

**A COMPARATIVE STUDY OF COMMUNICATION IN SIX TAXA OF SOUTHERN
AFRICAN ELEPHANT-SHREWS (Macroscelididae)**

BY

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Preface

This study was carried out in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from February 1992 to December 1996, under the supervision of Professor Michael R. Perrin and Dr. Edith R. Dempster.

This study represents original work by the author and has not been submitted in any form to another University. Where use was made of the work of others, it has been duly acknowledged in the text.



Alida S. Faurie

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ABSTRACT

Aspects of olfactory, auditory, visual and tactile communication were investigated in five *Elephantulus* species (*E. brachyrhynchus*, *E. edwardii*, *E. intufi*, *E. myurus*, *E. rupestris*) and *Macroscelides proboscideus*, facilitating comparisons among species and genera. The purpose of this study was to determine whether species specific patterns of communication could be identified in the southern African elephant-shrews.

Scent gland structure and location was investigated to determine whether species specific differences existed and to relate gland location to marking behaviour. Prominent scent glands were found in the oral angle, foot pads, anogenital region and tail of all elephant-shrew species. Marking behaviours such as sandbathing, digging and anal dragging correlated strongly with scent gland location, but no glandular size and/or structural differences were apparent among the different elephant-shrew species. Species specific differences in marking frequencies did exist among the six elephant-shrew taxa, but were unrelated to glandular development. Choice chamber preference tests indicated that *Elephantulus* species preferred conspecific odours, with males showing higher levels of discrimination than females.

Audible vocalizations and footdrumming were investigated and compared in the sex elephant-shrew taxa. Distinct differences were present in the acoustic repertoires of the southern African elephant-shrew species. Footdrumming showed very clear species specific patterns, and footdrumming characteristics were compared with an existing morphological phenogram to derive a possible path of evolution for footdrumming.

Visual and tactile communication were investigated by analysis of frequencies and sequences of behavioural acts. A comparison of male-female interactions of the different taxa showed differences in behavioural frequencies both between males and females of a species, and among the different species. Discriminant function analysis showed clear species specific patterns in the visual/ tactile signalling systems of southern African elephant-shrews, and this was more clearly defined in males.

Elephant-shrews showed higher levels of aggressive behaviour in interspecific encounters, indicating a possible role of aggression as a premating isolating mechanism between species. However, no differences in aggressive behaviour between allopatric and sympatric male-female interactions could be discerned. Elephant-shrew males showed high frequencies of submissive behaviour in intraspecific encounters, which may be a strategy to reduce aggression in conspecific females.

Species specific patterns of behaviour were found to exist in all three modes of communication investigated, and may all act to some extent as premating isolation mechanisms between species. However, many of these patterns are very subtle and it is suggested that a combination of all sensory modalities act together to form each species' signalling system.

CHAPTER 1

INTRODUCTION

Communication has been defined as the transmission of information, encoded into a signal, by one animal to another animal which decodes this information (Deag 1980, Green and Marler 1979). According to Green and Marler (1979) animal communication should satisfy three conditions: The signal must be of a shorter duration than any phase of the animal's life cycle; structural or behavioural specializations are necessary in both sender and receiver; signaller and receiver must be able to internalize signals, i.e. the signaller must be able to change the state of the receiver and influence its behaviour.

A communication system between conspecifics is essential for the maintenance of the group's social organization, and to achieve and modulate cooperative relationships (Marler 1977). One would expect intraspecific signals to evolve to be clearly and unambiguously transmitted and received (Ewer 1968), enabling receivers to discriminate on the level of the individual (Beecher 1989). The most elaborate and complex signalling systems should therefore be found in intraspecific relationships (Ewer 1968, Marler 1977). The complexity of intraspecific signalling systems will further depend on the social organisation of the species. For example, parent-offspring recognition systems in colonial species such as bats (Gelfand and MacCracken 1986, Scherrer and Wilkinson 1993) will need to be more developed than those of solitary species (Beecher 1989).

The evolution of an animal's communication systems is closely associated with speciation and adaptation (Alcock 1993, Nevo 1990). One would expect evolving signalling systems to benefit both the signaller and the receiver, i.e. there should be co-adaptation between signal and receiver (Alcock 1993). Green and Marler (1979) note that species specific signals often arise as a consequence of ecological rather than social adaptation. Divergence of mate recognition signals has been a controversial issue for a number of years. The best supported theory suggests that mate recognition signals diverge in allopatry as an incidental by-product of isolation, due to factors such as adaptation to different environmental conditions during isolation, or genetic drift, or sexual selection. This is in accordance with both Mayr's (1963) Isolation Concept and Paterson's (1985) Recognition Concept of species. However, Paterson argued that if enough change took place in the signalling systems, then new specific mate recognition systems will result, while Mayr argued that isolating mechanisms will come into play to reduce the chances of hybridization if isolation is not complete. Bush (1986), reviewing these theories argued in favour of sympatric speciation. He points out that reinforcement of reproductive isolating mechanisms in sympatric species may take place through enhanced species discrimination ability rather than morphological or signalling system divergence.

Nevo *et al.* (1987) argue that the crux of speciation is the development of reproductive isolation between populations. This reproductive isolation may either precede or follow chromosomal divergence. Capanna (1994) sees chromosomal rearrangement as preceding reproductive and spatial isolation. In his study on blind mole-rats Nevo (1990) found that auditory, olfactory, tactile and morphological characters all act, singly and in combination, as species specific recognition signals. He found that hybrid zones between mole rat species disappeared gradually due to the

progressive development of behavioural isolation. Nevo thus sees the sequence as chromosomal differences acting as postmating isolation mechanisms, developing first, followed by pre-mating ethological isolation.

Mammalian communication systems usually include visual, auditory, chemical and tactile signals. The specific sensory modalities chosen by a species will depend on factors such as phylogenetic history and environmental conditions (Marler 1977), and will evolve to interact with and complement one another (Nevo 1990).

Vision is the best medium for diurnal signalling (Marler 1977), and visual communication is common in many species with well developed visual and social systems (Hailman 1977). Many visual signals are accompanied by acoustic, olfactory or tactile signals, e.g. sandbathing in most desert rodents (Eisenberg 1967) and elephant-shrews (Rathbun 1979), aggressive postures accompanied by vocal and olfactory cues in shrews (Baxter and Irvine 1995), and sexual behaviours associated with ultrasonic vocalisations in gerbils (Brown *et al.* 1988, Dempster *et al.* 1991). Vision has the advantage that it may persist for long periods of time, can relay large amounts of information, and carry information about the possible subsequent behaviour of the sender (Hailman 1977). Vision is of limited value in dim light situations e.g. in dense vegetation and at night.

Auditory communication in mammals includes a wide variety of sound frequencies ranging from ultrasound to audible sound and seismic signals. Sounds are most commonly produced by the vocal apparatus of an animal, but other parts of the body are sometimes also employed, e.g.

footdrumming in rodents and elephant-shrews (Eisenberg 1967, Randall 1989, Rathbun 1979) and head thumping in mole rats (Heth *et al.* 1991). Mammalian auditory communication systems are parsimonious, since a small sound repertoire serves many functions in many situations (Gould 1983). Scherrer and Wilkinson (1993) found that bat isolation calls not only contain information about the individual pup, but also about family and colony. Footdrumming in elephant-shrews is used to deter predators, in territorial encounters, and possibly as an advertisement of the fitness of the particular individual (Rathbun 1979, Roeper 1981). Transmission quality of different sound frequencies may depend on specific habitat. Forest animals that need to maintain their group structure and spacing will use auditory signals in an environment where vision is very limited (Busnel 1977). Similarly, sea-otters rely heavily on acoustic communication under conditions that inhibit clear vision and olfaction (McShane *et al.* 1995). Animals seem to be able to select amplitude and frequencies for the best sound transmission in their particular habitat and spatial organization (Marler 1977). Acoustic signalling is of prime importance in some species, e.g. for maintaining mother-infant relationships in certain birds, bats (Scherrer and Wilkinson 1993) and otters (McShane *et al.* 1995), or for mate selection in certain insects (Busnel 1977), frogs (Cocroft and Ryan 1995), birds (Robertson 1996), and mammals (Heth *et al.* 1991, Randall 1989). In many species however, acoustic signalling is linked to other modalities of their communication systems (Busnel 1977).

Most mammals have well developed olfactory senses and use scent signals as part of their communication systems (Ralls 1971, Stoddart 1974). Many nocturnal animals such as mice (Bronson 1976), gerbils (Brown *et al.* 1988) and ferrets (Clapperton 1989) rely heavily on chemical signals for communication. The durability of a chemical signal depends on the substance used.

Low volatility chemical signals have larger molecular weights, carry higher information loads (since the number of structural isomers capable of transmitting information increases exponentially with molecular size), and are longer lasting than highly volatile substances (Alberts and Werner 1993). Locating these chemical signals can however be problematic because of their relatively low volatility. One solution to the problem seems to be combining this scent signal with another that is easy to locate, such as volatile components or visual signals (Alberts and Werner 1993). Glandular secretions usually consist of a combination of large non-volatile proteins and smaller volatile components (Alberts *et al.* 1992, Beauchamp *et al.* 1976). Elaborate marking behaviours in mammals such as ground scratching in dogs (Bekoff 1979), tarsal and maxillary gland marking in antelope (Müller-Schwarze 1983, Ralls 1971) and sandbathing in rodents (Eisenberg 1967) serve as composite signals to combine visual and olfactory cues.

Tactile communication involves close contact between two individuals, e.g. mother-infant interactions, social grooming, aggression and sexual behaviour. This mode of communication can be either socially destructive when contact is violent, or can promote peaceful interaction and reduce social aggression, e.g. social grooming (Marler 1977). Tactile communication is further used in species where vision is limited, e.g. the vibrissae of shrews are extremely sensitive, and active contact and aggressive interactions are frequently avoided by this tactile cue (Baxter and Irwin 1995). Tactile communication is often linked with olfaction (Baxter and Irwin 1995), especially where an individual scent marks on a conspecific (Ralls 1971), or where mutual sniffing serves to match individuals to deposited scent marks (Clapperton 1989).

The elephant-shrew family, Macroscelididae, includes a small number of species which are endemic to Africa. Fossil records of elephant-shrews have only been found in Africa, and go back as far as the Eocene (Butler 1995). Elephant-shrew taxonomy has been a controversial issue for many years, previously they have been associated with primates, ungulates and insectivores. They were for a long time included as a family of the order Insectivora, and it was Butler (1956) who first suggested that elephant-shrews were sufficiently distinct to be placed in a separate order. Patterson (1965) concurred with this, placing elephant-shrews in the order Macroscelidea. This view has been further supported by recent authors such as McKenna (1975), Meester *et al.* (1986) and Rathbun (1979).

The taxonomy of the family Macroscelididae was extensively revised by Corbet and Hanks (1968) and Corbet (1974, 1995). The family comprises two subfamilies; the Rhynchocyoninae, consisting of one genus, *Rhynchocyon*, and three species, and the Macroscelidinae, with three genera; *Macroscelides* (one species), *Petrodromus* (one species) and *Elephantulus* (nine species).

All three genera of the Macroscelidinae are represented in the southern African subregion (Skinner and Smithers 1990). The five *Elephantulus* and one *Macroscelides* species found in southern Africa occur in a range of semi-arid to arid habitats. Distribution ranges of elephant-shrews species were obtained from (Meester *et al.* 1986, Skinner and Smithers 1990) (Fig. 1.1).

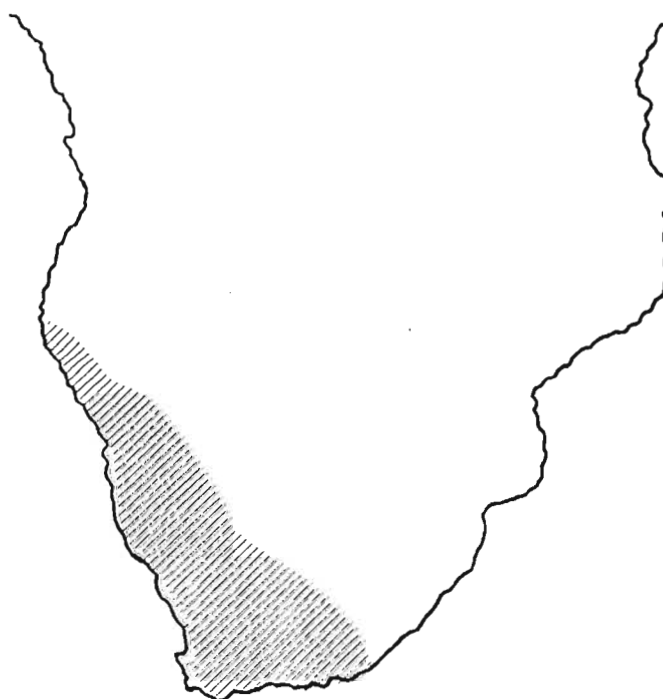
Elephantulus species*Macroscelides*

Figure 1.1 Geographical distribution of *Elephantulus* and *Macroscelides* species in southern Africa
 (from Skinner and Smithers 1990)

Although three *Elephantulus* species, *E. myurus*, *E. edwardii* and *E. rupestris* all utilize rocky habitats, their distributions do not overlap in the subregion (Skinner and Smithers 1990). Parts of the range of *E. myurus* and *E. brachyrhynchus* overlap, but in these areas they are separated by habitat requirements. *E. brachyrhynchus* prefers habitat with denser vegetation cover than *E. myurus*, which prefers a more rocky habitat. Skinner and Smithers (1990) reported that these two species often live within a few metres of each other on rocky hillsides where the two habitat types meet.

Similarly, the ranges of *E. brachyrhynchus* and *E. intufi* overlap, but the species are segregated by habitat requirements, with *E. intufi* preferring open grassland and scrub associated with sandy soil, while *E. brachyrhynchus* prefers areas with a richer vegetation and more cover. *E. edwardii* is confined to the areas of the southern and south western Cape Province, where they occur in sparsely vegetated areas associated with small rocky outcrops. *E. rupestris* is sympatric for most of its range with *M. proboscideus*, and shows a very small area of overlap with *E. myurus* and *E. edwardii*. *Macroscelides proboscideus* lives in the most arid area, and part of its range overlaps with that of *E. edwardii* and *E. myurus* in the south and *E. intufi* in the north

Only *M. proboscideus* is known to excavate the burrows in which they live. Members of the *Elephantulus* genus generally use cover provided by rocks and rocky outcrops with sufficient holes and crannies, as well as low vegetation. *E. intufi* has been found in burrows, but it is unclear whether they excavate these for themselves (Skinner and Smithers 1990). Both *E. intufi* and *M. proboscideus* make clearly defined runs radiating from their burrow entrances (Sauer 1973, Skinner and Smithers 1990). *M. proboscideus* and *E. brachyrhynchus* are active both day and night, with

peak activity at dawn and dusk. *E. intufi*, *E. myurus* and *E. rupestris* are active diurnally with high peaks of activity at dawn, while *E. edwardii* is predominantly nocturnal (Skinner and Smithers 1990, Woodall *et al.* 1989). Elephant-shrews are primarily insectivorous, but herbage forms a significant part of the diets of *M. proboscideus* (Kerley 1995), *E. brachyrhynchus* (Leirs *et al.* 1995), *E. intufi* and *E. rufescens* (Rathbun 1979).

Observations of most elephant-shrew species show them to be solitary but sometimes occurring in pairs. Fitzgibbon (1995), Rathbun (1979) and Sauer (1973) found that elephant-shrews of the species *E. rufescens*, *Rhynchocyon* species and *M. proboscideus* are facultatively monogamous. These species form monogamous pairs sharing overlapping territories, although pair association and interactions are quite infrequent. This territory is defended sex-specifically against other adults. Rathbun (1979) suggests that this system probably exists for all the elephant-shrew species. Elephant-shrews are reproductively active throughout the year, but in the temperate regions at higher latitudes young tend to be born during the warmer, summer months (Neal 1995, Skinner and Smithers 1990). Females usually produce litters of one or two precocial young, born fully haired and with open eyes (Dempster *et al.* 1992, Skinner and Smithers 1990).

Morphologically the five *Elephantulus* species occurring in the southern African subregion are very similar. Hindlimbs and feet are long and slender, and much longer than forelimbs which facilitates very fast movement. Footdrumming has been observed in most elephant-shrew species (Rathbun 1979, Skinner and Smithers 1990). The long trunk-like snout is a characteristic of all the members of the family. Scent marking behaviours such as ventral rubbing, anal dragging and sandbathing have been observed in *M. proboscideus* and most of the *Elephantulus* species (Rathbun 1979).

Pelage colour is quite similar among the *Elephantulus* species with seasonal and geographic variations between individuals. Classification has consequently been strongly dependent on dentition and ear morphology (Corbet and Hanks 1968, Meester *et al.* 1986, Skinner and Smithers 1990), and therefore communication signals may help to elucidate the taxonomy of the elephant-shrews.

Very few cytogenetic studies have been done on the elephant-shrew family. Diploid chromosome numbers for the six species used in this study have been established as *M. proboscideus* $2n=26$, *E. edwardii*, *E. intufi*, *E. rupestris* $2n=26$, *E. brachyrhynchus* $2n=28$ and *E. myurus* $2n=30$ (Ford and Hamerton 1956, Raman and Perrin 1997, Wenhold and Robinson 1987). Both Raman and Perrin (1997) and Wenhold and Robinson (1987) argue that *Petrodromus tetradactylus* diploid number $2n=28$ represents the ancestral condition, and that a reduction to $2n=26$ took place in the *Elephantulus* and *Macroscelides* genera. *E. brachyrhynchus* and *E. myurus* then underwent further chromosomal fission to arrive at the present diploid numbers. Systematic relationships among southern African elephant-shrew species have been examined using chromosomal and allozyme data by Raman and Perrin (1997) and Tolliver *et al.* (1989). Phenograms derived from data of Tolliver *et al.* (1989) and Raman and Perrin (1997) for genetic and protein characters differ considerably from that of Corbet and Hanks (1968) for morphological characters (Fig. 1.2).

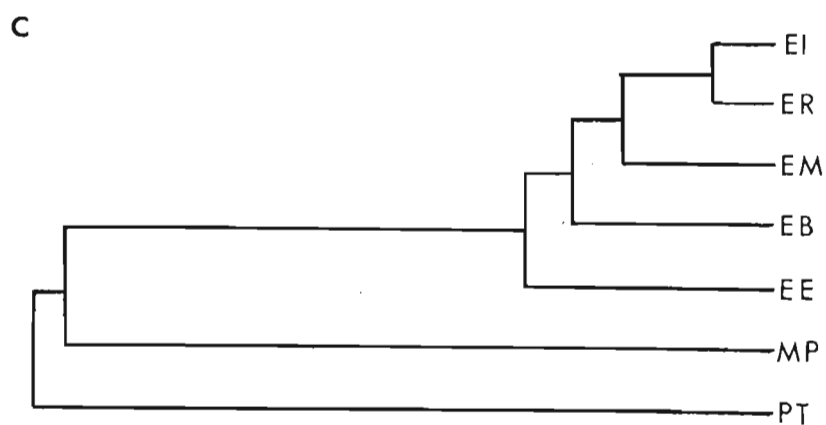
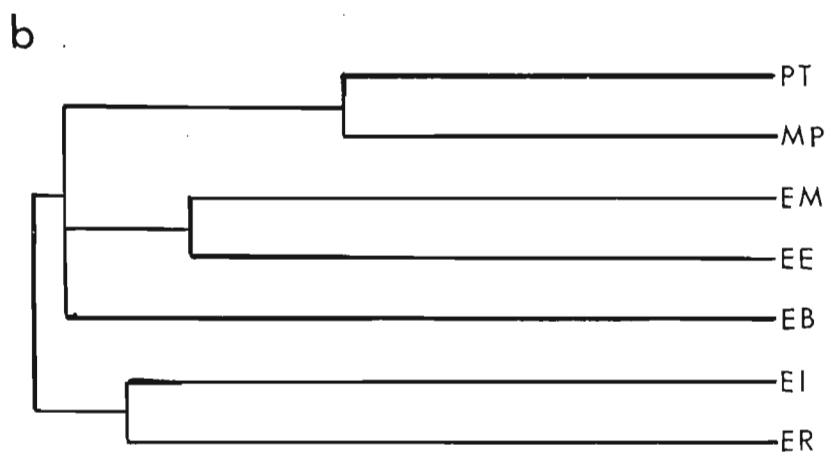
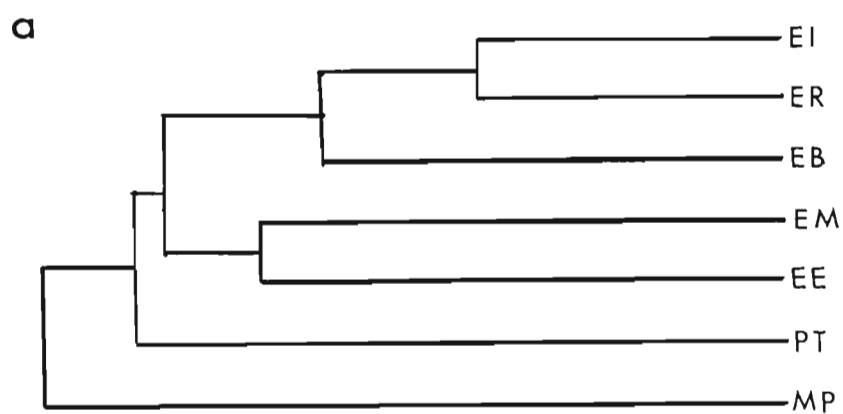


Figure 1.2 Phenograms showing relationships within the Macroscelidinae. (a) Tolliver *et al.* 1989, (b) Raman and Perrin 1997, (c) Corbet and Hanks 1968.

PT = *Petrodromus tetradactylus* MP = *Macroscelides proboscideus* EB = *E. brachyrhynchus*
 EE = *E. edwardii* EI = *E. intufi* EM = *E. myurus* ER = *E. rufus*

Tolliver *et al.* (1989) included 37 loci in their electrophoretic analysis. When subjected to cluster analysis considerable divergence among the species was shown, with all the *Elephantulus* species more closely related to each other than to *Macroscelides* or *Petrodromus*. Raman and Perrin (1997), investigating seven of the southern African elephant-shrew species, used three tissue types and examined 26 loci to test for differences in isozymes and allozymes. When subjected to cluster analysis the resulting phenograms divided the elephant-shrews into an *Elephantulus* group, and a *Petrodromus*/ *Macroscelides* group, similar to findings of Tolliver *et al.* (1989). Both the above mentioned cytogenetic phenograms cluster *E. myurus* and *E. edwardii* together, separated from the cluster of *E. rupestris* and *E. intufi*. However, Tolliver *et al.*'s analysis puts *E. brachyrhynchus* in a cluster with *E. rupestris* and *E. intufi*, while Raman and Perrin's phenogram shows a trichotomy between *E. brachyrhynchus* and the *E. myurus*/ *E. edwardii* and *Petrodromus*/ *Macroscelides* groups.

Corbet and Hanks (1968) used morphological characters to derive their phenogram. *Petrodromus* differed from the other elephant-shrew species in the number of toes (four instead of five) on the hindfeet, three pairs of mammae compared to two in the other species, and its relatively large size. *Macroscelides* has enormously inflated auditory bullae, differentiating it from the *Elephantulus* group. In the *Elephantulus* group, *E. brachyrhynchus* can be separated on the basis of an extra pair of posterior lower molars, but "the remaining forms of southern African *Elephantulus* have caused a great deal of confusion" (Corbet and Hanks 1968). Field identification is often difficult since pelage colour, body dimensions and geographical locations overlap among the species. Corbet and Hanks (1968) separated *Elephantulus* species using pelage colour, ear morphology and variations in dentition. In the phenogram derived from morphological characteristics, the

Elephantulus group is arranged with *E. edwardii* and *E. brachyrhynchus* splitting off first. In the *E. myurus*, *E. rupestris* and *E. intufi* group, *E. rupestris* and *E. intufi* are clustered together. This last grouping is the only area of close agreement between the cytogenetic and morphologically derived phenograms concerning the *Elephantulus* species.

Tolliver *et al.* (1989) notes that chromosomal evolution as deduced from standard karyotypes appears to have been conservative in the elephant-shrews, and is of little help in establishing finer relationships among the elephant-shrew taxa. Adding behavioural data to cytogenetic and morphological information would probably provide a clearer picture of phylogenetic relationships among the elephant-shrew taxa. Marler (1977) and Bekoff (1977) argued that behaviour can be as revealing as morphology in species diagnosis, since behaviour evolves and is thus phylogenetically traceable. Understanding how diversity in signalling systems evolved is of prime importance in ethology and behavioural ecology (Cocroft and Ryan 1995). Behavioural characteristics have long been used to establish taxonomic relationships, or to support and/or clarify taxonomies and phylogenies based on other characters (Brooks and McLennan 1991, Gittleman and Decker 1994, Kennedy *et al.* 1996, McLennan *et al.* 1988). One of the original studies relating behaviour to taxonomy was done by Lorenz (1941). Some recent studies include vocalizations from different gerbil taxa (Dempster and Perrin 1994), chipmunk species (Dunford and Davis 1975), pika species (Somers 1973), bird (Kennedy *et al.* 1996) and frog (Cocroft and Ryan 1995) species related to taxonomies and phylogenies, while Langtimm and Dewsbury (1991) used a cladistic analysis of rodent copulatory behaviour to confirm existing phylogenies based on morphology.

Information from all modalities in the signalling system of a species needs to be considered to get a

clear and complete picture of communication in that species. The aim of the present study was to investigate aspects of communication of six species of southern African elephant-shrews. Five *Elephantulus* species (*E. brachyrhynchus*, *E. edwardii*, *E. intufi*, *E. myurus* and *E. rupestris*) and *Macroscelides proboscideus* were studied, facilitating intraspecific, interspecific and intergeneric comparisons.

In the present study three modes of communication were investigated.

i) Acoustic: Footdrumming and vocalizations were described for the different elephant-shrew species. Vocal and footdrumming patterns were then compared among the species to determine whether they were species specific and could be used firstly as a taxonomic tool, and secondly to elucidate some of the phylogenetic questions still unanswered among the South African elephant-shrew species.

ii) Olfactory: Scent gland location and structure was investigated in each of the species, firstly to determine whether any species specific differences exist, and secondly to relate scent gland structure and location to marking patterns and functions.

