Journal of Zoology. Print ISSN 0952-8369

Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea

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Keywords
Macroscelidea; elephant-shrew; sengi; social organization; monogamy; mate guarding.

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Received 21 March 2005; accepted 19 October 2005

doi:10.1111/j.1469-7998.2006.00087.x

Abstract

The elephant-shrews or sengis (order Macroscelidea) represent a monophyletic radiation endemic to Africa with 15 extant species in four genera. Field studies of representatives from all four genera indicate that all are socially monogamous. Resource and female dispersion, indirect paternal investment and male mate guarding have been proposed as factors contributing to sengi monogamy. To better understand sengi social organization, we studied the behavioural ecology of the bushveld sengi *Elephantulus intufi* in Namibia. Radio-tags and direct observation were used to gather spatial and behavioural data during 5 months in 2000–2002. Bushveld sengis were distributed as monogamous pairs on exclusive territories, similar to other sengis. Maternal care was characterized by an 'absentee' strategy and there was no evidence of direct or indirect paternal care. Sengis share many life-history traits with small antelopes, including uni-parental monogamy. Unlike the antelopes, which exhibit strong pair bonds, bushveld sengi pairs spend little time in coordinated activities. Male mate guarding best explains why sengis are socially monogamous – a model largely developed from studies of small antelopes. The similarity in morphology, life history and behaviour among sengi species results in a distinctive adaptive syndrome, which explains the consistency of their social structure, even in the extremes of terrestrial habitats that they occupy. The degree of sengi social monogamy is labile, which is related to their weak pair bond, same-sex aggression and variable densities.

Introduction

The behavioural ecology of sengis or elephant-shrews (order Macroscelidea) is best understood in the context of their evolutionary history. Their phylogeny has long been the subject of much speculation and controversy (Patterson, 1965), but with the recent application of molecular methods to phylogenetic analyses there is increasingly convincing evidence that the Macroscelidea is part of a monophyletic African clade of mammals that represents one of four early eutherian radiations. This clade, the superorder Afrotheria, includes elephants, sea cows, hyraxes, the aardvark, sengis, tenrecs and golden moles (Springer *et al*., 2004). Macroscelidean diversity peaked during the Miocene, when there were at least six subfamilies (all in the family Macroscelididae), including several herbivorous forms (Butler, 1995). Today, there are only two subfamilies, four genera and 15 species that are all restricted to Africa (Corbet & Hanks, 1968). As small-bodied (35–550 g), highly cursorial and largely diurnal insectivores, their life history is similar to several small-bodied cursorial herbivores and frugivores (Rathbun, 1979).

Publications on the Macroscelidea are extensive (Rathbun & Woodall, 2002), but there have been relatively few field studies of their behavioural ecology and social organization. Those that have been carefully studied, however, are socially monogamous (Rathbun, 1979; FitzGibbon, 1995, 1997; Ribble & Perrin, in press), despite their occurrence in a wide range of habitats and climatic regimes, including coastal and montane deserts, bushlands, rocky outcrops and tropical forests (Corbet & Hanks, 1968).

Although monogamy is found in less than 10% of mammals (Kleiman, 1977), there is an expanding literature on its evolution (Reichard & Boesch, 2003). The necessity of paternal assistance in caring for the young is one of the main explanations for mammalian monogamy (e.g. Kleiman, 1977; Wittenberger & Tilson, 1980; Kleiman & Malcolm, 1981; Møller, 2003). Sengis have an absentee system of maternal care (Ralls, Kranz & Lundrigan, 1986), where a litter of one to two (rarely up to four) precocial young is infrequently visited for short bouts of nursing (Sauer, 1973; Rathbun, 1979; Ribble & Perrin, in press; this paper). This presents little opportunity for *direct* male care of the young. Indeed, no direct paternal care has been recorded for any

Figure 1 A monogamous pair of bushveld sengis *Elephantulus intufi* and their single young basking on top of a boulder at the Erongo Mountains study site in Namibia. Both adults on the right (RR2 male above DGL female, see Fig. 2) are radio-collared and in typical resting postures. The *c.* 43-day-old young (RP male) on the left is scratching its flank while standing, a common auto-grooming stance. The coloured ear-tags on far-side pinnae are not easily visible here.

sengi, including captives. Rathbun (1979, 1984), however, suggested that monogamy in the rufous sengi *Elephantulus rufescens* might be related to the advantages of *indirect* paternal investment. Rufous sengi pairs maintain an extensive trail system through surface leaf litter, and males spend about 40% of their active daylight hours trail cleaning, compared with only about 20% for female mates. The trails allow easy access by territory members to feeding areas, and more importantly permit the highly cursorial parents and neonates to escape predation effectively.

A convincing argument has been made for male mate guarding as the main factor in the evolution of monogamy in Kirk's dik-dik *Madoqua kirkii*, a dwarf antelope found in East Africa, Angola and Namibia (Brotherton & Rhodes, 1996; Komers, 1996*a,b*; Brotherton & Manser, 1997; Komers & Brotherton, 1997; Brotherton & Komers, 2003). On the basis of the dik-dik model, Ribble & Perrin (in press) discuss mate guarding as the best explanation for social monogamy in the eastern rock sengi *Elephantulus myurus*. Is it possible that male mate guarding explains monogamy in other sengis? To help elucidate this question, we carried out a field study of the bushveld sengi *Elephantulus intufi* (Fig. 1), which weighs about 40 g and occurs on bush-studded sandy plains from south-western Angola south through most of Namibia and Botswana, and into parts of northern South Africa (Corbet & Hanks, 1968).

