
Review article

Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology?

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Abstract

The seventeen species of sengis or elephant-shrews form a well-defined clade of mammals endemic to Africa that occupy the extremes of terrestrial habitats, from coastal deserts to montane forests. Because of their isolation on Africa soon after the break-up of Gondwanaland, theoretically sengis initially evolved with little competition from other placental radiations. Their life history features include myrmecophagy, saltatorial gaits, no or limited use of nests, social monogamy, small litters of precocial young and absentee maternal care of neonates. These traits together are unique to the Macroscelidea and represent a wedding of features usually associated with either small antelopes or anteaters. Combined, these features define an adaptive syndrome that presumably has been relatively immune to competition from contemporary mammals, partially due to phylogenetic inertia. Yet paradoxically, the syndrome is well suited to a wide range of terrestrial habitats, resulting in low taxonomic diversity. Because of their unusual phylogeny and low species diversity, conservation interest is high for those sengis with relatively low densities in fragmented forests.

Key words: Africa, conservation, distribution, elephant-shrews, life history, phylogeography

Résumé

Les 17 espèces de sengis (musaraignes éléphants) forment un clade bien déterminé de mammifères endémiques d'Afrique, qui occupe des habitats terrestres extrêmes

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allant de déserts côtiers à des forêts de montagne. En raison de leur isolement sur le continent africain très vite après la scission du Gondwana, les sengis ont théoriquement évolué au départ sans qu'il existe beaucoup de compétition avec les radiations d'autres placentaires. Les caractéristiques de leur histoire incluent de la myrmécophagie, des déplacements par bonds, un usage de nids limité, voire inexistant, la monogamie sociale, de petites portées de jeunes précoces et l'inexistence de soins maternels pour les nouveau-nés. Toutes ces caractéristiques sont uniques pour les Macroscélidés et représentent un regroupement de caractéristiques d'habitude associées à de petites antilopes ou à des fourmiliers. Combinées, ces caractéristiques définissent un syndrome d'adaptation qui, sans doute, fut relativement protégé de toute compétition avec des mammifères contemporains, à cause, en partie, de l'inertie phylogénétique. Mais, paradoxalement, ce syndrome est bien adapté à une vaste gamme d'habitats terrestres, ce qui n'entraîne donc qu'une faible diversité taxonomique. En raison de leur phylogénèse inhabituelle et de la faible diversité entre ces espèces, l'intérêt de la conservation est considérable pour ces sengis dont la densité, dans des forêts fragmentées, est relativement faible.

Introduction

Nearly all aspects of the biology of sengis or elephant-shrews have fascinated biologists since the first species was discovered by Western scientists near the end of the 18th Century. However, many ecologists are unaware of the unique features of this group, and there continue to be

misconceptions about their ecology in the literature (e.g. Panchetti *et al.*, 2008). Here, I review the more important aspects of the behavioural ecology and taxonomy of sengis, including some aspects that are often misunderstood or incorrectly reported in the literature, and then discuss why there are only 17 species of sengis, despite their occurrence in the extremes of terrestrial habitats. Lastly, I review their conservation status.

What are sengis?

There is little question among most biologists that the sengis represent a monophyletic family (Macroscelididae) and order (Macroscelidea) of endemic African mammals with a highly distinctive evolutionary history. However, this clarity in understanding has not always prevailed.

Confusing taxonomic history

During the three decades straddling the turn of the 19th century, Africa was being 'discovered' by western scientists and many new sengis were described (Corbet & Hanks, 1968). The taxonomists of the time were often faced with the dilemma of trying to fit new and exotic groups of mammals into the accepted mammalian taxonomy of the time, which resulted in the sengis being placed in the 'dumping ground' order Insectivora. However, it was evident from nearly the beginning that many of the clades included in the Insectivora only had superficial morphological resemblances to each other and represented multiple phylogenetic origins. This resulted in various different taxonomic schemes to accommodate sengis (reviewed by Patterson, 1965; Mckenna, 1975; Kingdon *et al.*, in press).

In the 1990s, with the development of molecular techniques to assess higher-order relationships, more and more analyses of proteins and DNA began to suggest that the sengis were in fact part of a relatively ancient radiation of African endemic mammals that included several seemingly improbable groups or clades. Now, the molecular evidence is overwhelmingly supportive of the supercohort Afrotheria (Springer *et al.*, 2004), which includes the long-recognized Paenungulata (elephants, hyraxes and sea cows) along with the tenrecs and golden moles (order Afrosoricidea), the aardvark (order Tubulidentata) and sengis (order Macroscelidea). Despite the molecular data, however, the morphological evidence for the Afrotheria continues to be weak (Seiffert, 2007), which is likely related to the c. 105 million years that have passed since

the isolation and then divergence of the various afrotheres (Hedges, 2001).

The fossil record

Several of the afrotherian clades with reasonably good fossil records (Proboscidea, Hyracoidea, Sirenia) show a pattern of declining taxonomic diversity from the Miocene to present (Kingdon *et al.*, in press). Even the Macroscelidea lost four of six known subfamilies (Holroyd & Mussell, 2005). Significantly, some of the representatives of now-extinct sengi radiations were likely herbivores, as suggested by the structure of their highly hypsodont dentition. Indeed, the extinct sengi genus *Myohyrax* had teeth that were so similar to those of the herbivorous hyraxes (order Hyracoidea) that specimens were initially misidentified (Patterson, 1965). All extant sengis have relatively hypsodont teeth and a caecum (Woodall & Mackie, 1987), which are features often associated with herbivory, which further suggests a herbivorous ancestry for extant sengis.