Odour preferences were tested among sympatric species to ascertain whether elephant-shrews can discriminate between conspecific and heterospecific odours.

iii) Visual/ tactile: Visual components of behaviour were classified for each species. Intra- and interspecific interactions were staged between different-sex and same-sex animals. Comparisons between species were made to identify species specific behaviours and/or behavioural components. Intra- and interspecific behaviours were compared to determine whether any behavioural changes take place indicating species discrimination. Elephant-shrews are known to defend their territories sex-specifically (Rathbun 1979), and intra- compared to intersexual encounters could indicate whether changes in behaviour (especially aggressive behaviour) were evident.

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CHAPTER 2

SCENT COMMUNICATION

INTRODUCTION

As part of their social communication systems most mammals use chemical signals found in urine, faeces and cutaneous scent glands. Eisenberg and Kleiman (1972) defined olfactory communication as the process whereby a chemical signal is generated and transmitted by a sender to a receiver who can identify and respond to this signal. When these signals are deposited on certain objects or on conspecifics, using specialized mechanical behaviour patterns, it is known as scent marking (Ewer 1968).

Although exocrine skin glands are found in many mammalian taxa (Ewer 1968, Ebling 1977, Müller-Schwarze 1983), the stimuli that elicit marking and the exact messages conveyed are still unclear in most cases. Scent marking is generally classed according to the apparent function that the mark serves or the reaction of individuals to the mark. The motivation behind a scent marking act can be inferred more effectively when the marking is frequent, vigorous and of high intensity. Where marking is less vigorous the motivation is usually less clear (Ralls 1971). Marks can be used for individual recognition (Dagg and Windsor 1971, Müller-Schwarze 1971, Johnson 1973, Rasa 1973, Gorman 1980) and species recognition (Bowers and Alexander 1967, Müller-Schwarze 1974, 1983). Many oestrus females use marking for sexual attraction (Johnson 1973, Müller-Schwarze 1974), while releaser and primer hormones in mice and rats influence and regulate reproduction (Bronson 1979, Müller-Schwarze 1979, Vandenberg 1983, Hurst 1993). Secretions are also used as alarm signals

(Müller-Schwarze 1983), although very few studies provide direct evidence for this (Johnson 1973), and for territorial marking (Randall 1987, Richardson 1990). In reviews of scent marking both Ralls (1971) and Johnson (1973) noted that animals mark frequently when they are dominant to or intolerant of conspecifics, and caution that although this may involve a territorial motivation, there are very few studies that directly support this claim.

Mammalian exocrine skin glands vary considerably among species in size, type and location (Quay 1977, Adams 1980). Exocrine glands can be classified according to their shape and secretory method. Three types of exocrine glands are found; eccrine sudoriferous glands (simple sweat glands), apocrine sudoriferous glands, and sebaceous glands. Sebaceous glands are thought to be evolutionarily ancestral to other types of glands (Müller-Schwarze 1983). Where an aggregation or enlargement of any of these glands occurs, specialized scent glands are formed (Ebling 1977, Adams 1980).

Eccrine sudoriferous gland, found in the foot pads of many rodent species (Sokolov 1962, Ropartz 1967 in Adams 1980, Green 1988), secrete a watery solution that plays a role in thermoregulation and excretion (Rhodin, 1974, Kivett 1978, Ham and Cormack 1979). In the lower mammals eccrine sweat glands on the palmar and plantar pads further function to reduce slipping during fast movement (Quay 1977).

Apocrine glands are found in most mammal species (Müller-Schwarze 1983). Ham and Cormack (1979) suggest that the main function of apocrine glands is to release relatively small amounts of secretion onto the skin surface, giving the animal a distinctive body odour. They are believed to secrete more or less continuously, but not abundantly, and are responsive to

sex hormones. Apocrine sudoriferous glands are stimulated by testosterone and inhibited by oestrogen Ebling (1977), and emotional and sensory stimuli further cause an increase in apocrine secretion (Rhodin 1974). Where odours are transmitted over some distance (i.e. released into the air) during social interactions, apocrine glands usually play a role (Müller-Schwarze 1983). The presence of apocrine glandular regions have been reported in the faces of bats (Haffner 1995), submandibular area of rabbits (Mykutowycz 1968 in Ebling 1977), dorsal skin of ground squirrels (Kivett 1978) and foot pads of porcupines (Green 1988). Apocrine glands are considered to be the most primitive of the two types of scent glands (Quay 1977). Adams (1980) states that a phylogenetic relationship exists between apocrine and eccrine sweat glands; most mammals have apocrine glands over the entire body while higher primates have both eccrine and apocrine glands. Eccrine glands in the lower mammals are restricted to specific areas of the body.

Sebaceous glands secrete an oily substance (sebum) that normally serves to lubricate the skin. They are strongly influenced by sex hormones, being stimulated by testosterone and to a lesser degree by progesterone, while oestrogen inhibits the production of sebum (Ebling 1977, Ham and Cormack 1979). Where secretions are deposited on the substrate, sebaceous glands are usually involved (Müller-Schwarze 1983). Sebaceous gland form the sternal gland of gerbils (Thiessen *et al.* 1968), facial gland of bats (Haffner 1995) and oral angle and posterolateral gland of many rodent species (Quay 1965, Jannett 1990).

The same chemical substances or secretions may serve a number of functions, i.e. individual and/or species recognition, sexual attraction, territorial defence, reassurance marking, etc. (Johnson 1973, Müller-Schwarze 1979, 1983). Simultaneously many species mark with

several scent areas on the body in response to a single stimulus (Ralls 1971). Clearly the effect of a chemical signal depends on the receiver's state and experience and on the situation in which the signal is encountered. The message contained in any chemical signal may be modified by visual, tactile and auditory signals received simultaneously (Müller-Schwarze 1979).

A number of studies have investigated the chemical structure of mammalian pheromones (Müller-Schwarze 1983 for a review). The concept of a pheromone as used in entomology does not apply to the vertebrates, since the pheromones of insects usually consists of single components or simple mixtures, while vertebrate pheromones consist of complex mixtures (Wilson 1970, Bronson 1976, Beauchamps *et al.* 1976, Mykytowycz 1979). Wilson (1970) suggests that the reason for the complexity of vertebrate pheromones is that the behaviour of vertebrates is "personal", i.e. based on the recognition of individuals. To individualise a scent comprising a range of components simply requires a variation in the components of the mixture. These variations in odour may be caused by a) genetically determined metabolic variations in the species or group, b) dietary differences, c) individual genetic differences which would also influence the community odour (Eisenberg and Kleiman 1972). It is well documented that many mammalian species can distinguish between the odours of their own and another, closely related species, and that they show a preference for own species odour (Bowers and Alexander 1967, Dag and Windsor 1971, Doty 1972, Müller-Schwarze 1974), and use odours such as urine for mate recognition (Brown *et al.* 1988). Johnston and Robinson (1993), and Halpin (1986) found that mammals can discriminate not only between individual conspecific odours, but also between those of heterospecific individuals, which could mean that mechanisms involved in odour detection and discrimination are general

purpose ones and not species specific. However, the fact that most species show a preference for conspecific odours indicate that olfactory cues could act as reproductive isolating mechanisms in areas of sympatry (Eisenberg and Kleiman 1972, 1977).

Observations recorded for six elephant-shrew species demonstrated a series of similar behaviour patterns which could be classed as scent marking actions. These include perineal and ventral drag, sandbathing, ventral and substrate-rubbing and digging. These behaviours are used by rodents as part of their chemical communication systems (Eisenberg 1967). Marking behaviours together with the characteristically long, trunk-like, and mobile proboscis of elephant shrews, with which they constantly smell the surrounding air, combined with the presence of a highly developed nasal epithelium (pers. obs.) suggests a very keen sense of smell. Odour discrimination is thus indicated to play an important role in the southern African elephant-shrew species. All the elephant-shrews used in this study were collected from geographically separated populations, but they are sympatric in parts of their distribution range (Meester *et al.* 1986, Skinner and Smithers 1990). Odour preference trials were conducted using sympatric species, as it would be in areas of sympatry that animals would most likely show odour discrimination if chemical signals play a role in species recognition.

The aims of this part of the study were:

- 1) to determine the location of elephant shrew scent glands, and to investigate the histology of these glands. Scent gland location may help to explain whether specific behaviour patterns such as anal dragging were related to scent marking. Furthermore, different types of glands may indicate different functions. Müller-Schwarze (1983) in a review of skin gland in different mammalian taxa concluded that where odours are released directly into the air

apocrine glands dominate, while sebaceous glands are mainly responsible where a secretion is deposited on a substrate.

2) to determine whether the elephant-shrews species discriminated between conspecific and heterospecific odours.

METHODS

Histology

The six elephant-shrew species examined for the presence of scent glands were *Elephantulus brachyrhynchus*, *E.edwardii*, *E. intufi*, *E. myurus*, *E. rupestris*, and *Macroscelides proboscideus*. Probable location of scent glands were determined firstly by observing marking behaviours such as digging (feet), sandbathing (ventral and lateral body surface and side of the face) and ventral and anal dragging (anogenital region), and second, by taking skin samples from these areas to examine them for the presence of glandular tissue. In addition tissue samples were taken at the "usual" sites that glands occur in most small mammals that scent mark (i.e. front foot, hind foot, sternal, perineal, subcaudal and anal regions, and the oral angle) (Green 1988). During social interactions animals sniffed each others' noses, sides of face/ oral angle, side of body and anogenital areas. Skin samples from these areas were included in the histological investigation.

Tissue samples were collected immediately after death and fixed with Bouin's fixative for 18 hours, after which they were stored in 70% alcohol. After processing, tissues were embedded in paraffin wax, and sectioned at 7-10 μm . Ehrlich's haematoxylin and eosin was used to stain

the sections. Photographs of the sections were taken using a Zeiss photomicroscope. Samples were taken from 6 male and 5 female *E. brachyrhynchus*, 6 male and 5 female *E. edwardii*, 1 male and 2 female *E. intufi*, 5 male and 5 female *E. myurus*, 3 male and 4 female *E. rupestris* and 1 male and 1 female *M. proboscideus*.

Odour preference trials

Elephant-shrews are extremely sensitive to the presence of human observers, and for this reason odour preference trials were filmed using a video camera and analysed later. A test animal was put into a glass tank (60x60x30 cm) with an odour source placed at each end of the tank. Half a cotton bud rubbed in the fur and over glandular areas of a donor animal was used as odour source. They were then filmed for 20 minutes after sniffing the first odour source. Each test animal was exposed to odours of (a) a conspecific of the opposite sex, and (b) an animal of the opposite sex from a sympatric species. Thus males were tested with female odours as odour sources, and *vice versa*. Blank cotton buds were placed in the test animals' cage for several hours before the start of each trial to familiarize the animal with the buds. Species used in these trials were *E. brachyrhynchus*, *E. edwardii*, *E. myurus* and *E. rupestris*. *E. myurus* was tested with *E. brachyrhynchus* as the sympatric species, and *vice versa*. *E. edwardii* was tested with *E. rupestris* as sympatric species, while *E. rupestris* was tested with both *E. myurus* (Trial 1) and *E. edwardii* (Trial 2). Between eight and eleven individuals of each species were tested. Some individuals were tested two to three times, but never with the same odour source. Total time sniffing each cotton bud was recorded. Trials in which only one odour source was investigated were discarded. Results were analysed using a Wilcoxon signed-rank test (Statgraphics 6.1).

RESULTS

Histology

Three types of exocrine glands were found in the skin samples from the various regions examined: eccrine and apocrine sudoriferous glands, and sebaceous glands (Table 2.1). Due to small sample sizes of animals available for dissection, samples were not available for certain species, indicated as blank spaces in Table 2.1. Eccrine sudoriferous glands were simple, coiled tubular glands. Apocrine sudoriferous glands were usually small glands with the terminal part of the duct secreting into a hair follicle. Only in a few areas were the apocrine sweat glands enlarged (Table 2.1). These glands, like all sweat glands, were coiled, tubular glands but with much larger lumens. Apocrine glands were classed according to duct diameter as: small (<0.05 mm), medium (0.05-0.1 mm) and large (>0.1 mm).

Sebaceous glands were, with one exception, always associated with hair follicles in the skin of the elephant-shrews. The size and morphology of these glands differed considerably depending on the area where they were found. Based on this they were separated into different types, similar to the classification for bats (Haffner 1995). Four types of sebaceous glands were distinguished:

- 1) Normal, un-enlarged sebaceous glands associated with hair follicles. These are small, simple glands (acinus length 0.08-0.15 mm). They do not reach to the base of the hair follicle and are either single or simple branched acinar glands (Fig. 2.4).

- 2) Slightly enlarged, simple branched glands (acinus length 0.15-0.3 mm) associated with hair follicles, but with no obvious muscle association (Fig. 2.4).
- 3) Large branched, simple glands (acinus length 0.3-0.5 mm) associated with hair follicles, and with some thin muscle fibres around the acini (Fig. 2.2).
- 4) Very enlarged, branched sebaceous glands with muscle fibres surrounding the lobes. They were either simple or compound with the acini surrounding the hair follicle (when present) and extending well into the dermis (acinus length 0.5-1.5 mm) (Fig. 2.7b).

Table 2.1. Anatomical positioning and classification of skin glands of elephant-shrews

(SB = Sebaceous; SE = Eccrine sudoriferous; SA = Apocrine sudoriferous)

	<i>M. proboscideus</i>		<i>E. brachyrhynchus</i>		<i>E. intufi</i>	
	Male n=1	Female n=1	Male n=6	Female n=5	Male n=1	Female n=2
Oral angle	SB types 3-4 SA small		SB types 3-4	SB type 3 SA small	SB type 3 SA small	SB type 3 SA small
Ear	SB type 4		SB type 1	SB type 1	SB type 2	SB type 2
Front foot	SE		SE	SE	SE	SE
Hind foot	SE		SE	SE	SE	SE
Anal	SB type 2 SA small	SB type 3-4 SA medium	SB type 2 SA large	SB type 2 SA large	SB type 1 SA small	SB type 1 SA small
Genital	SB type 2 SA small	SB type 1 SA small	SB type 1-2 SA medium	SB type 1-2 SA medium		SB type 2 SA medium
Thigh patch			SB type 1	SB type 1	SB type 2 SA large	
Tail patch			SB type 1	SB type 1	SB type 1-2 SA medium	
Tail		SB type 2	SB type 2 & 4	SB type 2-3	SB type 2 & 4	SB type 2

Table 2.1. Anatomical positioning and classification of skin glands of elephant-shrews

(SB = Sebaceous; SE = Eccrine sudoriferous; SA = Apocrine sudoriferous)

	<i>E. edwardii</i>		<i>E. myurus</i>		<i>E. rupestris</i>	
	Male n=6	Female n=5	Male n=5	Female n=5	Male n=2	Female n=1
Oral angle	SB types 3-4 SA small	SB types 3-4 SA small	SB types 3-4 SA medium	SB type 3 SA medium	SB type 3-4 SA small	SB type 3 SA small
Ear	SB type 1-2	SB type 1	SB type 1	SB type 1	SB type 1	SB type 1
Front foot	SE	SE	SE	SE	SE	SE
Hind foot	SE	SE	SE	SE	SE	SE
Anal	SB type 2-3 SA medium	SB type 2 SA medium	SB type 2-3 SA large	SB type 2-3 SA large	SB type 3 SA medium	SB type 2 SA medium
Genital	SB type 3 SA medium	SB type 2-3 SA medium	SB type 1-2	SB type 2 SA medium		SB type 1-2 SA small
Thigh patch	SB type 1 SA medium	SB type 1 SA medium	SB type 1 SA medium	SB type 1 SA medium	SB type 1-2 SA large	SB type 1 SA medium
Tail patch	SB type 1-2 SA medium	SB type 1-2 SA medium	SB type 1 SA small	SB type 1 SA small	SB type 1-2 SA large	SB type 1-2 SA medium
Tail	SB type 2 & 4	SB type 2	SB type 2 & 4	SB type 2-3	SB type 2 & 4	SB type 2

Glandular areas in the skin included:

Feet

The foot and toe pads of both the front and hind feet all of species investigated showed simple, tubular sudoriferous glands. These glands were densely distributed throughout the foot and toe pads, but with a higher concentration towards the centre of the pads. The external layer of the feet and toes consisted of a thick, cornified squamous epithelial layer through which the terminal parts of the sweat ducts spiralled (Fig. 2.1). Pedal glands of each species were of a similar size.

Oral angle

Enlarged acinar (alveolar) sebaceous glands were found at the oral angle of all the elephant-shrew species investigated. The glands were branched and quite large in size (type 3-4). Small to medium sized apocrine glands were also present in most cases (Fig. 2.2).

Ear

Alveolar sebaceous glands were found in the small (± 1 cm diameter) hairless area behind the ear of most species. In all the *Elephantulus* species these were small, unbranched glands (type 1-2) associated with hair follicles surrounding the hairless area. *M. proboscideus* in contrast had very enlarged (type 4), compound glands in this area (Fig. 2.3). These glands were not associated with hair follicles and the glandular acini were associated with blood vessels and muscle fibres.

Thigh patch

The back of the thigh in all *Elephantulus* species examined was hairless. Sections of the skin in this area showed small, undeveloped sebaceous glands (type 1-2) associated with the hair follicles surrounding the patch. In *E. edwardii* and *E. myurus* small to medium apocrine glands were present, while the sections of the *E. intufi* and *E. rupestris* males showed extensive, enlarged apocrine glands (Fig. 2.4).

Tail patch

The area around the tail insertion in all the *Elephantulus* species was hairless, and at the dorsal side of the tail base a bald patch of ± 1 cm was formed. Histological sections of this area showed small, undeveloped sebaceous glands (type 1-2) associated with the hair surrounding the patch, and some apocrine elements. In *E. brachyrhynchus* and *E. myurus* these apocrine glands were very small, in *E. intufi*, *E. edwardii* and female *E. rupestris* they were medium sized, while *E. rupestris* males had large apocrine glands in this area.

Anal

E. intufi showed only small sebaceous glands (types 1-2) associated with hair follicles in the anal area, and small apocrine elements. The rest of the *Elephantulus* species as well as *M. proboscideus* had enlarged (type 2-3) sebaceous glands in the anal region (Fig 2.5). *E. brachyrhynchus*, *E. myurus* and male *M. proboscideus* had large apocrine glandular areas (Fig 2.6), while female *M. proboscideus* and the rest of the *Elephantulus* species had medium sized apocrine glands in this area.

Genital

Overall the six species showed very little sebaceous enlargement in the genital area, except for one male *E. edwardii* which had enlarged, branched sebaceous glands with muscle strands surrounding the acini. Some small to medium apocrine glands were also present in the genital areas of most species.

Tail

Tail glands were externally visible in all species, although the length and thickness of these glands differed among individuals. Tail glands were situated on the ventral side of the tail about 1-2 cm from the tail insertion. They appeared as a dark, slightly raised area of approximately 1-2cm in length. Tail glands in males were more prominent than those of females. Histological studies of the tail skin around the tail gland revealed that every hair follicle in this area had two small (type 2) sebaceous glands associated with it. The tail gland itself was formed by the enlargement of the glands associated with the ventral hair follicles. In all the females the tail glands consisted of relatively small, branched, simple sebaceous glands (type 2-3) (Fig. 2.7a). In comparison, male tail glands were considerably enlarged, branched, compound sebaceous glands (type 4) that form a glandular area of approximately 2x1.5x20mm (Fig. 2.7b).

The remaining areas tested, *ie.* the ventral, dorsal and lateral body surface, side of the face, top of the nose and lacrymal area showed no unusual or enlarged glandular areas.

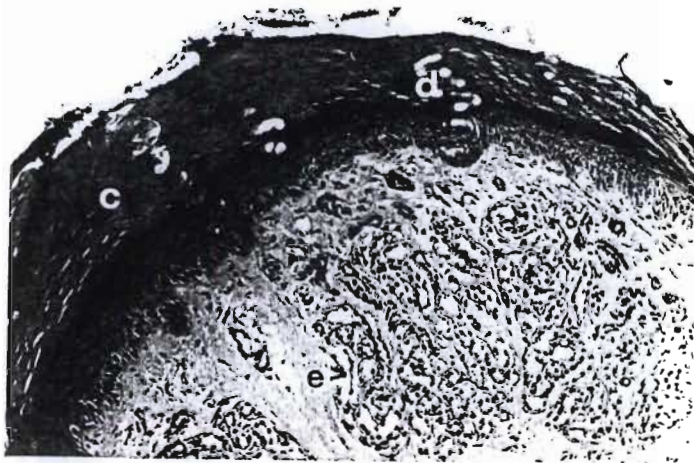


Figure 2.1 Eccrine sudoriferous glands in footpad of *E. myurus*
e = eccrine gland **d** = duct of gland
c = cornified layer

Mag. 70x

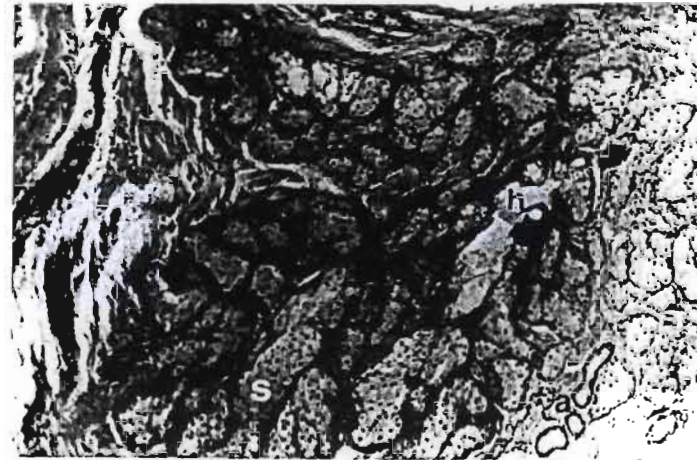


Figure 2.2 Section through oral angle of *E. brachyrhynchus* ♀
h = hair follicle **s** = sebaceous gland
a = apocrine gland

Mag. 80x

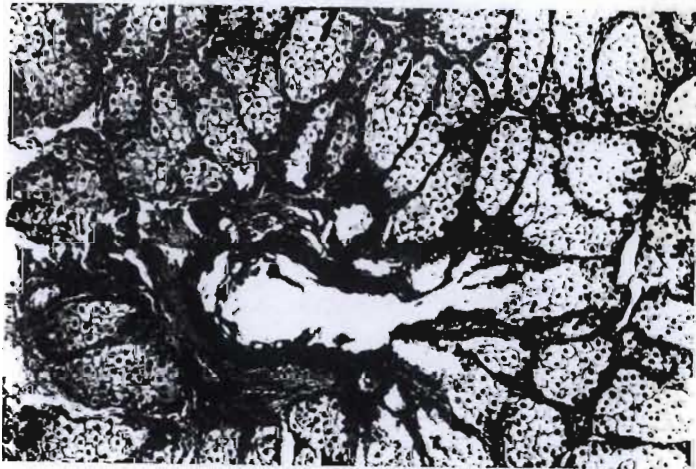


Figure 2.3 Compound sebaceous glands behind ear of
M. proboscideus ♀

Mag. 70x



Figure 2.4 Section through skin glands on thigh of *E. rupestris* ♂
s = sebaceous glands **a** = apocrine gland
h = hair follicle

Mag. 70x

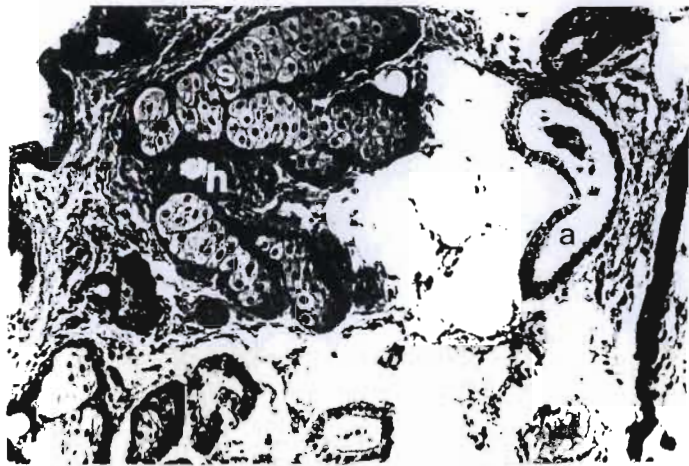


Figure 2.5 Section through anal area of *E. edwardii* ♂
s = sebaceous gland **a** = apocrine gland
h = hair follicle
 Mag. 70x

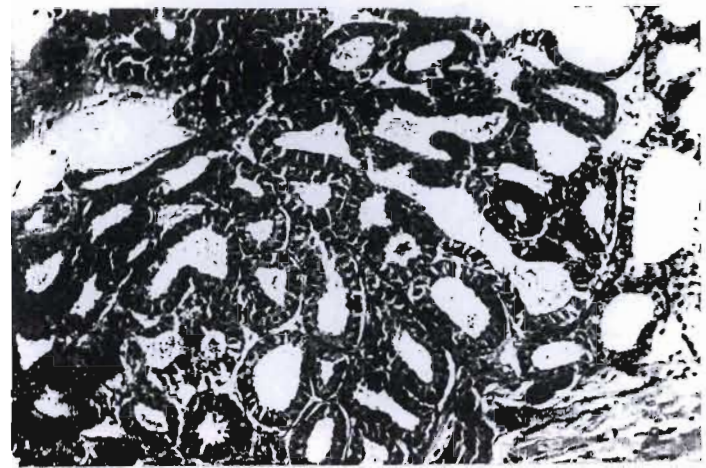


Figure 2.6 Enlarged apocrine glands in anal area of
E. brachyrhynchus ♂
 Mag. 128x

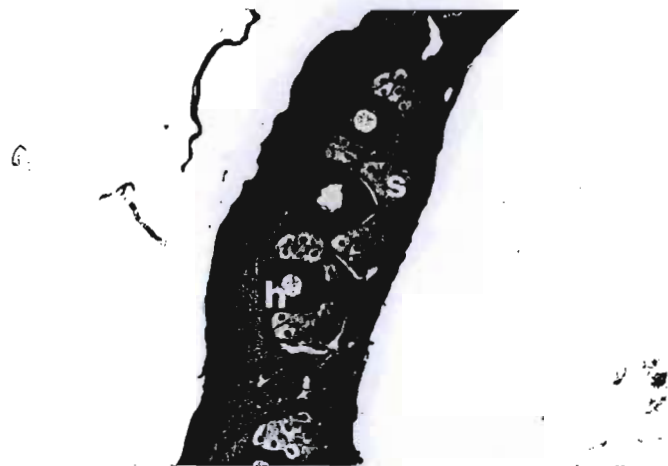


Figure 2.7a Section through tailskin of *M. proboscideus* ♂
s = sebaceous gland **h** = hair follicle
 Mag. 70x



Figure 2.7b Section through tailgland of *E. brachyrhynchus* ♂ showing
 enlarged branched sebaceous glands
s = sebaceous glands **h** = hair follicle
 Mag. 70x

Odour preference trials

The average time spent at each of the scent sources, results of statistical tests and the average total time spent investigating the scent sources for each species is given in Table 2.2.