Because there have been no previous field studies of *E. intufi*, we were particularly interested in determining whether it fit the monogamous pattern of other well-studied macroscelids. In addition, we hypothesized that sengi species that reproduce seasonally in the higher latitudes (Neal, 1995) would show seasonal variation in their behaviours and social organization and thus perhaps further elucidate the factors associated with sengi monogamy. Although little information has been published on *E. intufi*, Skinner & Smithers (1990) indicate that they breed seasonally during the warm and wet months of August–March, making this species a potentially good model to test our hypothesis.

Methods

Study site

Our study was done near the Erongo Wilderness Lodge (21°27.679′S, 15°52.523′E) on Okapekaha Farm, about 10 km west of Omaruru town in the foothills of the Erongo Mountains in Namibia. The site is 1240 m above sea level and is characterized by rounded granite dikes that rise about 100 m above the surrounding peneplain and smaller 10–20 m high granite outcrops or kopjes surrounded by intruding fingers of the surrounding bushveld. The vegetation at the study site is composed of widely spaced low trees and bushes interspersed with seasonally dense annual and perennial forbs and bunch grasses. The dominant trees include *Terminalia prunoides*, *Acacia* spp. and *Boscia albitrunca* and the more common bushes included several species of *Grewia* and *Combretum*, *Dichrostachys cineria* and *Dombeya rotundifolia.*

The annual mean rainfall at Omaruru Prison is 292.9 mm, with virtually all of this falling during the months of November–April. Annual average minimum and maximum temperatures at the prison are 11.4–31.0 °C, with May–August being the coolest months (Rathbun & Rathbun, in press).

After determining the suitability of the study site in June 2000, we radio-tracked and observed sengis during three subsequent periods: 14 December 2000 to 8 January 2001, 4 September to 21 October 2001 and 28 April to 29 June 2002, inclusive.

Trapping and tagging

We captured sengis with 10 × 10 × 30.5 cm folding aluminium Sherman live traps baited with a dry mixture of rolled oats, peanut butter and Marmite (a yeast spread). To prevent hyperthermia in captured animals, we avoided trapping during mid-day. After dark we checked traps every hour or two to reduce the risk of trap predation. Some sengis became 'trap happy' whereas others avoided capture by going around or jumping over the traps. To recapture trap-shy animals, we used nylon mist nets (50 denier/2-ply, 38 mm mesh) that we cut into panels 10–20 m long and about 1 m deep. We positioned these nets vertically along the ground across known travel routes and then gently drove targeted sengis into the nets or allowed them to entangle themselves during their normal movements. To prevent entangled sengis from escaping, injuring themselves or becoming prey, we monitored nets constantly while set. The most effective time to net was from late afternoon to dusk.

We permanently marked our sengis for subsequent visual identification by sandwiching an ear pinna between two 7-mm-diameter disks cut from coloured vinyl embossing tape. The sandwich was held together with a short rod of nylon monofilament fishing line threaded through pin-holes in the pinna and centres of each disk and melted on each end (Rathbun, 1979). This ear-tag also allowed us to identify unmarked individuals in our study area and target these for trapping and marking.

We initially attached radio-transmitters (Holohil Systems Ltd, Carp, Ontario, Canada; model BD-2G, 1.7 g weight, 90-day battery life, 8-pound-test wire and 10-cm-long whip antenna) to collars made of beaded chain (Harker, Rathbun & Langtimm, 1999). However, the chain attachment resulted in abrasions on the back of the neck of some animals. We eliminated the abrasion problem by replacing the chain with wire (10-pound-test fishing leader) inside Tygon tubing and fitted with a single bead on each end for quick attachment to the same transmitter connector that we used with the chain collars. Both these radio-tag designs weighed less than 2.0 g. Our sengis had a propensity to entangle their front feet in the collars, unless they were fitted very snugly.

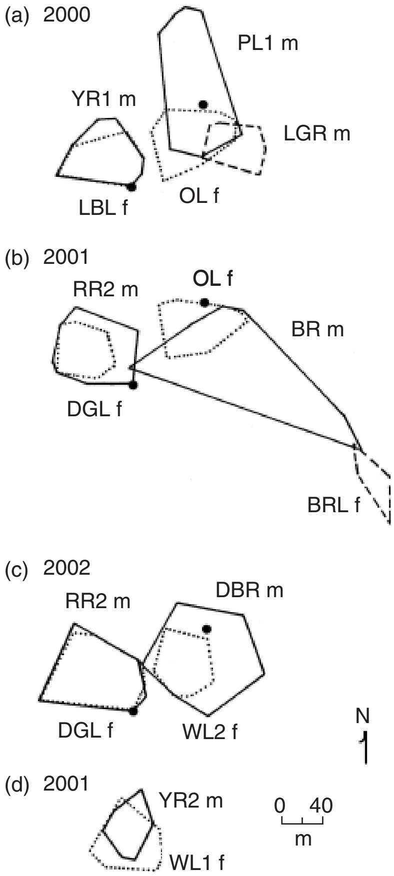

Figure 2 Minimum convex polygon home ranges (95% of fixes) for adult bushveld sengis *Elephantulus intufi* (identified by two or three characters) at the Erongo Mountains study site in Namibia. Areas in (a)–(c) are the same (paired solid black circles are identical reference points) during consecutive years 2000–2002. Area in (d) during 2001 is different. The scale is common to all panels. Male (m) and female (f) pairs are represented by solid-line and dotted-line polygons, respectively. Dash-lined areas are temporarily paired adults of either sex (see text). Sengi BRL (b) was only ear-tagged.