Current and future taxonomy

The understanding of the taxonomic and distributional relationships of the various extant forms of sengis was bordering on chaotic until the seminal revision by Corbet & Hanks (1968). In addition to the new taxa being described as Africa was explored by Western biologists, the problem was rooted in the relatively minor and often cryptic phenotypic cranial and pelage colour differences distinguishing many forms. Corbet & Hanks (1968) consolidated the many taxa into fourteen species in four genera and two subfamilies. The giant sengi (subfamily Rhynchocyoninae with a single genus *Rhynchocyon*) included only three relatively distinct species with several subspecies in the confusingly variable *Rhynchocyon cirnei*. The soft-furred sengi (subfamily Macroscelidinae) contained three genera (the monospecific *Macroscelides* and *Petrodromus*, along with nine species of *Elephantulus*). In 1974, a subspecies was elevated to a full species (*Elephantulus fuscipes*), resulting in fifteen species (Corbet, 1974). Although the phylogeny of this taxonomic arrangement (Table 1) is still debated, it seems to be generally supported by numerous molecular studies (Tolliver *et al.*, 1989; Raman & Perrin, 1997; Smit, Robinson & Van Vuuren, 2007) and morphological studies (Rautenbach & Schlitter, 1977; Matson & Blood, 1997; Panchetti *et al.*, 2008).

Table 1 Summary of Macroscelidea taxonomy (based on Corbet, 1974; Rovero *et al.*, 2008; and Smit *et al.*, 2008) including common names (Nicoll & Rathbun, 1990) and subspecies (Corbet & Hanks, 1968)

Scientific Name	Common name (+ sengi)	No. of Ssp.	Approx. weight (g)	Litter size	Countries of Occurrence	Red list
Subfamily Rhynchocyoninae	Giant	–	300–750	–	–	–
<i>Rhynchocyon chrysopygus</i> Günther, 1881	Golden-rumped	0	540	1–2	Kenya endemic	EN
<i>Rhynchocyon cirnei</i> Peters, 1874	Chequered	6	450	1–3	Central Afr. Repub.?, Dem. Repub. Congo, Uganda, Tanzania, Mozambique, Malawi, Zambia	NT
<i>Rhynchocyon petersi</i> Bocage, 1880	Black-and-rufous	2	540	1–2	Kenya & Tanzania	VU
<i>Rhynchocyon udzungwensis</i> Rathbun & Rovero, 2008	Grey faced	0	710	1–2	Tanzania endemic	VU
Subfamily Macroscelidinae	Soft-furred	–	35–200	–	–	–
<i>Petrodromus tetradactylus</i> Peters, 1846	Four-toed	10	200	1–2	Dem. Repub. Congo, Kenya, Tanzania, Mozambique, Malawi, Zambia, Zimbabwe, Angola?, Namibia?, South Africa	LC
<i>Macroscelides proboscideus</i> (Shaw, 1800)	Round-eared	2	35	1–3	Namibia, Botswana, South Africa	LC
<i>Elephantulus brachyrhynchus</i> (A. Smith, 1836)	Short-snouted	0	45	?	Dem. Repub. Congo, Uganda, Kenya, Tanzania, Mozambique, Malawi, Zambia, Zimbabwe, Angola, Namibia, Botswana, South Africa	LC
<i>Elephantulus edwardii</i> (A. Smith, 1839)	Cape rock	0	50	1–2	South Africa endemic	LC
<i>Elephantulus fuscipes</i> (Thomas, 1894)	Dusky-footed	0	45	?	Dem. Repub. Congo, Sudan, Uganda	DD
<i>Elephantulus fuscus</i> (Peters, 1852)	Dusky	0	45	?	Mozambique, Malawi, Zambia	DD
<i>Elephantulus intufi</i> (A. Smith, 1836)	Blushveld	2?	45	1–2	Angola, Namibia, Botswana, South Africa	LC
<i>Elephantulus myurus</i> Thomas & Schwann, 1906	Eastern rock	0	60	1–2	Zambia?, Mozambique, Zimbabwe, Botswana, South Africa	LC
<i>Elephantulus pilicaudus</i> Smit, 2008	Karoo rock	0	45	?	South Africa endemic	?
<i>Elephantulus revoilii</i> (Huet, 1881)	Somali	0	50	?	Somalia endemic	DD
<i>Elephantulus rozeti</i> (Duvernoy, 1833)	North African	2	50	1–4	Western Sahara, Morocco, Algeria, Libya, Tunisia	LC
<i>Elephantulus rufescens</i> (Peters, 1878)	Rufous	0	55	1–2	Somalia, Ethiopia, Sudan, Uganda, Kenya, Tanzania	LC
<i>Elephantulus rupestris</i> (A. Smith, 1831)	Western rock	0	60	?	Namibia, South Africa	LC

Weight and litter size from the literature (Rathbun & Woodall, 2002). Countries of occurrence with a ? are based on ambiguous records, often on or near borders (G. Rathbun, unpublished data). Conservation status from IUCN, 2008 Red List: EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern, DD = data deficient.

