biomasses, it is evident that the Bushwhackers area had a greater density of potentially available invertebrates than the coastal forest areas; 161.2 and 33.0 individuals/m^2, respectively. The biomass densities for Bushwhackers and the coast were more similar; 1.42 and 1.12 gm/m^2, respectively. This indicates that the average invertebrate size at the coast was larger than at Bushwhackers. This was mostly due to the greater contribution made by termites (small, but numerous) at Bushwhackers, and orthopterans (large and relatively less numerous) at the coast. The seasonal difference in invertebrate density was greatest at Bushwhackers, with a dry season figure of 98.0 individuals/m^2 and a wet season density of 222.0 individuals/m^2. The corresponding figures for the coast were 31.6 and 51.6 individuals/m^2.

These data are consistent with the greater climatic and habitat seasonality at Bushwhackers as compared to the coastal forest. The rainfall, and thus habitat, at Bushwhackers (DWA Plantations data) was less predictable than that at the coast, as indicated by the mean of each month's coefficient of variation; 137.9 % and 117.3 %, respectively.

Assuming the sampling techniques were not greatly affecting the variances of the means from the 2 areas (the rationale for combining the invertebrate samples from Bushwhackers), the invertebrates were less homogeneously distributed at Bushwhackers than in the coastal forests. This is demonstrated by a comparison of the coefficient of variation figures for densities; 77.7 % and 66.4 %, respectively, and a variance ratio test ($p<0.05$). These data are supported by the highly clumped distribution of foraging termites, and the greater seasonality and heterogeneity of the habitat at Bushwhackers compared to the coastal forest.

If one compares the invertebrate groups forming the principal diet of each species of elephant-shrew (termites for *E. rufescens* and beetles for *R. chrysopygus*), the differences in prey homogeneity between the two habitats are even more pronounced than the general invertebrate faunas.

VII. Interspecific Ecology

A. Predation

1. Rhynchocyon chrysopygus

At Gedi Ruins, only 2 predation attempts on elephant-shrews were observed, not including those of man. A Southern Banded Harrier Eagle, *Circaetus fasciolatus,* was seen carrying a known juvenile (Y-4) in its talons. On another occasion, an unidentified diurnal raptor, possibly a Harrier Eagle, swooped down and chased an adult (? Ragged-ear ♀) for 50 m. The elephant-shrew, running at full speed in a straight line, escaped by heading into a patch of undergrowth and freezing. In order to demonstrate the swiftness of *R. chrysopygus* locomotion, I tethered and ran with a captive. Its maximum speed was estimated at about 7.5 m/s (27 km/h). Based on ciné film taken of 3 tethered individuals, they used a half bound gait (rh = lh, rf, lf) (RATHBUN 1973).

I examined over 50 Barn Owl *(Tyto alba)* pellets and 27 genet (*Genetta* sp.) fecal boli from Gedi Forest and found no remains of *R. chrysopygus.* A single *Petrodromus* milk tooth molar was found in one genet bolus. Although other carnivores were present at Gedi (Egyptian Mongoose, *Herpestes ichneumon;* Slender Mongoose, *Herpestes sanguineus;* and White-tailed Mongoose, *Ichneumia albicauda*), I do not believe any of the mammalian predators captured *R. chrysopygus* frequently.

No encounters were seen between the elephant-shrews and the numerous potential reptilian predators at Gedi (Monitor Lizard, *Varanus* sp.; Black Mamba, *Dendroaspis polylepis;* Forest Cobra, *Naja melanoleuca;* Spitting Cobra, *Naja nigricollis;* Python, *Python sebae* and Puff Adder, *Bitis arietans*). JACKSON IHA (pers. comm.), curator of the Nairobi Snake Park, caught a Black Mamba at Gede town with a *R. chrysopygus* in its digestive tract, indicating that reptiles may have occasionally preyed on Gedi elephant-shrews.

The Giriama people along the northern coast of Kenya hunt both *Rhynchocyon* and *Petrodromus* for food using snares and they probably have a considerable effect on local populations. This is especially true of *Petrodromus,* which is preferred and easier to snare.

Judging from the Golden-rumped Elephant-shrew's reaction to disturbances, its senses are very keen. At the slightest unusual sound or sight, it froze and cautiously sniffed the air (Fig. 46). After a disturbance or potential predator passed, *R. chrysopygus* walked quietly away and continued its activity. If a predator was close and obviously aware of its presence, then 1 of 3 things happened. The elephant-shrew either (1) slowly walked away while loudly slapping its tail on the leaf litter every 1—3 s; (2) ran away in a gait that was very similar to the stotting of gazelle; or (3) ran away in its typical, swift, cursorial bounding gait. While stotting or bounding, it hammered the leaf litter loudly with its rear feet, producing a very characteristic "crunch, crunch, crunch" sound as it fled. After running 10—15 m, the elephant-shrew stopped and froze. Depending on the predator's action, it then either began to forage or took one of the evasive actions just described. If suddenly and violently

Fig. 46:
Adult *R. chrysopygus* sniffing the air

disturbed, an elephant-shrew immediately took flight. If a pair or a ♀ and her newly emergent juvenile were disturbed, they fled in different directions.

On several occasions tail slapping or rear foot hammering elephant-shrews that were out-of-sight caused individuals under observation to become alert or even to take flight, which suggests that these behaviours may serve as intraspecific predator warning signals.

The response of *R. chrysopygus* to being captured and handled was rather atypical of a predatory animal, for they never attempted to bite defensively. They would alternately be passive and then burst into a violent bout of struggling and kicking, a behaviour often resulting in claw wounds and in effecting escape from one's hands. Some captured individuals screamed loudly, similarly to a rabbit's distress cry.

2. *Elephantulus rufescens*

While at Bushwhackers, 5 instances of Speckled Sand Snake *(Psammophis punctulatus)* predation attempts on *E. rufescens* were observed. One of these was successful, when the snake managed to capture and ingest a 1—2 day old elephant-shrew. Other potential reptilian predators included the Monitor Lizard, Spitting Cobra and Puff Adder, although none of these were known to prey on the elephant-shrews.

There were numerous potential mammalian predators in the area, including jackals, *Canis* sp., and various viverrids and felids. I examined about 20 Genet *(Genetta tigrina)* fecal boli and found no elephant-shrew remains. On several occasions I observed *E. rufescens*' reaction to the presence of a Slender Mongoose, but I never saw this predator hunt elephant-shrews.

Birds-of-prey were also numerous, but I found no evidence of those species most likely to prey on elephant-shrews doing so (Pale-chanting Goshawk, *Melierax poliopterus;* African Goshawk, *Accipiter tachiro;* Verraux's Eagle Owl, *Bubo lacteus;* and the Pearl-spotted Owlet, *Glaucidium perlatum).* In the Serengeti National Park, Tanzania, the Barn Owl infrequently feeds on *Elephantulus.* LAURIE (1970) found 0.8 % of the owl pellets (n = 346) contained elephant-shrew remains. Barn Owls were not seen in the Bushwhackers area.

The elephant-shrews' reaction to Slender Mongooses and their initial reaction to me (before they became habituated in 3—4 weeks) can be used to summarize their generalized anti-predator behaviour. The first reaction of *E. rufescens* to an approaching predator was to remain immobile, but if closely approached they ran away swiftly. After fleeing, they returned within 30—60 s by a different route and while maintaining a safe flight distance, loudly drummed one or both rear feet on the ground. This resulted in a "prrrr, prrrr, prrrr" sound which attracted other members of the territory to the disturbance. Between bouts of drumming the elephant-shrews darted towards and around the predator, keeping the predator in view and within a safe flight distance.