Radio-tracking and visual observations

We radio-located each of our sengis several times a day between 04:30 and 22:30 h. We separated consecutive fixes by at least 45 min, which we believe was sufficient to reduce inter-fix autocorrelation because the animals moved frequently on their home ranges. The sengis were exceedingly alert and wary and prone to flee from disturbances, which required that we use stealth in radio-tracking. Sengi behaviour, along with radio-signal deflection because of the numerous granite boulders and kopjes, often made triangulation impractical. Therefore, we used a combination of homing and triangulation (Kenward, 2001) to determine radio-locations (fixes), which varied in number from 44 to 290 (mean = 126) for the 15 home ranges by 12 individuals (Fig. 2). We flagged locations made at night and determined coordinates the next day.

We calculated universal transverse Mercator (UTM) coordinates for our visual and radio-fixes by first determining the location of a prominent target site in our study area with a global positioning system (GPS) receiver. We then used rangefinder distances and compass azimuths and the computer software program UTM CALC (O'Leary, 1998) to calculate coordinates for several other prominent targets (kopjes or trunks of trees) so that at least one was visible within 100 m from any spot on the study area. UTM CALC was similarly used to calculate sengi locations. The precision of our laser rangefinder (Bushnell, Proctor, Minnesota, USA; model × 400) and sighting compass (Brunton, Riverton, Wyoming, USA; model 16-FSM360LA-SME) was ± 1.0 m and ± 0.5°, respectively. The accuracy of our location calculations was less than ± 2.0 m at 100 m. This was considerably better than the GPS accuracy of ± 5.5 m that we determined from nine fixes (averaged over 3 min) taken during 24 h at a single site. The accuracy of our initial GPS location had no significance in our home range analyses because all our subsequent sengi fixes were determined relative to the initial site.

We used the software program RANGES 6 (Kenward, South & Walls, 2002) to calculate home range areas. Minimum convex polygon (MCP) areas and their overlaps were calculated using the arithmetic mean when less than 100% of fixes were used. The default settings in RANGES 6 were used to calculate fixed kernel home range areas.

During morning and late afternoon, when air temperatures were usually below 30 °C and thus tolerable, we sat on top of granite boulders that were about 1–3 m high and with 8 × 40 binoculars watched our tagged sengis. Even with the advantage of radio-transmitters and sitting above the surrounding habitat, unhindered observation was often difficult because of the frequent movements of our sengis and obstructing dense annual grass growth, bushes and trees, and numerous boulders. In addition, our sengis were not as active during the day as we had expected.

Results

Spatial organization

During the study periods, we were able to capture and mark all sengis in our study areas, based on subsequent sightings of only ear-tagged individuals, and found that male and female sengis were distributed as pairs (Fig. 1). Some pairs had nearly congruent home ranges, as illustrated by the dyads on the left side of Fig. 2a and b, both pairs in Fig. 2c and the single pair in Fig. 2d. The triad on the right side of Fig. 2a was associated with the loss of LGR male and his replacement by PL1 male, and Fig. 2b was related to an attempt by BR male to include unpaired female BRL within his home range. In the latter case, BR's excursions to visit BRL female, which was ear-tagged but not radio-tagged, only involved night visits during a 2-week period (she was unintentionally removed when she accidentally escaped while being photographed about 500 m from her home range).

The average area (± SD) of the 95% MCP home ranges for males of the five nearly congruent pairs (see above, Fig. 2) was 0.47 ± 0.25 ha, slightly larger than that of females (0.32 ± 0.11 ha). Because of our small sample size and the large variances the difference was not statistically significant (paired *t*-test, two-tailed $P = 0.24$). If we include the home ranges of the two pairs with temporarily polygynous associations (OL female with mates PL1 and BR, Fig. 2a and b), the average home range area for the seven males was 0.61 ± 0.35 ha compared with 0.34 ± 0.11 ha for their mates; the difference is nearly significant (paired *t*-test, two-tailed $P = 0.09$).

The average 95% MCP home range area overlap of females by their male mates for the four pairs with nearly congruent home ranges (same individuals as above, but excluding the pair in Fig. 2d) was 98.7%, and of males by their female mates was 64.1%. Only two individuals from neighbouring pairs overlapped, and both areas were less than 1% (Fig. 2b and c).

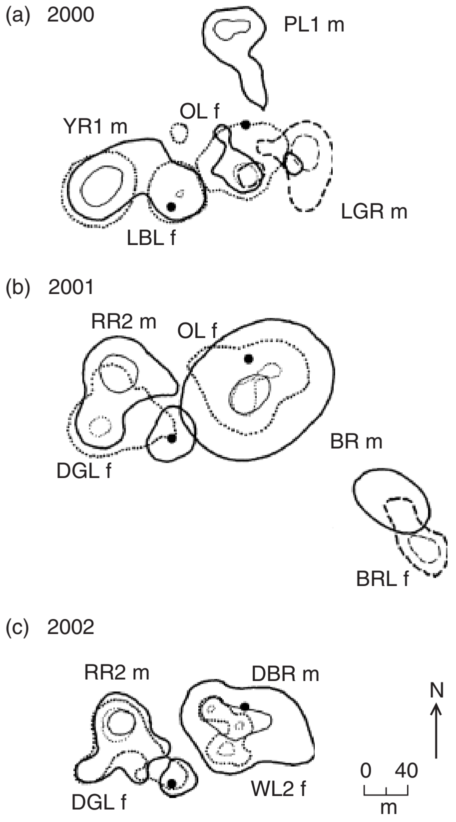

Figure 3 Fixed kernel contour home ranges for adult bushveld sengis *Elephantulus intufi*. Data and scale same as in Fig. 2a–c. For each individual, the outermost bold-line contour includes 95% of location fixes and the inner thin-line contour includes 50% of fixes.