Dashes = not relevant. ? = no data.

Sengi systematics started to change with the publication of the results from an extensive (but not complete) molecular phylogeny of the soft-furred sengis (Douady *et al.*, 2003). Although the species-level morphological systematics of Corbet & Hanks (1968) was largely supported by this effort, the authors suggested that the highly disjunct North African sengi (*Elephantulus rozeti*) was more closely related to the four-toed sengi (*Petrodromus*

tetradactylus) of sub-Saharan Africa than to all the other sub-Saharan species of *Elephantulus*. Penis morphology (Woodall, 1995) was cited as supportive of this hypothesis, although this phylogeny remains controversial (Panchetti *et al.*, 2008). No taxonomic changes have been published to accommodate the Douady view, which leaves the current systematics somewhat unresolved (Holroyd & Mussell, 2005), but unchanged (Table 1).

Recently, two unexpected and exciting changes to sengi taxonomy occurred. *Rhynchocyon udzungwensis*, a completely new species, was described from two isolated montane forests in the northern Udzungwa Mountains of Tanzania (Rovero *et al.*, 2008). Then, *Elephantulus pilicaudus*, a morphologically cryptic and completely new species endemic to South Africa was described (Smit *et al.*, 2008), which was discovered serendipitously while exploring the molecular biogeography of *Elephantulus edwardii*, its sister species (Smit *et al.*, 2007). Thus, for the first time in over 35 years, the taxonomic diversity of sengis increased from fifteen to seventeen species in 2008 (Table 1). This was not the result of shuffling already described taxa, but establishing species that were never described before.

The past and recent taxonomic changes reviewed above raise the question as to whether sengi systematics is nearly definitive, or are there more species to be found? It is likely that using DNA analyses additional species will be resurrected, split, or named for the first time. For example, Corbet & Hanks (1968) suggested that *R. cirnei stuhlmanni* Matschie 1893 and *P. tetradactylus tordayi* Thomas 1910, which are isolated in the Congo Basin, may actually be full species. Similarly, there is increasing molecular and morphological evidence that *Macroscelides* may not be monospecific (G. Rathbun, pers. obs.; H. Smit & J. Dumbacher, pers. comm.). It is also possible that completely new species of *Rhynchocyon* might be found in restricted and isolated forests that have not been explored carefully by biologists such as the Boni Forest in north-eastern Kenya (Rathbun, 1979; Mwangi, 2007; G. Rathbun, pers. obs.). However, given the extent of past and current morphological and molecular studies of sengis, as reviewed above, and the fact that there is minimal unexplored territory in Africa, there is little reason to believe that a landslide of new species is waiting to be found or resurrected. The Macroscelidea appears to be a taxonomically well-defined order with low species diversity, considering its distribution throughout much of Africa (see below).

Biogeography

None of the smaller Afrotherian clades has a pan-African distribution. For example, the tenrecs are absent from most of Africa save the middle latitudes, but reach a remarkable diversity on the island of Madagascar. Golden moles are largely absent from much of central, western and northern Africa, with their greatest diversity in southern Africa. The

sengis are more widely distributed, only being absent from western Africa and the Sahara Desert, and their peak diversity is in southern Africa, followed by eastern Africa (Fig. 1, Table 1).

It remains unclear why no sengis occur in western Africa. The current western-most sub-Saharan distributions are along the Congo River system (Fig. 1). There is little doubt that large rivers define the distribution of some sengis. For example, in south-western Africa, the Orange and Kunene rivers appear to limit the distributions of some soft-furred species. In eastern Africa, the lower Tana, Rufiji and Zambezi rivers define the distributions of giant sengis and may even be associated with speciation events. The influence of rivers is probably related to the sheltering habits of sengis (see below), which are not compatible with standing surface water or flooding (G. Rathbun, pers. obs.). However, it is difficult to imagine that the Congo River system could prevent sengis from dispersing into western Africa for millions of years. Perhaps there are other biogeographical factors involved.

One feature of sengi distribution that is often overlooked is that the various species occupy the extremes of terrestrial habitats (Table 2, Fig. 2). For example, *E. rozeti* is a boulder-dweller that occurs from the coast to 2700 m in the Atlas Mountains (Cuzin & Séguignes, 1990) with apparently minimal regard to vegetative cover (G. Rathbun, pers. obs.). South Africa has four boulder dwellers: *Elephantulus rupestris*, *Elephantulus myurus* and the sister species *E. edwardii* and *E. pilicaudus*. It is not clear whether the Somali sengi (*Elephantulus revoilii*) is also an obligate boulder-dweller (Table 2). The remaining species of *Elephantulus* occur in a wide range of arid habitats with relatively fine-grained but compact soils (sand dunes are avoided). *Macroscelides* is largely restricted to arid gravel plains, which vary from the Namib Desert of Namibia with no significant vegetation, to the High Karoo of South Africa, where the gravel plains support scattered bushes and experience freezing winter temperatures and occasional winter snows. At the opposite extreme, the four species of *Rhynchocyon* occupy various closed canopy forests, dense woodlands, riparian and coral rag thickets, and fallow agricultural lands adjacent to forests that now support secondary closed-canopy thickets and forest. *Petrodromus* occupies the same habitats as *Rhynchocyon*, but also occurs in mesic woodland scrub habitats with less dense cover.