Table 2.2. Results of odour trials.

SPECIES	Ave. Time Spent \pm SD (sec)		n	P	Ave. Tot. Time (sec)
	Conspecific	Heterospecific			
<i>E. brachyrhynchys</i> M	11.11 \pm 11.8	7.89 \pm 9.9	9	0.05	19.0
<i>E. brachyrhynchus</i> F	10.44 \pm 6.9	6.89 \pm 4.0	9	0.5	17.3
<i>E. edwardii</i> M	10.17 \pm 9.4	9.0 \pm 7.1	12	0.4	19.2
<i>E. edwardii</i> F	22.13 \pm 26.0	15.75 \pm 9.9	16	0.2	37.6
<i>E. myurus</i> M	7.53 \pm 8.2	4.88 \pm 5.4	17	0.06	12.4
<i>E. myurus</i> F	11.93 \pm 11.9	11.06 \pm 9.1	16	0.9	23.0
<i>E. rupestris</i> M (trial 1)	6.44 \pm 2.9	5.78 \pm 4.9	9	0.2	13.0
<i>E. rupestris</i> F (trial 1)	14.5 \pm 19.7	12.25 \pm 13.5	8	0.8	
<i>E. rupestris</i> M (trial 2)	9.56 \pm 15.6	5.11 \pm 2.7	9	0.8	18.2
<i>E. rupestris</i> F (trial 2)	4.38 \pm 2.9	5.25 \pm 3.9	8	0.7	

The elephant-shrews spent very little time investigating the scent sources; between 1 and 100 sec per 20 min test period. All species spent on average more time investigating the scents from conspecifics than those from heterospecifics, however, these results were statistically significant only for males of *E. brachyrhynchus* and *E. myurus*.

In four out of five combinations, males showed a stronger discrimination than females for conspecific odours, although this was not statistically significant. The opposite was true for *E. edwardii* where females showed more evidence of discrimination than males. With the exception of *E. brachyrhynchus*, females spent more time overall in investigating odour sources than males. Female *E. edwardii* spent significantly more time than any other group investigating the scent sources, whereas *E. rupestris* and *E. myurus* males spent the least amount of time at this activity

DISCUSSION

All three types of exocrine scent glands (eccrine sudoriferous, apocrine sudoriferous and sebaceous) were present in different areas in the skin of elephant-shrews. Haffner (1995) suggested three modes of secretion from sebaceous and apocrine glands:

- 1) passive secretion from normal, small glands with no muscle fibres around the acini. (Type 1 glands in elephant-shrews).

2) passive secretion combined with secretion caused by pressing the glandular area against an object. (Type 2 glands in elephant-shrews, especially in the anogenital region which is pressed onto the substrate during anal dragging).

3) secretion caused by the contraction of the muscle fibres surrounding the glandular acini, and the underlying subcutaneous musculature. This may be combined with pressing the glandular area against objects. (Type 3 and 4 glands in elephant-shrews). Secretions from glands at the oral angle fall in this category. Glandular secretion would be stimulated during face washing (muscle contractions around the gland), and sandbathing (pressing of the glandular area against the sand). Tail glands of elephant-shrews also fall into this category.

The three major marking behaviours involving skin glands were: 1) digging in the sand, 2) anal and genital dragging, and 3) sandbathing.

Digging

All four feet were used, although they dig more often with the forefeet than the hindfeet. A variation of digging behaviour found in all the species investigated, consisted of vigorously rubbing both the front and hind feet in the sand. Rathbun and Redford (1981) observed this behaviour in *E. rufescens* and termed it substrate-rubbing. In the present study digging and substrate-rubbing was usually associated with sandbathing. Rathbun and Redford (1981) found a variation of substrate-rubbing in juvenile *E. rufescens* where the young climbed onto the back of a parent and rubbed their feet in the back fur of the parent with a similar motion.

Histological examinations showed no glandular activity in the back skin of the adults, but considerable glandular development on the plantar surfaces of toes from front and hind feet of the neonates. They termed this behaviour back-rubbing, and suggested that this form of pedal scent-marking may serve as an initial scent exchange between the parents and neonates. This would be an effective means of odour exchange in a species where there is infrequent contact between parents and offspring, and where the young are highly precocial. This mixture of adult and juvenile scents obtained during back rubbing is then distributed across the territory when the parents sandbathe, creating a family scent on the territory which enables the parents to recognise their young and the young to learn the extent of the parental territory (Rathbun and Redford 1981). Pedal glands have been found in many mammals (Ewer 1968, Johnson 1973, Green 1988), several of which have been found to function as scent glands. Both foot pads and the toes of the six elephant-shrew species showed extensive glandular development. From the digging and substrate-rubbing behaviour exhibited by the elephant-shrew species studied, it would appear that the sudoriferous glands found in the foot and toe pads have a communication function in addition to a probable thermoregulatory function.

Dragging

This involved pressing or dragging the anal and/or genital region onto the sand or other objects such as rocks and nest boxes in their cage areas. Eisenberg (1967) hypothesized that marking behaviour such as anal and genital dragging evolved from common cleaning movements. Furthermore, tail glands were inevitably dragged over, or pressed onto the substrate during anal dragging and ventral rubbing. Medium to large sebaceous glands were present in the anal and genital regions of all species examined, with the anal area showing

more glandular development than the genital region. The apocrine glands found in the anogenital region of all the elephant-shrew species were involved in odour deposition during dragging since they were in direct contact with the substrate. These glandular areas can be quite extensive (eg. *E. myurus* and *E. brachyrhynchus*), and would further likely play an important role in mutual naso-anal sniffing performed when two individuals meet. A mixture of apocrine and sebaceous glands are often found in the anal area of mammals (Kivette 1978).

Sandbathing

Sandbathing is a common behaviour in most arid-adapted mammal species. Signalling systems such as sandbathing, that involve both visual and chemical components are usually favoured in open habitats (Eisenberg 1967). Müller-Schwarze (1983) found that where visual signals accompany chemical signals, elaborate behaviour patterns optimize odour release. Sandbathing in elephant-shrews was usually quite vigorously performed, and involved wriggling the ventral surface in the sand and rolling with the sides and dorsal part of the body and head in the sand. This sandrolling behaviour was usually preceded by digging and substrate rubbing at the spot where they sandbathe. Rodents living in arid habitats usually have very active sebaceous glands (Sokolov 1962), and although the increased sebum secretion prevents the skin from drying out, excess oil has to be removed through sandbathing (Eisenberg 1967, Eisenberg and Kleiman 1972). This results in sebum from the hair and secretions from other skin glands (and in some cases urine) being deposited at sandbathing sites, thereby giving sandbathing both a grooming and marking function (Eisenberg 1963, 1967).

In many rodent species, conspecifics tend to use the same sandbathing spots, which indicates that such sandbathing spots likely play an important role in scent communication. (Eisenberg 1963). In social species this is a way to maintain the group odour throughout the colony (Eisenberg and Kleiman 1972). Randall's (1991) study on sandbathing in kangaroo rats further supports the familiarity hypothesis. She found that chemical signals at sandbathing sites play a role in neighbour recognition. This is important in the maintenance of a stable social structure, especially in territorial species.

The social system of all elephant-shrews species investigated consists of monogamous pairs occupying a territory (Rathbun 1979, Fitzgibbon 1995). Sandbathing could well serve as a means of transferring scent gland secretions onto one another's fur, and distributing a family odour throughout the territory. Rathbun and Redford (1981) found that rufous elephant-shrews (*E. rufescens*) frequently scent marked and sandbathed in the same spot, usually on the trails in their territory. Mutual sandbathing areas have been reported for a number of other elephant-shrew species (Rathbun 1979), but this has not been verified for all of the southern African species.

During staged encounters in the laboratory between pairs of elephant-shrews, mutual sniffing was common. The area most often sniffed was the facial area, followed by the side of the body, the anogenital area and the tail (pers obs.). As part of their grooming routine elephant-shrews wash their faces by licking the forepaws and wiping them over the mouth and nose area. This may spread the secretions of the large oral angle glands as well as some saliva over the side of the head and face, which in turn would be added to the general body odour when

the animal sandbathes. Sebaceous and especially apocrine secretions from glands in the anogenital regions (and possibly also vaginal secretions) and apocrine secretions from tail patches and thigh patches likely explain why these regions are preferentially sniffed during social interactions. During agonistic encounters the aggressor usually holds the body well above the substrate and the tail high in the air, either straight out behind the animal, or curled over its body. This posture exposes all the posterior glandular areas on the body and probably optimises odour release. Fur on the side of the body contains the general body odour obtained from sandbathing sites.

It is well documented that androgens influence scent glands, and the influence of sex hormones on scent marking has been demonstrated for several mammals (Johnson 1973, Ebling 1977, Müller-Schwarze 1983). In mammals where both sexes scent mark, males usually mark more frequently than females (Thiessen *et al.* 1970, Johnson 1973). However, this hormonal effect may vary in intensity depending on the species and glands involved. Both sexes in the elephant-shrews seem to have similar sized glands, with the exception of the tail gland that is noticeably larger in males. In the South African *Elephantulus* species studied, females urinated and dragged more than males, while males sandbathed more frequently. In *M. proboscideus* however, males sandbathed and marked more frequently than females (Chapter 4). Although differences in marking frequencies exist among the different elephant-shrew species, with *M. proboscideus* and *E. rupestris* marking most often followed by *E. edwardii*, *E. brachyrhynchus* and *E. myurus*, this seems unrelated to glandular development.

Comparison of the position of glandular areas with specific behaviour patterns in elephant-shrews lead to the following conclusion:

Elephant-shrews use secretions from all three types of exocrine gland in their communication system. Sandbathing serves as a means of distributing the animals' body odour throughout its home area. No sternal glands were found in the six southern African elephant-shrew species examined, and sebaceous secretions were mainly deposited from tail and anal glands during dragging and from oral glands during sandbathing. Apocrine sudoriferous gland secretions were probably more important during mutual sniffing and in creating a general body odour.

Eccrine sudoriferous glands also contributed to the general odour of an elephant-shrew, and the creation of "familiar" odours at sandbathing sites. Elephant-shrews are monogamous and territorial (Rathbun 1979, Fitzgibbon 1995), and the creation of a familiar "home scent" by the two individuals occupying a territory probably reduces aggression between mates and stabilises territorial maintenance.

Mayr (1970) states that "differences in chemical signals often serve as isolating mechanisms", especially amongst mammals. Nevo *et al.* (1976) found that olfactory discrimination is very distinct in mole rats (*Spalax ehrenbergi*), and that the role of sexual odour in maintaining reproductive isolation is clear. Smith's (1965) study on two species of *Peromyscus* indicated that sympatric males showed a stronger preference for conspecific female odours than allopatric males, thus supporting Dobzhansky's hypothesis that isolating mechanisms are reinforced in areas of sympatry. Brown *et al.* (1988) suggest that recognition of the scent of a

territory mate reduces aggression and thus plays an important role in pair maintenance in this monogamous species.

Elephant-shrews showed a preference for conspecific odours, although the results were statistically significant in only two cases. Reviewing olfactory communication in rodents, Eisenberg and Kleiman (1972) noted that males showed distinction in preferences for specific scents more often than females, similar to the results obtained in these trials with elephant-shrews. However, females elephant-shrews spent more time overall investigating odour sources. Doty (1972) found that female *Peromyscus maniculatus* showed a preference for male conspecific odours only when they were in oestrus. This may explain the inconclusive results obtained from females in the results of the preference trials presented here. Oestrus is very difficult to determine in elephant-shrews, and Lumpkin & Koontz (1986) found a distinctive vaginal secretion to be one of the best indicators of the oestrus condition. None of the animals used in these trials showed any signs of oestrus, and were probably all reproductively inactive. Dempster and Perrin (1990) found no evidence for preference for conspecific odours in four *Gerbillurus* species. They suggested that odour deposition is not an important mode of communication in these arid adapted species, and that visual/tactile/acoustic signals have to be used in conjunction with odour cues. Pheromones with a complex structure and large molecular weight are better suited as chemical signals, since they can potentially transmit more useful information (Alberts and Werner 1993). Larger molecules usually have reduced volatility and can thus transmit information when the signaller is absent, but they may be difficult for the recipients to locate. This problem can be solved by either combining scent signals with visual signals (Alberts 1989), or by including a volatile

component in the pheromone (Alberts and Werner 1993). Müller-Schwarze (1974) notes that olfactory recognition of species or individuals is normally accomplished by direct contact or over short distances.

The ability to discriminate at a species level between the body odours of two animals could indicate that chemical cues may act in the mate recognition systems of the elephant-shrews. However, the variability of the results suggest that chemical cues are likely to be used in conjunction with other signals to be most effective.

Specific research on behaviour and chemical communication in the different elephant shrew species is still needed to understand more about the general biology of each species, and their relationship to their environment, as well as to point to the taxonomic and evolutionary relationships between them.

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CHAPTER 3

ACOUSTIC COMMUNICATION

INTRODUCTION

The acoustic repertoires of elephant-shrews consist of audible vocalisations ("mewing" and "clicking") and footdrumming. Footdrumming is the most commonly observed signal, and is produced by hitting one or both of the elongated hind feet on the ground in rapid succession. In our laboratory colonies of elephant-shrews, footdrumming was elicited by disturbances and during agonistic encounters, whereas vocalizations were only observed in agonistic encounters.

Footdrumming has been reported for several elephant-shrew species in the wild (Ansell and Ansell 1969, Critch 1969, Rathbun 1979, Skinner and Smithers 1990), as well as for several rodent (Bridelance and Paillette 1985, Dewsbury 1971, Eisenberg 1963, 1967, Kenagy 1976, Randall 1993) and Lagomorph species (Eisenberg and Kleiman 1977). Studies on a variety of rodent species have shown a difference in footdrumming rhythms between different species (Daly and Daly 1975, Fiedler 1973). Bridelance and Paillette (1985), however, were the first to describe the structure of, and to measure various parameters of footdrumming in several *Meriones* species. In their study they found that species-specific footdrumming patterns exist in these rodents.

The physical structure of most mammalian vocalizations appears to be genetically fixed, and can be used as a taxonomic character when measuring species differences (Brooks and McLennan 1991, Cocroft and Ryan 1995, Gould 1983). For example, Somers (1973) found significant differences in the vocal dialects of different pika populations in North America, and suggested the use of these

vocalisations as a taxonomic tool. Similarly, Dunford and Davis (1975) related chipmunk vocalizations to their taxonomy. Vocalisations and footdrumming from a range of rodent species have been related to phylogeny and taxonomy (Bridelance 1989, Bridelance and Hemim 1989, Dempster and Perrin 1991, 1994). In a study on mole rats (*Spalax*), Nevo *et al.* (1987) found significant differences in vocal dialects between four chromosomal mole rat species, with the call of the last derived species not yet fully differentiated. The structure of the elephant-shrew footdrumming patterns could therefore be used as a taxonomic tool to elucidate the phylogenetic relationships among the species.

Elephant-shrews are a monophyletic group of animals endemic to Africa. Five *Elephantulus* species, one *Macroscelides* species and one *Petrodromus* species occur in South Africa (Skinner and Smithers 1990). With the exception of *Petrodromus* all elephant-shrews occur in a range of semi-arid to arid habitats. The five *Elephantulus* species are morphologically very similar. Differences in dimensions among the species are very subtle, and pelage colour varies among regions (Corbet 1974, 1995, Skinner and Smithers 1990) and among seasons (pers. obs.), making them very difficult to differentiate. Corbet and Hanks (1968) and Corbet (1974, 1995) revised the taxonomy of the family Macroscelididae based on morphological characters. However, as Marler (1977) noted, behaviour can be as revealing as morphology in species diagnoses, and the purpose of the present study was therefore to describe the acoustic signals of the five South African *Elephantulus* species, and to determine whether species specific patterns exist.

METHODS

The five *Elephantulus* species included in this study were *E. edwardii*, *E. rupestris*, *E. myurus*, *E. brachyrhynchus* and *E. intufi*. Footdumming data were also collected from *Macroscelides proboscideus*. *E. edwardii* were trapped at Nieuwoudtville, Western Cape, and *E. rupestris* at Richmond and at Deelfontein, both in the Cape province. *E. myurus* were trapped in two localities; at Bloemfontein, OFS, and Deelfontein, Cape province, while *E. brachyrhynchus* were trapped near Louis Trichardt in the northern Transvaal. In the present study *E. edwardii* did not footdrum readily once they had become habituated to the laboratory situation. The three *E. intufi* individuals died shortly after the start of the study, and therefore recordings from most *E. edwardii* and all of the *E. intufi* were from a preliminary study conducted in the Department of Zoology (Dempster, pers. com.). The results of the preliminary study, as well as the sonograms obtained were used for comparison in the present study. Animals were housed individually in glass tanks of 60x30x30 cm, and provided with a layer of sand, rocks and a nest box. Food (Pronutro, catfood and sunflower seeds) and water were provided *ad. lib.*, and a 12L:12D light cycle and temperature of 25°C was maintained.

Recordings were made of animals footdrumming in cardboard nest boxes while audible vocalizations were recorded during staged encounters and when handling the animals (clicking). A Marantz tape recorder with a TECT super-cardioid condenser microphone was used. The tape speed was 475 mm/sec with a frequency response at -20 dB of 20 Hz to 18 kHz. The recordings were analysed with a Multigon Uniscan II sonograph.

Footdrumming

Footdrums were recorded from six male and five female *E. myurus*, five male and five female *E. rupestris*, five male and seven female *E. brachyrhynchus*, three male and two female *E. edwardii* and two male and three female *E. intufi*. Footdrumming data from *M. proboscideus* were very limited (one recording consisting of two series of footdrumming, each comprising three footdrumming bouts). Footdrums were produced by hitting the hindfeet on the ground. One foot at a time was used, but feet were alternated between, and sometimes during, bouts of footdrumming.

Footdrummings were classified according to the system of Bridelance and Paillette (1985), who used the term "podophony" to describe this type of communication. Footdrums were emitted in a series that lasted from a few milli-seconds to several minutes. A series consisted of one or more bouts of footdrumming, with the shortest footdrumming bout consisting of a single footdrum. These footdrumming bouts could be regular or irregular. A regular footdrumming bout consisted of regularly spaced footdrums, while irregular bouts, by implication, had varying footdrum intervals. A new series was defined when a pause of more than 500 msec elapsed between footdrums.

Sonograms were analysed, and the mean frequency of footdrum intervals calculated for each of the *Elephantulus* species. These were then graphically presented to show the distribution of intervals for each species and to facilitate comparison among species. Footdrumming patterns of all the elephant-shrew species were further compared to determine a possible evolutionary path of footdrumming development.

The following characteristics were used in the comparison:

- 1) footdrums per regular footdrumming bout
- 2) footdrums per irregular footdrumming bout
- 3) regular footdrum intervals
- 4) irregular footdrum intervals
- 5) footdrumming bouts per series

Vocalizations

Recorded vocalizations were measured for duration, and for the frequency limits of each call. Two types of vocalizations were recorded; 1) clicks which were brief, discrete sound, and 2) mews which were longer and more modulated. Sonograms from clicking vocalizations were analysed from two *E. edwardii* and one *E. myurus* recording, while sonograms of mewing vocalizations were obtained from two *E. edwardii*, three *E. myurus*, two *E. rupestris* and six *E. brachyrhynchus* during staged encounters. Seven *E. intufi* mewing vocalizations collected by Dempster (pers com) during the preliminary investigation were reported together with the present results for comparison.

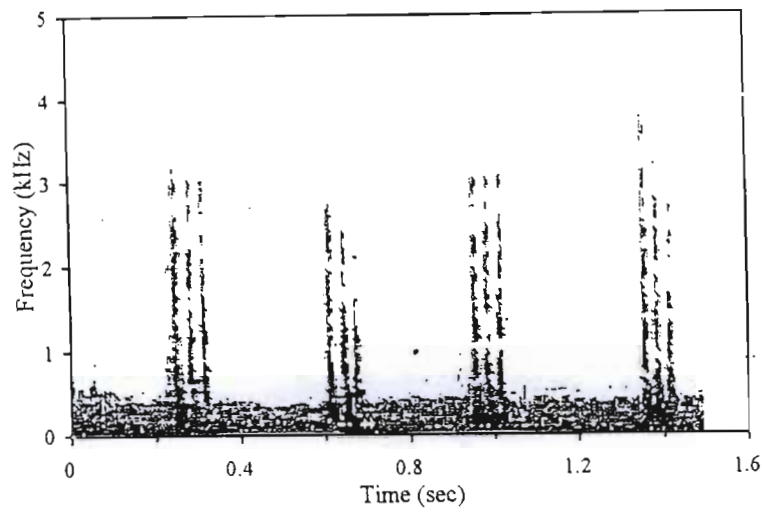
RESULTS

Footdrumming

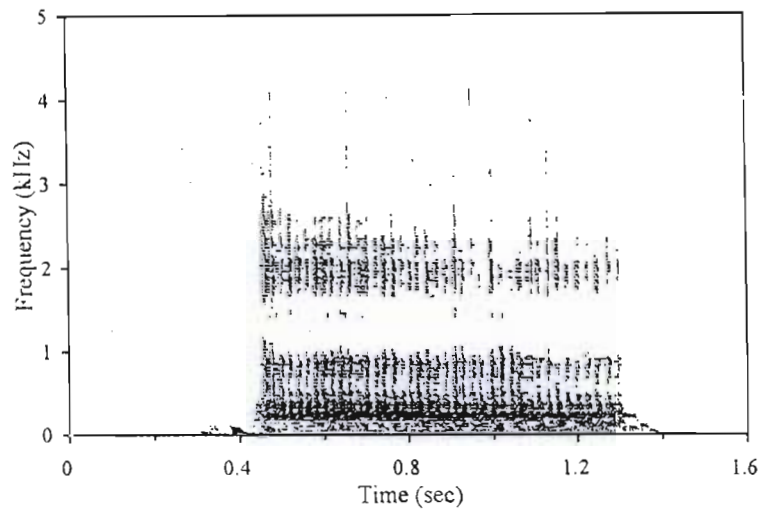
It was easy to discern distinct footdrumming patterns by simply listening to the different elephant-shrew species. Footdrumming patterns were similar for males and females of the same species.

The footdrums of the five *Elephantulus* species are illustrated in Figure 3.1:

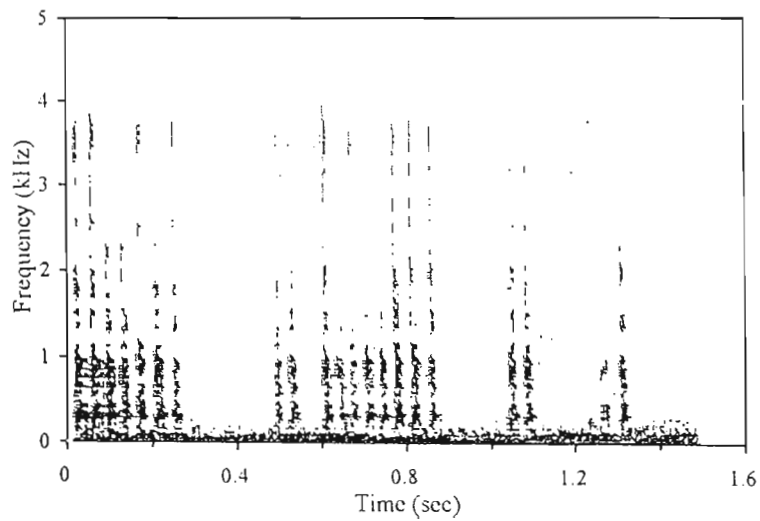
E. myurus



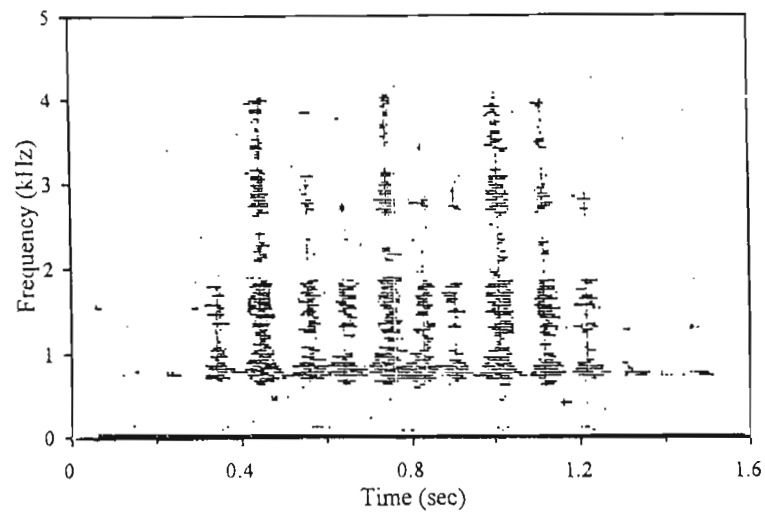
E. rupestris



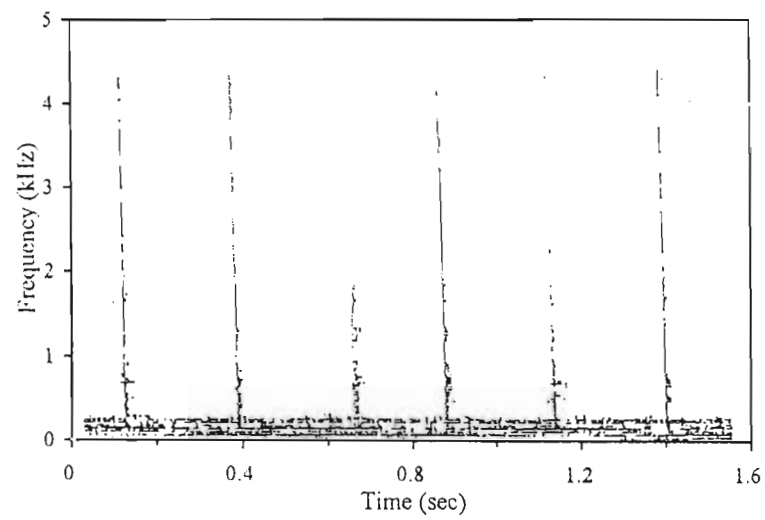
E. brachyrhynchus



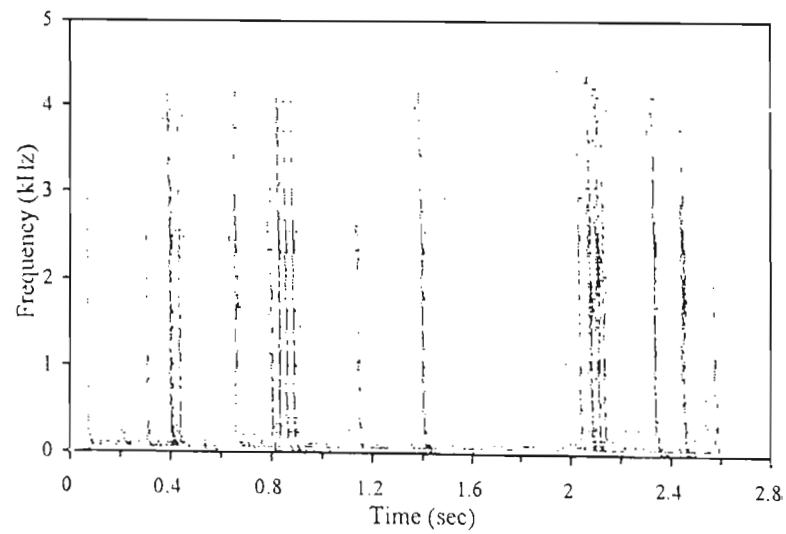
E. edwardii (regular)



E. intufi (regular)



E. intufi (irregular)



E. myurus

E. myurus emitted regular footdrums in short bouts of 2-4 footdrums with intervals of 25-40 msec between footdrums in a bout, and 250-350 msec between footdrumming bouts. The length of a series varied between individuals, but was usually between five and 20 seconds, although it varied in length from less than one second up to several minutes. No irregular footdrumming bouts were present.