Mobbing continued until the predator moved out of the territory. On one occasion, when a pair mobbed a Speckled Sand Snake, one of the 2 elephant-shrews made a very aggressive rush towards the metre-long snake and stopped just short of making actual body contact with the retreating reptile. *E. rufescens* also reacted to the warning calls of birds and the warning whistles of Dik-dik, *Madoqua kirki,* by becoming very alert, facing the direction of the warnings, and slowly moving towards the disturbance.

I spent 7.5 h observing a newborn elephant-shrew, which was crouched at the base of a *Combretum* bush 10 m away. The ♀ was nervous at my proximity and on her periodic visits to the area she faced me and softly drummed for a few s before leaving again. She finally approached the juvenile at 18.25 h and took it by the skin of the back or neck and carried it away. I believe that the ♀ moved her juvenile away from me as a potential predator.

Twice when pairs had neonates somewhere on their territories and a Speckled Sand Snake appeared, the pair mobbed the snake as described, but every few min the ♀ left for 30—60 s, always going and coming from the same direction. From several observations I strongly suspect that when predators approach a neonate too closely the ♀ moves her young to a safer area of the territory and periodically interrupts the mobbing activity to check it while the ♂ continues mobbing and distracting the predator.

One of the Speckled Sand Snake predation attempts on *E. rufescens* is of particular interest because it demonstrates the importance of the elephant-shrews' keen senses, swift locomotion and trail network in escaping predators. The pair, Red ♀ and Yellow ♂, and one of their 8-day-old twins were all resting or sleeping within 2 m of each other (a rare situation) in the shade of a low *Barleria* bush at 15.15 h. The snake appeared some 4 m away and slowly approached the elephant-shrews, pausing every few cm for 1 or 2 min before moving closer. When the snake was about 1 m from the resting animals, all the elephant-shrews suddenly fled down trails in 3 different directions with the snake in pursuit of one of them. The speed at which this all took place was too fast for immediate comprehension, but during the next min, amid much drumming and darting about, all 3 elephant-shrews were accounted for as they mobbed the snake, which slowly moved away without further attempts to attack the very alert and active elephant-shrews.

B. Commensalism

Foraging parties of birds were frequently seen in the Gedi Forest and on 9 occasions they included 1 or 2 *R. chrysopygus*. I believe the birds were attracted to the elephant-shrews' activity, because in all cases the elephant-shrews were passive participants, neither attracted to nor agonistic towards the birds.

The Red-capped Robin-chat, *Cossypha natalensis,* was a common seasonal (May through November) resident of the forest floor with an estimated density of about 4 individuals/ha. At Gedi the robin-chat foraged in the leaf litter, in the low vegetation and also in association with *R. chrysopygus.* The birds followed foraging elephant-shrews and hawked flushed insects or foraged on recent feeding or nest excavations. In the months of September, October and November 1971, I made 827 pair or individual elephant-shrew observations and in 63 cases (7.6 %) a robin-chat was within 1 m of an elephant-shrew. In addition to being physically close to the elephant-shrews, the birds were intensely interested in the foraging or nest building activity and often approached to within 15 cm while watching for flushed prey. Of 155 observed associations, agonistic behaviour was only once shown towards a bird and *R. chrysopygus* never reacted to the birds' warnings. The relationship was commensal, the elephant-shrews neither benefiting nor being harmed by the association.

VIII. Life History Traits from the Literature

Zoogeographically and morphologically, the Macroscelidea is an exceedingly well-defined taxon (Corbet and Hanks 1968), which lends itself well to life history comparisons, especially since different species within the taxon have radiated into the extremes of terrestrial habitats: tropical forest, semi-arid bushlands, boulder fields, and deserts. My studies include species that occupy the first two habitats. Life history data published on other species, especially the desert dwelling *M. proboscideus,* are thus of special interest for comparative purposes (see Discussion, Section IX).

A. *Rhynchocyon* species

"While it was not unusual to hear these elephant-shrews scratching aside the fallen leaves in search of insects, they were very timid and rarely exposed themselves. On one occasion in the Matipa Forest, however, my gunbearer, slashing a way through the undergrowth with his machete, was ascending the mountain side above me. I was some distance below him, engaged in searching beneath a log I had overturned, when an elephant-shrew, doubtless disturbed by the gunbearer, came racing down the hillside so fast that the noise of its flying feet on the carpet of dead leaves made a single continuous rushing sound like that produced by a startled snake. Though the animal passed quite close to me and in full view for 20 feet, all I saw was a brown streak, the handsome cream-colored markings being quite indistinguishable." This is Lawrence and Loveridge (1953) commenting on a *R. cirnei* on the Nyika Plateau, Nyasaland.

The chequered elephant-shrew, *R. cirnei,* apparently is diurnal and constructs a nest similar to that described for *R. chrysopygus* (Allen and Loveridge 1927, 1933; Brown 1964). It feeds mainly on invertebrates, especially insects (Lawrence and Loveridge 1953; Ansell and Ansell 1973). Based on 4 records from Uganda and Zambia, *R. cirnei* has a litter of 2 (Lawrence and Loveridge 1953; Brown 1964; Ansell and Ansell 1973), but a specimen of *R. c. shirensis* in the British Museum of Natural History that was collected on Mlanje Mountain, Malawi, at 6,300 feet on 3 January 1932 has a label with the remark: "3 foetuses removed and preserved in spirit" (G. Corbet, pers. comm.). Kingdon (1971) cites Ionides as having found *Rhynchocyon* (? *R. cirnei)* killed by Gaboon Viper, *Bitis gabonica,* and Forest Cobra, *Naja melanoleuca.*

I have watched single *R. petersi* foraging, similarly to *R. chrysopygus,* during the day in the Diani Forest, south of Mombasa, Kenya. TRIPP (1971) records 2 embryos from a preserved specimen.

It is generally thought that the 3 species of *Rhynchocyon* are similar in their life histories; their colouration perhaps being their most distinctive variable feature. KINGDON (1974) considers the different forms of *Rhynchocyon* as subspecies of *R. cirnei.*

B. *Elephantulus* species

There are numerous short publications and references on the different species of *Elephantulus* and many of these are contradictory, but there are some patterns which are discernible in certain species and there is a high degree of overall similarity in the life history traits within the genus.

TRIPP (1970) considers *E. myurus, E. intufi,* and *E. rozeti* polycyclic and judging from the contradictory accounts of the activity periods in the literature for all species of *Elephantulus,* they are probably all polycyclic (see BROWN 1964, for a literature review).

E. rufescens apparently makes and uses trails throughout its range, even where the vegetation is not particularly dense (LORRING in ROOSEVELT 1910; HOOGSTRAAL 1950; BROWN 1964; J. SALE and B. NEAL, pers. comms.; pers. obs.). This elephant-shrew seems to be the only one which makes extensive use of trails, although TRIPP (1970) describes trail cleaning behaviour in captive *E. intufi.*

All *Elephantulus* species occupy arid and semi-arid habitats. *E. myurus* is apparently restricted to rocky outcrops, or kopjes, where it shelters among the boulders and crevices (HORST 1946; CRITCH 1969; TRIPP 1972). *E. brachyrhynchus,* which has the widest range, lives in burrows (SHORTRIDGE 1934; TOSCHI 1949; BROWN 1964; RANKIN 1965). SHORTRIDGE (1934) indicates *E. rupestris* and *E. intufi* also inhabit burrows, as does *E. rozeti* (CABRERA 1932). There are no reports of nests for any Macroscelidinae and WALKER (1955) and TRIPP (1971) comment on captive *E. rufescens* refusing to use nest material.