Although the overall distribution of sengis is well documented (California Academy of Sciences, 2008; IUCN, 2008), regional patterns are much less understood. Rapid

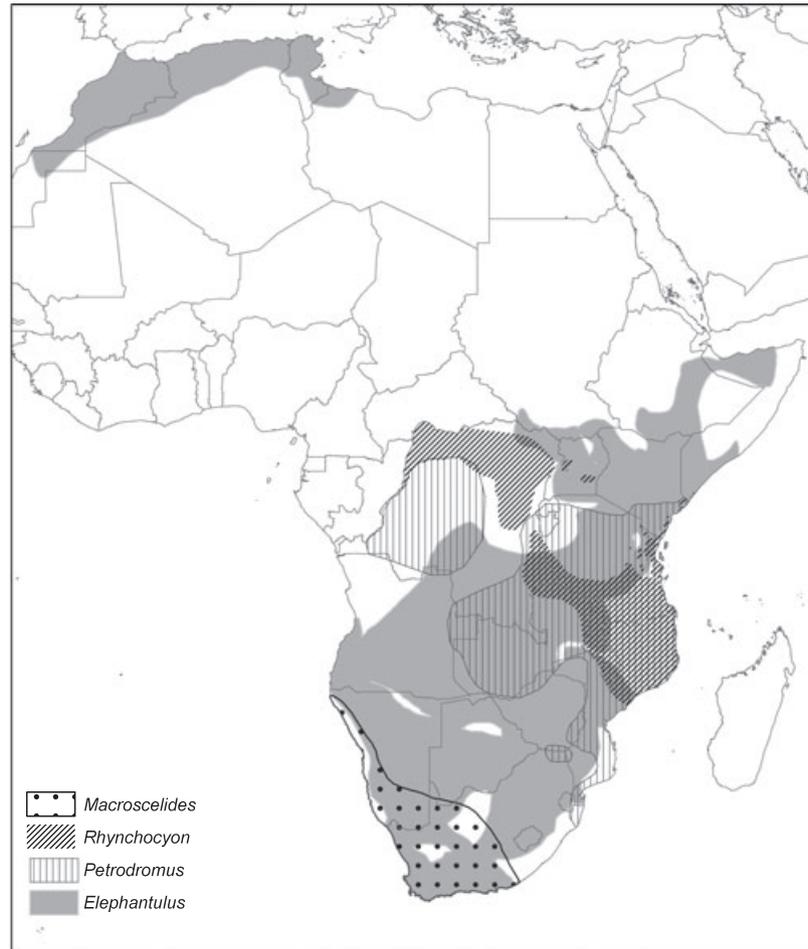


Fig 1 Distribution of the four genera of Macroscelidea based on individual species ranges (G. Rathbun unpublished data, IUCN, 2008, California Academy of Sciences, 2008). Cartography courtesy of Mike Hoffmann, IUCN

progress, however, is expected in understanding the fine-grained details of the sometimes confusing distribution patterns with the application of DNA sequencing methods. This has been demonstrated with *E. rozeti* in northern Africa (Douady *et al.*, 2003) and a suite of soft-furred species in South Africa (Smit *et al.*, 2007). Of special interest will be the application of these new methods to understand better the complicated pelage colouration and distribution patterns found in the giant sengis, especially in eastern Africa (Corbet & Hanks, 1968; Kingdon, 1974; Rovero *et al.*, 2008; G. Rathbun, pers. obs.). Explaining the absence of sengis from western Africa, however, will be particularly challenging.

Behavioural ecology

The relatively well-defined external morphology of extant sengis was noted by Corbet & Hanks (1968). Consequently,

it is not surprising that they show relatively little variation in many of their behavioural and ecological traits (Rathbun, 1979; Rathbun & Rathbun, 2006b). The most distinctive differences separate along the two extant sub-families, the giant sengis and soft-furred sengis, as detailed below.

Diet

Early on it was recognized that living sengis were mostly insectivorous, which supported their inclusion in the order Insectivora, even if their relatively hypsodont dentition was suggestive of a herbivorous diet (see discussion above on phylogeny and fossil record). The soft-furred species prey predominately on small invertebrates, especially ants and termites, but sometimes supplement this diet (often seasonally) with small fruits, seeds and green plant tissue (Rathbun, 1979; Kerley, 1995; Leirs *et al.*,

Table 2 Ecological relationships of sengi species. Genera are *Elephantulus*, *Macroscerlides*, *Petrodromus*, and *Rhynchocyon*. Microhabitats are closely associated with sheltering habits