E. rupestris

A footdrumming series of *E. rupestris* consisted mostly of single footdrumming bouts containing 30-50 footdrums very closely spaced (usually 15-25 msec apart). These bouts may taper off, with the last few footdrums being 30-40 msec apart. Each series lasted about 1.0 to 1.5 seconds. Only regular footdrumming bouts were present.

E. brachyrhynchus

Recordings from *E. brachyrhynchus* showed elements in common with the above two species in certain of their regular footdrumming bouts. However, they also had irregular footdrumming bouts. A series usually consisted of one to several regular footdrumming bouts, with the longest of these being 10-30 footdrums long, as well as some short irregular bouts. The interval between footdrumming bouts ranged from 100 to 200 msec, while footdrum intervals were between 30 and 40 msec. The length of the series varied from about 200 msec to just over five seconds.

E. edwardii

E. edwardii showed regular footdrums with more variable footdrum intervals (30-50 msec) and many more irregular footdrumming bouts (not shown in figure) than the other species. The irregular part of the footdrumming series typically consisted of footdrums with varying drum intervals ranging between 50 and 130 msec. Footdrumming series varied in length, but were normally less than two seconds in duration.

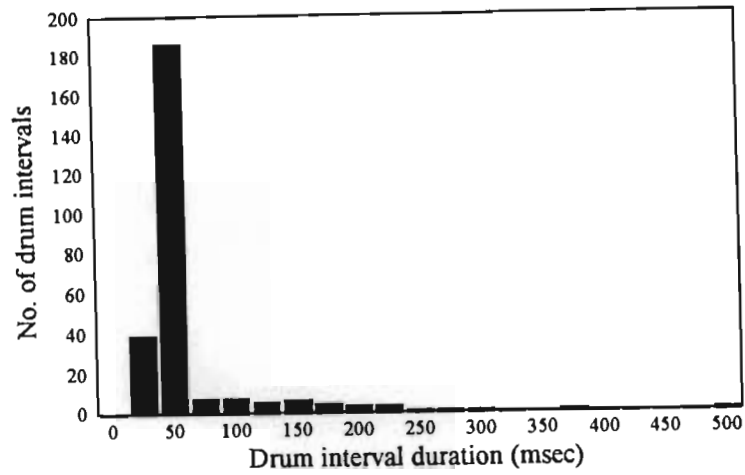
E. intufi

E. intufi showed regular and irregular footdrumming patterns. The regular footdrumming bouts had widely spaced footdrums (200-300 msec), whereas the irregular bouts were of a shorter duration and consisted of groups of footdrums of varying lengths but with predominantly small drum intervals. Series lengths were variable, and could last up to several seconds or even minutes.

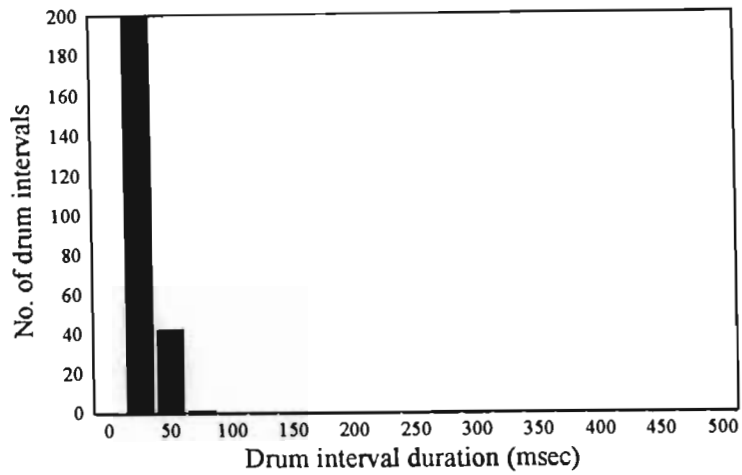
The footdrumming series of *M. proboscideus* (not shown in Fig. 3.1) consisted of only regular footdrumming bouts, but with footdrum intervals ranging between 50 and 80 msec.

The distribution of footdrum intervals in a series was graphically represented for each of the five *Elephantulus* species (Fig. 3.2), to compare the differences among the species.

E. brachyrhynchus (n=12)



E. rupestris (n=12)



E. myurus (n=11)

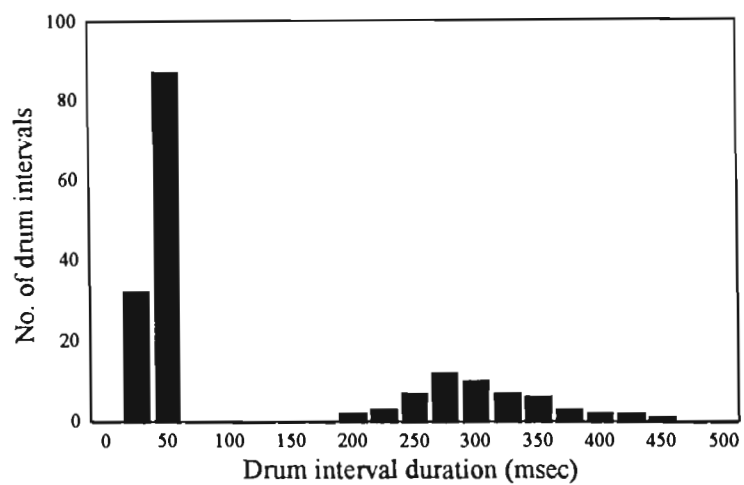
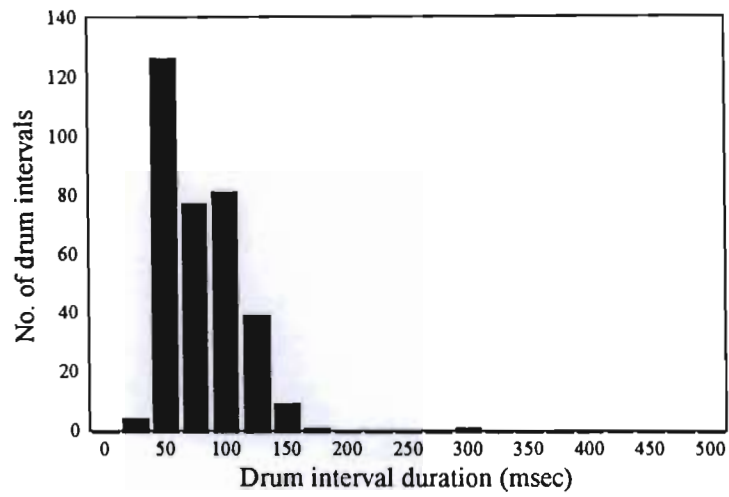


Figure 3.2 Distribution of footdrum intervals per series for five *Elephantulus* species.

E. edwardii (n=5)



E. intufi (n=3)

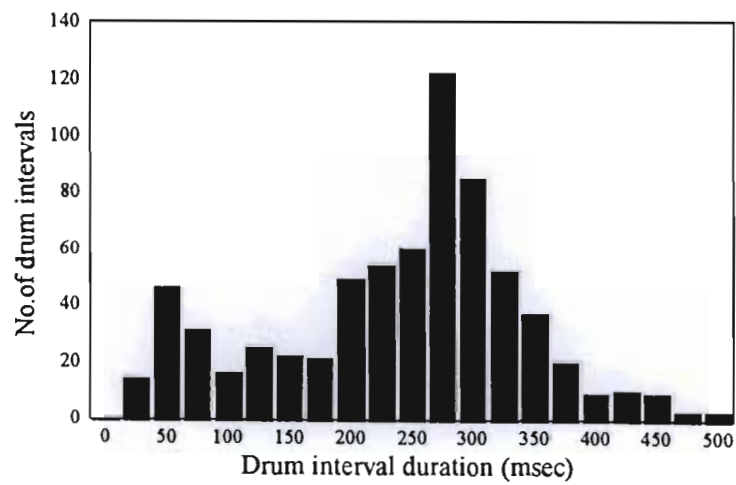


Figure 3.2 Distribution of footdrum intervals per series for five *Elephantulus* species.

Footdrum interval distribution for the average *E. myurus* footdrum series showed the majority of footdrum intervals falling between 1 and 50 msec. These were the intervals within footdrumming bouts. The intervals between bouts were naturally less common and ranged between 175 and 450 msec.

In the case of *E. rupestris*, where a single regular footdrumming bout also formed a series, all the footdrum intervals were between 1 and 50 msec in duration. The majority ranged between 12 and 30 msec, while the smaller group of footdrum intervals between 25 and 50 msec represented the deceleration of footdrumming towards the end of each bout or series.

Regular footdrumming bouts formed the major part of an *E. brachyrhynchus* footdrumming series, with footdrum intervals between 1 and 50 msec, whereas the shorter and less common irregular footdrumming bouts comprised the remainder of the series.

The regular footdrumming bouts of *E. edwardii* with footdrum intervals of 25-50 msec is represented by the second bar of the histogram, and represents the majority of footdrums. The area between 50 and 200 msec represents the irregular footdrumming bouts.

Footdrum distributions of *E. intufi* showed two peaks. The first represented the irregular portion of the footdrumming series, while the second peak showed the regular portion, where the footdrum intervals were more widely spaced (200-350 msec).

Footdrumming patterns differed among elephant-shrew species not only in the length and regularity or irregularity of the footdrumming bouts and series, but also in the intervals between successive footdrums and the number of footdrums per bout (Table 3.1).

Table 3.1 Footdrumming characteristics of six elephant-shrew species.

FOOTDRUMMING CHARACTERISTICS	SPECIES					
	Mp	Eb	Ee	Ei	Em	Er
1. Footdrums/bout						
>10	*	*	*	*		*
<10					*	
2. Irregular bouts present		*	*	*		
Irregular bouts absent	*				*	*
3. Regular footdrum intervals				*		
>80sec						
51-80sec	*					
26-50sec		*	*		*	
15-25 sec						*
4. Irregular footdrum intervals:					*	*
none	*					
<50sec				*		
>50sec		*	*			
5. Bouts per series						
<10	*	*	*	*		*
>10					*	

Mp *M. proboscideus*
Ei *E. intufi*

Eb *E. brachyrhynchus*
Em *E. myurus*

Ee *E. edwardii*
Er *E. rupestris*

Each species had specific regular footdrumming bouts in their footdrumming series, while irregular elements were found only in three species; *E. brachyrhynchus*, *E. intufi* and *E. edwardii*. In *E. intufi* regular footdrumming bouts had relatively long footdrum intervals (200-300 msec.), while the irregular sections of these series usually had shorter footdrum intervals. This was the directopposite of the footdrumming patterns of *E. brachyrhynchus* and *E. edwardii*. In the latter species the regular sections consisted of closely spaced footdrums (similar to those found in *E. myurus* and *E. rupestris*), while the irregular portion of the footdrum series had wider spaced footdrum intervals.

Vocalizations

Very few recordings were made of vocalizations during encounters. Audible vocalizations were uttered rarely, and then only during agonistic encounters, usually by the defensive animal. This is especially true of the mewling calls. All these vocalizations were therefore interpreted as stress calls. The mewling vocalizations consisted of one to several short calls. Each mew had a duration of between 200 and 800 msec. Where a call consisted of more than one vocalization, the first one was usually the shortest, with the following ones increasing in duration. Table 3.2 presents the duration and frequency limits of these calls. Because of the small number of *E. rupestris* and *E. edwardii* recordings, no means were calculated for frequencies and durations for these species.

Table 3.2. Duration and harmonic frequencies (mean \pm sd) for mew vocalizations of five *Elephantulus* species.

SPECIES	CALL DURATION (msec)	FUNDAMENTAL (kHz)	HARMONICS(kHz) (n)
<i>E. intufi</i> ⁺	520.3 \pm 321.7	1.39 \pm 0.1 (n=19)	2nd: 2.8 \pm 0.2 (19) 3rd: 4.3 \pm 0.3 (19)* 4th: 5.7 \pm 0.3 (19)* 5th: 7.0 \pm 0.3 (18) 6th: 8.1 \pm 0.6 (13) 7th: 9.0 \pm 0.6 (9)
<i>E. myurus</i>	467.7 \pm 185	1.47 \pm 0.1 (n=6)*	2nd: 2.7 \pm 0.1 (6) 3rd: 3.8 \pm 0.1 (6) 4th: 5.1 \pm 0.2 (6)* 5th: 6.4 (1)
<i>E. edwardii</i>	370; 750; 520	1.80 (n=1)	2nd: 2.7 (1) 3rd: 3.7 (3) 4th: 4.5 (1) 5th: 5.2 (3)* 6th: 6.3 (3) 7th: 7.5 (3)
<i>E. rupestris</i>	250; 260	0.70; 0.75	2nd: 1.5 (2) 3rd: 3.0 (2)* 4th: 4.5 (2) 5th: 6.2 (2)
<i>E. brachyrhynchus</i>	545.0 \pm 255	1.65 \pm 0.1 (n=15)	2nd: 2.7 \pm 0.2 (18) 3rd: 3.6 \pm 0.1 (13)* 4th: 4.8 \pm 0.2 (13)* 5th: 5.6 \pm 0.2 (14)* 6th: 6.6 \pm 0.1 (14) 7th: 7.6 \pm 0.1 (13) 8th: 8.6 \pm 0.2 (10)

* Harmonics with highest amplitude

⁺ Dempster (pers. com.)

Mew calls were characterised by a number of harmonics, up to eight in some of the vocalizations. The fundamental (first harmonic) had a very low frequency modulation, but this increased slightly in the higher harmonics (Fig. 3.3). In these vocalizations the harmonics with the greatest amplitude (ie. the loudest part of the call) were at 4.3 and 5.7 kHz (third and fourth harmonics) for *E. intufi*; 5.1 kHz (fourth harmonic) for *E. myurus*; 5.2 and 6.3 kHz for *E. edwardii*; 3 kHz (third harmonic) for *E. rupestris* and 3.6, 4.8 and 5.7 kHz (third, fourth and fifth harmonics) for *E. brachyrhynchus* (Table 3.2).

E. intufi and *E. brachyrhynchus* vocalized most often during encounters (17 calls in 7 encounters for *E. intufi* and 12 calls in 23 encounters for *E. brachyrhynchus*). This was followed by *E. edwardii* (4 calls in 29 encounters), *E. myurus* (3 calls in 34 encounters), and *E. rupestris* (2 calls in 32 encounters). The mew calls of *E. rupestris* were not only rarer, but also of a much shorter duration and with a much lower fundamental frequency than those of the other species.

The short (10-50 msec.), unstructured clicks produced by elephant shrews in some agonistic situations as well as when being handled in the laboratory were observed in all *Elephantulus* species and in *Macroscelides*. The animals normally produced single clicks during aggressive encounters, but when being handled they uttered a whole series of clicks. Recordings of clicking vocalizations made during handling were only recorded for *E. edwardii* and *E. myurus*. These sounds were produced at the back of the throat with the mouth wide open. The clicks produced by *E. myurus* (Fig. 3.4) ranged in frequency from 1.0 to 6.5 kHz, with the area of highest amplitude being at \pm 1.5 kHz. The intervals between clicks were variable, and ranged from 100 to 200 msec. The intervals between clicks produced by *E. edwardii* (Fig. 3.4) were shorter (140-150 msec apart) and more regular. These clicks had a frequency range of up to 8 kHz, with the greatest amplitude falling between 6 and 7 kHz.

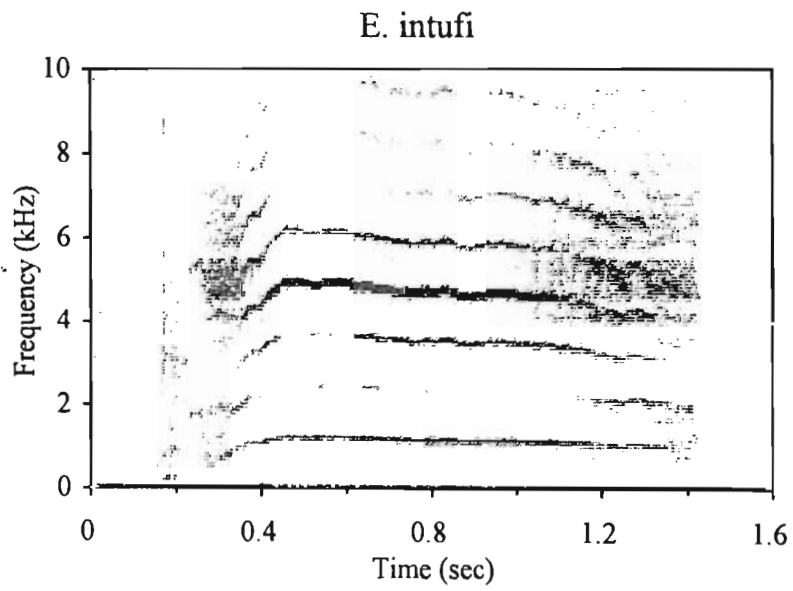
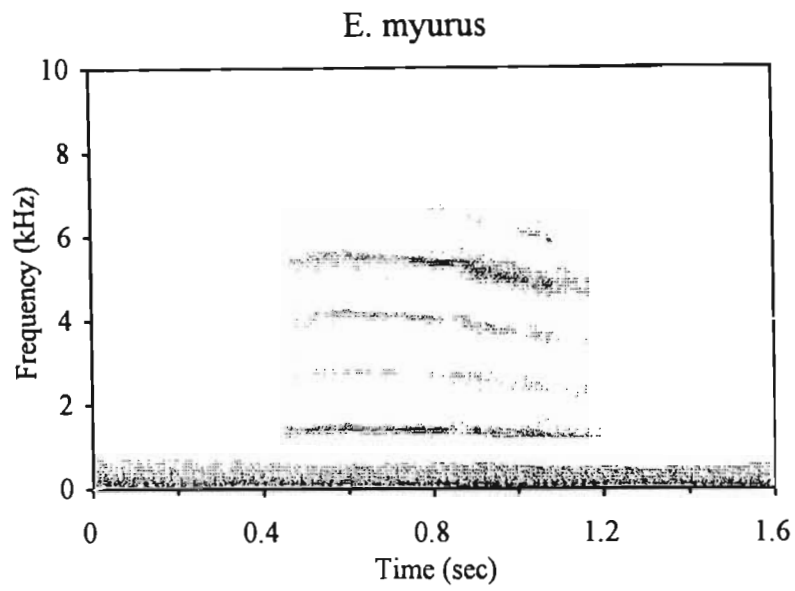


Figure 3.3 Sonograms of mew calls of *E. myurus* and *E. intufi*.

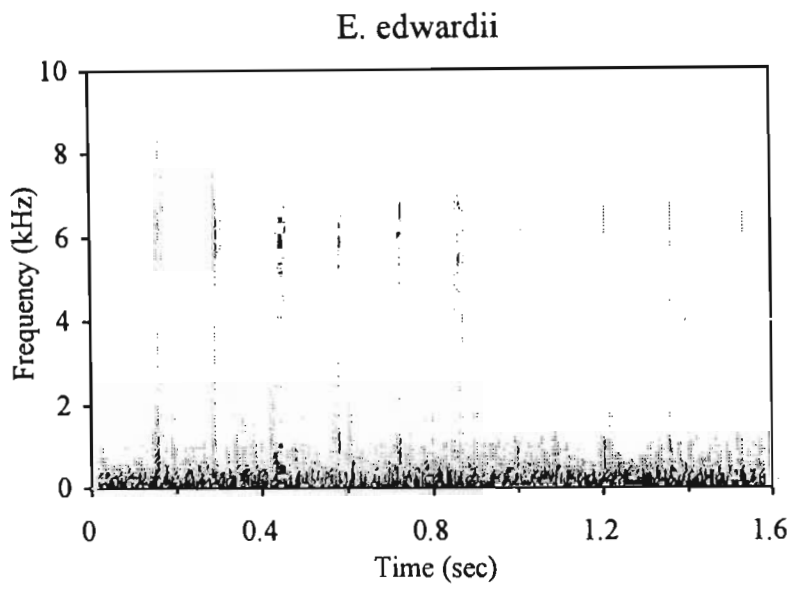
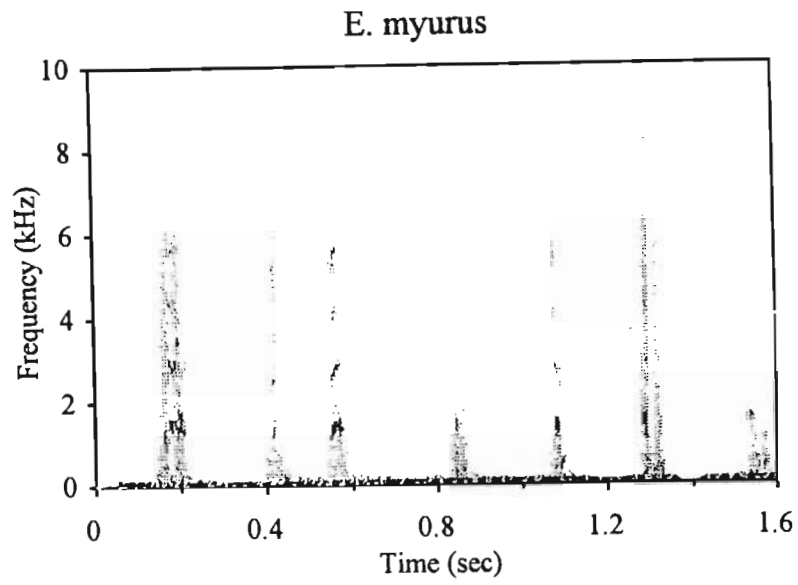


Figure 3.4 Sonograms of click vocalizations of *E. myurus* and *E. edwardii*.

DISCUSSION

Eisenberg (1963) described footdrumming in five kangaroo rat species, but could not ascribe a specific function to it. In recent years there have been several studies of footdrumming in rodents in which some specific communicatory functions have been demonstrated (Randall 1993). Footdrumming in mammals generally occur when animals are in an agitated condition (Roeper 1981), such as during agonistic encounters with conspecifics (Bridelance 1986, Randall 1984, 1994), when exploring a new territory (Bridelance & Paillette 1985), when confronting ground predators (especially snakes) (Cross & Owings 1978, Randall & Stevens 1987, Rathbun 1979) and during or after mating (Bridelance & Paillette 1985, Dewsbury 1971, Kenagy 1976).

Elephant-shrews are very sensitive to human presence and any sudden movement or loud sound caused a footdrumming response in our laboratory populations. In the wild, elephant-shrews footdrum during agonistic encounters and when encountering ground predators (Rathbun 1979). In studies of footdrumming in *E. rufescens* in the wild (Rathbun 1979), and in the laboratory (Roeper 1981), these elephant-shrews footdrummed in stress situations. Rathbun (1979) found that *E. rufescens* footdrum during aggressive territorial encounters on territory borders, while both Rathbun and Roeper found that they used footdrumming as an anti-predator device. When a snake enters an elephant-shrew territory, the animal remains immobile until the snake is quite close, after which it darts away, and then approaches from a different direction. On return the elephant-shrew footdrums loudly, attracting other members from within the territory. The elephant-shrews then mob the snake by charging at it between bouts of footdrumming, until it finally moves away. Footdrumming on sandy substrates and on rocks produces low frequency sounds and vibrations

which would be sensed by snakes. Roeper (1981) concluded that *E. rufescens* used footdrumming to deter pursuit, and that footdrumming may further be indicative of the fitness of the drummer.

Macroscelides proboscideus has greatly hypertrophied auditory bullae (Corbet and Hanks 1968, Skinner and Smithers 1990). The bullae of *Elephantulus* species show much less expansion, but in *E. edwardii* and *E. myurus* the ectotympanic part of the bullae is greatly swollen (Corbet and Hanks 1968). Lay (1972), studying species of Gerbillinae, found a very strong correlation between middle and inner ear specialization and the aridity of habitat. This hypertrophy of the middle ear volume is further associated with a specialized ability for hearing low frequency sounds. Lay suggests that the hearing specialisation of the Gerbillinae has evolved as a primary response to predator avoidance in arid habitats. He found that the attack flight of owls produced frequencies of up to 1.2 kHz, while snake movements produced sound frequencies of up to 2.2 kHz. Many elephant-shrew species inhabit semi-arid to arid habitats, where owls and snakes are significant predators.

Eisenberg and Kleiman (1977) hypothesized that predation may have been the primary selective force for low frequency sensitivity, but that certain classes of auditory signals have undergone further selection to conform to the optimal sensitivity of the adult ear. Randall (1984) concluded from her studies on kangaroo rats that their hearing sensitivity at low frequencies is an adaptation for conspecific communication. According to Knudsen (1935, in Lay 1972) and Gould (1983) the transmission of sounds with a frequency of more than 1 kHz is considerably reduced in air with a low humidity and/or high temperature (i.e. semi-arid to arid conditions). Thus the higher the frequency, the more rapid the attenuation of the sound in air. All elephant-shrew vocalizations in

this study comprised sound with frequencies below 10 kHz. In mew calls and clicks the areas of greatest amplitude fell between 1.5 and 5.5 kHz, while footdrums produced on sand or rocks had frequencies below 2 kHz. What part, if any, the seismic component of footdrumming plays is as yet unknown. However, recordings of footdrumming of kangaroo rats suggest a substantial seismic component (Randall 1989).