E. myurus of southern Africa apparently scent marks with a subcaudal or perineal gland, creates dung piles, is intraspecifically aggressive, foot drums, and scratches, grooms and sand bathes similarly to *E. rufescens* (CRITCH 1969). TRIPP (1970) reports that both *E. intufi* and *E. rozeti* drum their rear feet.

There is general agreement in the literature that most species of *Elephantulus* eat mainly ants and termites (see BROWN 1964, for a review). Plant matter is utilized to a limited extent by at least *E. rufescens, E. intufi, E. myurus, E. brachyrhynchus* and *E. rozeti* (SHORTRIDGE 1934; HOOGSTRAAL 1950; RANKIN 1965; CRITCH 1969; TRIPP 1970).

Nearly all species of *Elephantulus* have precocial litters of 1—2 (HOLLISTER 1918; SHORTRIDGE 1934; BROWN 1964; RANKIN 1965; CRITCH 1969; TRIPP 1970, 1971) except *E. rozeti* which has been reported to have up to 4 embryos (TRIPP 1970, 1971).

E. intufi from southern Africa, with a mean body weight of 49.2 g, has a gestation period of about 51 days, a mean neonatal weight of 10.0 g, and a postpartum estrus. The young increase in weight by about 1 g a day (TRIPP 1972).

C. *Petrodromus tetradactylus*

Individually housed *Petrodromus* (1.2 x 2.4 m cage with a 12-h artificial light cycle) at the National Zoological Park in Washington. D. C. (RATHBUN, research in progress) exhibit diel activity patterns very similar to those of

E. rufescens at Bushwhackers (Fig. 18). Major activity peaks occur just prior to "day-break" and just after "night-fall." Between these two peaks there is a decrease of activity during the night, with a slight peak at mid-night. Minimal activity occurs during the day, with a very slight peak at mid-day. *Petrodromus,* like *E. rufescens,* is polycyclic (Tripp 1970; Rathbun, pers. obs.).

Petrodromus builds an extensive trail network similar in appearance to that of *E. rufescens* (Ansell and Ansell 1969 a; Rathbun, pers. obs.). Comparing captive *Petrodromus* and *E. rufescens* at the National Zoological Park, the former is less fastidious about making and maintaining trails through the wood-chip cage substrate.

Tripp (1970) and Ansell and Ansell (1969 a) indicate *Petrodromus* takes refuge in burrows and hollow tree trunks when pursued. A pair, which I kept in a 4 m diameter pen in the forest at Gedi, often retreated, when disturbed, into a 30 cm deep burrow, which I built for them. They did not sleep or use nest material in the burrow. Captives at the National Zoological Park also retreat into shelters when disturbed, but prefer to sleep and rest outside, and often on top, of the wood tunnel shelters. In connection with this behaviour, the animals always appear alert. They never lie down on their sides and apparently only very rarely (if at all) close their eyes completely.

When animals of the same sex are confined together, they fight by rearing up on their hind legs and attempt to bite and strike one another with their front feet.

Petrodromus grooms, scratches and face-washes just like *E. rufescens* and also foot drums similarly (Ansell and Ansell 1969 a; Tripp 1970; pers. obs.).

During one week of sooted-card tracking near Gedi Forest, Betty Eidemiller (pers. comm.) tracked a toe-clipped adult individual and apparently one other unmarked adult animal on the same trail network. The overall impression I have, based on occasional observations of free-living and captive animals and the literature, is that *Petrodromus* is probably paired on overlapping home ranges of at least 1 ha in area.

Loveridge (1922) examined some *Petrodromus* stomachs from Tanganyika and concluded that the diet was composed mainly of ants and termites. A similar conclusion was arrived at by Sheppe (1973) after examining dung in Zambia. Ansell and Ansell (1969 b) commented on two stomach contents of *Petrodromus* from Zambia as containing invertebrates and "... also plant material consisting of small leaflets, rootlets and some seeds, not definitely identifiable, but possibly *Acacia nilotica.* ... both (stomachs) seemed to contain a noticeable percentage of plant matter." Tripp (1970) writes of *Petrodromus:* "... incidental observations of stomachs and droppings indicated that the diet consisted largely of insects, but considerable proportion (up to about 40 %) of vegetable matter appeared to be eaten."

In Kenya I found *Petrodromus* (n = 8) had a litter of one, which is the same as Tripp (1971) found in specimens (n = 9) from northern Natal. Brown (1964) reviewed the published litter sizes and all 17 records were for single births. Sheppe (1973), however, records a specimen from Zambia with 2 embryos. The young are born in a highly precocial state (Tripp 1972).

These data indicate *P. tetradactylus* has a life history similar to that of *E. rufescens.*

D. *Macroscelides proboscideus*

E. G. F. Sauer's 1973 paper is the last of 4 which he, with Eleonore M. Sauer on 2 occasions, has published on the short-eared elephant-shrew, *M. proboscideus.* It is based on field studies in the Namib Desert in Southwest

Africa during December 1969, July and August 1970, and December through March 1972. Although this is a total of 7 months, the longest continuous period of study was a maximum of 4 months. SAUER apparently did not mark elephant-shrews for individual recognition nor does he provide any evidence that he could individually identify animals, except for a statement that he successfully used behaviour to determine sex. ROSENTHAL (1975) carried out a behavioural study of captive *M. proboscideus* at the Lincoln Park Zoological Garden, Chicago, Illinois, which along with SAUER's (1973) material forms the basis for the following life history summary.

This elephant-shrew is polycyclic, with the majority of its activity restricted to dawn, dusk and night. It spends most of the day in a rock shelter, gerbil burrow, or self-excavated burrow. The temporal pattern of shelter use is similar to the nest-use pattern of *R. chrysopygus*.

Macroscelides builds and maintains an extensive trail network, which interconnects its numerous rock shelters and burrows with its invertebrate feeding grounds. The behaviour patterns used to construct the trails are very similar to those *E. rufescens* uses. SAUER (1973) claims *Macroscelides* can run along the trails at a speed of 5.5 m/s (20 km/h).

CORBET and HANKS (1968) indicate a subcaudal gland is present and ROSENTHAL (1975) describes scent-marking behaviour, but SAUER (1973) makes no mention of the scent gland nor marking behaviour.

Snakes, raptorial birds and small carnivorous mammals are potential predators and the animals' escape pattern involves swift flight along a trail into a shelter or burrow. Apparently this species does not foot drum.

Macroscelides feeds principally on invertebrates, but supplements this diet with plant matter when available.

The single or pair of highly precocial young are born in a shelter separate from the female and male shelters and no nest material is used. The juveniles are visited for short sessions of nursing and feeding at dusk and during the night; a pattern that led SAUER to use the term "♀ absentee system" for this elephant-shrew. MARTIN (1968) used this term to describe the tree-shrew (Tupaiidae) system of infrequent, minimal maternal care towards highly *altricial* juveniles. I do not think the elephant-shrew and tree-shrew systems are, as SAUER (1973) implies, analogous or homologous. Apparently the female *M. proboscideus* provisions her young with masticated invertebrates, which she gathers in cheek pouches. ROSENTHAL does not describe this behaviour in his captive breeding pairs.

SAUER (1973) considered that free-living animals typically occupied individual, undefended home ranges of about 1 km². During periods of sexual inactivity the animals lived a solitary life and during mating periods ♂♂ were free to successively mate with numerous ♀♀. The mother-family was the only known family unit and the most complex group SAUER (1973) found. ROSENTHAL (1975) kept his animals as permanent pairs and achieved a high degree of breeding success.