Habitat	Microhabitat	Sengi species	Sheltering habits
Rock	Kopjes and scattered boulders in savannah woodlands	<i>E. myurus</i>	Among boulders
	Rock, scree, and boulders associated with ridges and mountains	<i>E. rozeti</i> <i>E. edwardii</i> <i>E. pilicaudus</i> <i>E. rupestris</i> ? <i>E. revoilii</i> ?	Among boulders and in cracks & crevices of rock
Gravel plains	Karoo, with scattered bushes	<i>M. proboscideus</i> <i>proboscideus</i>	Dense vegetation & shallow burrows
	Namib Desert with sparse grass between widely spaced rocky outcrops or boulders	<i>M. proboscideus</i> <i>flavicaudatus</i>	Among rocks and boulders, shallow burrows
Arid woodland & bushland	Open canopy with compact sandy soils, little grass, dominated by scrub	<i>E. intufi</i> <i>E. rufescens</i>	Base of bushes, among rocks, occasionally abandoned rodent burrows
Mesic savannah woodland & bushland	Areas providing cover, such as brush in riparian areas, fallow agricultural land interspersed with grasslands	<i>E. brachyrhynchus</i> <i>E. fuscus</i> ? <i>E. fuscipes</i> ?	Thickets and dense grass and abandoned rodent burrows
Mesic Woodland and bushland	Closed canopy, with or without dense leaf litter on variable soils	<i>P. tetradactylus</i>	Dense thickets & undergrowth, retreats to hollow logs and tree trunks
Forests, riparian corridors, mesic dense scrub	Closed canopy, with or without dense leaf litter on variable soils	<i>P. tetradactylus</i>	Dense thickets & undergrowth, retreats to hollow logs and tree trunks
	Closed canopy with dense leaf litter on loamy, sandy, or coral rag soils, but rarely ground water forests.	<i>R. chrysopygus</i> <i>R. cirnei</i> <i>R. petersi</i> <i>R. udzungwensis</i>	Dense leaf litter to build nests on forest floor, retreats to hollow logs and tree trunks.

Data are from personal observations and the literature (Rathbun & Woodall, 2002). Species with ? have limited or no data.

1995; Neal, 1995). The giant sengis, however, are more strictly invertebrate specialists, eating whatever they can glean from the leaf litter and soil (Rathbun, 1979; Fitz-Gibbon, 1995). All species use their long nose as a probe to search for prey, while their long tongue, which can be extended several millimetres beyond the tip of the nose, is used to flick food items into their small, under-slung mouths. Sengis are morphologically poorly equipped to eat large prey items, such as small vertebrates, and they rarely if ever do so. As their diet and facial morphology (Fig. 3) suggest, they are essentially miniature 'ant-eaters'.

Locomotion

No sengis are known to be bipedal or ricochetal, despite claims to the contrary (Panchetti *et al.*, 2008). However, all are highly saltatorial and capable of exceedingly fast qua-

drupedal gaits, including half-bounds (Rathbun, 1973) and a peculiar footfall pattern among the soft-furred species, where one hind foot is suspended and out of action when walking (Schmidt & Fischer, 2007; G. Rathbun, pers. obs.). Their highly antelope-like cursorial habits are reflected by their long legs, large ears and eyes, flighty and skittish temperament, and a laterally compressed body, especially in *Petrodromus* and *Rhynchocyon* (Fig. 3). *Rhynchocyon* even uses a stotting gait when pursued by a predator (Rathbun, 1979), which is similar to the behaviour found in some ungulates. Indeed, the distinctive gold-coloured rump patch of *Rhynchocyon chrysopygus* (Fig. 3), with its associated dermal shield, probably functions similarly to rump patches and dermal shields of some ungulates (Rathbun, 1978). The pedal scent glands of sengis and some ungulates probably have similar functions that are associated with their cursorial habits (Rathbun, Beaman & Maliniak, 1981; Rathbun & Redford, 1981; Faurie & Perrin, 1995).