The clicks produced by the five *Elephantulus* species, and by *M. proboscideus* were observed in agonistic encounters. Clicks are amongst the most widespread sounds uttered by mammals, since they are easy to produce, hear and locate. They can function in both affiliative or agonistic contexts (Gould 1983). According to Andrew (1964, in Gould 1983) clicks have two sources, one derived from the motor controls for suckling which involves the tongue or lips, and the other from closure of the glottis which is associated with a protective response. The clicks produced by the elephant shrews are probably related to the latter, since the production does not involve lip or tongue movements.

The mewing calls produced by elephant shrews were all relatively short (<1 sec), low frequency sounds. These calls were very rarely produced, and usually only when animals were under severe stress (i.e. in very aggressive agonistic encounters). Rankin (1965) and Skinner and Smithers (1990) have reported *E. myurus*, *E. intufi* and *E. brachyrhynchus* vocalizing under natural conditions as well as in the laboratory. However, the exact context and circumstances under which these vocalizations took place was not very clear. Skinner and Smithers (1990) reported that these vocalizations of *E. myurus* consists of a series of squeaks trailing off towards the end, similar to the vocalization patterns found in the present study. The number of audible vocalizations recorded for

the five elephant shrew species were too limited to compare for species specific patterns.

Definite species specific footdrumming patterns could, however, be discerned among the five *Elephantulus* species tested. Roeper (1981) found that males and females of *E. rufescens* footdrum with equal frequency, which is similar to the results obtained from the South African elephant-shrew species (Chapter 4). The regular footdrumming bouts of the *Elephantulus* species, like those found in the *Meriones* species studied by Bridelance and Paillett (1985), were very stereotyped, which likely indicates a genetic basis.

Comparison of the footdrumming patterns suggested an evolutionary path of footdrumming which splits the *Elephantulus* group from *Macroscelides* by a decrease in footdrum intervals (character 3). These footdrum intervals are then further decreased in the case of *E. rupestris*. Although *E. intufi* proves the exception, an explanation for the exceptionally large footdrum intervals found in *E. intufi* may be that a reversal of regular and irregular elements took place. Comparison of regular and irregular footdrum intervals in the footdrumming series of *E. intufi*, *E. edwardii* and *E. brachyrhynchus* shows the latter two species have exactly the opposite arrangement to that of *E. intufi*. In *E. myurus* it appears that the regular footdrumming bouts have become much shorter (characters 1 and 3), while *E. brachyrhynchus*, *E. edwardii* and *E. intufi* acquired irregular elements in their footdrumming series (character 2 and 4).

Animal vocalizations are often considered as a single unit of behaviour. However, most vocalizations consist of sets of characters that evolve at different rates (Cocroft and Ryan 1995). In a study on call evolution in toads and frogs, Cocroft and Ryan (1995) treated mating calls as a

behavioural pattern, and mapped the different call characters onto existing trees based on morphological and molecular data. This supported the topology of the trees, and they were further able to deduce patterns of call evolution among the different species. Similarly, it could be useful to map the different characters of elephant-shrew footdrumming patterns onto existing morphological and cytogenetic phylogenetic trees to derive a possible path of evolution for footdrumming. Using Corbet and Hanks' (1968) phenogram (Fig. 1.2) to superimpose footdrumming characteristics on makes the most evolutionary sense. The split in the *Elephantulus*/ *Macroscelides* genera agrees with a decrease in footdrum intervals (character 3). *E. edwardii* and *E. brachyrhynchus* then split from the rest of the *Elephantulus* species by the acquisition of irregular elements in their footdrumming series, while *E. myurus* splits from *E. rupestris* by a shortening/ breaking up of regular footdrumming bouts into small sections. The position of *E. intufi* is difficult to interpret, but a reversal of footdrumming characteristics (discussed above), could provide a solution.

In a study on North American pikas (*Ochotona*), Somers (1973) observed that the main morphological characters used in the classification of this group tend to intergrade from one area to the next (skull size and dimensions), and to vary considerably with geography (pelage colour). He suggested that vocalizations are strong indicators of evolution, since they are less subject to selection for local characteristics. Although information about elephant-shrew vocalizations is too limited to include in the present analysis, the initial results show sufficient variation among the species to suggest possible species specific patterns. Gould (1983) pointed out that vocalizations which promote interspecific segregation and/or intraspecific cohesion are much more species-specific than any other vocalizations. Applied to elephant-shrews this indicates that footdrumming, and possibly other vocalizations, may play a role in the maintenance of the territory structure

through individual and mate recognition. However, more in-depth studies on the role of vocalizations, and especially footdrumming, in the laboratory as well as in the field is necessary to give a clearer understanding of function. Footdrumming and vocalizations form only a part of the behavioural repertoire of elephant-shrews, and the present study provides valuable additional data needed to resolve the uncertainties still present in the *Elephantulus* classification. It is obvious from results using different data sets, that a combination of data from morphological, behavioural and biochemical/karyological sources are necessary to obtain a complete picture of elephant-shrew evolution.

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CHAPTER 4

VISUAL AND TACTILE COMMUNICATION

INTRODUCTION

A visual signal could be anything about an animal that can be perceived by another individual (Hailman 1977). The assumption that, during social interactions animals exchange stimuli among themselves, leads to the conclusion that all interactive behaviour must by definition have a communication function (Eisenberg 1981). Visual signals usually combine two, or all three of the dimensions of orientation, shape and movement (Hailman 1977), and are often combined with structural (eg. elaborate plumage or horns) and surface elements (eg. striking colours/patterns). Visual communication has the advantage over other modalities in that it (a) can persist for a long time, (b) is very diverse and consequently has a large information content, and (c) can be directed at a specific receiver (Hailman 1977). Many maintenance behaviours such as dragging, sandbathing, grooming and shaking serve more than one function. All these behaviours originated from primitive pelage dressing and cleaning movements (Eisenberg 1967, 1981), but have taken on an additional role as composite signals in communication (Alcock 1993). For example, behaviours such as dragging and sandbathing serve an additional olfactory as well as a visual communication function (Eisenberg 1967, 1975, Halloran and Bekoff 1995).

The analysis of behavioural patterns and their classification into discrete units that can be used, in a manner similar to morphological characters, for comparison between species have long been used in ethology (Lorenz 1941, Tinbergen 1951, Eisenberg 1967). Butlin and Ritchie (1994) point out that observing behaviour, and especially mating signals in closely related (recently diverged) species provides an insight into the involvement of each of the different behaviours in speciation. The

usefulness of behavioural characters in phylogenetic studies have been much debated (Brooks and McLennan 1991, Cocroft and Ryan 1995, Kennedy *et al.* 1996), but recent advances in comparative methodology have given rise to renewed interest in this area (Alcock 1993, Brooks and McLennan 1991, Gittleman and Decker 1994, Kennedy *et al.* 1996, McLennan *et al.* 1988, Prum 1990). Furthermore, comparison of frequencies of occurrence of different units in an animal's behavioural repertoire elucidates species specific patterns (Bridelance and Paillette 1985, Eisenberg 1967, Dempster *et al.* 1992, Goltsman and Borisova 1993, Koepl *et al.* 1978). Species specific signals have the function of ensuring conspecific aggregation and preventing hybridization and gamete wastage in reproductive behaviour (Hailman 1977). Konishi (1970) suggests that the major reason for the evolution of species specific communication signals are to ensure reproductive isolation.

The aims of this part of the study were firstly to classify and compare visually identifiable behavioural components of the five South African elephant-shrew species, and secondly to test the following hypotheses:

- 1) to determine whether any sexual dimorphism exists in behaviour between males and females of a species.
- 2) to test for species specific behavioural patterns among the South-African elephant-shrew species.
- 3) to determine whether changes occur due to species discrimination in interspecific encounters. In interspecific encounters animals were paired with both sympatric and allopatric heterospecifics. The hypothesis tested was that sympatric species would show higher levels of those behaviours that can act as possible isolating mechanisms when the two species meet (e.g. aggression, fighting and avoidance behaviour).
- 4) studies on several elephant-shrew species have shown that these animals defend their territories sex-specifically (Rathbun 1979, Skinner and Smithers 1990). Intra- and intersexual encounters

were compared for each species to test the hypothesis that higher levels of aggressive behaviour would occur between animals of the same sex.

METHODS

The elephant-shrew species used in this study included *Elephantulus brachyrhynchus*, *E. edwardii*, *E. myurus*, *E. rupestris* and *Macroscelides proboscideus*. Elephant-shrews were kept in the animal house with a 12L:12D light cycle at a temperature of 25° C and a relative humidity of 35 %, and provided with *ad lib.* food and water. At the time of testing, two animals were put into a glass tank (60x30x30 cm) and separated by a wire-mesh partition. Each animal was provided with a nestbox and *ad lib.* water. After 8 hours the partition, water and nestboxes were removed, and the animals were filmed for 20 minutes. Elephant-shrews were filmed during the last 1-2 hours of their light cycle, one of the periods when they were most active. After filming, animals were returned to their home cages. Some animals were used in 2 or 3 different encounters, but never with the same partner, and with a rest period of at least one week between subsequent encounters.

Videotapes were analysed and the different components of visual behaviour were classified, and frequencies of occurrence determined for each elephant-shrew species. Most of the behaviours lasted only fractions of a second to a few seconds. However, where a behaviour lasted for a long period of time (eg. watch and explore), it was subdivided into 10 second units, with every 10 second unit thus counting as one behavioural act. The following encounters were staged:

Male-female intraspecific encounters

- 1) frequencies of male and female behaviours in intersexual encounters were compared using Mann-Whitney-U tests to investigate possible sexual differences in behaviour.
- 2) to determine whether species differed significantly in behaviour of males and females separately, the data were subjected to a Kruskal-Wallis one way analysis of variance by ranks (Statgraphics 6), followed by a multiple comparison test (Siegel and Castellan 1988). Frequencies of behaviours of the elephant-shrews were then used in discriminant function analysis (Statgraphics 6) to determine how well these behaviours separate the individuals of the five species out.
- 3) frequencies of all possible dyadic behaviours were calculated for male act → male act, male act → female act, female act → male act, and female act → female act for each species. Conditional frequencies for each dyad was calculated from transition matrices as: cell total/ row total x 100. Frequencies of less than 30%, as well as dyads that occurred less than 10 times were omitted from the analyses. The most common dyads were thus identified and used in sequence diagrams to illustrate most likely sequences of behaviour for each species.

Male-female interspecific encounters

- 3) to determine any behavioural frequency changes in intraspecific vs. interspecific encounters using male-female groupings, Mann-Whitney-U tests were employed. These encounters were staged only for the four *Elephantulus* species. Behavioural frequencies in intraspecific vs. interspecific allopatric encounters, and intraspecific vs. interspecific sympatric encounters were analysed for significance separately, but plotted in the same graph for comparison.

Same-sex intraspecific encounters

Mann-Whitney-U tests were used to test for any significant behavioural differences between same-sex and mixed-sex encounters for each species. Thus behavioural frequencies of male acts in male-male encounters were compared with behavioural frequencies of male acts in male-female encounters for each species.

Behavioural frequency data were very variable, and consequently non-parametric statistical tests were appropriate for data analysis.

RESULTS

The following list of behaviours comprised the visual/ tactile repertoire of the South-African elephant-shrew species.

ex	explore - moving around the arena investigating and sniffing
wa	watch - sitting inactive and watching opponent, sometimes sleeping
gr	groom - scratching, biting fur and feet/tail
mk	mark - urinating, anal and ventral drag
sb	sandbathe - rolling body in sand
sk	shake - jumping in the air and shaking body rapidly
ap	approach - definite movement towards other individual
ma	move away - definite movement away from other individual
sf	sniff - sniffing any part of other animal (most often naso-nasal, side of the face, side of the body, anal region)
ev	evade - movement with head/body away from opponent, while staying in the same spot
cr	crouch - crouching down, body and head held low, eyes half closed, mouth sometimes half open
fl	flee - run away from opponent
ot	open mouth threat - opening mouth wide in nervous/ submissive reaction, usually when opponent approaches
at	attack threat - threat by opening mouth and making lunging movement with head at opponent, but staying in the same spot
al	attack lunge - lunge and chase
fh	fight - both animals involved in locked fight, rolling and mutual biting

- cl circle - circling opponent closely, usually associated with sniffing (naso-side and naso-anal).
 Mostly performed by both animals simultaneously.
- fo follow - either following after or running parallel with animal moving away
- fd footdrum - rapid hitting of one or both hindfeet on substrate (usually associated with
 aggressive encounters)
- vo vocalize - producing mewling or clicking sounds

No sexual behaviour was observed.

For interspecific and same-sex comparisons certain behaviours were pooled where acts had the same motivation/function. These were marking behaviours, submissive behaviour, aggressive behaviour and vocalizations:

- mrk mark - combined behaviours: mk and sb
- sub submissive - combined behaviours: ev, cr, ot and fl
- agr aggressive - combined behaviours: at and al
- voc vocalizations - combined behaviours: fd and vo

Male-female intraspecific encounters

Comparison of male and female behaviours in intraspecific encounters are shown in Figure 4.1.

E. brachyrhynchus

Females are more active than males, exploring and approaching significantly more than males do. At the same time males watch more than females, and show significantly more submissive behaviour (evading and crouching) when approached and sniffed by females. Overall females

showed higher frequencies of aggressive behaviour, while males acted more submissively. Although not significant, females urinated/dragged more frequently, while males sandbathed and shook themselves more often.

E. edwardii

Females explored significantly more, while males watched more often. Females approached males significantly more frequently and also sniffed, followed and moved away more often than males. Although not significant, males showed more submissive behaviour (evade, crouch and open mouth threat) than females, but also more aggressive behaviour, causing females to flee more often than males. Males showed more grooming and sandbathing behaviour than females, while females urinated and dragged significantly more frequently. Males shook themselves more frequently than females, which is understandable since shaking usually follows either sandbathing or aggressive interactions.

E. myurus

Females explored, while males watched significantly more frequently. Females approached and sniffed significantly more frequently than males. They also followed and showed aggression more often than males, while males showed significantly more submissive behaviour (crouch, open mouth threat, evade). Females further showed significantly higher frequencies of marking and grooming behaviour than males.

E. rupestris

E. rupestris, like *Macroscelides*, showed very little difference in exploratory/watching behaviour between males and females. In contrast with previous species male *E. rupestris* tended to explore, approach and move away more frequently than females, but this difference was not statistically

significant. Although males showed more submissive behaviour (with the exception of crouching) than females, they also attacked and threatened females more often. However, none of these differences were significant. Females showed higher frequencies of marking behaviour (urination and drag), while males sandbathed more often. The only significant difference in behaviour frequencies between the sexes was that males shook themselves more often than females, a behaviour associated with aggression or sandbathing.

M. proboscideus

Males and females had very similar frequencies of exploratory and watching behaviour, although the trend was for males to explore more often, and for females to watch more often. Males groomed and marked (sandbathed and urinated/dragged) significantly more often than females. They also approached and sniffed more often than females did, although this was not significant. Males did however move away from females significantly more frequently than females did.

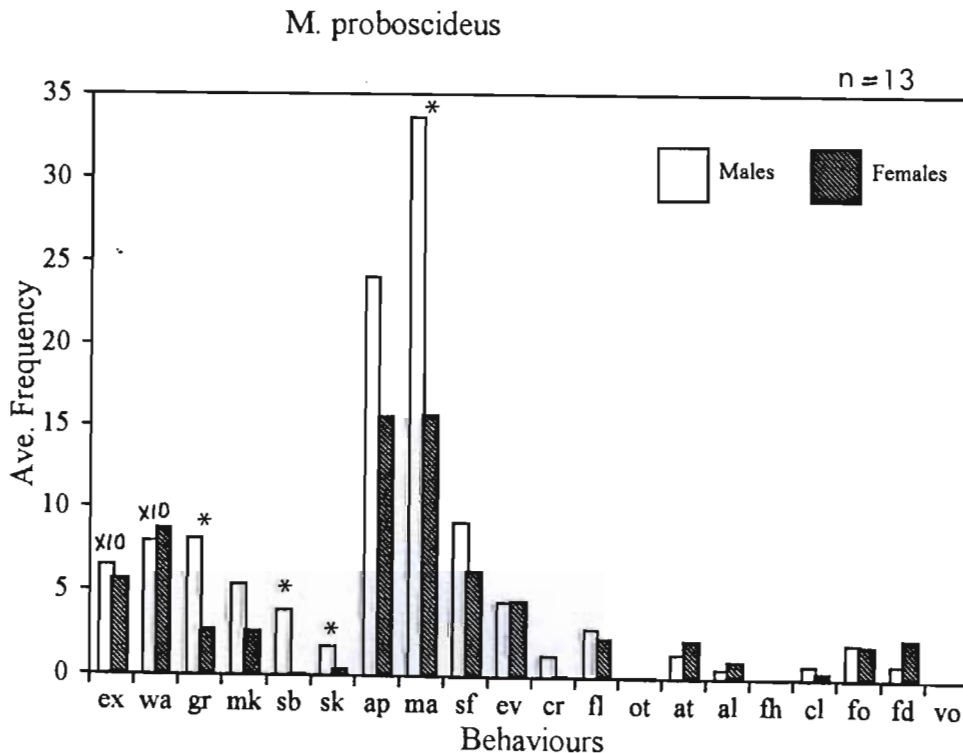


Figure 4.1 Intraspecific behavioural frequencies: males vs. females (* = significant differences)

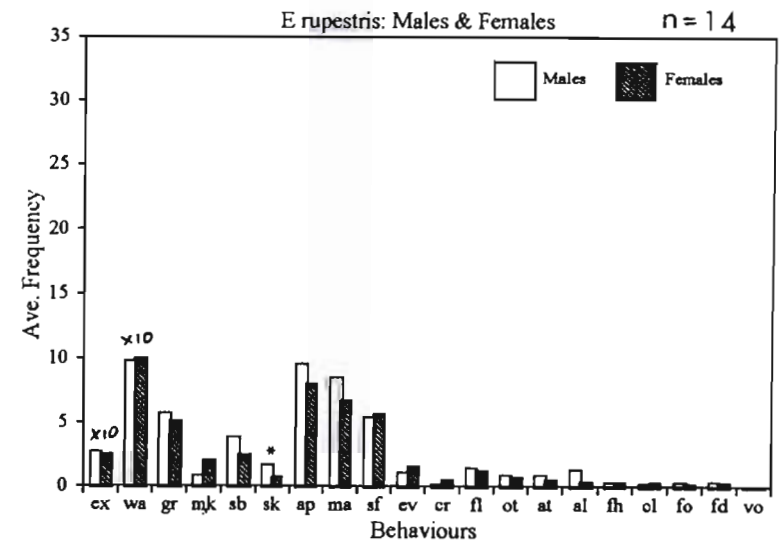
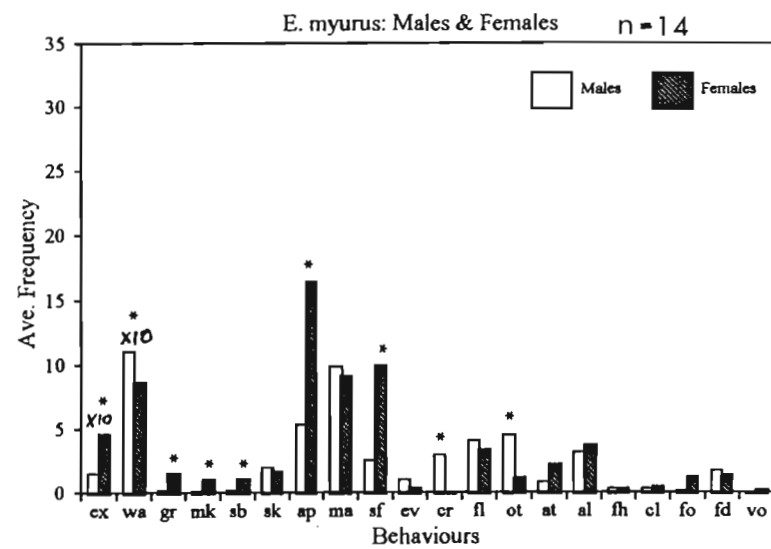
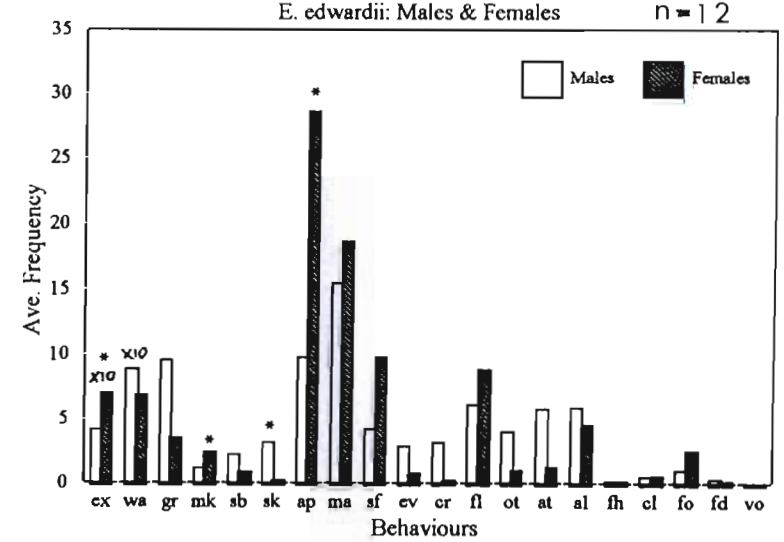
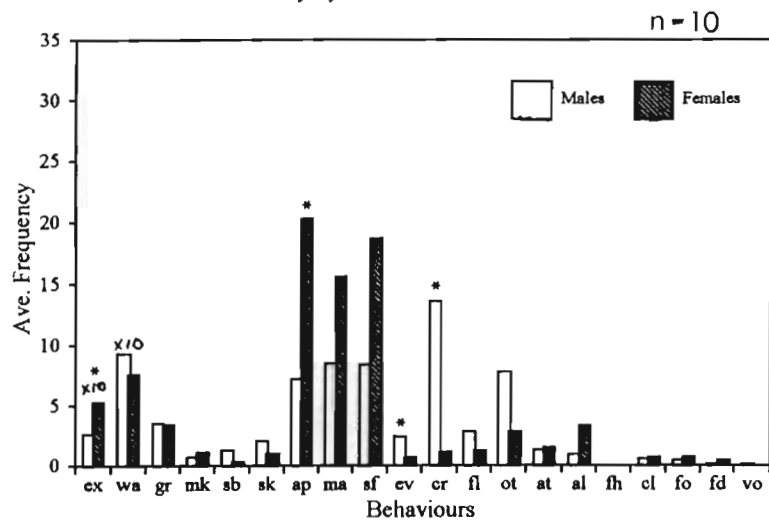


Figure 4.1 Intraspecific behavioural frequencies : males vs. females

* = significant differences

Comparison of different behavioural frequencies among the five elephant-shrew species using a Kruskal-Wallis test indicated significant differences in certain behaviours. This test however, only points to differences between the groups but does not identify which group is different or how many groups differ significantly from one another. A multiple comparison test was used to determine which of the groups were significantly different (Table 4.1). Nine behaviours showed significant differences for males (explore, watch, groom, mark, approach, move away, submissive, aggressive, follow), while only five were significantly different amongst females (explore, watch, approach, move away, vocalize).

Results of discriminant function analyses were as follows:

Males

The first discriminant function accounted for 55.67% of the variance, while the second function accounted for 28.23%. These first two functions thus together accounted for 83.90% of the variance, and both functions showed highly significant correlations between behaviour and species.

Two further functions were identified, but these were not significant at the 95% level (Table 4.2).

By examining standardized discriminant function coefficients the contribution of specific behaviours to each function could be determined, especially when used together with the Kruskal-Wallis results (Table 4.3).

For function 1 move away had the highest coefficient, with shake, sniff and mark also contributing.

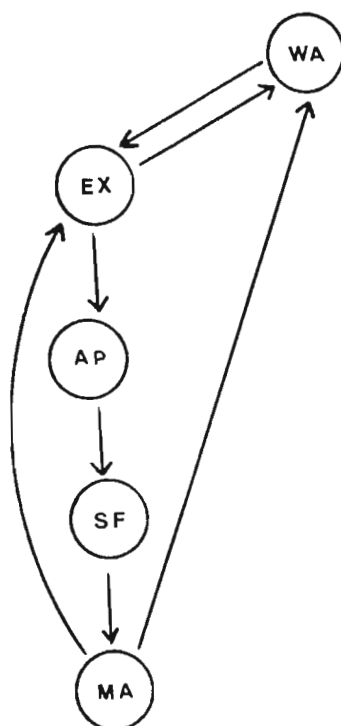
Results from the Kruskal-Wallis tests showed that *M. proboscideus* moved away more often than any of the *Elephantulus* species, with *E. edwardii* intermediate between *M. proboscideus* and the rest of the *Elephantulus* species. *M. proboscideus* males also marked more frequently than the *Elephantulus* species. *E. myurus* marked the least frequently, followed by *E. brachyrhynchus* and

then *E. edwardii* and *E. rupestris*. Kruskal-Wallis tests showed no significant differences between sniffing and shaking behaviour among the species. The first discriminant function could thus be defined by avoidance/markings behaviour.

Exploring had the highest coefficient in the second function. However, approach, submissive and aggressive behaviour also contributed to this function. *M. proboscideus* explored and approached more frequently than the *Elephantulus* species, followed by *E. edwardii*, *E. rupestris*, *E. brachyrhynchus* and lastly *E. myurus*. *E. brachyrhynchus* showed the highest levels of submissive behaviour, with *E. myurus*, *E. edwardii* and *M. proboscideus* intermediate, and *E. rupestris* having the lowest levels. In contrast *E. edwardii* showed the highest frequencies of aggressive behaviour followed by *E. myurus* and *E. brachyrhynchus* and lastly *E. rupestris* and *M. proboscideus* displaying comparatively low levels of aggression. The second function could be defined by exploratory/interactive behaviour.