We assessed the use of individual home range areas with fixed kernel methods and the same individuals and fixes used in the MCP home range calculations (Fig. 2). The kernel densities (Fig. 3) indicate that dyads with the most congruence in home range boundaries also used their areas more similarly than those animals with less congruent boundaries. For instance, the greatest differences between male–female pairs occurred in 2000 when male PL1 had two main centres of activity that corresponded with centres of activity before and after he moved onto adjacent female OL's home range when LGR male disappeared. Similarly, in 2001 the bimodal centres of activity of male BR reflect his nightly visits during 2 weeks to adjacent female BRL before we removed her.

The MCP home range analyses illustrate that members of dyads used their shared home range nearly exclusive of neighbouring pairs (Fig. 2), suggesting that they were territories. This is corroborated by the comparable 95% fixed kernel home range areas, showing that the sengis centred their activity well away from areas of potential overlap with neighbours (Fig. 3). We spent numerous hours in these interface areas with the hope of seeing territorial behaviours such as agonistic encounters or scent marking, but we saw none. These areas were also nearly devoid of secondary signs of high use by the sengis, including sheltering sites or dung.

Reproduction

On two home ranges we observed single young. In December 2000, OL visited her presumed young (not marked) on two different days. Neither she nor her mate was seen with the young on any other occasions, despite our attempts over many hours. On the first visit, the female left her favoured shelter at 18:18 h and travelled about 40 m to where the young was sheltering at the base of a kopje. After some initial darting about interspersed with nose–nose greetings, the female sat up on her rear legs and the young nursed for about 2 min. Once nursing was finished, the female immediately left the area. We tried to repeat these observations, but were only able to catch the two together again 4 days later, when the female again briefly visited the young at the same location at 18:40 h. Unfortunately, our view of their interactions was hidden by rocks, vegetation and failing daylight. After several minutes the female left the area.

On 2 May 2002, we first spotted a very small sengi under dense shrubs in a *c*. 100-m^2 area in the south-eastern corner of the home range of DGL female and RR2 male (Fig. 2c). After several days of focused trapping, on 14 May we captured, weighed (29.0 g) and ear-tagged a young male (PL2), which we estimated (based on the growth curve for *E. rufescens* in Rathbun, Beaman & Maliniak, 1981) was 20 days old. Despite numerous attempts to observe interactions between the young and adult pair, we were not successful until PL2 expanded his range on about 19 May to include an area used more frequently by the radio-tagged adults. Although these three sengis were often within several metres of each other, we did not observe the female and young together until 2 June, when they were seen resting while touching sides. Three days later we again saw them resting together, his nose on her rump. The only time we observed adult male RR2 close to the young was on 9 June, when all three basked together on top of a rock at 16:05 h in the last rays of the sun (Fig. 1). This close association, however, represented a resource (sunlight) rather than social gathering.

When we found little evidence of seasonal variation in *E. intufi* behaviours or use of space, we examined more closely the timing of reproduction. We extrapolated birth dates for museum specimens with weight data from Namibia based on the birth weight and growth rate of *E. rufescens* (Rathbun *et al*., 1981). Out of 45 records (five personal observations, 28 specimens in the Los Angeles County Museum of Natural History, eight in the National Museum of Namibia and four reported in Shortridge, 1934), one each occurred in March and October, two each in January, June and August, three in April; seven in November, 12 in February and 15 in December. Only May and July had no evidence of births. Unfortunately, an assessment of the monthly effort that resulted in these data is not possible, but bushveld sengis in Namibia apparently are not highly seasonal breeders.

Sheltering behaviour

Each sengi used and maintained several basking and rest spots. For example, in 2002 an average of 73% of the total radio-fixes ($n = 938$) for two pairs (WL2–DBR and DGL–RR2, Fig. 2) were located at five to 12 different sites, and these sites were each used between five and 59 different times. For the same two pairs, 12% of fixes were at two to four locations that were used two to four times, and 15% at multiple sites used only once. Although members of a dyad were closely associated in space, their favoured rest sites were often different. For instance, we radio-located WL2 and DBR at 17 different shelter locations six or more times, but only two of the loci were common to both. DGL and RR2 were less independent; they used 15 different shelter locations six or more times, and both individuals used 10 of these loci.

We rarely radio-located or observed more than one sengi using the same shelter site at the same time, although members of a pair often used sites 2–5 m apart at the same time. We observed members of a pair meet at a sheltering spot only four times, and in three cases the animals exchanged nose–nose contact before one or both departed. In the fourth case, a radio-collared female and an unmarked intruding animal exchanged nasal contact, and then the two nervously foot drummed and darted around each other before both ran off in separate directions; we did not see the unmarked animal again. We saw no aggression or dominance in these four interactions. In only two instances did we see a male and female pair remain together at rest sites. In 2001, WL1 female and YR2 male rested rump to rump for about 2 min and then the female pushed the male off the site by constantly backing into him. On 6 June 2002 at 15:45 h, we observed DGL female and RR2 male basking flank to flank in a spot of sunlight for about 1 min.

We focused much of our observation efforts on basking and resting sites, and accumulated about 20 h of sengi observations. These sites were positioned under the cover of bushes that were about 1 m high or in 15- or 20-cm-wide gaps under or between large boulders sitting on the ground or on flat rock surfaces. Depending on the angle and exposure of the sun, some of the resting sites were used for basking. Sheltering sites under bushes were often covered with 1–5 cm of leaf litter, whereas rock surfaces and the relatively large areas between trees and bushes usually lacked litter (Fig. 1). When leaves and twigs were present on favoured travel routes or at sheltering locations, the sengis cleared the material with sweeping motions of their front feet. Sites that were frequently used typically had dozens of dung pellets scattered about the surface.