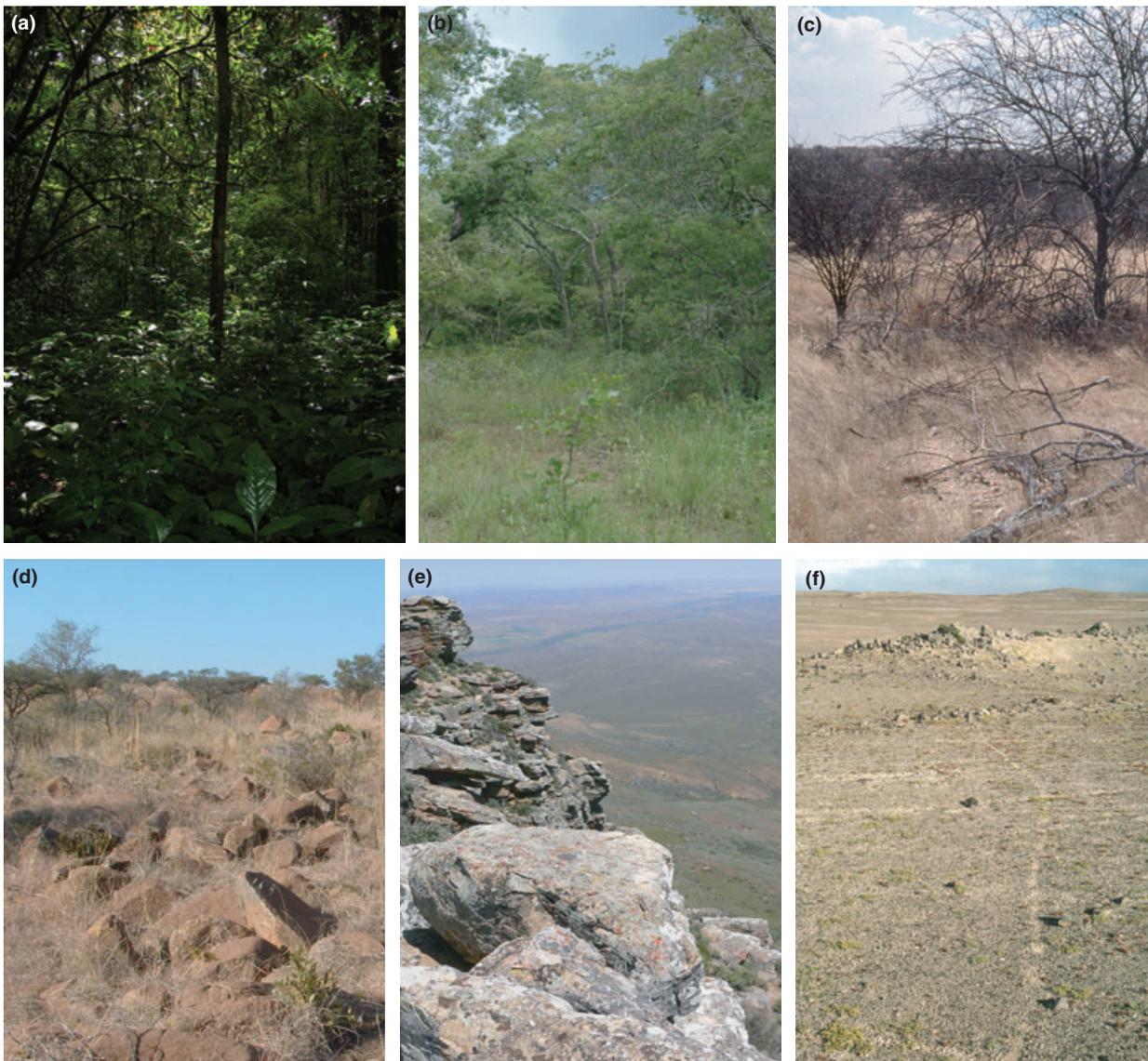


Fig 2 Representative habitats of sengis, including the species found at each location: (a) Montane forest, West Kilombero Scarp Forest Reserve, Udzungwa Mountains, Tanzania – *Rhynchocyon udzungwensis* and *Petrodromus tetradactylus* (photo G. Rathbun). (b) Mesi (Miombo) woodland, Nansai Farm, Choma Province, Zambia – *Petrodromus tetradactylus* and *Elephantulus brachyrhynchus* (photo Tim Osborne). (c) Arid bushland, Omaruru, Namibia – *Elephantulus intufi* (photo G. Rathbun). (d) Savannah woodland boulder field, Weenen Nature Reserve, KwaZulu Natal, South Africa – *Elephantulus myurus* (photo D. Ribble). (e) Montane rock and boulders, Nuweveld Mountains, Calvinia, Northern Cape Province, South Africa – *Elephantulus pilicaudus* (photo H. Smit). (f). Gravel plain, Namib Desert, Wlotzkasbaken, Namibia – *Macrosclides proboscideus*. Sengi path of oval bare patches is prominent up through centre of image (photo G. Rathbun)

Sheltering

In many respects, the giant sengis are more specialized than the soft-furred species, but this is not the case in sheltering habits. *Rhynchocyon* builds and uses leaf nests

on the forest floor, whereas none of the *Macrosclidinae* builds or uses nests (Rathbun, 1979; Table 2). Depending on the habitat and species (Table 2), the soft-furred sengis shelter in rock crevices and among boulders (Ribble & Perrin, 2005), at the bases of bushes in thickets (Rathbun,



Fig 3 The four genera of Macroscelidea, illustrating distinctive external morphology, including typical pelage colouration; pelage texture; large ears and eyes; long legs, tail, and nose; and laterally compressed body, especially in *Petrodromus* and *Rhynchocyon*. (a) *Elephantulus rupestris* (c. 60 g), Namibia. (b) *Macroscelides proboscideus* (c. 35 g), Namibia. (c) *Petrodromus tetradactylus* (c. 200 g), Kenya. (d) *Rhynchocyon chrysopygus* (c. 540 g), Kenya. (All photos G. Rathbun)

1979) and less commonly in shallow burrows abandoned by rodents (Rathbun & Rathbun, 2006b) or in termite mounds. Some sengis may excavate their own burrows in soft substrates (Sauer, 1973).

The soft-furred sengis, especially *Petrodromus*, *Macroscelides*, and *Elephantulus rufescens*, actively maintain distinct paths through surface litter by removing small stones, leaves, twigs, or grasses with forefoot sweeping motions, biting, and forehead pushing actions (Rathbun, 1979). The giant sengis do not actively build or maintain paths, but in dense habitats, indistinct trails through thickets can sometimes be found, which are the result of habitual use by sengis as well as other small mammals. Swift ungulate-like locomotion and the use of paths where surface structure warrants, allow sengis to effectively escape predation (Rathbun, 1979). When pursued, most sengis will eventually take refuge in hollow logs, tree trunks, or shallow burrows.