Within group correlation matrices (Table 4.4) were examined to determine whether any of the variables in the discriminant functions were closely related. Most acts had a negative or low positive correlation, with a few exceptions. Explore and approach were highly correlated (0.749), as were explore and move away (0.415), and explore and sniff (0.447). Reasons for this could be the relatively small size of the arena, which makes it inevitable that a large part of approaching and moving away behaviours are correlated to exploration, since these behaviours could have been unintentional as part of exploration. Approach was further correlated with follow (0.667), sniff (0.600), and to a lesser extent with move away (0.385). Moving away also showed a high correlation with sniff (0.558). The correlation between approach, sniff and move away is not surprising, since most of the initial contact behaviour between elephant-shrews consisted of a large amount of rapid approach/ sniff/ move away manoeuvres. Sequential analysis of male act → male

act, and female act → female act confirmed this as an important behavioural sequence occurring at high frequencies in both males and females in all species investigated.



Aggressive behaviour shows correlations with follow (0.339), fight (0.379) and shake (0.414). Grooming, marking and shaking behaviours showed positive correlations which indicates probable similar motivational states.

Scatterplots (Figure 4.2), together with group centroids (Table 4.5) showed a relatively clear separation of the species. The first function separated *M. proboscideus* from the *Elephantulus* species. The second function separated *E. brachyrhynchus* and *E. edwardii* from the other two *Elephantulus* species.

Finally, classification results (Table 4.6) indicate that 69% of *M. proboscideus* individuals were correctly identified. Of the *Elephantulus* species, *E. myurus* and *E. rupestris* were correctly identified in 71% of the individuals, while *E. brachyrhynchus* and *E. edwardii* were correctly identified in 70% and 67% of the individuals respectively.

Table 4.1 Results from Kruskal-Wallis and Multiple Comparison tests.

MALES							
Behaviour	Ave Rank					Test stat.	P
	M.p.	E.b.	E.e.	E.m.	E.r.		
Explore	45.73	29.4	35.62	19.64	30.36	14.46	0.006
Watch	22.69	28.65	26.71	46.11	33.46	13.08	0.011
Groom	41.73	28.25	39.71	14.85	36.18	20.38	0.0004
Mark	49.54	25.05	31.38	16.64	36.57	25.75	<0.0005
Shake	29.46	30.05	37.88	32.14	30.57	1.75	0.78
Approach	42.81	29.3	35.54	21.18	31.68	10.13	0.04
Move Away	50.27	26.6	31.5	25.18	26.14	17.21	0.002
Sniff	37.88	36.1	29.25	23.07	34.89	5.86	0.21
Submissive	32.42	43.7	32.54	34.11	20.68	9.67	0.046
Aggressive	24.46	31.4	47.46	31.82	26.36	12.82	0.01
Fight	29	29	34.08	31.43	35.71	5.25	0.26
Circle	35.69	34.75	32.92	29.21	28.61	2.44	0.65
Follow	38.88	30.2	39.5	23.39	29.07	10.58	0.032
Vocalize	33.92	28.6	30.29	38.11	28	4.61	0.33
FEMALES							
Behaviour	Ave. Rank					Test stat.	P
	M.p.	E.b.	E.e.	E.m.	E.r.		
Explore	36.73	35.35	44.37	29.57	17.04	16.25	0.003
Watch	33.15	25.75	20.12	34.79	42.29	11.43	0.02
Groom	28.54	35.05	35.5	24.29	37.75	5.35	0.25
Mark	33.65	23.65	35.33	28.61	36.96	4.23	0.37
Shake	25.19	37.35	24.5	40.03	32.89	9.13	0.058
Approach	31.73	38.85	41.37	31.86	19.46	11.11	0.025
Move Away	35.58	37.2	42.21	28.61	21.61	10.79	0.03
Sniff	28.77	45.7	31.58	31.29	26.29	7.42	0.11
Submissive	32.46	31.75	43.96	26.43	27.07	7.52	0.11
Aggressive	35.42	33.8	34.17	35.29	22.39	5.45	0.24
Fight	29	29	34.08	31.43	35.71	5.25	0.26
Circle	31.73	37.65	31.42	31.64	29.07	2.04	0.73
Follow	37.88	31.3	36.46	30.04	25.18	6.56	0.16
Vocalize	40.04	25.9	25.04	40.14	26.68	14.08	0.007

M.p. *Macroscelides proboscideus*

E.e. *Elephantulus edwardii*

E.r. *Elephantulus rufestris*

E.b. *Elephantulus brachyrhynchus*

E.m. *Elephantulus myurus*

Table 4.2. Discriminant function analysis for male elephant-shrews.

Discriminant Function	Eigenvalue	Relative Percentage	Canonical Correlation
1	2.195	55.97	0.828
2	1.113	28.23	0.725
3	0.351	8.92	0.510
4	0.283	7.18	0.469

Functions Derived	Wilks Lambda	Chi-Square	DF	Sig. Level
0	0.085	129.209	56	0.000
1	0.272	68.212	39	0.002
2	0.576	28.922	24	0.223
3	0.779	13.093	11	0.287

Table 4.3 Standardized discriminant function coefficients for male elephant-shrews.

	1	2	3	4
Explore	-0.456	-1.158	-0.731	-0.677
Watch	-0.449	-0.007	-0.536	-0.614
Groom	0.032	-0.654	-0.234	-0.639
Mark	0.732	-0.043	0.503	-0.109
Shake	-0.960	0.217	0.091	0.257
Approach	0.204	0.888	-0.090	-0.337
Move Away	1.174	0.328	-0.182	0.570
Sniff	-0.841	-0.252	1.032	-0.130
Submissive	-0.293	-0.818	0.151	0.334
Aggressive	0.161	-0.810	-0.426	-0.190
Fight	-0.009	0.138	0.011	-0.398
Circle	0.317	-0.014	-0.350	0.493
Follow	0.353	-0.035	0.033	0.571
Vocalise	-0.030	0.511	-0.165	0.345

Table 4.4 Correlation matrix of male elephant-shrew behaviours.

	ex	mrk	sk	ap	ma	sf	sub	agr
ex	1.000							
mrk	0.183	1.000						
sk	0.119	0.411	1.000					
ap	0.749	0.044	0.045	1.000				
ma	0.415	0.053	0.369	0.385	1.000			
sf	0.447	-0.022	-0.028	0.600	0.558	1.000		
sub	-0.181	-0.190	-0.160	-0.058	0.050	-0.080	1.000	
agr	-0.052	-0.121	0.414	0.107	0.217	0.079	-0.168	1.000

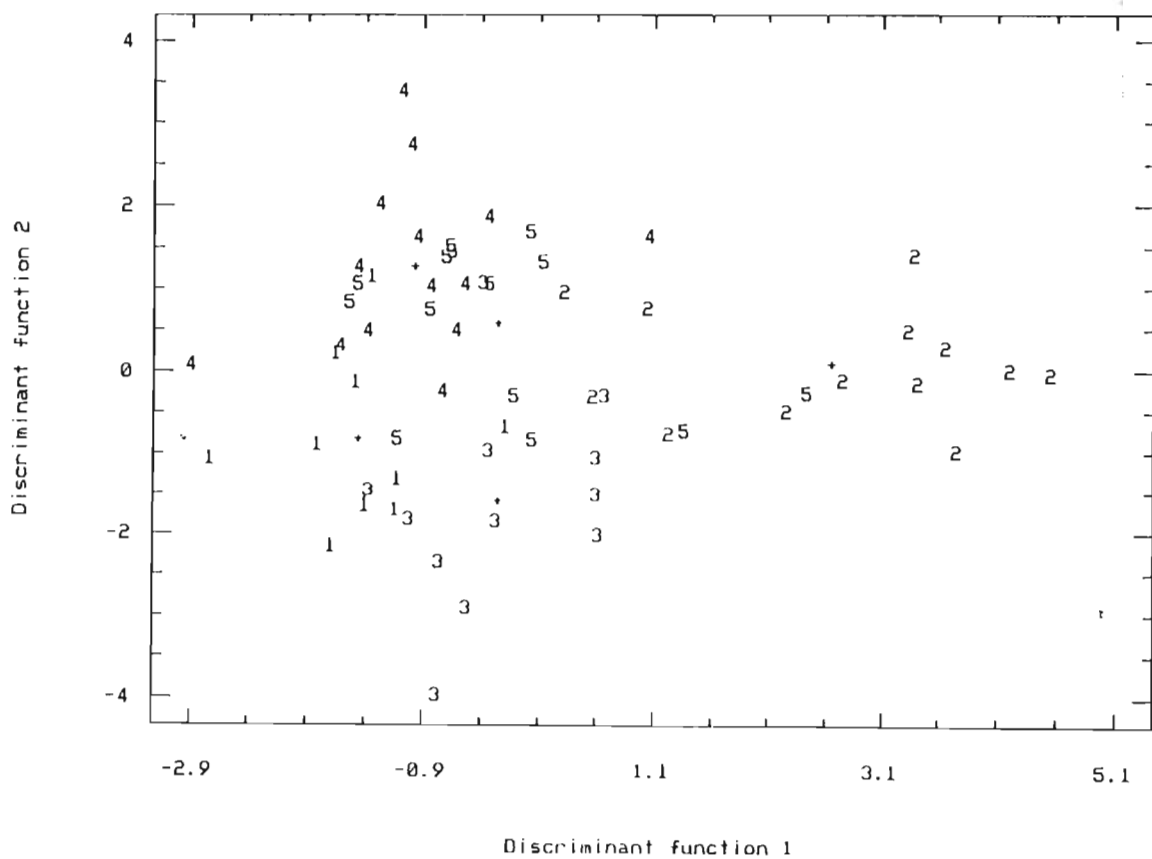


Figure 4.2 Scatterplot of discriminant functions for male elephant-shrews.

1 = *E. brachyrhynchus*
 4 = *E. myurus*

2 = *M. proboscideus*
 5 = *E. rupestris*

3 = *E. edwardii*

Table 4.5 Group Centroids for male elephant-shrews.

	1	2	3	4
E. brachyrhynchus	-1.454	-0.813	0.904	0.532
E. edwardii	-0.246	-0.587	-0.718	-0.211
E. myurus	-0.970	1.278	-0.529	0.387
E. rupestris	-0.243	0.586	0.363	-0.843
M. proboscideus	2.653	0.082	0.147	0.275

Table 4.6 Classification Results for elephant-shrew males.

Actual group	Predicted Group					
	<i>E. brachyrhynchus</i>		<i>E. edwardii</i>		<i>E. myurus</i>	
	Count	Percent	Count	Percent	Count	Percent
<i>E. brachyrhynchus</i>	7	70.00	1	10.00	1	10.00
<i>E. edwardii</i>	2	16.67	8	66.67	1	8.33
<i>E. myurus</i>	2	14.29	0	0.00	10	71.43
<i>E. rupestris</i>	0	0.00	0	0.00	3	21.43
<i>M. proboscideus</i>	0	0.00	1	7.69	0	0.00

Actual Group	Predicted Group					
	<i>E. rupestris</i>		<i>M. proboscideus</i>		TOTAL	
	Count	Percent	Count	Percent	Count	Percent
<i>E. brachyrhynchus</i>	1	10.00	0	0.00	10	100.00
<i>E. edwardii</i>	1	8.33	0	0.00	12	100.00
<i>E. myurus</i>	2	14.29	0	0.00	14	100.00
<i>E. rupestris</i>	10	71.43	1	7.14	14	100.00
<i>M. proboscideus</i>	3	23.08	9	69.23	13	100.00

Females

The first discriminant function accounted for 46.32% of the variation, while the second accounted for 26.23%, and the third for 18.66%. One further function was identified but this was not significant at the 95% level. The first two functions were highly significant, showing a strong correlation between behaviour and species. The third discriminant function was also used since the Wilkes-Lambda values were still close to the 95% significance level. The first three discriminant functions thus accounted for 91.21% of the variance (Table 4.7).

Using standardised discriminant function coefficients (Table 4.8) in conjunction with the Kruskal-Wallis results, behaviours contributing to each function could be determined. Explore and sniff had the highest coefficient in the first function. *E. edwardii* did the largest amount of exploring, followed by *M. proboscideus* and *E. brachyrhynchus* with very similar ranks, then *E. myurus* and lastly *E. rupestris* females which showed comparatively low frequencies of exploratory behaviour. Female *E. brachyrhynchus* showed the highest frequencies of sniffing, followed by *E. edwardii* and *E. myurus*, and then by *M. proboscideus* and *E. rupestris*. However, these frequencies were not significant in the Kruskal-Wallis tests. The first function could be defined as exploratory.

For the second function sniffing and fighting had the highest coefficients. Neither of these behaviours were significant in the Kruskal-Wallis analysis. *E. rupestris* fought most often, followed by *E. edwardii*, *E. myurus*, *E. brachyrhynchus* and *M. proboscideus*. Watch, mark, aggressive and submissive behaviour contributed to the second function to a lesser degree. The second function could thus be defined as sniffing/fighting.

Explore, watch and approach had the highest coefficients in the third function. *E. rupestris* watched most often, followed by *M. proboscideus* and *E. myurus* which were very similar and then *E. brachyrhynchus* and lastly *E. edwardii* females which did the least amount of watching. *E.*

edwardii females approached more often than any of the other species, followed by *E. brachyrhynchus* and then *E. myurus* and *M. proboscideus* with similar values, and *E. rupestris* with the lowest frequencies.

Within group correlation matrices (Table 4.9) showed most acts with negative or low positive correlations, although a few high correlations were present. Explore and approach (0.743), explore and move away (0.531) and explore and sniff (0.622) were highly correlated. Similarly to the results found in males, the small size of the arena could mean that a large part of approaching and moving away behaviours were correlated to exploration, since these behaviours could have been unintentional as part of exploration. There is furthermore a positive correlation between approach and move away (0.596), approach and sniff (0.838) and approach and follow (0.710) similar to that found in the males, and these behaviours are probably correlated for the same reason; they are often performed together as part of the initial contact behaviour as confirmed by sequence analysis. Submissive behaviour has a slight positive correlation with move away and fight, while aggressive behaviour is correlated with approach, circle, sniff and follow. Grooming, marking and shaking show low positive correlations, similarly to males.

Scatterplots (Figure 4.3) and group centroids (Table 4.10) showed, similarly to males, a separation of the species, although not as clearly as was found in males. Function one separated *M. proboscideus* and *E. edwardii* from the rest of the elephant-shrew species. The second function separated *E. rupestris* from the rest, while the third function (not shown on the scatterplot) further separated *E. edwardii* from the other species, with *M. proboscideus* and *E. myurus* forming an intermediate group, and *E. brachyrhynchus* and *E. rupestris* forming the last group.

Actual and predicted classification results identified only 46% of the *M. proboscideus* females as the correct species. 92% of *E. rupestris* females were correctly identified, while 67% of *E.*

edwardii females, 60% of *E. brachyrhynchus* and 50% of *E. myurus* females were correctly identified.

Table 4.7 Discriminant function analysis for female elephant-shrews.

Discriminant Function	Eigenvalue	Relative Percentage	Canonical Correlation
	1.362	46.32	0.759
1	0.771	26.23	0.660
3	0.549	18.66	0.595
4	0.259	8.80	0.453

Functions Derived	Wilks Lambda	Chi-Square	DF	Sig. Level
0	0.123	110.192	56	0.000
1	0.290	65.060	39	0.005
2	0.513	35.043	24	0.067
3	0.794	12.079	11	0.358

Table 4.8 Standardized discriminant function coefficients for female elephant-shrews.

	1	2	3	4
Explore	1.067	-0.213	1.712	-0.662
Watch	0.373	0.581	1.401	-0.689
Groom	0.290	0.095	-0.288	-0.635
Mark	-0.026	0.680	-0.141	0.193
Shake	-0.475	0.127	0.372	0.637
Approach	0.296	0.485	-1.145	0.924
Move away	-0.057	0.225	-0.105	-0.423
Sniff	-1.544	-0.748	0.498	-0.665
Submissive	0.118	-0.559	-0.508	0.057
Aggressive	0.379	-0.593	-0.063	0.007
Fight	-0.292	0.718	0.126	0.324
Circle	-0.007	-0.089	-0.209	-0.052
Follow	0.773	0.355	0.326	0.193
Vocalize	0.410	-0.282	0.440	-0.101

Table 4.9 Correlation matrix of female elephant-shrew behaviours.

	Ex	Wa	Mrk	Ap	Sf	Sub	Agr	Fh
Ex	1.000							
Wa	-0.904	1.000						
Mrk	0.229	-0.234	1.000					
Ap	0.744	-0.642	0.134	1.000				
Sf	0.622	-0.588	0.206	0.838	1.000			
Sub	0.098	0.153	-0.115	0.087	-0.118	1.000		
Agr	0.182	-0.115	0.091	0.439	0.377	-0.067	1.000	
Fh	0.126	-0.067	-0.133	0.118	0.022	0.345	0.294	1.000

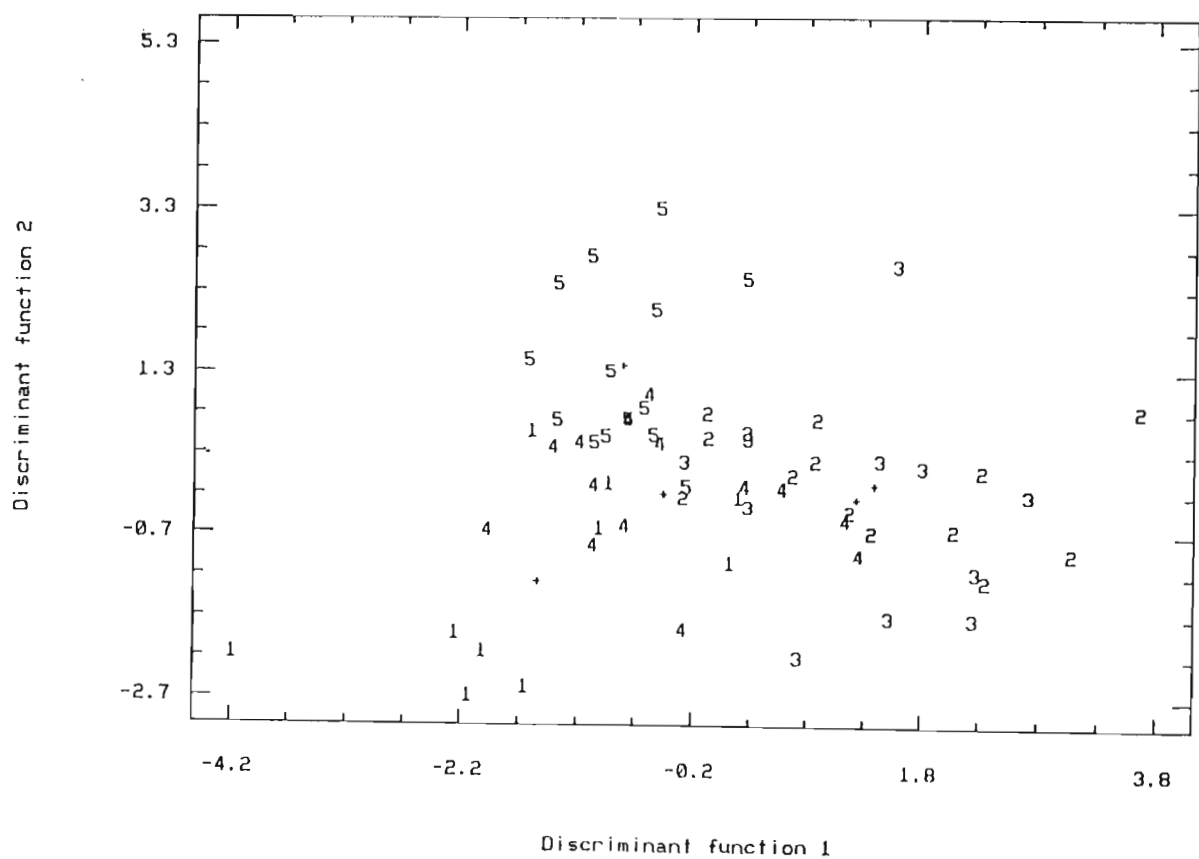


Figure 4.3 Scatterplot of discriminant functions for female elephant-shrews.

1 = *E. brachyrhynchus*
 4 = *E. myurus*

2 = *M. proboscideus*
 5 = *E. rupestris*

3 = *E. edwardii*

Table 4.10 Group centroids for female elephant-shrews.

	1	2	3	4
E. brachyrhynchus	-1.537	-1.277	-0.268	-0.482
E. edwardii	1.239	-0.257	-1.150	0.273
E. myurus	-0.451	-0.187	0.657	0.761
E. rupestris	-0.802	1.390	-0.229	-0.195
M. proboscideus	1.389	-0.076	0.806	-0.491

Table 4.11 Classification Results for elephant-shrew females.

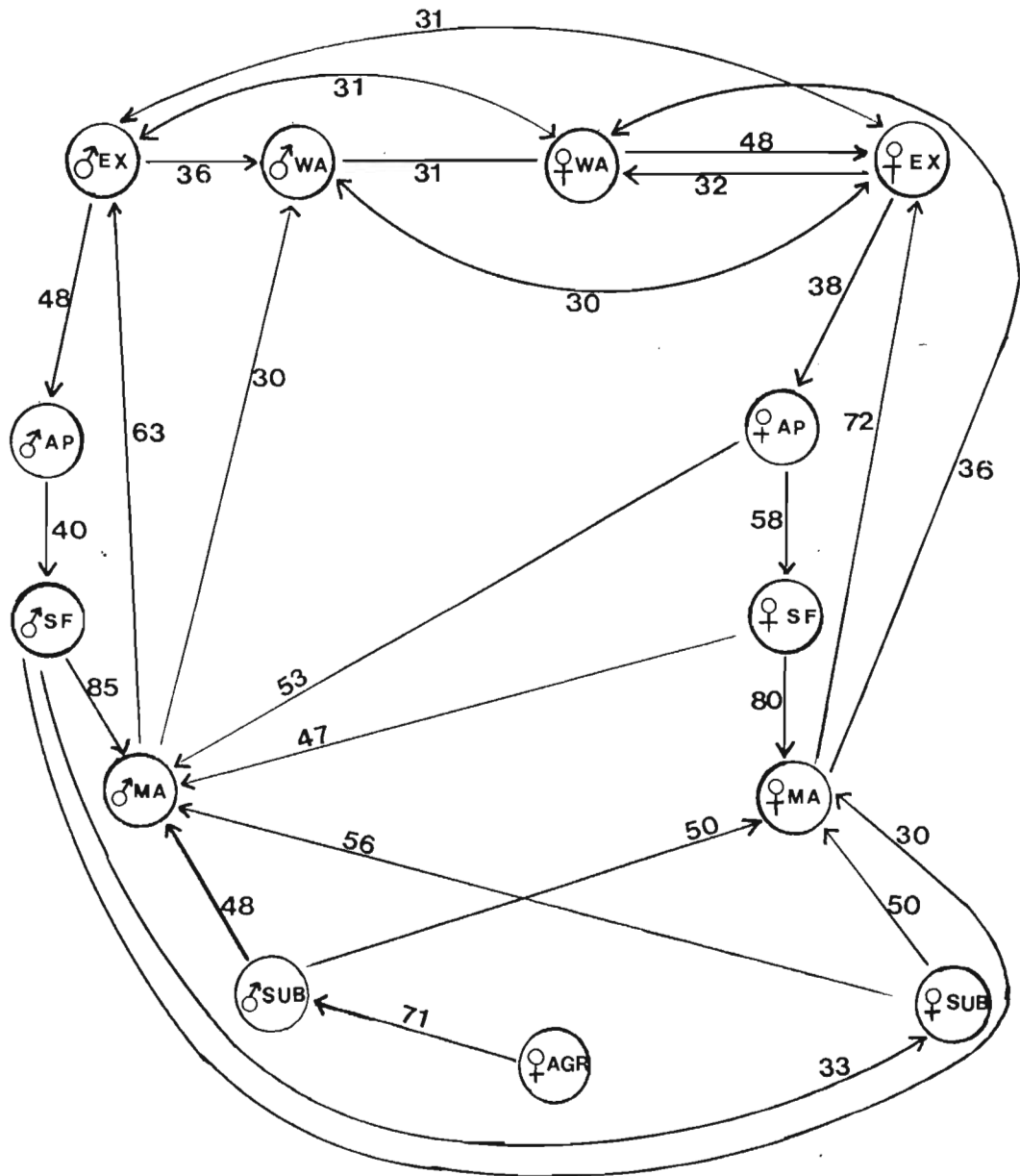
Actual Group	Predicted Group					
	E. brachyrhynchus		E. edwardii		E. myurus	
	Count	Percent	Count	Percent	Count	Percent
E. brachyrhynchus	6	60.00	1	10.00	2	20.00
E. edwardii	0	0.00	8	66.67	2	16.67
E. myurus	2	14.29	1	7.14	7	50.00
E. rupestris	0	0.00	0	0.00	1	7.14
M. proboscideus	1	7.69	4	30.77	0	0.00

Actual Group	Predicted group					
	E. rupestris		M. proboscideus		TOTAL	
	Count	Percent	Count	Percent	Count	Percent
E. brachyrhynchus	1	10.00	0	0.00	10	100.00
E. edwardii	1	8.33	1	8.33	12	100.00
E. myurus	1	7.14	3	21.48	14	100.00
E. rupestris	13	92.86	0	0.00	14	100.00
M. proboscideus	2	15.38	6	46.15	13	100.00

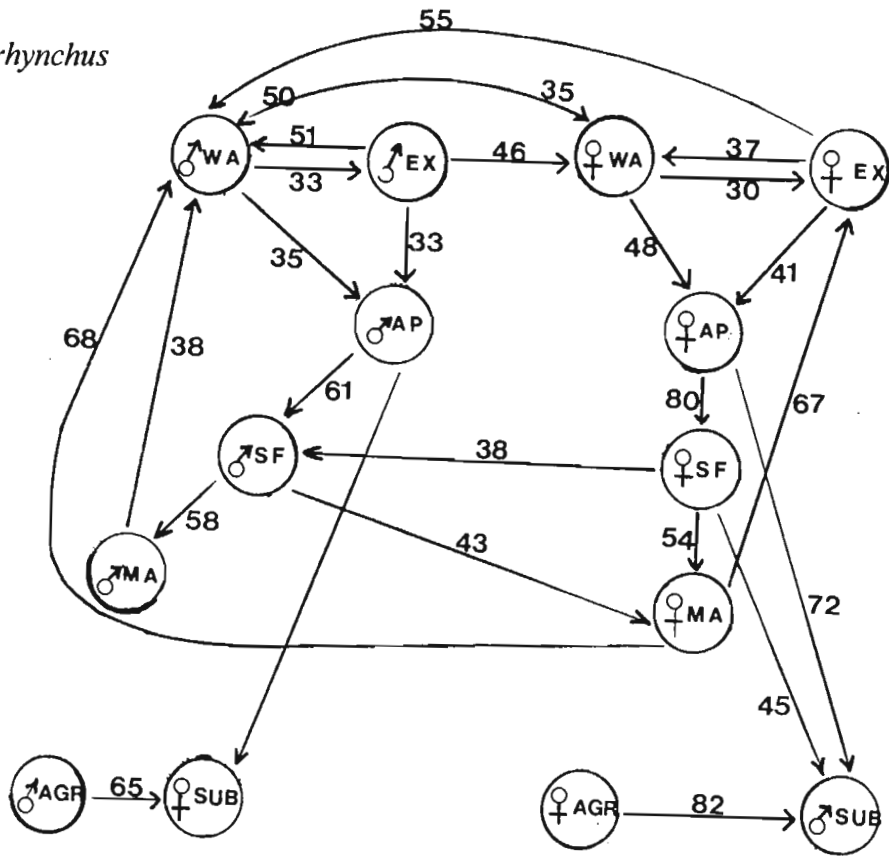
Behavioural sequences

Analysis of male act → female act, and female act → male act for the different species are illustrated in below. Arrows indicate direction of action, and numbers indicate conditional probabilities.