While basking, resting or sleeping at sheltering sites, sengis crouched down on top of all four legs and rested their heads on their forefeet (Fig. 1). We never observed them lying on their sides with their legs or feet out to one side. Sengis appeared to sleep for periods of 1–10 min in the crouched position, although we never saw them completely shut their eyes. The slightest unusual sight or sound would cause resting or sleeping sengis to jump to their feet and nervously flick their tails side to side and up and down while foot drumming – all the while twitching and twisting their noses in the air as though searching for unusual scents.

Rodent burrows were common and widespread in the study area, but only three of our 15 radio-tagged sengis intermittently used holes during our study. Male PL1 (Fig. 2) habitually used two widely separate burrows that were each part of a cluster of holes, perhaps abandoned by gerbils *Tatera leucogaster* or rock mice *Aethomys namaquensis*. One of the holes used was under a dense pile of cut and dead acacia branches and the other was under a 1-m-high living bush. YR2 and WL1 (Fig. 2) sometimes used the same hole that was located under a dense tangle of vegetation. We often found one or the other resting 15–20 cm outside the burrow entrance, and if disturbed the sengi would quickly retreat into the hole or run off to another area. There was no evidence that the radio-tagged pair used the burrow at the same time. Out of 67 captures on and adjacent to our study site, only two sengis fled into burrows 3–4 m away when released, and we never found sengis in these burrows again. The remaining sengis swiftly ran many metres off and disappeared from sight beyond vegetation or rocks. Three of our radio-tagged sengis entangled their front feet in their collars and uncharacteristically began using burrows until their feet were untangled and collars tightened. We found no evidence of nest material being used by any sengis and believe that only the entrances to the burrows were being used as shelters.

Discussion

We found bushveld sengis in Namiba to be socially monogamous, but they did not reproduce seasonally, so we were unable to explore our hypothesis that their social organization would vary with seasonal reproduction. However, *E. myurus* does reproduce seasonally (Woodall & Skinner, 1989), and apparently is socially monogamous during nonreproductive periods (Ribble & Perrin, in press), which demonstrates that sengi social monogamy persists regardless of seasonal changes in the reproductive condition of females.

The results from our study are relevant to two important questions: First, why are most, if not all, sengis monogamous, and second, what are the adaptive factors associated with social monogamy in the Macroscelidea? We begin by identifying the importance of a suite of uniquely derived traits among Macroscelidea that relate to the first question. We then examine several models that relate to the second question. Lastly, we discuss variation in sengi social monogamy, especially in relation to different densities.

Corbet & Hanks (1968) noted the remarkable similarity in external morphology of all 15 sengi species, which includes their long nose and tongue, small under-slung mouth, large eyes and pinnae, long legs, laterally compressed body, etc. (Fig. 1). All sengis also appear to have similar life-history traits (Brown, 1964; Rathbun, 1979; Perrin, 1995), including small litters of precocial young, multi-year longevity, mostly insectivorous diet, unremarkable metabolic rates, etc. Sengi morphological traits (and presumably their life history, too) have remained remarkably static over geological time. For example, based on fossils recovered from once-forested areas in Kenya, *Rhynchocyon* has hardly changed over the last 20 million years (Novacek, 1984).

Many of the behaviours exhibited by captive and free-ranging sengis are also notably similar. For example, most of the behaviours we observed in free-ranging *E. intufi* are also found in captives (Hoesch, 1959), as is the case with free-ranging and captive *E. rufescens* (Rathbun, 1979; Rathbun *et al*., 1981; Lumpkin & Koontz, 1986). Similarly, behaviours between species are remarkably similar, as remarked by Nöthen (1982) for *E. intufi* and *E. rufescens*. These behaviours include the use of relatively exposed shelter sites, lack of nesting material, auto-grooming patterns, solar basking, scent marking, trail cleaning, foot drumming, surface gleaning of invertebrates, etc. Indeed, all *Elephantulus* studied to date exhibit these same behaviours. For example, solar basking is well documented in several species, especially the North African sengi *Elephantulus rozeti* (Séguignes, 1989), the eastern rock sengi (Mzilikazi, Lovegrove & Ribble, 2002) and bushveld sengi (Fig. 1). Most species also foot drum when disturbed (Faurie, Dempster & Perrin, 1996), and all are exceedingly alert and prone to antelope-like behaviours, including swift cursorial flight when disturbed (Brown, 1964; Kingdon, 1974; Rathbun, 1979; this paper).

The similarities within the order also extend to social organization. The rufous sengi (Rathbun, 1979), eastern rock sengi (Ribble & Perrin, in press) and bushveld sengi (this paper) exhibit social monogamy, where male–female pairs have overlapping home ranges that are relatively stable through time and function as territories. However, few pair-bond behaviours are exhibited. A similar structure is also found in *Elephantulus brachyrhynchus* (Neal, 1995), *Macroscelides proboscideus* (Sauer, 1973; Rosenthal, 1975), *Petrodromus tetradactylus* (Rathbun, 1979; FitzGibbon, 1995) and *Rhynchocyon chrysopygus* (Rathbun, 1978, 1979; FitzGibbon, 1995). Even though all these species have the same social structure (i.e. social monogamy), variation in their monogamy does occur, which we will discuss later.