Activity period

It is well established that the four species of *Rhynchocyon* spend each night, and sometimes short periods during the day, alone in leaf nests on the forest floor (Rathbun, 1979; FitzGibbon, 1995). The situation with the diurnal habits of the soft-furred sengis is not as clear. Based on quantitative data from captives and free-ranging animals, most soft-furred species are crepuscular, with some activity during the day and night (Rathbun, 1979; Woodall, Woodall & Bodero, 1989; FitzGibbon, 1995; Neal, 1995; Ribble & Perrin, 2005). The reports of daylight activity are probably biased because sengis have acute senses of sight, sound and smell, and tend to flee from their exposed sheltering sites when disturbed (see Sheltering above). Thus, anecdotal reports of diurnal activity may largely reflect the activity of casual observers, rather than that of sengis.

Thermoregulation

Solar basking is a prominent behaviour of soft-furred sengis (Sauer, 1973; Rathbun, 1979; Ribble & Perrin, 2005; Rathbun & Rathbun, 2006b). Basking is usually done alone, but parents and dependent young sometimes bask together when suitable sunny sites are limited, as is often the case during peak basking periods of early morning and late afternoon (Rathbun & Rathbun, 2006b). Although the overall metabolic traits of sengis do not deviate remarkably from what would be expected for their body sizes (Perrin, 1995), the importance of basking is thought to be associated with sengi metabolism and energy conservation, especially considering the occurrence of nocturnal (daily) torpor in some species (Mzilikazi, Lovegrove & Ribble, 2002; Mzilikazi & Lovegrove, 2004). Because energetics may be an important factor in the ecology of many sengis, perhaps it is not surprising that the boulder-dwelling sengis (Table 2) are restricted to the higher latitudes (and altitudes) where cold air temperatures (including snow and ice) are buffered by large rock masses (Rathbun & Rathbun, 2006a). Giant sengis are not known to bask, which is not surprising given the closed-canopy habitats in the mid-latitudes where they occur. The metabolic traits of the Rhynchocyoninae, however, are not known because of past difficulties in maintaining captives (Nicoll & Rathbun, 1990), but this may soon change (Baker *et al.*, 2005).

Social structure and reproduction

All sengis studied so far are socially monogamous despite the wide range of habitats that they occupy (Rathbun & Rathbun, 2006b). The pair bond is weak, with the animals spending relatively little time in coordinated activities, except when a female is in oestrus (Rathbun, 1979; Lumpkin & Koontz, 1986). The home ranges of each member of a pair can be nearly congruent, or only partially overlapping, but the home ranges of neighbouring pairs rarely overlap, which suggests territoriality. However, actual defence has only been observed in some species (Rathbun & Rathbun, 2006b). Replacement of mates that disappear is usually swift, but sometimes when a male of a pair disappears, the neighbouring male will form a temporary polygynous association with the lone female, which supports the mate-guarding hypothesis for sengi monogamy (FitzGibbon, 1997; Ribble & Perrin, 2005; Rathbun & Rathbun, 2006b).

Sengi reproduction is antelope-like in numerous respects. Mating is brief (Rathbun, 1979; Lumpkin & Koontz, 1986), which partly explains the anterior position of the penis, at the base of the sternum (Woodall, 1995). The soft-furred sengis all give birth to highly precocial young that are small versions of adults and are able to run swiftly within an hour of birth (Rathbun, 1979; Rathbun & Rathbun, 2006b). This trait is closely associated with their cursorial locomotion and sheltering habits (see above, Table 2). The giant sengis, however, give birth to less precocial young that are restricted to a nest for about 2–3 weeks before emerging to forage (Rathbun, 1979; Baker *et al.*, 2005). In all sengis, litters are usually 1–2 (Sauer, 1973; Rathbun, 1979; Rathbun *et al.*, 1981; Neal, 1995; Bernard *et al.*, 1996), rarely as large as three or four (Séguignes, 1989; Olbricht, 2007; Table 1). There is no evidence of any relationship between litter size and habitats occupied, as indicated by Panchetti *et al.* (2008). Larger litters, however, are associated with seasonal reproduction at higher latitudes and elevations (Neal, 1995; Tables 1 & 2). Female sengis practise an ‘absentee’ system of neonatal care, sometimes only visiting the neonates once a day for a brief nursing bout (Rathbun, 1979; Rathbun & Rathbun, 2006b). In some soft-furred species, the location of nipples and upright nursing posture (Rathbun *et al.*, 1981) are probably related to their unguigrade locomotion and exposed sheltering habits. No direct paternal investment in neonates has been documented.

The adaptive syndrome

Although none of the life history traits summarized above is unique to the Macroscelidea, in combination they are. There is no other species or clade of small mammal in Africa or any of the other biogeographical regions of the world that combines highly cursorial locomotion, relatively exposed sheltering habits (at least the soft-furred species), mostly myrmecophagy, social monogamy, small precocial litters, female absentee neonatal care and small body size (<1 kg). This combination of features might be described as the melding of the characteristic life history traits of small antelopes typified by dik-diks (*Madoqua* spp.) with those of ant-eaters such as tamanduas (*Tamandua* spp.). This odd assemblage of features has been defined as the ‘micro-cursorial adaptive syndrome’ (Rathbun, 1979).