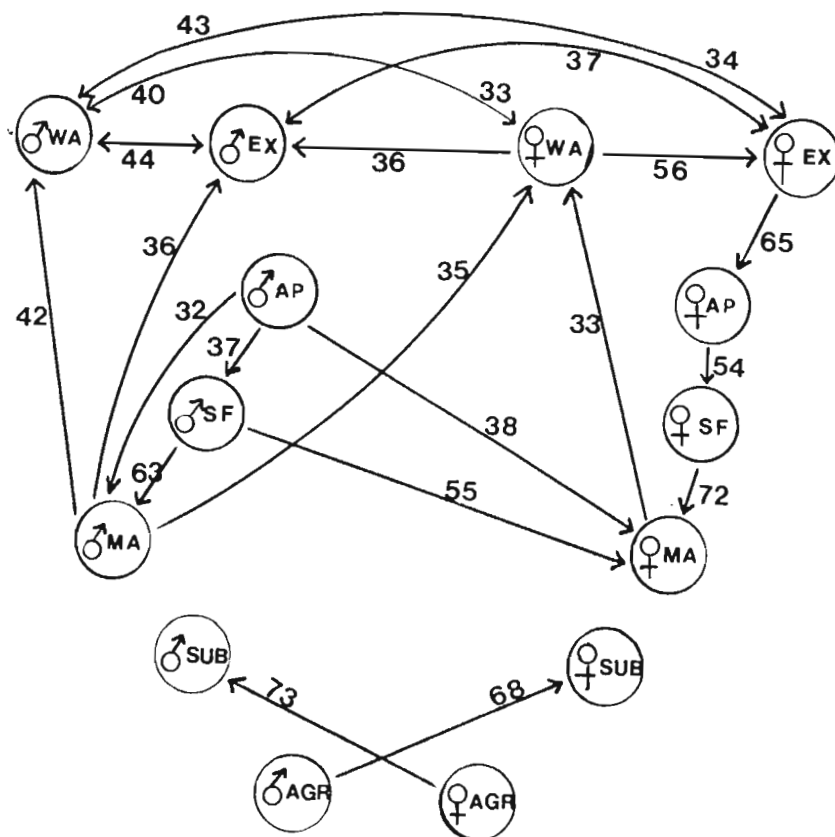
M. Proboscideus



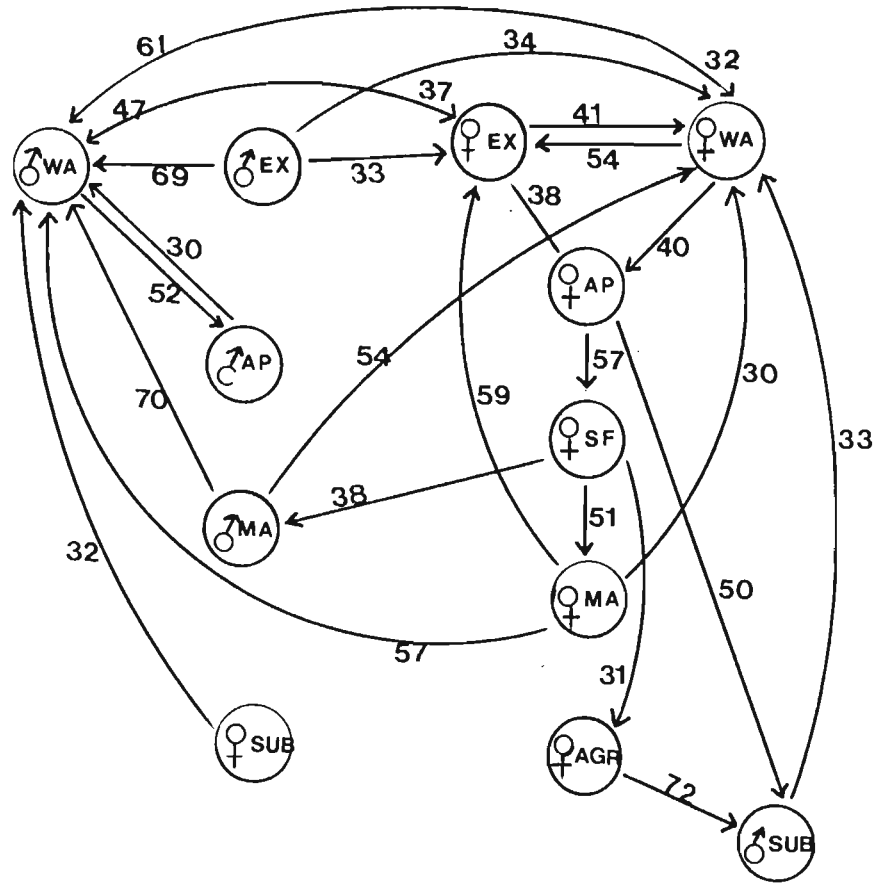
E. brachyrhynchus



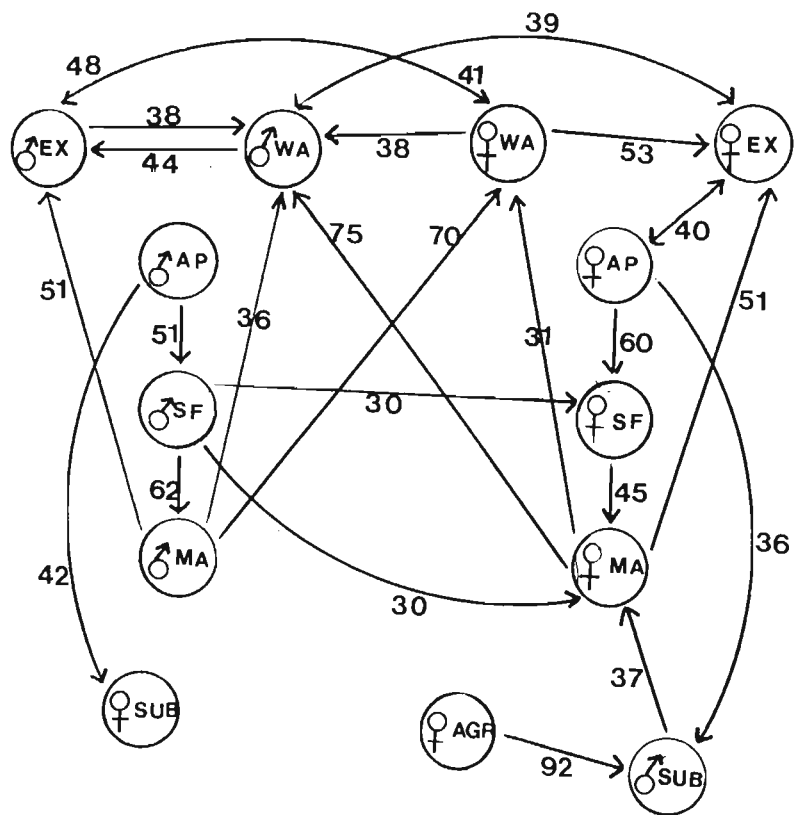
E. edwardii



E. myurus



E. rupestris



The contact promoting/ exploratory behaviours of explore/watch → approach → sniff → move away is noticeable in males and females of all species. Exploratory and watching behaviours seem to have a corresponding response in the opposite sex in all the elephant-shrew species. The size of the arenas made this inevitable, since the slightest movement by one animal, would be noticed and/or acted on by the other animal.

Sequence analysis further indicated that aggressive behaviour by females lead to high frequencies of submissive behaviour in all the elephant-shrew males. However, aggressive behaviour in males caused high frequencies of submissive behaviour only in *E. brachyrhynchus* and *E. edwardii* females.

In both sexes of *E. brachyrhynchus* and *E. rupestris*, and in *E. myurus* and *M. proboscideus* females submissive behaviours were also caused by approach/ sniff acts from an opponent. In *E. brachyrhynchus*, *E. edwardii*, *E. rupestris* and *M. proboscideus* males, as well as *E. myurus* females approaching and sniffing frequently resulted in the other animal moving away.

Male-female interspecific encounters

Results of interspecific vs intraspecific encounters are shown in Figure 4.4.

E. brachyrhynchus

E. brachyrhynchus males and females explored more and watched less in intraspecific than interspecific encounters. Both sexes performed more contact promoting behaviour (approach/move away, sniff and follow) with conspecifics than heterospecifics. However, males were more submissive in intraspecific encounters (especially when compared with allopatric interspecific encounters), while females in contrast, showed less submission and more aggression in intraspecific encounters. Males showed higher aggression frequencies in

interspecific encounters with sympatric species than with conspecifics. Both male and female *E. brachyrhynchus* footdrummed more often in interspecific encounters than in intraspecific encounters, while females marked (especially sandbathed) and groomed more often in interspecific encounters with sympatric heterospecifics.

E. edwardii

Both male and female *E. edwardii* explored significantly less in interspecific encounters with allopatric heterospecifics than with conspecifics. Both sexes performed more contact behaviour (approach/move away, sniff, follow) in intraspecific encounters. However, this trend is much more pronounced when comparing encounters with conspecifics and allopatric heterospecifics. Encounters with sympatric species showed similar behavioural frequencies as encounters with conspecifics. Both sexes showed considerably more submissive as well as aggressive behaviour in intraspecific encounters. However, both sexes sandbathed significantly more in interspecific encounters (especially with sympatric species), and females footdrummed more often in interspecific encounters with sympatric species, although the result is not significant.

E. myurus

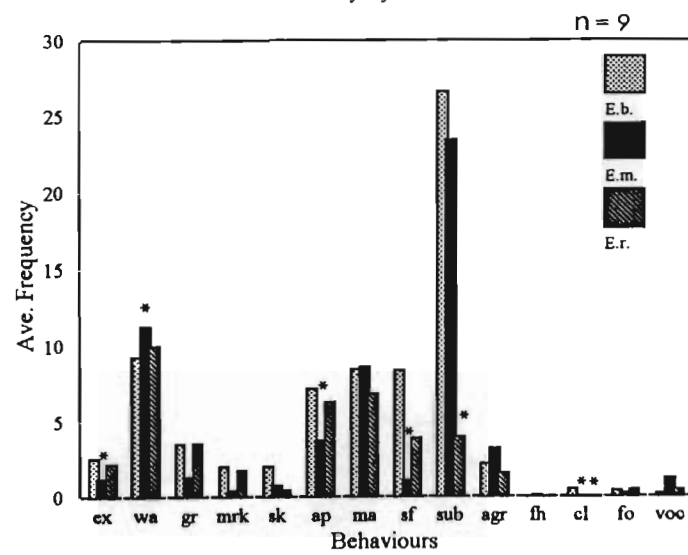
There were no significant differences in exploratory and watching behaviours in *E. myurus* in intraspecific compared with interspecific encounters. Male *E. myurus* moved away, and showed submissive behaviour more often in intraspecific encounters than in any interspecific encounters. Males showed higher frequencies of aggressive behaviour in conspecific encounters than compared with allopatric encounters, and much lower aggression frequencies with conspecifics when compared with sympatric heterospecifics. Females moved away more frequently, but also showed higher frequencies of aggression when paired with sympatric species, and lower frequencies of aggressive behaviour with allopatric species when compared

to conspecific pairings.

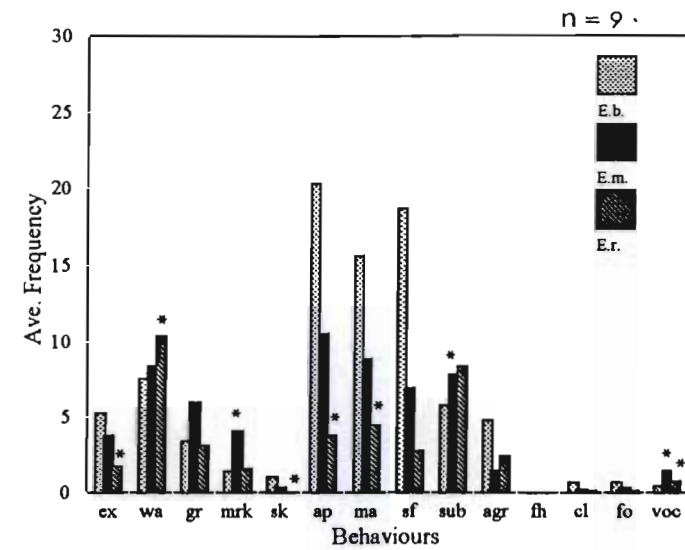
E. rupestris

E. rupestris did not differ significantly in exploring and watching behaviours in intraspecific and interspecific encounters. *E. rupestris* females explored more and watched less in interspecific encounters with *E. edwardii*, with which it is sympatric, than with conspecifics or allopatric heterospecifics. *E. rupestris* males groomed and marked significantly more often in intraspecific encounters, while for females the only statistically significant difference was that they sandbathed more in intraspecific encounters than encounters with interspecific allopatric species, however, they marked less often in encounters with conspecific males than sympatric heterospecific males. *E. rupestris* males showed similar results in approach/move away and sniffing behaviours in all encounters, while females tended to approach/move away more with sympatric heterospecifics (*E. edwardii*). However, both sexes followed significantly more often and showed more aggressive behaviour in interspecific encounters with *E. edwardii* (sympatric heterospecific). Only *E. rupestris* males showed significantly more submissive behaviour in encounters with *E. edwardii*.

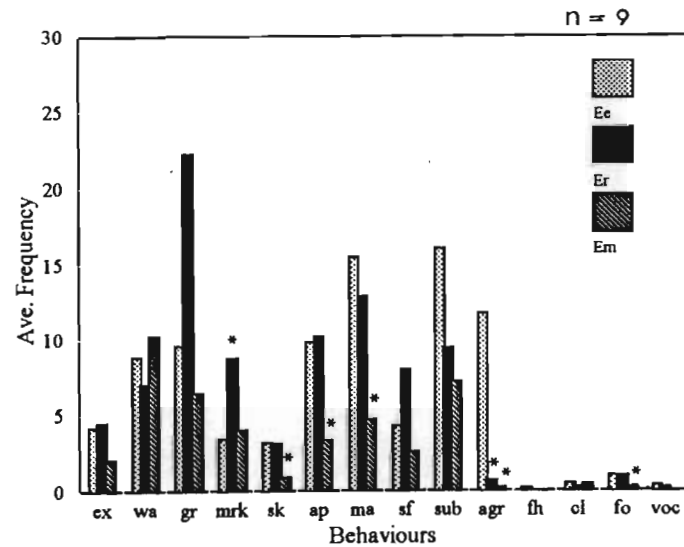
E. brachyrhynchus males



E. brachyrhynchus females



E. edwardii males



E. edwardii females

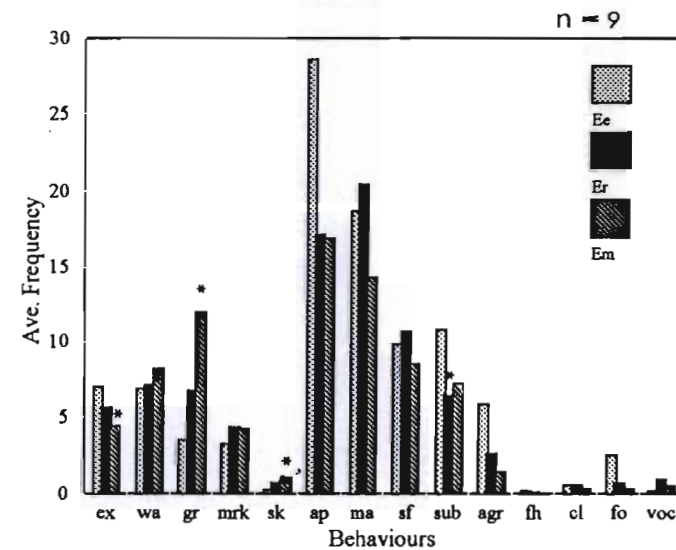


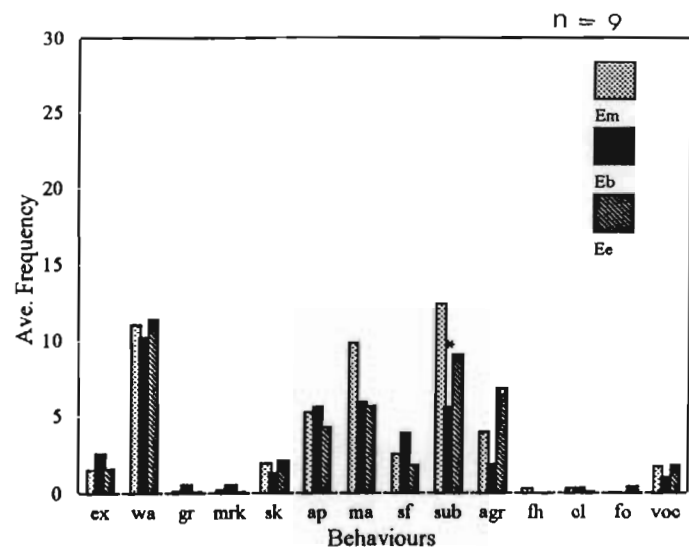
Figure 4.4 Comparison in intraspecific and interspecific behaviour frequencies among four *Elephantulus* species.

* = significant differences.

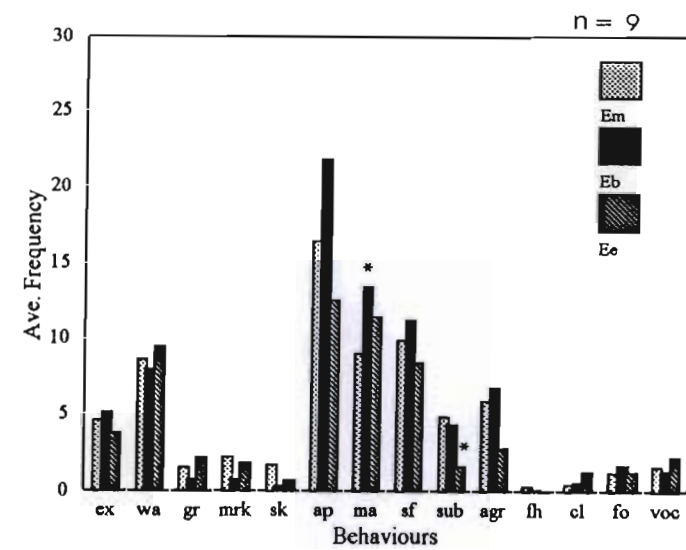
■ = Intraspecific

■ = interspecific (sympatric)

■ = interspecific (allopatric)



E. rupestris males



E. rupestris females

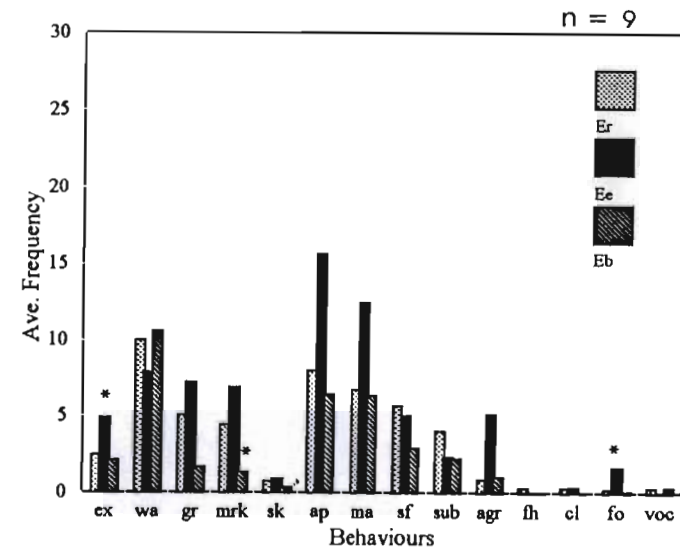
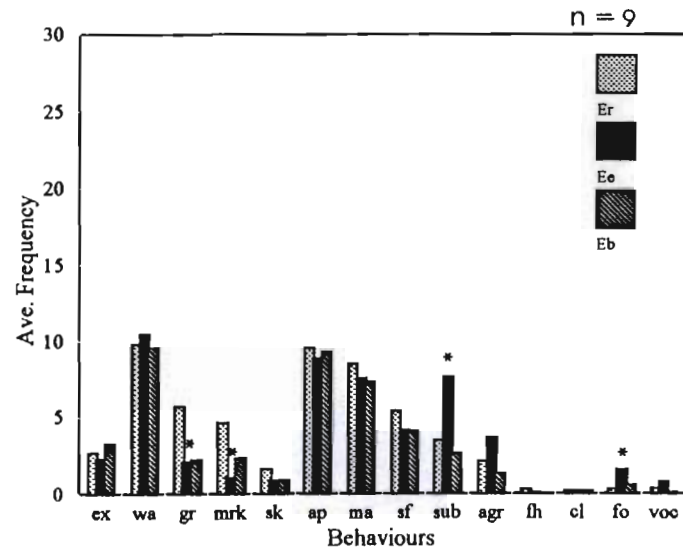


Figure 4. Comparison of intraspecific and interspecific behaviour frequencies among four *Elephantulus* species.

* = significant differences

▨ = intraspecific

■ = interspecific (sympatric)

■ = interspecific (allopatric)

Same-sex encounters

Results from same-sex versus mixed-sex encounters are shown in Figure 4.5.

E. brachyrhynchus

Both males and females explored more and watched significantly more in same-sex encounters than mixed-sex encounters. Contact promoting behaviours (approach/move away) also occurred more frequently in same-sex encounters. Males showed significantly more submissive behaviour in mixed-sex encounters than females. Both males and females displayed higher aggression levels, as well as circling and following behaviour in same-sex encounters, although this was only significant for female aggression. Females furthermore footdrummed significantly more often in same-sex encounters, which is not surprising considering that footdrumming is generally associated with aggression. Both sexes groomed significantly more often during same-sex encounters.

E. edwardii

Both *E. edwardii* sexes showed higher behaviour frequencies in all acts in same-sex encounters compared with mixed-sex encounters. Both sexes watched significantly more often and females shook and groomed more often in same-sex encounters. Contact promoting behaviour was significantly higher in same-sex encounters (approach in females and move away in males). Submissive behaviour showed the same trend, with female *E. edwardii* evading others significantly more often in same-sex encounters, however, although males showed higher levels of aggression in same-sex encounters, females showed levels similar to mixed-sex encounters. Both sexes footdrummed and vocalized more often in same-sex encounters, but this was only significant for females.

E. myurus

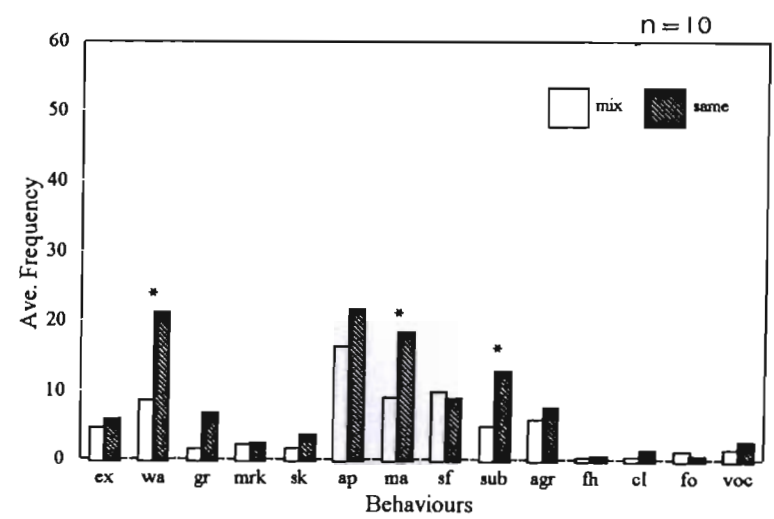
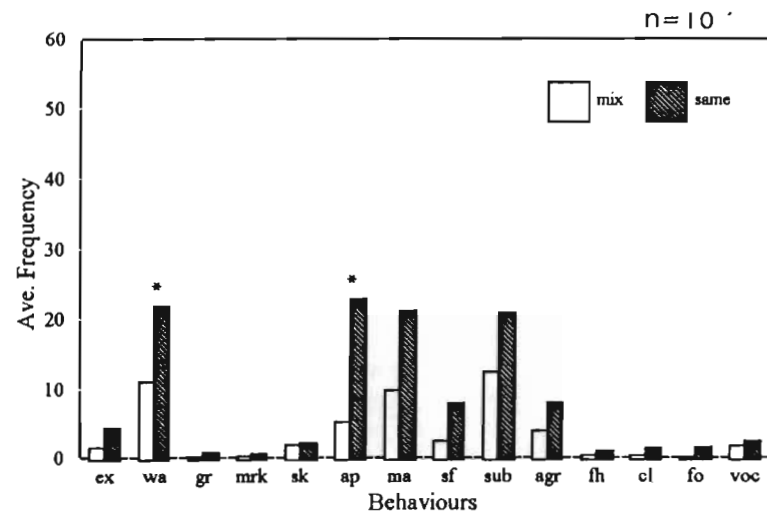
E. myurus males and females, as with the previous species watched significantly more often in same-sex encounters. Both sexes also approached and moved away, while males sniffed more often in same-sex encounters. All *E. myurus* individuals showed significantly more submissive behaviour in same-sex encounters. Aggressive behaviour and footdrumming also occurred at higher frequencies in same-sex encounters, but these differences were not significant.