The numerous attempts to breed sengis in captivity have mainly succeeded when animals are housed as monogamous pairs (Tripp, 1972; Rosenthal, 1975; Rathbun *et al*., 1981; Lumpkin & Koontz, 1986; Nicoll & Rathbun, 1990; Unger, 1999; Baker *et al*., 2005). When multiple adults of the same sex are kept together they often fight, which results in wounded and stressed animals that either do not breed or kill and eat their neonates (Rathbun *et al*., 1981). Same-sex aggression among adults has also been found in sengis that have been closely observed in the wild (Rathbun, 1979), which suggests that this behaviour may be relatively invariable.

The well-defined and similar morphology, life history and ethology of most, if not all, sengis, as reviewed above, results in an adaptive syndrome that includes a highly integrated and similar social structure. The relatively invariable adaptive syndrome of sengis, which has no ecological equivalent outside of Africa and might best be described as that of a very small antelope-like anteater, is surprising. Why have sengis not evolved more specializations related to the wide range of habitats they occupy? Perhaps the concept of phylogenetic inertia is applicable, especially given their evolutionary stasis and ancient association with the Afrotheria.

Although the well-defined suite of highly integrated traits in sengis provides an explanation for the generality of their social monogamy, it does not explain the ultimate adaptive factors associated with this social organization. If indirect paternal assistance (e.g. trail cleaning) were an important factor in sengi monogamy, it should occur in all species. Trail cleaning by *E. intufi* was not as important as in *E. rufescens* and trails are not used by rock-dwelling sengis (*E. myurus*, Ribble & Perrin, in press; *E. rozeti*, *Elephantulus edwardii* and *Elephantulus rupestris*; G. B. Rathbun & C. D. Rathbun, pers. obs.) or forest-dwelling *R. chrysopygus* (Rathbun, 1979). Nevertheless, these sengis are socially monogamous, which suggests that some other indirect factor, such as maintenance of a territory or vigilance for predators, might be involved. On the other hand, indirect paternal investment may not be important at all.

Rathbun (1979, 1984) proposed that the social monogamy exhibited by the golden-rumped sengi *R. chrysopygus* in the coastal forests of Kenya was the result of female dispersion in relation to widely dispersed invertebrate prey, year-round (but brief) oestrous periods and several behaviours shared with monogamous ungulates, including swift cursorial locomotion, small litters of precocial young, absentee maternal care, etc. These factors resulted in the most productive male strategy being to associate with a single female. FitzGibbon (1997) for *R. chrysopygus* and Ribble & Perrin (in press) for *E. myurus* present evidence that mate guarding is responsible for monogamy in these species. An important component of their argument is the relative size of male and female home ranges of mated pairs, where males often use areas that are large enough to encompass more than one female, but they do not (see the discussion below on temporary liaisons of *E. intufi*). On the basis of detailed observations of the reproductive behaviour of captive *E. rufescens*, Lumpkin & Koontz (1986) suggested that the cryptic, short and variable duration of oestrus results in male mate guarding being particularly adaptive. In addition, the vulnerability of sengis to predation, especially because of their exposed habits, makes same-sex territorial aggression especially adaptive in terms of rapid and easy mate replacement (Lumpkin & Koontz, 1986). Although several factors may be involved with the evolution of sengi social monogamy, male mate guarding is the most parsimonious with published information and our observations.

A review of sengi behavioural ecology suggests that the amount of intra-pair home range overlap is associated with their density. Under high-density conditions home ranges are nearly congruent, whereas at low densities there is less overlap. For example, golden-rumped sengi pairs at Gedi Ruins in Kenya (Rathbun, 1979) had smaller home ranges that were more congruent than pairs in the nearby Arabuko-Sokoke Forest, where densities were lower because of the less productive forest (FitzGibbon, 1997). Our data on *E. intufi* intra-pair home range overlap also show the effect of density. In the south-eastern corner of our study site, pairs showed more home range overlap than in other areas (Fig. 2). The south-eastern pairs were boxed into a high-density situation by unsuitable rocky areas on the southern and north-western sides of a triangle, and on the remaining side by a neighbouring pair. This restricted configuration did not occur in the other areas of the study site, where home ranges were less congruent.

The round-eared sengi *M. proboscideus* in the Namib Desert of Namibia occurs at very low densities compared with all other sengis studied to date. The home ranges of *M. proboscideus* can be up to a kilometre across (Sauer, 1973; G. B. Rathbun & C. D. Rathbun, pers. obs.), and under these conditions Sauer (1973) found minimal (but unmeasured) home range overlap and so few intra-pair interactions that he characterized the species as solitary, but with an insipient tendency for monogamy. In the higher density conditions of captivity (Rosenthal, 1975; Unger, 1999), *M. proboscideus* exhibits monogamous associations typical of other sengis.

The rufous sengi is highly territorial, as shown by their dung piles on home range boundaries, agonistic displays (e.g. 'mechanical walk') and aggressive pursuit of conspecific home range intruders (Rathbun, 1979). We did not observe these behaviours in bushveld sengis, although their home ranges were nearly exclusive of neighbouring pairs and thus functioned as territories. Territorial behaviours may have been rare at our study site because *E. intufi* densities were relatively low, resulting in little need and few opportunities for neighbouring pairs to interact.