SAUER's (1973) descriptions of *M. proboscideus* behaviour, if considered without his terminology and conclusions, agree with ROSENTHAL's (1975) descriptions and are very similar to my observations of *E. rufescens* behaviour, which suggests that *M. proboscideus* and *E. rufescens* have a very similar social structure: Monogamous pairs that interact at low frequencies but occupy overlapping, and possibly congruent, home ranges that are probably defended against other adults. SAUER (1973) continually hints at pair associations, but apparently due to the low interaction frequency of pairs, he concluded that the animals were solitary, and inhabited individual home ranges. SAUER's descriptions (1973) of aggressive behaviour not only suggest territorial defense, but possibly sexspecific defense. ROSENTHAL (1975) interprets observations of his animals' aggressive and scent-marking behaviours as probably being related to territoriality.

The diverse habitats the Macroscelidea occupy and the overall conformity in life history traits that species in this old taxon exhibit suggest a considerable amount of evolutionary inertia (MAYR 1970). This principle has also been implied as a factor resulting in life history similarity within other taxa, such as the hystricomorph rodents (ROWLANDS and WEIR 1974), canids and felids (KLEIMAN and EISENBERG 1973) and primates (STRUHSAKER 1969; EISENBERG, MUCKENHIRN and RUDRAN 1972). The similar and specialized morphology and reproductive biology among the different elephant-shrew species probably are important factors contributing to the inertia and much of the remaining life history conformity in the taxon (see Discussion Section D).

IX. Discussion

> "For almost every topic discussed in the following pages the data are insufficient. The student who attempts interpretations under these circumstances does so in the certainty that some of the conclusions will be rejected. It is, however, pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow. Indeed there would be no tomorrow for science if this common attitude were universal."
>
> GEORGE GAYLORD SIMPSON 1944

The way a species utilizes and distributes the limited, basic resources of time, energy and space between its life processes is its life history strategy, which is the result of natural selection and is therefore adaptive (GADGILL and BOSSERT 1970).

In this discussion I compare the forest-dwelling *R. chrysopygus*, bushland-dwelling *E. rufescens*, and, when sufficient data warrant, other elephant-shrew species, such as the desert-dwelling *M. proboscideus*. Suggestions are offered regarding the causes of some of the variations and similarities between the elephant-shrews' life histories.

Because of the complexity of comparing the adaptive nature of entire life histories, the comparison is subdivided into 3 sections: anti-predator, feeding and reproductive strategies. The discussion concludes with some speculation as to the elephant-shrew's relationship to other mammals.

A. Defense strategies

Both *R. chrysopygus* and *E. rufescens* use a swift cursorial gait to outdistance predators as a principal method of escape, but defense strategies differ considerably in other aspects.

R. chrysopygus spends the night in a well camouflaged nest, entirely concealed from visually oriented predators, but during the day it is completely exposed, only initially and very briefly attempting to be cryptic in the presence of a potential predator. Once detected and disturbed, it probably employs the opposite of concealment. SMYTHE (1970 a) proposes that some mammalian behaviour patterns exhibited by prey species are directed towards predators in an attempt to induce premature attack. These "pursuit invitation signals" include both visual and auditory displays, such as mobbing, stotting, short flight followed by a pause, rump patch displays and alarm calls. He suggests that a healthy individual can successfully escape a premature attack, and once a predator has failed, it often loses interest in the individual which may result from having lost the advantage of a surprise ambush. The occurrence of the rump patch, short flight followed by a pause, stotting, tail slapping and rear foot hammering of *R. chrysopygus* all support SMYTHE's hypothesis (RATHBUN 1978.). Although the pursuit invitation strategy may seem to be less than optimal, prey species whose life histories preclude them from adopting the presumably "fittest" anti-predator strategy (such as crypsis) must settle for "less fit" solutions (SCHOENER 1971). The diurnal, conspicuous feeding of *R. chrysopygus* prevents it from effectively using crypsis.

Elephantulus rufescens spends all of its time physically exposed, relying on cryptic behaviours and colouration to avoid detection by predators. Associated with this is the geographic variation in pelage colour which corresponds to the differences in soil colouration (KINGDON 1974), and the facial pattern that is probably disruptive and thus increases crypsis (EDMUNDS 1974). Although this elephant-shrew relies mostly on camouflage and then flight, its subsequent drumming behaviour towards disturbances also reduces predation, not only by serving as a warning signal but also by assembling other elephant-shrews within the territory for a mobbing effort. As in birds, mobbing tends to intimidate and drive small predators away. Drumming may also serve as a pursuit invitation signal towards large predators.

The temporal and spatial pattern of nest use by *R. chrysopygus*, rest/sleep-spot use by *E. rufescens* and burrow/shelter use by *M. proboscideus* are all similar and probably have evolved in response to the ability of predators to develop search images. The inconsistent and transitory use of these spaced sites (and the low density of the animals themselves) creates a pattern on which it is difficult for a predator to form and maintain a search image (CROZE 1970).

The 3 species of elephant-shrew use refugia to different degrees when pursued. *R. chrysopygus* and *E. rufescens* flee through dense thickets of vegetation. Only as a last resort do they retreat into holes in the ground, tree-trunks and fallen logs (HOOGSTRAAL 1950; WATSON 1951; BROWN 1964). *M. proboscideus* apparently flees more readily into rock shelters or burrows (SAUER 1973). This difference is probably related to the effect of the dense vegetation of the forest and bushland habitats on pursuing predators. SAUER (1973) probably is correct in also explaining shelter use by *M. proboscideus* as protection from the adverse desert climate.

The difference in trail use between *R. chrysopygus*, *E. rufescens* and *M. proboscideus* may be due to the differences in body size in relation to substrate obstructions. The larger elephant-shrew can easily run on top of the forest floor litter, whereas the 2 smaller species are not able to run on top of the grass, twigs, leaves and stones that litter the substrate in their habitats. This is supported by KINGDON's (1974) observation that *R. cirnei* in southern Tanzania uses trails in densely vegetated woodland situations and the apparent lack of trail-use by species of *Elephantulus* which occupy habitats where it would not be adaptive. For example, *E. myurus*, which lives among large boulders, builds no trails (SHORTRIDGE 1934; CRITCH 1969).

R. chrysopygus and *E. rufescens* have substantial amounts of energy invested in their territories in terms of the nests or trails that they have built and in maintaining their familiarity with the area. The occurence of territoriality is also probably associated with defending the resources that are important in their anti-predator strategies (EISENBERG 1966, FISLER 1969).

SAUER (1973) describes the maternal care system of *M. proboscideus* as an anti-predator adaptation. Likewise, *E. rufescens* and possibly *R. chrysopygus* exhibit a minimum of parental care, which reduces the attraction of predators, and thus predation, on young and parents. It is predictable that elephant-shrews, just as most ungulates (LENT 1974), exhibit minimal parental care (see Discussion Section C).

B. Feeding strategies

R. chrysopygus and *E. rufescens* are both behaviorally and morphologically adapted to feeding on small invertebrates, but the strategies appear to be different in terms of the amount of energy gained per food item in relation to the amount of energy spent in capturing each food item (SCHOENER 1971).

R. chrysopygus feeds exclusively on invertebrates, which in the coastal forest are a relatively low density resource uniformly dispersed in time and space. In order to gather sufficient energy, *R. chrysopygus* must spend much of its active time foraging, moving over all the available habitat within its territory in search of small individual food items. This affects its relationship to potential predators, as already discussed.