E. rupestris

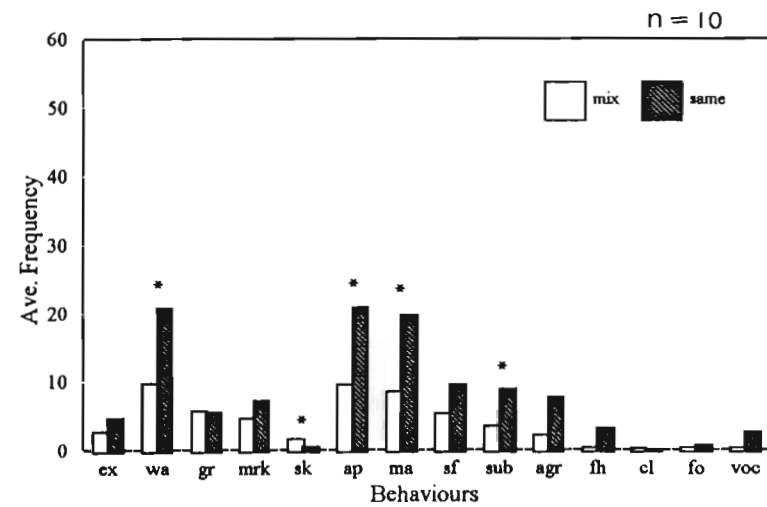
E. rupestris males explored, and females explored and watched significantly more often in same-sex encounters. Females shook themselves more often during same-sex encounters, while males in contrast, shook significantly more frequently during mixed-sex encounters. Both sexes approached/moved away significantly more frequently, and sniffed and followed (significant only in females) more often in same-sex encounters. Males showed more submissive, aggressive and fighting behaviour during same-sex encounters, while females only showed higher levels of submissive behaviour.

M. proboscideus

All *M. proboscideus* individuals explored and watched significantly more often in same-sex encounters. Contact behaviours (approach/move away, sniff and follow) were much higher in same-sex encounters, however, this was only significant for females. Both sexes had significantly higher submissive behaviour frequencies in same-sex encounters, but only females showed higher aggression levels. Females also showed significantly higher circling behaviour in same-sex encounters. *M. proboscideus* females and males footdrummed only during mixed-sex encounters.



E. rupestris males



E. rupestris females

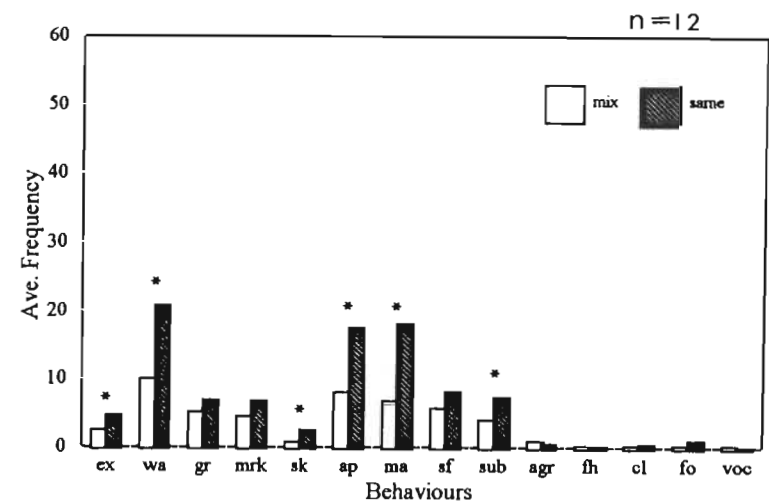
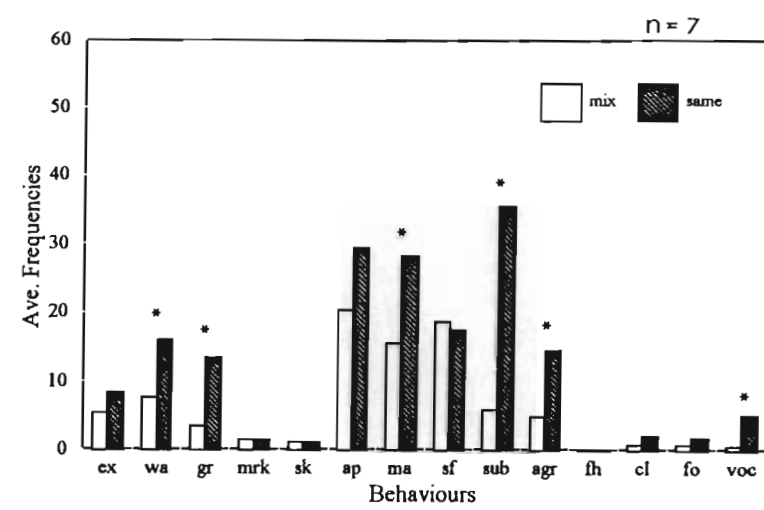
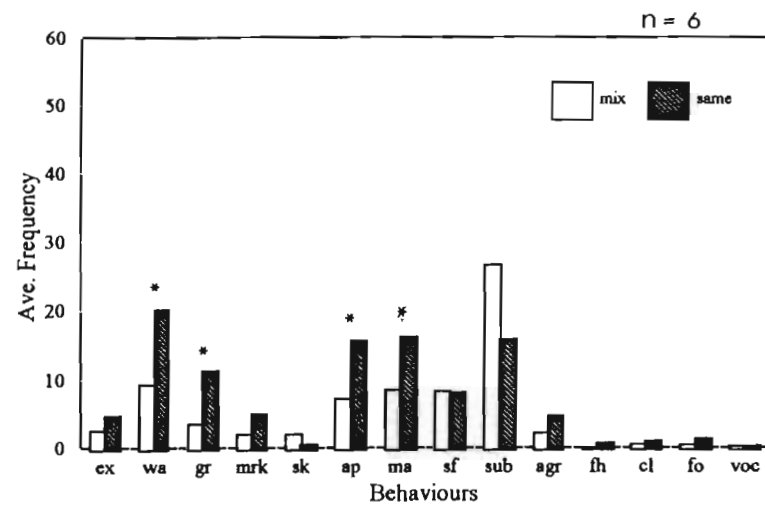


Figure 4.5 Comparison of same-sex and mixed-sex behavioural frequencies among five elephant-shrew species.

* = significant differences



E. edwardii males

E. edwardii females

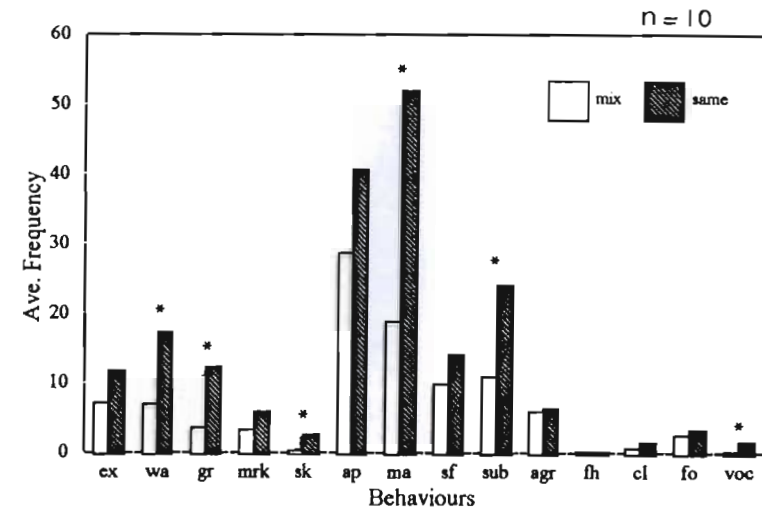
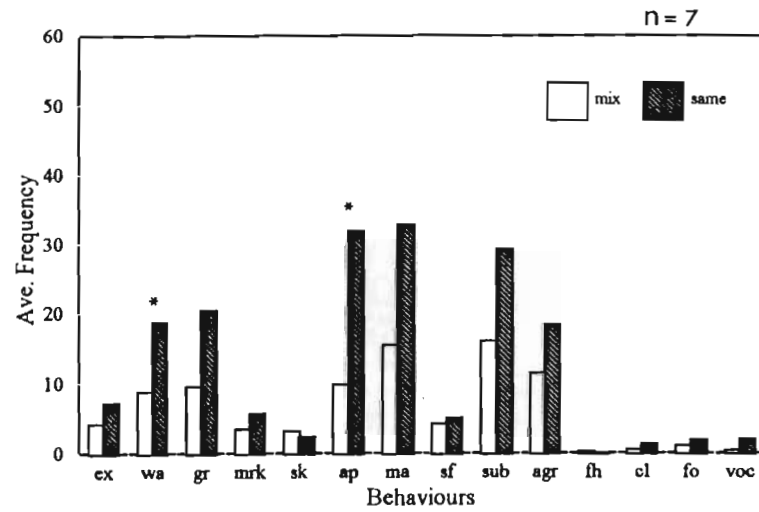
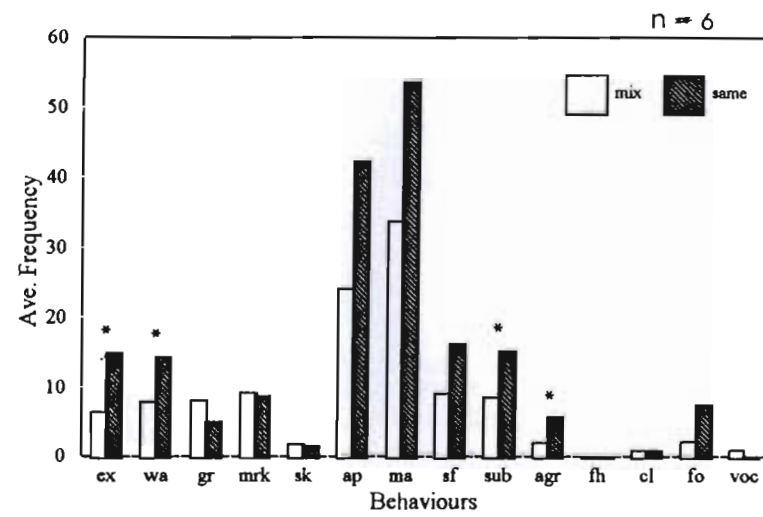


Figure 4.5 Comparison of same-sex and mixed-sex behavioural frequencies among five elephant-shrew species.

* = significant differences.



M. proboscideus females

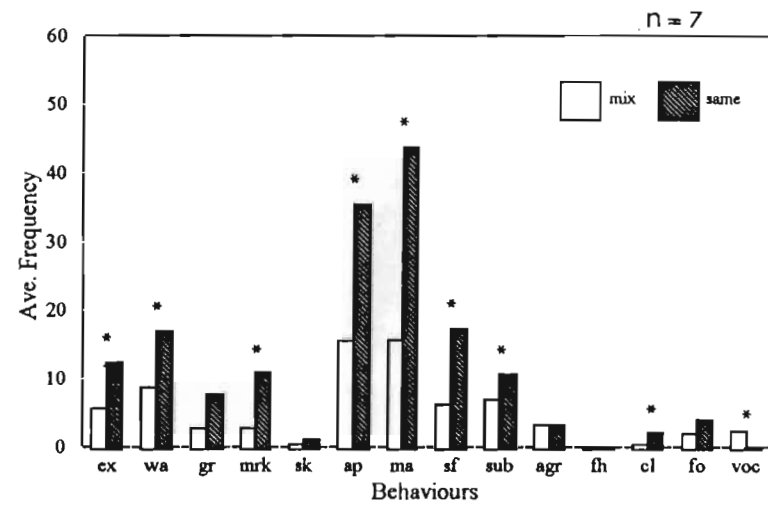


Figure 4.5 Comparison of same-sex and mixed-sex behavioural frequencies among five elephant-shrew species

* = significant differences

DISCUSSION

Behavioural postures of South African elephant-shrew species were similar to many of those described for rodents (Eisenberg 1963, 1967, Grant and Mackintosh 1963), gerbils (Swanson 1974, Dempster and Perrin 1989a, 1989b) and *Elephantulus rufescens* (Lumpkin and Koontz 1986). No allogrooming, upright/sparring or sexual behaviours were observed. All the elephant-shrew species showed similar behavioural repertoires. Eisenberg (1967) states that differences in behavioural frequencies rather than the behaviours themselves are the most important criterion for delineating taxon specific differences in closely related species.

Male-female intraspecific encounters

Differences in behavioural frequencies between males and females of a species were evident. Overall, females of *E. brachyrhynchus*, *E. edwardii* and *E. myurus* explored more frequently, while males watched more often. These differences were statistically significant. In contrast *E. rupestris* and *M. proboscideus* males and females had very similar exploration and watching frequencies, with males exploring more often and females watching more frequently than males. Females of *E. brachyrhynchus*, *E. edwardii*, *E. myurus* approached, sniffed and followed more frequently than males, while *E. rupestris* and *M. proboscideus* males approached, sniffed and moved away significantly more frequently than females.

Males of all four *Elephantulus* species showed significantly more submissive behaviour than the females, and males of all species generally exhibited submissive behaviour in response to female aggression. However, only *E. brachyrhynchus* and *E. myurus* females showed higher aggression levels than males. *E. rupestris* and *E. edwardii* males showed more aggression than females. *M. proboscideus* showed very little aggressive and submissive behaviour with

only slight difference between male and female frequencies. Lumpkin and Koontz (1986) and Rathbun (1979) found that *E. rufescens* females are generally more aggressive than males, and dominate their males. Examples of female dominance over males are also found in gerbils (Daly and Daly 1975, Dempster and Perrin 1989b), and hamsters (Payne and Swanson 1970). This trend was only shown in *E. brachyrhynchus* and *E. myurus* in the present study.

There were furthermore behavioural differences in marking/ grooming behaviour between males and females. Females dragged (anal- and ventral-) and urinated more frequently than males in all *Elephantulus* species, while the opposite was true for *M. proboscideus*. *E. brachyrhynchus*, *E. edwardii*, *E. rupestris* and *M. proboscideus* males sandbathed more often than females in contrast to *E. myurus* where females sandbathed more often. Shaking is usually performed either after sandbathing or after an aggressive encounter. Although only significant in three cases (*M. proboscideus*, *E. edwardii* and *E. rupestris*) males in all species shake more than females.

Comparison of behaviour frequencies among the species in male-female interactions indicated that *M. proboscideus* males had higher marking frequencies than the *Elephantulus* species, and also explored, approached and moved away more frequently in encounters than the *Elephantulus* males. *M. proboscideus* males were thus overall more active and exploratory. However, *M. proboscideus* males showed relatively low frequencies of aggressive behaviour. *M. proboscideus* females also showed comparatively high frequencies of exploratory behaviour and low levels of aggression and fighting. *E. rupestris* males and females showed, similar to *M. proboscideus* very low overall levels of aggressive and submissive behaviour.

Discriminant function analysis determines relationships among two or more known groups/species. This method uses multiple behavioural variables to assess the discriminability of these groups, and classifies individuals among these groups (Aspey and Blankenship 1971).

Discriminant function analyses indicated that individuals of the five elephant-shrew species could be separated out using these behaviour variables. For males, *M. proboscideus* showed behaviour patterns distinctly different from those of the *Elephantulus* species tested, while the four *Elephantulus* species showed behaviour frequencies/ patterns that differed sufficiently from one another to separate the groups reliably. In females, *E. rupestris* showed distinctly different behaviour patterns from the rest of the species, while the remainder of the *Elephantulus* species were identified to an accuracy of $\geq 50\%$. In contrast to results found in male elephant-shrews, however, *M. proboscideus* females were identified with the least amount of certainty, with 6 out of 14 animals classified as *Macroscelides* and 3 out of 14 as *E. myurus*. Bekoff (1977) found discriminant function analysis useful to distinguish closely related canid species on the basis of behavioural characteristics, since it allows a detailed analysis of similarities and differences among a number of species. These canid species had the same basic behavioural repertoires, but differed in relative frequencies of agonistic and social play behaviours. Similarly Goltsman and Borisova (1993) found differences in durations of behavioural acts among different gerbil (*Meriones*) species. The noticeable similarity in the signalling systems of many closely related species (eg. Cocroft and Ryan 1995, Dempster *et al.* 1992, Eisenberg 1976) suggest that species recognition only requires slight, but consistent differences (Hailman 1977).

Although frequency differences in behaviour components of the different elephant-shrew species were evident, species recognition usually involves a combination of all communication

modalities (i.e. visual, tactile, olfactory and acoustic). Differences in mating signals most often form the barrier in gene exchange (Butlin and Ritchie 1994). However, Uzendoski and Verrell (1993) and West-Eberhard (1983) caution against the assumption that species specific differences in behaviour is always responsible for species incompatibility/ recognition. Other modalities (eg. scent, sound) may be needed to trigger courtship.

Male-female interspecific encounters

Arguments have been, and are still raging in speciation theories debating whether divergence in signalling systems occurs in sympatry or allopatry. If divergence occurred during allopatry there should be a greater difference in behavioural repertoires between allopatric species than sympatric species. The converse would be expected if divergence of signalling systems occurred in sympatry. Dempster *et al.* (1992) and Dempster and Perrin (1991) found that allopatric gerbils (*Gerbillurus*) species show no significant divergence in ultrasonic or behavioural repertoire, while sympatric gerbil species do show significant differences in behavioural and vocal signals. Similar results were obtained for sympatric and allopatric *Tatera* species, giving support to Mayr's isolation theory. Higher levels of aggression would thus be expected between heterospecifics than conspecifics if aggressive behaviour acts as an isolating mechanism between sympatric species of elephant-shrews.

The *Elephantulus* species showed changes in behaviour frequencies in intraspecific compared to interspecific encounters. However, males and females showed similar amounts of behavioural change. Overall *E. brachyrhynchus* and *E. edwardii* males and females explore more in intraspecific encounters, but this was not apparent in *E. myurus* and *E. rupestris*. Similarly, both *E. brachyrhynchus* and *E. edwardii* showed higher frequencies of contact behaviour (approach/move away, sniff and follow) in intraspecific encounters than interspecific

encounters, but no similar trend was present in *E. myurus* and *E. rupestris*.

Males of *E. brachyrhynchus*, *E. edwardii* and *E. myurus* showed higher frequencies of submissive behaviour in intraspecific encounters, the same is only true for *E. edwardii* females.

Both sexes of *E. edwardii* showed more submissive as well as aggressive behaviour in intraspecific encounters. Apart from *E. edwardii*, only *E. brachyrhynchus* females showed higher aggressive frequencies in intraspecific encounters. *E. rupestris* in contrast with the above three species showed lower levels of submissive behaviour in intraspecific encounters than interspecific encounters with allopatric species. However, both sexes of *E. rupestris* followed less and showed less aggressive behaviour towards conspecifics.

Males of *E. brachyrhynchus*, *E. edwardii* and *E. myurus* thus showed more submissive behaviour in intraspecific encounters. The amount of submissive behaviour shown towards sympatric and allopatric heterospecifics is very variable among species. Although *E. rupestris* showed less submissive behaviour in intraspecific encounters, they also showed lower aggression levels. High levels of submissive behaviour (or reduction in aggressive behaviour in the case of *E. rupestris*) may indicate a strategy to reduce aggression in conspecific females.

Only *E. brachyrhynchus* and *E. edwardii* females showed higher aggressive frequencies in intraspecific encounters, but this was not statistically significant, and may be partially explained by higher frequencies of exploratory and contact promoting behaviour during intraspecific encounters. Nevo (1990) found that high levels of aggression act as premating isolation mechanisms between chromosomal species of mole rats.

E. brachyrhynchus males and females, and *E. edwardii* females footdrummed significantly less

in intraspecific encounters. Both *E. brachyrhynchus* females and *E. edwardii* males and females sandbathed/marked less in intraspecific encounters, while *E. rupestris* males and females sandbathes more often in intraspecific encounters.

Levels of behavioural frequencies vary considerably among the species in sympatric and allopatric interspecific parings, and no definite trends could be discerned pertaining to differences in discrimination between allopatric and sympatric species.

Same-sex encounters

All four *Elephantulus* species, as well as *M. proboscideus* were much more active/interactive in same-sex encounters than different-sex encounters. These results agreed with finding for Mongolian gerbils (Swanson 1974), but were in contrast to those found in *Gerbillurus* species by Dempster and Perrin (1989b). Contact promoting behaviours (approach, sniff, move away) were higher for same-sex encounters in all the species, and in many cases these differences were statistically significant.

Submissive behaviours were significantly more often performed in all encounters with animals of the same sex. Similarly aggressive, circling and following behaviours were performed more frequently by all species in same-sex encounters.

M. proboscideus footdrummed more frequently in mixed-sex encounters in contrast to the *Elephantulus* species that footdrummed more frequently in same-sex encounters. Marking (dragging and sandbathing) frequencies were generally higher in same-sex encounters, but this was not statistically significant. Shaking behaviour was variable among the species, with some showing higher frequencies in same-sex encounters and others in mixed-sex encounters.

This study shows that the visual/tactile behavioural repertoires of elephant-shrews, although comprising the same basic behavioural units, differ significantly between species in the frequencies with which behaviours are performed. This results in clear species specific patterns in the visual signalling systems of the five elephant-shrew species, particularly males.

Results from field observations of elephant-shrews (Rathbun 1979) showed that females are dominant over males. This was only found in two of the species investigated here. However, the restricted area of the arenas that prevented complete escape from an opponent, may have influenced the results. The increase in male submissive behaviour in interspecific encounters does, however, suggest a strategy for reducing aggression in female conspecifics. Furthermore, higher aggression levels in both sexes in interspecific encounters may play a role in reproductive isolation.

Higher activity levels and levels of interactive and aggressive behaviour between animals of the same sex lends support to the field observations that elephant-shrews defend their territories sex specifically.

Footdrumming and mutual sniffing found in encounters of all the elephant-shrew species indicates that a combination of sensory modalities comprise the elephant-shrew signalling system.

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CHAPTER 5

CONCLUSION

The communication systems of six southern African elephant-shrew species were investigated and the different modalities involved were described. The major aim of this thesis was to identify and describe species specific patterns in the signalling systems of the southern African elephant-shrew species.

Both the *Elephantulus* species and *M. proboscideus* showed scent marking behaviours that would serve to deposit secretions from skin glands onto the substrate throughout their territory, creating a "familiar" scent. Familiarising the territory would serve not only as reassurance for the territory owners (Ewer 1968), but also reduce aggression between males and females sharing a territory (Randall 1991). Elephant-shrew scent marking behaviours included sandbathing, ventral and anal dragging, digging and substrate rubbing. Unlike certain central African species (Rathbun 1979), southern African elephant-shrews do not possess sternal glands. They do however have conspicuous tail glands, as well as several well developed glandular areas distributed over the body. With the exception of the tail gland which is more developed in males, there were no size difference in glandular areas between males and females.

Species specific differences in marking behavioural frequencies were shown to exist among the elephant-shrew species, with *M. proboscideus* marking more often than the *Elephantulus* species. However, these frequencies seemed unrelated to glandular development. In the southern African *Elephantulus* species, females urinated and dragged more frequently than males, while males sandbathed more often. In contrast, *M. proboscideus* males sandbathed, urinated and dragged

more often than females.

Elephant-shrews have long, mobile probosces, and a well developed nasal epithelium. Mutual sniffing formed an important part of interactive behaviour among all the elephant-shrew species, indicating that olfaction and odour discrimination likely plays a role in elephant-shrew signalling systems. This was confirmed by odour preference trials which showed that elephant-shrews preferred conspecific odours to heterospecific odours, and that males have higher levels of odour discrimination than females.

Distinct species differences were discerned in the acoustic repertoires of the six southern African elephant-shrew species. Elephant-shrews employed two types of audible vocalizations; mewing calls and clicking. Species differences were apparent in harmonic characteristics of the calls, as well as in the duration and frequencies of vocalizations. Although data were too limited to identify species specific patterns, the above differences indicate that they would likely exist.

Footdrumming, the acoustic signal most commonly used by elephant-shrews, showed distinct species specific patterns among the southern African species. Using an existing morphological phenogram (Corbet and Hanks 1968) on which to map footdrumming characteristics suggested an evolutionarily plausible path of footdrumming development. Footdrumming patterns in the *Elephantulus* species appears to have evolved via a split from *Macroscelides* through a decrease in footdrum intervals. Certain of the *Elephantulus* species then acquired irregular element in their footdrumming repertoires (*E. brachyrhynchus*, *E. edwardii*, *E. intufi*), followed by a divergence in footdrum intervals (*E. brachyrhynchus* and *E. edwardii*) and a regular/ irregular bout reversal (*E. intufi*). These results are in agreement with current trends and studies in ethology that use behavioural characteristics to support and resolve phylogenies (Brooks and McLennan 1991,

Cocroft and Ryan 1995, Gittleman and Decker 1994).

Behavioural components of the visual communication systems of elephant-shrews were similar to those found in rodents (Eisenberg 1967, Grant and Mackintosh 1963). Although the species studied here used the same behavioural repertoire, significant differences in behavioural frequencies were present, both between males and females of a specific species, and among the different species. Differences in behavioural frequencies of the five elephant-shrew species studied here were sufficiently defined to classify individuals into the correct species in 44 out of 63 individual males, and 40 out of 63 females. Definite species specific patterns in the visual signalling systems of the South African elephant-shrew species were thus apparent.

Comparison of intra- and interspecific encounters showed that males generally had higher frequencies of submissive behaviour in intraspecific encounters, which may be a strategy to reduce aggression in conspecific females. This is supported by sequencing data indicating that female aggression resulted in male submissive behaviour in intraspecific encounters. With the exception of *E. edwardii* males and females and *E. brachyrhynchus* females, elephant-shrews also displayed higher levels of aggressive behaviour in interspecific encounters, indicating that elevated aggression levels may act as premating isolation mechanisms. Elephant-shrews thus showed a decrease in submissive behaviour and an increase in aggressive behaviour in encounters with heterospecifics compared to conspecifics. However, no indication of higher levels of aggression in interactions with allopatric heterospecifics compared to sympatric heterospecifics were found.

To fully understand a species' signalling system, and how it relates to species recognition, one must look at the combined actions of all sensory modalities employed by the individuals of that species. In the southern African elephant-shrews a combination of olfactory, acoustic and visual/tactile

signals are likely used in species recognition.

The systematic relationships of the elephant-shrew family have been examined using morphological (Corbet and Hanks 1968, Corbet 1995) and cytogenetic (Raman and Perrin 1997, Tolliver *et al.* 1989) methods. Results obtained from these studies are not always in agreement, and further investigation is therefore needed. Species specific behavioural characteristics from the different signalling systems could likely provide important information towards resolving these phylogenies.

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