In studies of individually marked free-ranging sengis, a male will sometimes expand its home range to include a neighbouring unpaired (often widowed) female (Rathbun, 1979; FitzGibbon, 1997; this paper). These polygynous associations are ephemeral – when an unpaired male begins to associate with a widowed female (and presumably guards her) the would-be polygynous neighbouring male retreats to his original mate and home range. These observations support the mate guarding hypothesis for social monogamy (FitzGibbon, 1997; Brotherton & Komers, 2003), but they also illustrate the weak pair bond in sengis (Rathbun, 1979; this paper) compared with the strong bond of the monogamous dik-dik (Kranz, 1991). The temporary sengi home range expansions also represent the collapse of social monogamy in temporarily low-density situations where females outnumber males. In Ribble & Perrin's (in press) study of *E. myurus*, apparently there was no shortage of males because widowed females were quickly paired with nearby unpaired males, thus quickly eliminating the opportunity for polygyny by adjacent paired males. Home range expansions and shifts by sengis show the importance of the weak pair bond and same-sex aggression in mate replacement.

To further advance our understanding of indirect paternal investment and mate guarding, studies must be designed and completed where individually identifiable males and females are manipulated and paternity established to determine the various effects on social monogamy. Longer term studies are also needed to document variation in social monogamy as population densities change through time. As pointed out by Ribble & Perrin (in press), sengis are ideal for these studies.

In conclusion, the ubiquity of social monogamy in sengis across remarkably different habitats may be the consequence of the interaction and conservation of a suite of uniquely derived traits. The ultimate factor that makes social monogamy adaptive for sengis is probably male mate guarding. The Macroscelidea also exhibit density-dependent monogamy, with decreasing densities resulting in male–female home range associations varying from highly congruent, through temporarily polygynous, to insipiently monogamous. The variability of sengi social monogamy is also closely related to a weak pair bond and same-sex aggression.

Acknowledgements

We are grateful for the logistical support and fellowship in Namibia provided by Mike Griffin of the Ministry of Environment and Tourism, Tim and Laurel Osborne of Windpoort Farm, and Seth Eisab of the National Museum. We thank our friends at the Erongo Wilderness Lodge for enthusiastically hosting us, especially designer/builder Danie Holloway, managers Roger Fussell, Mike Warren and Lindy van den Bosch, and the entire staff. Tom O'Shea generously provided us with mist nets. Paquita Hoeck translated several papers from German to English. We appreciate the assistance of Emcé Bouwer of the Marietha Bouwer Agencies in obtaining research visas from the Ministry of Home Affairs. Our work was completed under research permit no. 505 from the Ministry of Environment and Tourism. We benefited greatly from the insightful comments and suggestions made by David Ribble and two anonymous reviewers on early versions of this paper.

References

Baker, J.A., Lengel, K., McCafferty, K. & Hellmuth, H. (2005). Black-and-rufous sengi *(Rhynchocyon petersi)* at the Philadelphia Zoo. *Afrotherian Conservation – Newsletter of the IUCN-SSC Afrotheria Specialist Group*, No. 3:6–7.

Brotherton, P.N.M. & Komers, P.E. (2003). Mate guarding and the evolution of social monogamy in mammals. In *Monogamy – mating strategies and partnerships in birds, humans and other mammals*: 42–58. Reichard, U.H. & Boesch, C. (Eds). Cambridge: Cambridge University Press.

Brotherton, P.N.M. & Manser, M.B. (1997). Female dispersion and the evolution of monogamy in the dik-dik. *Anim. Behav*. **54**, 1413–1424.

Brotherton, P.N.M. & Rhodes, A. (1996). Monogamy without biparental care in a dwarf antelope. *Proc. Roy. Soc. Lond. (Biol.)* **263**, 23–29.

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

Butler, P.M. (1995). Fossil Macroscelidea. *Mamm. Rev*. **25**, 3–14.

Corbet, G.B. & Hanks, J. (1968). A revision of the elephant-shrews, family Macroscelididae. *Bull. Br. Mus. Nat. Hist. (Zool.)* **16**, 47–111.

Faurie, A.S., Dempster, E.R. & Perrin, M.R. (1996). Foot-drumming patterns of southern African elephant-shrews. *Mammalia* **60**, 567–576.

FitzGibbon, C.D. (1995). Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. *Mammal Rev*. **25**, 19–30.

FitzGibbon, C.D. (1997). The adaptive significance of monogamy in the golden-rumped elephant-shrew. *J. Zool. (Lond.)* **242**, 167–177.

Harker, M., Rathbun, G.B. & Langtimm, C.A. (1999). Beaded-chain collars: a new method to radiotag kangaroo rats for short-term studies. *Wildl. Soc. Bull*. **27**, 314–317.

Hoesch, W. (1959). Elefanten-Spitzmause in Freiheit und in Gefangenschaft. *Nat. Volk*. **89**, 53–59.

Kenward, R.E. (2001). *A manual for wildlife radio tagging*. London: Academic Press.

Kenward, R., South, A. & Walls, S. (2002). *RANGES 6*. Wareham, Dorset, UK: AnaTrack Ltd.

Kingdon, J. (1974). *East African mammals; an atlas of evolution in Africa*. New York: Academic Press.

Kleiman, D.G. (1977). Monogamy in mammals. *Quart. Rev. Biol*. **52**, 39–69.

Kleiman, D.G. & Malcolm, J.R. (1981). The evolution of male parental investment in mammals. In *Parental care in mammals*: 347–387. Gubernick, D.J. & Klopfer, P.H. (Eds). New York: Plenum Press.

Komers, P.E. (1996*a*). Obligate monogamy without paternal care in Kirk's dik-dik. *Anim. Behav*. **51**, 131–140.

Komers, P.E. (1996*b*). Conflicting territory use in males and females of a monogamous ungulate, the Kirk's dik-dik. *Ethology* **102**, 568–579.

Komers, P.E. & Brotherton, P.N.M. (1997). Female space use is the best predictor of monogamy in mammals. *Proc. Roy. Soc. Lond. (Biol.)* **264**, 1261–1270.