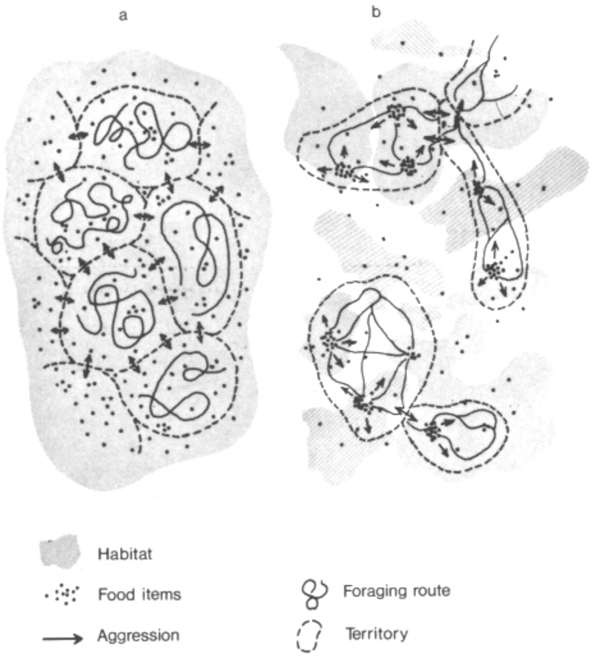

Fig. 47: Hypothetical diagrams of *R. chrysopygus* (a.) and *E. rufescens* (b.) foraging strategies

Because of the dispersed food resource, there is little advantage to an individual in expending energy in defending individual food items. This may partially explain the lack of intra-pair and parental-offspring aggression and the symbiotic relationship with the robin-chat. Inter-pair aggression may serve to space the pairs in relation to the overall food resource, thus assuring a supply of invertebrates for the adults and their young. The similarity of territory sizes and their stability are predictable in the relatively homogeneous habitat with its evenly distributed and temporally stable food supply (SCHOENER 1971) (Fig. 47).

When compared with the coastal forest, the habitat at Bushwhackers is more seasonal and heterogeneous, producing an invertebrate litter fauna which is characterized by a more patchy distribution and a wider seasonal fluctuation in numbers. This fauna is dominated by the concentrations of termites. These contribute greatly to the elephant-shrews' diet and because of the distribution little foraging time or energy is required after a concentration is located.

The importance of trails in utilizing a food resource efficiently has been suggested by Smythe (pers. comm.) in Agoutis, *Dasyprocta punctata,* which feed on clumped, temporary concentrations of fallen fruit in South American forests. The trail network of the Rufous Elephant-shrew is highly adaptive in terms of escaping predators, but may also serve to increase the efficient detection and utilization of invertebrate and fruit concentrations by allowing the animals to cover their entire territory easily and quickly. *E. rufescens* predictably spends a comparatively small proportion of its active hours conspicuously moving about in search of food. This is important when considering the animal's defence strategy. The significance of familiar trails in foraging by *M. proboscideus* has been discussed by Sauer (1973).

The temporally and spatially localized and presumably limited availability of food favours its defense by *E. rufescens.* Thus, inter-specific, intra-pair, and parental-offspring aggression is predictable (Schoener 1971). Inter-pair aggression may serve to space individuals and their progeny in relation to the overall food supply. The instability of the territories through time and the large variations in their size is probably associated with the spatially heterogeneous and temporally variable nature of the habitat and invertebrate fauna (Fig. 47).

The importance of cursorial locomotion in the elephant-shrews' anti-predator and feeding strategies has been described. If this trait is as critical to the animals' survival as it appears, then considerable individual advantage is to be gained by achieving the trait as soon after birth as possible; precocial births are probably a correlate of cursorial locomotion.

C. Reproductive strategy

Monogamy in the Mammalia is rare (Eisenberg 1966), occurring in only about 3 % of the species (Kleiman 1977). This is not surprising, as there is normally little advantage for a ♂ to invest large amounts of energy in a ♀ or young after insemination, and so a male mammal's strategy is usually to increase his reproductive success by being polygynous and mating with as many ♀♀ as he can (Orians 1969). Why then does monogamy occur at all?

Kleiman (1977), in her review of monogamy in mammals, approached the question mainly from a behavioural point of view and concluded that 2 forms of monogamy could be distinguished. Obligate monogamy is characterized by strong, frequent pair-bond behaviours, direct paternal investment in young, and older sibling assistance with parental duties. Examples include the Wolf, *Canis lupus,* the Beaver, *Castor fiber,* and the Lion Tamarin, *Leontopithecus rosalia.* Facultative monogamy is described as including few and infrequent pair-bond behaviours, little direct paternal investment and parental aggression towards maturing young. The Dik-dik, *Madoqua kirkii,* Acouchi, *Myoprocta pratti,* and Elephant-shrew, *Rhynchocyon chrysopygus,* are examples.

The Macroscelidea generally produce highly precocial young. There is little a father can do to directly assist a highly developed neonate, for it needs little more than milk, which the ♀ must provide. The lack of *direct* paternal investment in elephant-shrew young is probably a secondary effect of precociality. If the father is to invest any assistance, it will be *indirect.* In terms of paternal reproductive fitness, it makes little difference whether the investment is direct or indirect, since both require an expenditure of time and energy and both presumably increase the survivorship of progeny. The absence of older sibling assistance with parental duties is also probably related to the high degree of neonatal development as well as the fact that the parents and young have evolved an optimal resource utilization and reproduction strategy. Do the parents increase their reproductive fitness most by forcing their young out into the "cold, cruel, territorial world," so that the young, with luck, find a territory and reproduce? Or do they allow the juveniles to hang around and utilize their resources until a territorial vacancy arises? The evidence for the elephant-shrews suggests that food and/or shelter are important factors in deciding this question. The coastal forest provides abundant cover and a relatively homogeneous, constant food supply for *R. chrysopygus*. The parents do not drive their offspring away; instead they allow them to remain and wander "in search" of vacant territorial areas. The vegetation at Bushwhackers is less homogeneous and the invertebrates are more localized in time and space. There is probably a premium on these resources and the parents drive their older offspring away in favour of supplying the resources to their neonates.

Eisenberg, Muckenhirn and Rudran (1972) define the mammalian pair-bond as being characterized by ". . . social relationships between specific individuals based on performance of mutually reinforcing activities; in addition to mating behaviours. It follows then that grooming, huddling, and other nonsexual behaviours define the pair bond." The infrequent occurrence of pair-bond behaviours in the elephant-shrews is probably related to their precocial neonates. The offspring require minimal parental attention in terms of feeding, warmth, protection and grooming, thus they do not serve as a focus for maternal and paternal behaviours. Outside of mating, there is little need for ♂ or ♀ social activity and minimal selection favouring pair-bond interactions. The dispersed food resource and the elephant-shrews' feeding strategies reinforce their largely independent existence. This, however, does not mean a pair bond is absent. In all the species studied so far there is considerable scent-marking activity which perhaps plays a significant role in pair bond maintenance.

For elephant-shrews, cursorial locomotion is essential in avoiding predation and in foraging. This type of locomotion and its correlate of highly developed neonates may explain much of the elephant-shrews' reproductive strategy, especially facultative monogamy.

The question still remains as to why elephant-shrews are monogamous. The data available for the Macroscelidea seem sufficient to construct a preliminary, simplified model explaining why monogamy is adaptive to members of this taxon (Fig. 48). No single factor is sufficient to explain macroscelidean monogamy; it is a complex of environmental factors operating in conjunction with their distinctive phylogeny.