So few sengi species in so many habitats

Comparing taxonomy and ecology of mammals in Africa

In some respects, it is difficult to make comparisons between the macroscelidean radiation and other terrestrial mammal radiations, such as artiodactyls, rodents and carnivores, because of their disparate phylogeography. Nevertheless, using Nowak (1999), I tallied the number of extant terrestrial endemic African genera in these three radiations for comparison with sengis. The Artiodactyla is represented by 36 endemic genera (44% of total artiodactylid genera found in Africa), Carnivora 20 (21%), and Rodentia 76 (17%), whereas the Macroselidea is represented by only four genera, all of which are endemic. The three nonsengi orders occupy terrestrial habitats equally as diverse as those used by sengis, but clearly the diversity of taxa far surpasses that found in the sengis.

Phylogenetic inertia, the adaptive syndrome and competition

'When pigs fly' is sometimes used in casual conversations to indicate the near impossibility of an event occurring. The principle being expressed is essentially 'phylogenetic inertia' as used by E. O. Wilson (Blomberg & Garland, 2002), where the various morphological, physiological, behavioural, etc. features of a species or clade (its adaptive syndrome) inhibit it from evolving in some directions (pigs will probably never fly, no matter what the selection pressures and time frame).

The Afrotheria evolved in relative isolation on 'island Africa' after Gondwanaland broke up about 105 Ma, and I assume that they remained largely isolated from competition from other mammals until about 40 Ma, when Africa and Europe collided (Hedges, 2001). With a bridge from Europe, an inflow to Africa of northern placental mammals occurred. By the time of this mixing, however, the ancestors of the living insectivorous sengis had evolved their adaptive syndrome (Novacek, 1984; Holroyd & Mussell, 2005) and presumably radiated into most terrestrial habitats. At the time of the invasion from the north, I theorize that the insectivorous sengis were relatively immune to the incoming competition because of their specialized and unique adaptive syndrome and phylogenetic inertia. On the other hand, Kingdon *et al.* (in press) have hypothesized that the lineages of herbivorous sengis perhaps were driven to extinction by competition from similarly adapted northern invaders.

Often, mammals with specialized adaptive syndromes have similarly specialized habitat requirements. Paradoxically, the unique and specialized sengi adaptive syndrome appears to be well suited to a wide range of terrestrial habitats because there has been relatively little phenotypic modification (speciation), and that which has occurred is often cryptic (Corbet & Hanks, 1968; Smit *et al.*, 2008). However, not all habitats support the same diversity of taxa. Rocky and forested habitats together are associated with eleven species compared with the six species that occur in gravel plain, bushland and woodland habitats (Table 2). If subspecies are considered (Table 1), the ratio is even greater (26 : 8). Diverse climatic regimes, rifting and volcanism have resulted in the dynamic distribution of forested areas in eastern Africa (Lovett & Wasser, 1993) and, along with erosion and river dynamics, the fragmentation of rock and boulder habitats in southern Africa (Smit, 2008). This dynamism explains much of the bewilderingly diverse biota of Africa (Kingdon, 1989) and probably has resulted in the high diversity of rock-dwelling sengis (Smit, 2008). I hypothesize that these environmental mechanisms also explain the remarkable diversity of *Rhynchocyon* and *Petrodromus* taxa (Table 1) in the forested areas of eastern Africa.

The various components of the sengi adaptive syndrome are relatively well documented compared with the paucity of data on sengi speciation and biogeography. This disparity has led to some of my speculation on the relationship between systematics and biogeography. I anticipate that further research in these areas will eventually lead to a much better understanding of sengi phylogeography.

Conservation

Because there are only seventeen extant species of Macroselidea, their conservation status is of interest in terms of protecting Africa's unique biodiversity (Seiffert, 2002). Among the soft-furred species, most occur in relatively arid habitats (Table 2) that are not prone to intense agricultural or urban development, thus despite small distributions for some (Nicoll & Rathbun, 1990; IUCN, 2008; Table 1) and generally low densities for most (Kerley & Erasmus, 1992; Linzey & Kesner, 1997), none appear to be threatened at present (IUCN, 2008; Table 1). Although intense grazing and fire can reduce population densities, there is no indication that these activities eliminate populations (Hoffmann & Zeller, 2005; Yarnell *et al.*, 2007).

The giant sengis, on the other hand, occupy forest habitats that have undergone remarkable reductions and fragmentation as a result of timber extraction and agriculture and urban development (Nicoll & Rathbun, 1990). In addition, giant sengis often occur at low densities (FitzGibbon, 1994; Coster & Ribble, 2005) and some are hunted for subsistence (FitzGibbon, Mogaka & Fanshawe, 1995; Rathbun & Kyallo, 2000). As a result, the four species of *Rhynchocyon* carry various categories of threat (IUCN, 2008; Table 1). It would be tragic if any of the extant sengis in this highly unique radiation were extirpated.

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