Kranz, K.R. (1991). Monogamy in the dik-dik. *Appl. Anim. Behav. Sci*. **29**, 87–105.

Lumpkin, S. & Koontz, F.W. (1986). Social and sexual behavior of the rufous elephant-shrew (*Elephantulus rufescens*) in captivity. *J. Mammal*. **67**, 112–119.

Møller, A.P. (2003). The evolution of monogamy: mating relationships, parental care and sexual selection. In *Monogamy – mating strategies and partnerships in birds, humans and other mammals*: 29–42. Reichard, U.H. & Boesch, C. (Eds). Cambridge: Cambridge University Press.

Mzilikazi, N., Lovegrove, B.G. & Ribble, D.O. (2002). Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. *Oecologia* **133**, 307–314.

Neal, B.R. (1995). The ecology and reproduction of the short-snouted elephant-shrew, *Elephantulus brachyrhynchus*, in Zimbabwe with a review of the reproductive ecology of the genus *Elephantulus*. *Mamm. Rev*. **25**, 51–60.

Nicoll, M.E. & Rathbun, G.B. (1990). *African Insectivora and elephant-shrews, an action plan for their conservation*. Gland: International Union for Conservation of Nature and Natural Resources (IUCN).

Nöthen, D. (1982). Putz- und Komfortverhalten bei der Bushveld-Elephantenspitzmaus *Elephantulus intufi*. *Zool. Beitr*. **28**, 17–32.

Novacek, M. (1984). Evolutionary stasis in the elephant-shrew, *Rhynchocyon*. In *Living fossils*: 4–22. Eldredge, N. & Stanley, S.M. (Eds). New York: Springer Verlag.

O'Leary, R. (1998). *UTM CALCULATOR, v. 2.1*. The Lane at Stillwater Lake, Stillwater Lake, Nova Scotia, Canada.

Patterson, B. (1965). The fossil elephant shrews (family Macroscelididae). *Bull. Mus. Comp. Zool*. **133**, 297–336.

Perrin, M.R. (Ed.) (1995). The biology of elephant-shrews – Proceedings of a symposium held during the 6th International Theriological Congress, Sydney, 5 July 1993. *Mamm. Rev*. **25**, 1–100.

Ralls, K., Kranz, K. & Lundrigan, B. (1986). Mother–young relationships in captive ungulates: variability and clustering. *Anim. Behav*. **34**, 134–145.

Rathbun, G.B. (1978). Evolution of the rump region in the golden-rumped elephant-shrew. *Bull. Carnegie Mus. Nat. Hist*. **6**, 11–19.

Rathbun, G.B. (1979). The social structure and ecology of elephant-shrews. *Adv. Ethol*. **20**, 1–75.

Rathbun, G.B. (1984). Elephant-shrews: order Macroscelidea. In *Encyclopedia of mammals*: 728–735. Macdonald, D. (Ed.). New York: Facts-On-File.

Rathbun, G.B., Beaman, P. & Maliniak, E. (1981). Capture, husbandry and breeding of rufous elephant-shrews. *Int. Zoo Yearbook* **21**, 176–184.

Rathbun, G.B. & Rathbun, C.D. (in press). Noki or dassie-rat (*Petromus typicus*) feeding ecology and petrophily. *Belg. J. Zool*. **135** (Suppl.).

Rathbun, G.B. & Woodall, P.F. (2002). A bibliography of elephant-shrews or sengis (Macroscelidea). *Mammal Rev*. **32**, 66–70.

Reichard, U.H. & Boesch, C. (Eds) (2003). *Monogamy – mating strategies and partnerships in birds, humans and other mammals*. Cambridge: Cambridge University Press.

Ribble, D.O. & Perrin, M.R. (in press). Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belg. J. Zool*. **135** (Suppl.).

Rosenthal, M. (1975). *The management, behavior and reproduction of the short-eared elephant shrew Macroscelides proboscideus (Shaw)*. MA thesis, Northeastern Illinois University.

Sauer, E.G.F. (1973). Zum sozialverhalten der kurzohrigen elefantenspitzmaus, *Macroscelides proboscideus*. *Z. Saugetierkd*. **38**, 65–97.

Séguignes, M. (1989). Contribution a l'etude de la reproduction d'*Elephantulus rozeti* (Insectivora, Macroscelididae). *Mammalia* **53**, 377–386.

Shortridge, G.C. (1934). *The mammals of Southwest Africa*. London: Heinemann.

Skinner, J.D. & Smithers, R.H.N. (1990). *The mammals of the southern African subregion*. 2nd edn. Pretoria: University of Pretoria.

Springer, M.S., Stanhope, M.J., Madsen, O. & DeJong, W.W. (2004). Molecules consolidate the placental mammal tree. *Trends Ecol. Evol*. **19**, 430–438.

Tripp, H.R.H. (1972). Capture, laboratory care and breeding of elephant-shrews (Macroscelididae). *Lab. Anim*. **6**, 213–224.

Unger, R. (1999). *Verhalten, Aktivitat und Ernahrung von Kurzohr-Russelspringern, Macroscelides proboscideus, Smith 1829 (Macroscelididae) im Tiergarten Schonbrunn*. Thesis, Universitat Wien.

Wittenberger, J.F. & Tilson, R.L. (1980). The evolution of monogamy: hypotheses and evidence. *Ann. Rev. Ecol. Syst*. **11**, 197–232.

Woodall, P.F. & Skinner, J.D. (1989). Seasonality of reproduction in male rock elephant shrews, *Elephantulus myurus*. *J. Zool. (Lond.)* **217**, 203–212.