The tropical, African environment produces a condition of relative stability for the elephant-shrews, due mainly to the mild temperatures. This, in turn, allows a relatively constant food resource (invertebrates) to exist, even when the environment experiences definite seasonal rainfalls. These stable conditions are unique when compared to those found in most temperate environments and permit elephant-shrews to reproduce constantly throughout the year. The dispersed invertebrates and/or shelters are important factors resulting in the establishment of relatively large, dispersed territories. Under these conditions the most efficient strategy for a ♂ may be to establish an association with a single ♀ and ensure his presence when she comes into estrus,

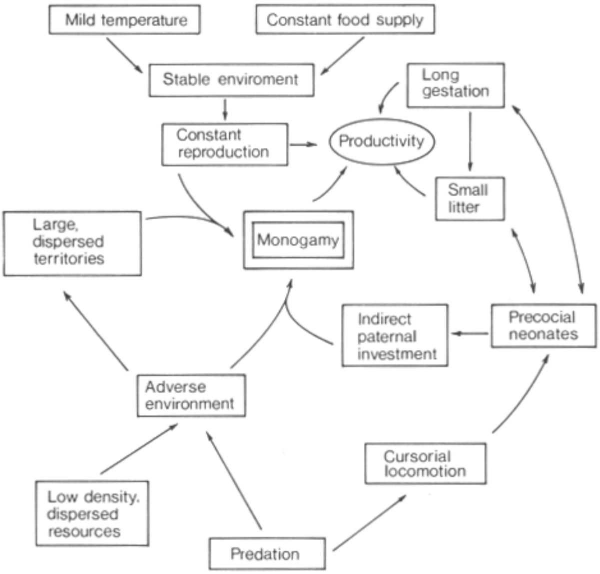

Fig. 48: Hypothetical flow diagram summarizing the relationships of some factors that influence the reproductive strategy of the Macroscelidea (see Discussion Section IX for a full explanation)

a frequent although brief event for these small, but relatively longlived mammals. This is exactly what the ♂♂ of both *R. chrysopygus* and *E. rufescens* appear to do, especially the former, where ♂♂ continuously attend ♀♀.

The environment has some aspects which may be considered adverse. The dispersed distribution of suitable shelters and/or invertebrates is such that they are probably a limited, essential resource. Many predators of the appropriate size might also be an adverse factor. The assistance by ♂♂ in overcoming these conditions may be necessary for the ♀♀ to successfully raise young to reproductive age (Eisenberg 1966; Wilson 1975). If this is true, then a ♂'s best strategy to increase his reproductive fitness is to remain with the ♀ he bred, ensuring that his young attain sexual maturity. The ♂♂ of *E. rufescens* invest considerable time and energy in building and maintaining a trail network, which is clearly of benefit to the precocial juveniles.

The sex-specific defense of the territories may be a refinement on the "defend-against-all" system. It increases individual reproductive success within a monogamous structure by allowing either animal to breed quickly with a new individual if a mate should suddenly disappear. When one sex is temporarily in short supply and pairs cannot be established immediately, polygamy can and does occur, thereby maintaining maximum individual productivity. This is especially adaptive for ♂♂.

A mammal's productivity is probably a complex balance of trade-offs between its various reproductive traits, which include neonatal developmental state, litter size, gestation, interbirth interval, longevity and social structure. Some of these reproductive parameters contribute to a relatively low potential productivity, such as small litters, long gestation periods and seasonal births. There are some correlations among these parameters; for example, long gestation periods are correlated with precocial births and small litters (Sacher and Staffeldt 1974). Other correlations are much more complex and less clear, as in the relationship of body size (and thus metabolism) to gestation, litter size and productivity (Leitch et al. 1959; Kihlström 1972; Sacher and Staffeldt 1974; Western 1976). The balance is thus largely intuitive and still awaits quantification (see Eisenberg, in prep.), but in principle it is a sound and useful approach to understanding the elephant-shrew's reproductive strategy (Fig. 48).

The occurrence of an elephant-shrew population, as with any mammal, is determined, in part, by the ability to maintain the birth rate equal to or above the death rate. The Macroscelidea have a potentially low productivity due mainly to small litters, so that a premium is placed on traits that would increase their birth rate. The monogamous social structure, longevity and continuous reproduction are such factors. As already discussed, the mild environment is probably important in allowing continuous breeding in elephant-shrews and thus may have an effect on their geographical distribution.

D. The adaptive syndrome

The existence of a group of small, tropical, cursorial mammals that utilize selected browse has been often noted (Dubost 1968; Eisenberg and Lockhart 1972; Estes 1974; Kleiman 1974; Eisenberg and McKay 1974; Ralls 1975; Barrette 1977b; Leuthold 1977). The members of this group include species of the Rodentia, Artiodactyla, and possibly Lagomorpha (Tab. 10) that have convergently evolved similar anti-predator, feeding and reproductive strategies. The theoretical aspects of the evolution of the components of this adaptive syndrome[1]) have been synthesized and discussed by Jarman (1974), Geist (1974), Eisenberg and McKay (1974) and Barrette (1977b). Complete life history data are not available for most of these species, yet there is still an obvious similarity among them. The variability that exists is within the framework of the following criteria, that characterize what might appropriately be called the "microcursorial adaptive syndrome":

1. tropical and sub-tropical distribution
2. body size less than 20 kg
3. swift, cursorial locomotion
4. browsing on high energy foods
5. precocial young
6. monogamous social structure.

Due to the lack of adequate field data and its uniform interpretation, there is some uncertainty as to whether the social structures of this group of species are, in fact, similar. For example, the Muntjac, *Muntiacus muntjak*, has been described as being "solitary" by Barrette (1977 b), while the Dikdik, *Madoqua kirki*, has been said to be "paired" by Hendrichs and Hendrichs (1971). I believe there is a real difference here, but, as in *M. proboscideus* and *E. rufescens*, it is exaggerated by the authors' terminologies. I feel that Kleiman's (1977) facultative monogamy nicely acommodates and unifies the variability in social structure exhibited by the different species.

The life history traits of *R. chrysopygus*, *E. rufescens*, and *M. proboscideus* closely fit the criteria that I have suggested characterize the microcursorial adaptive syndrome, with the exception of the elephant-shrews' mainly insectivorous diet. This makes them secondary and tertiary consumers compared to the other species, which is a relatively unimportant distinction for two reasons. First,

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[1]) A syndrome is any set of characteristics regarded as identifying a certain type, condition, etc. (Webster's New World Dictionary, 2nd ed., The New World Publ. Co., N.Y., 1970). Eisenberg, Muckenhirn and Rudran (1972) state: "... when a group of allopatric species shares the same relative narrow range of adaptations, then this group begins to exhibit a predictable 'adaptive syndrome' with respect to feeding, antipredator behaviors and social structure."

there is evidence that animal matter is eaten by some species of ungulates (Jarman 1974; Barrette 1975) and caviomorphs (Smythe 1970b), thus making them secondary consumers to some extent. Second, the trophic composition of the diet is probably not as important in the evolution of the syndrome as is the relatively high caloric value of the food and its dispersion in relation to the consumer, as pointed out by Jarman (1974) and Geist (1974).

I believe that *R. chrysopygus*, *E. rufescens* and *M. proboscideus*, and probably all elephant-shrews, are good examples of the microcursorial adaptive syndrome and their life history traits provide some new insights into the evolution of the syndrome as well as supporting existing hypotheses.

Table 10: List of species possibly exhibiting the "microcursorial adaptive syndrome"

Taxon	Common name	Authority
Lagomorpha		
Leporidae		
Lepus alleni	Antelope Jackrabbit	Seton 1953
Rodentia		
Caviidae		
Dolichotis patagonum	Mara	Smythe 1970 b Dubost and Genest 1974
Dolichotis salinicola	Dwarf Mara	Smythe 1970 b
Dasyproctidae		
Cuniculus paca	Paca	Smythe 1970 b
Dasyprocta punctata	Agouti	Smythe 1978
Myoprocta pratti	Acouchi	Morris 1962 Kleiman 1972
Artiodactyla		
Tragulidae		
Hyemoschus aquaticus	Water Chevrotain	Dubost 1975
Tragulus meminna	Mouse Deer	Eisenberg and Lockhart 1972
Tragulus napu	Mouse Deer	Ralls 1975
Cervidae		
Muntiacus reevesi	Muntjac	Barrette 1977 a, b
Muntiacus muntjak	Muntjac	Barrette 1977 a, b
Pudu pudu	Pudu	Cabrera and Yepes 1960 Fräderich 1975
Bovidae		
Cephalophus maxwelli	Duiker	Aeschlimann 1963 Ralls 1974
Cephalophus monticola	Duiker	Dubost 1968
Sylvicapra grimmia	Duiker	Wilson and Clarke 1962 Dunbar and Dunbar 1974
Oreotragus oreotragus	Klipspringer	Hendrichs 1972 Dunbar and Dunbar 1974
Ourebia ourebia	Oribi	Dorst and Dandelot 1970 Monfort and Monfort 1974
Raphicerus campestris	Steinbok	Chalmers 1963 Hendrichs 1972
Nesotragus moschatus	Suni	Dunbar and Dunbar 1974 pers. obs.
Neotragus batesi	Pygmy Antelope	Dubost 1968 Dorst and Dandelot 1970
Madoqua kirki	Dik - dik	Tinley 1969 Hendrichs and Hendrichs 1971

E. The phylogeny dilemma

Ever since the elephant-shrews were first described, there has been a continuing controversy as to their relationship within the Mammalia (see HORST 1950; EVANS 1942; MARTIN 1968; SAUER 1973, for reviews and examples). It is now obvious from PATTERSON'S (1965) revision of the fossil elephant-shrews, recent blood protein studies (GOODMAN 1974) and the elephant-shrews' ecology and behaviour that the group is a unique, monophyletic taxon with only pleisiomorph similarities to members of their traditional taxonomic associates, the Insectivora.

The time is ripe for a fresh approach in considering the elephant-shrew's morphology and phylogeny. MCKENNA (1974) has suggested, based on preliminary osteological and dental comparisons, that the Macroscelididae, Anagalidae (extinct) and Lagomorpha may have had a relatively close, ancient, common ancestry. A unique and distinct phylogeny such as this makes it unnecessary to attempt an awkward and complex explanation as to how a member of the conservative Insectivora attained the specialized morphology and life history exhibited by the Macroscelidea. MCKENNA'S (1974) hypothesis has some interesting implications regarding the elephant-shrews' ecology and behaviour and their association with the microcursorial adaptive syndrome.

It is likely that the extant elephant-shrews' insectivory is secondarily derived, as suggested by their relatively hypsodont dentition and large caecum, and the occurrence of extinct plant-eating forms (PATTERSON 1965) in addition to the plant-eating habits of some extant species, especially *Petrodromus*. If this is true, it is not difficult nor unrealistic to visualize the evolution of the extant insectivorous elephant-shrews from an ancestral plant-eater that had evolved convergently to the Artiodactyla and Rodentia representatives of the microcursorial adaptive syndrome (SMYTHE 1970b; BARRETTE 1975). The change in diet may have occurred when the small, cursorial ancestral form began to feed on the invertebrates attracted to the fallen fruits, flowers and seed pods that possibly made up its diet. Similar shifts in diet, with accompanying morphological changes, are not unusual (MAYR, 1970) as demonstrated by two rodents, the sciurid *Rhinosciurus* and the murid *Deomys* (WALKER et al. 1975; KINGDON 1974).

What is now needed is a fresh, careful, comparative re-examination and analysis of morphology, taking into consideration recently discovered fossil materials and new ideas (MCKENNA 1974; COLDIRON 1977).

Summary

1. The elephant-shrews (Macroscelidea) are a distinct and well defined group of mammals which are endemic to Africa and have radiated into the extremes of terrestrial habitats: forest, bushland and desert. There has been no previous, extensive field research carried out on their behaviour and ecology.

2. Life history data were gathered during two consecutive projects in Kenya. The forest dwelling Golden-rumped Elephant-shrew, *Rhynchocyon chrysopygus*, was studied at the coast, and the bushland dwelling Rufous Elephant-shrew, *Elephantulus rufescens*, was studied near Tsavo National Park. The field work lasted 33 months, during which time intensive, direct observation was carried out on marked, free-living individuals of each species. Limited data were also gathered on *Petrodromus tetradactylus*. SAUER'S material (1973) on *Macroscelides proboscideus* of the Namib Desert is used for comparison in the discussion.

3. *R. chrysopygus* is diurnal and individuals sleep in different leaf nests on the forest floor each night. It does not use or build trails.

4. It is monogamous, occupying contiguous territories that are consistent in size (mean, 1.7 ha) and saturate the habitat. A pair intraspecifically defends its territory sex-specifically. The pair bond is characterized by infrequent association and a permanency that only changes at death, which may be at 3—4 years of age. There is little intra-pair or parental-offspring aggression. While foraging widely on their territories, both sexes scent mark the substrate with a subcaudal gland.

5. *R. chrysopygus* spends about $^3/_4$ of its active hours foraging in the leaf litter for invertebrates and it eats them in approximate proportion to their availability, with the exception of millipedes. There is no evidence of food related interspecific aggression.

6. The Golden-rumped Elephant-shrew breeds throughout the year with a mean inter-birth interval of 82 days and a gestation of about 42 days. A single young is always born and the precocial neonate remains hidden for approximately two weeks, after which it emerges already weaned and almost fully independent of the ♀. It stays on the parental territory until it finds a vacant territory or is preyed upon. The main predators are snakes and raptors.

7. *E. rufescens* is polycyclic, with activity peaks at dusk and dawn, when it builds and maintains a trail network and forages. Nests are neither built nor used. All activities of an individual, such as resting, sleeping, grooming, foraging and nursing, occur on favoured spots on its trail network. Nearly $^1/_8$ of its active hours is spent maintaining trails.

8. The rufous elephant-shrew is monogamous on territories that vary from 0.16—0.52 ha. The habitat is not saturated, although most territories are contiguous with at least one other territory. The pair defends its area sex-specifically. Pair-bond behaviours are infrequent and the ♀ is dominant over the ♂. The pair association is stable and lasts as long as the individuals live, which may be 2—3 years. Contiguous territory boundaries are characterized by dung piles, which all individuals use. Both sexes scent mark with a sternal gland.

9. *E. rufescens* feeds on invertebrates. It defends concentrations of termites, which make up the major part of its diet, inter- and intraspecifically. A limited amount of plant matter is eaten.

10. It breeds throughout the year. The mean birth interval is 61 days and the gestation is about 50 days. The litter size is 1—2 and the young are highly precocial. The juveniles are weaned by 30 days and both parents aggressively drive the young from their territory by the time the next litter is born. Juveniles either disperse to a vacant territory, try to establish a new territory, or are preyed upon. Snakes are the main predators.

11. *Petrodromus tetradactylus* and *Macroscelides proboscideus* are most similar in their life history traits to *E. rufescens*. The members of the Macroscelidea exhibit a remarkable degree of life history conformity.

12. The ecological and behavioural data are compared and discussed in terms of defence, foraging and reproductive strategies. These strategies are subject to environmental as well as genetic constraints and show certain consistencies within the taxon and certain variations due to the different selection pressures operating on each species in its different environment.

13. Differences in the life histories, such as trail use and maintenance, amount of time spent foraging, home range size, and level of aggression may be related to the different environments occupied.

14. The reproductive and anti-predator aspects of the elephant-shrew life histories are very similar to those of some ungulates, rodents and lagomorphs and together these form a unique adaptive syndrome.

15. The monophyletic nature of the elephant-shrew taxon is supported by the behavioural and ecological data.

Zusammenfassung

Die Elefantenspitzmäuse (Macroscelididae) bilden eine eigene, in Afrika endemische Säugetiergruppe und bewohnen verschiedene terrestrische Extrembiotope: Wald, Buschland und Wüste. Dies ist die erste umfassende Freilandstudie über Verhalten und Ökologie dieser Tiere.

In zwei Etappen von insgesamt 33 Monaten wurden in Kenya beim Tsavo-National-Park freilebende, individuell markierte Rüsselhündchen *(Rhynchocyon chrysopygus)* und Elefantenspitzmäuse *(Elephantulus rufescens)*, kurzfristig auch die Vierzehenrüsselratte *(Petrodromus tetradactylus)* beobachtet.

Das waldlebende Rüsselhündchen ist tagaktiv; nachts schläft es in Blattnestern am Boden. Es legt keine Pfade an, besitzt etwa 1,7 ha große Reviere, die das Gebiet vollkommen ausfüllen, und lebt monogam. Die Paarbindung hält bis zum Tod (im Alter von 3—4 Jahren). Jedes Tier verteidigt das Revier gegen gleichgeschlechtliche Artgenossen. Aggression unter Familienmitgliedern ist selten. Beim Futtersuchen im Revier duftmarkieren beide Geschlechter mit einer subcaudal gelegenen Drüse. ¾ der Aktivitätszeit werden mit der Suche nach Invertebraten im Laub am Boden verbracht. Gefressen wird alles — außer Tausendfüßern — in der Häufigkeit, in der es vorkommt. Das ganze Jahr hindurch kommt alle 82 Tage — nach einer Tragzeit von 42 Tagen — jeweils ein Junges zur Welt, das zwei Wochen verborgen bleibt und dann, bereits entwöhnt, unabhängig von der Mutter lebt. Es bleibt im Elternrevier bis es ein eigenes findet oder Schlangen und Raubvögeln zum Opfer fällt.

Die im Buschland lebende Elefantenspitzmaus ist morgens und abends in der Dämmerung aktiv und legt dann ein Wegsystem an und frißt. ⅛ der Aktivitätszeit wird auf den Wegebau verwendet. Nester werden nicht angelegt. Für alle Aktivitäten gibt es bevorzugte Orte auf dem Wegenetz. Auch diese Art ist monogam und lebt in bis zu ½ ha großen Revieren, die das vorhandene Gebiet aber nicht völlig ausfüllen. Jedes Tier verteidigt das Revier gegen gleichgeschlechtliche Artgenossen. Das ♀ ist dominant über das ♂. Die Paarbindung hält bis zum Tod im Alter von 2—3 Jahren. Auf den Grenzen zwischen Nachbarrevieren liegen Kothaufen, die von allen Individuen benutzt werden. Beide Geschlechter duftmarkieren mit einer Sternaldrüse. Die Nahrung besteht aus wenig Pflanzenmaterial, überwiegend Invertebraten, speziell Termiten. Termitenansammlungen werden gegen Freßrivalen verteidigt. Das ganze Jahr über werden alle 61 Tage nach 50 Tagen Tragzeit jeweils 1—2 Junge geboren, 30 Tage gesäugt und von beiden Eltern aus dem Revier vertrieben, wenn der nächste Wurf zur Welt kommt. Die Jungen suchen ein verlassenes Revier, oder gründen ein neues, oder werden — meist von Schlangen — gefressen.

Sehr ähnlich wie diese Elefantenspitzmaus verhalten sich *Petrodromus tetradactylus* und *Macroscelides proboscideus.*

Die Monophylie des ganzen Taxons der Elefantenspitzmäuse zeigt sich auch in den Verhaltens- und Ökologiemerkmalen. Verschiedenheiten im Verhalten (Fortpflanzungsweise, Feindvermeidung, Aggression, Wegenetz-Benutzung) lassen sich den verschiedenen Lebensräumen zuordnen. Die Freß-, Fortpflanzungs- und Verteidigungs-Strategien werden genauer erörtert. Die beiden letzteren zeigen viele Übereinstimmungen mit einigen Huftieren, Nagetieren und Lagomorphen und bilden ein klares Anpassungs-Syndrom.

Acknowledgments

The financial support of the National Geographic Society, the East African Wildlife Society, the Ford Foundation, through their grant to the Department of Zoology, University of Nairobi, and the Smithsonian Institution, are all gratefully acknowledged.

Various people and institutions identified organisms for me: Plants, Dr. Faden, Mr. J. Gillett, and Ms. C. H. S. Kabuye, all of the East African Herbarium, Nairobi. Invertebrates, Mr. M. Cliffton of the National Museums of Kenya, Nairobi. Termites, Dr. J. Darlington of the International Centre for Insect Physiology and Ecology, Nairobi. Dr. G. B. Corbet supplied some elephant-shrew measurements from the British Museum of Natural History, London. The time and effort these people contributed is appreciated.

Many people have participated in both formal and casual discussions over the years, which have been of considerable value. Among these people are Professors M. Hyder, F. A. Mutere, J. B. Sale and T. A. Vaughan, Drs. H. Croze, B. Foster, H. Hoeck, P. Jarman, H. Kruuk, T. O'Shea, C. Pennycuick and T. Struhsaker; Mr. T. Huels, Mr. and Mrs. L. Hurxthal, Mr. J. Kingdon and Mr. J. Malcom. The discussions with Drs. J. F. Eisenberg, D. G. Kleiman and D. Western have been especially stimulating.

Mr. Kashuru Mumba and his family collected many of the coastal elephant-shrew specimens and Ms. L. Perez helped with some of the coastal invertebrate sampling work. Mr. T. Huels, Ms. C. Ryan and Dr. J. Frazier assisted in the capture of *Elephantulus* at Bushwhackers. The hospitality of Mr. and Mrs. H. Stanton, proprietors of Bushwhackers, took some of the "hardship" out of existing in the bush. The Office of Zoological Research (National Zoological Park) Keeper Staff have done an excellent job of caring for the captive elephant-shrews.

Mr. Richard Leakey has been encouraging from the beginning of the work and his moral and material support, through the National Museums of Kenya, has been invaluable. While a Smithsonian Institution Postdoctoral Fellow, Drs. John Eisenberg and Devra Kleiman have been exceedingly helpful with encouragement and discussions. My warmest appreciation to all these people.

I am grateful to Drs. J. F. Eisenberg, D. G. Kleiman, Ms. C. Dorsey and Mr. K. Redford for their comments on drafts of this paper and to Mrs. W. Holden for typing the manuscript.

To my parents who continually offer inspiration and encouragement, my loving gratitude.

Some of the material was originally submitted to the Department of Zoology, University of Nairobi, Kenya, as partial fulfilment of the degree of Doctor of Philosophy (Rathbun, 1976).

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