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Abstract

Animal dispersion in space and time results from environmental pressures, and affects the outcome of a species' social organization. When females are solitary, males may either roam or be pair-living. We studied possible environmental influences affecting the social organization of the round-eared sengi (*Macroscelides proboscideus*) in a semi-desert in South Africa, using trapping and radio-tracking across 2.5 yr. Adult sex ratios did not deviate from 1:1 and we found no indication of sexual dimorphism in body mass. Females maintained exclusive areas, which had little overlap (<4%) with neighbouring females (NF), and males overlapped predominately only with the home range of single females. Generally, inter- and intra-sexual overlap with neighbouring individuals was low (3–6%) for both sexes, indicating territoriality and pair-living. Pairs were perennial and territories were maintained year-round. However, males generally maintained much larger areas than females, which were sensitive to population density. Male space use appeared to be primarily limited by the presence of neighbouring males. Female home ranges were smaller-sized despite changes in population density, possibly for energetic efficiency. Some paired males attempted to take over widowed females, but shifted back to their original home range following the intrusion of an un-paired male. We conclude that social monogamy is the predominant social organization in round-eared sengis in a semi-desert that may have resulted from females living solitarily in small exclusive territories, balanced sex ratios, and from a low variation of body mass between males.

Introduction

Animal dispersion in space and time results from environmental pressures and affects the outcome of a species' social organization (Brown & Orians 1970). In species lacking paternal care, dispersed living females present an important prerequisite for the evolution of social monogamy, i.e. pair-living, because for males, the chances to encounter other potential mating partners are reduced (Komers & Brotherton 1997; Brotherton & Komers 2003). However, social systems are rarely attributable to a single factor (Sandell & Liberg 1992), and female dispersion *per se* is insufficient to account for the evolution of monogamy, since males could opt for other tactics, such as roaming (Kraus et al. 2003; Eberle & Kappeler 2004; Martin & Martin 2007). Thus, other factors may constrain males into socially monogamous relationships. Low population densities have been emphasized in some species, like prairie voles

(*Microtus ochrogaster*, Getz et al. 2003) or Mentawai snub-nosed langurs (*Simias concolor*, Watanabe 1981), and balanced adult sex ratios have been acknowledged to drive the occurrence of social monogamy in other mammalian species, such as Townsend's voles (*M. townsendii*, Lambin & Krebs 1991) and oribis (*Ourebia ourebi*, Adamczak & Dunbar 2007).

Social monogamy is rare in mammals (Kleiman 1977), but is believed to occur in all species of a unique order, the sengis (Macroscelidea, Ribble & Perrin 2005; Rathbun & Rathbun 2006). Sengis (or elephant-shrews) represent an ancient monophyletic clade with an early radiation from the Eutheria (Corbet & Hanks 1968), and comprise 17 species from four genera that are all endemic to the African continent. The assumption that all sengi species are monogamous is based on field studies of six sengis species (Rathbun 1979; FitzGibbon 1995, 1997; Leirs et al. 1995; Neal 1995; Ribble & Perrin 2005; Rathbun & Rathbun 2006). The social organization of sengis in these studies has been determined by investigating space use predominately, but to date, detailed studies regarding environmental parameters related to the social organization are absent.

In the present study, we investigated potential ecological and physical parameters affecting the social system in the round-eared sengi (*Macroscelides proboscideus*), a small-bodied (35 g) omnivorous mammal (Sauer 1973; Kerley 1995), which is found in the more arid regions of South Africa, Namibia and Botswana (Skinner & Smithers 1990). In contrast to other sengi species, individual round-eared sengis occupy undefended home ranges, reaching over 100 ha and resulting in a solitary life style with non-territorial females and roaming males (Sauer & Sauer 1971, 1972; Sauer 1973). In Sauer's studies, the habitat was characterized by low food abundance and few shelter sites for individuals, and associated with an extremely low population density of one individual per 100 ha and an irregular dispersion of round-eared sengis, resulting in small isolated populations.

Generally, population density of round-eared sengis is positively correlated with cover (Joubert & Ryan 1999) and food availability (van Deventer & Nel 2006). Since Sauer's study was conducted in a desert and the present study in a semi-desert, demographical differences between the two study sites, which reflect the differential availability of key resources, may promote different social organizations (Lott 1984; Schradin & Pillay 2005a). Thus the aim of the current study was to determine the social

organization of the round-eared sengi in a semi-desert, by testing for ecological and physical correlates of social organization. The following predictions were made:

Firstly, we investigated space use of female round-eared sengis. Environmental factors that influence female space use ultimately influence the social organization of a population, because male space use is affected by female distribution in space and time (Emlen & Oring 1977). We predicted that females live independently of each other, thereby decreasing male monopolization potential for several females. If males employ a roaming strategy, we suggest that they will maintain much larger home ranges than females in order to search widely for fertile females in breeding season (Michener & McLean 1996), and that male home ranges will be characterized by large overlap with male competitors (Sandell 1989; Gliwicz 1997). Alternatively, males may monopolize single females resulting in pair-living. In this situation, male space is predicted to be similar to that of females, i.e. pairs use similar-sized areas that have little intra- and inter-sexual overlap with neighbouring individuals of both sexes (Komers & Brotherton 1997).

Secondly, given that males may roam, we expected that round-eared sengis lack sexual dimorphism, because male body mass is not necessarily related to the roaming ability for female mates (Schwagmeyer & Woonter 1986). Alternatively, the lack of sexual dimorphism may also be a characteristic of pair-living (Kleiman 1977).

Thirdly, we studied the male searching efficiency for female mates by documenting adult sex ratios in round-eared sengis. Since sex ratios co-evolve with social systems, we assume that sex ratios will be more female biased promoting a male roaming tactic, because of a high searching efficiency for female mates (Sandell & Liberg 1992; but see Eberle & Kappeler 2004). In contrast, low searching efficiency caused by balanced adult sex ratios may favour the monopolization of single females (Sandell & Liberg 1992).

Fourthly, we determined the length of breeding season and synchronization of female receptivity. Generally, if females reproduce asynchronously it is more likely that males will adopt a roaming strategy, since this provides the opportunity to obtain matings with multiple females (Ims 1987; Ostfeld 1990). Asynchronous breeding may also intensify male–male competition because it increases the costs of territorial defence and decreases the monopolizability of potential mates (Emlen & Oring 1977).

Methods

Study Area

This study was conducted in the Goegap Nature Reserve (29°37′S; 17°59′E), South Africa from Aug. 2005 to Oct. 2007. This nature reserve is approx. 15 000 ha and is situated approx. 15 km south-east of the town of Springbok in the Northern Cape Province. In this semi-desert area, the vegetation consists mainly of *Zygophyllum retrofractum* and *Lycium cinerum* shrubs, and is classified as succulent karoo (Cowling et al. 1999; Mucina & Rutherford 2006). The average annual rainfall is 160 mm/yr (Rösch 2001) and occurs mostly during winter (Jun./Jul.). Maximum plant growth occurs in spring, consisting of annuals and perennials. Spring is followed by a long dry summer with decreasing plant abundance (Schradin & Pillay 2005b). The study site was characterized by dry riverbeds and sandy areas with soft sand parts, as well as parts with coarse sand surface with patchily distributed shrubs interspersed. The size of the study area varied during the study from 11.93 to 36.70 ha, because of a decline in population density of sengis (see Results).

Study Animal

The round-eared sengi is crepuscular to nocturnal, with activity peaks at dusk, dawn and through the night. Activity is affected by ambient temperatures and food availability, with a decrease in activity during cold nights (Sauer & Sauer 1971). Furthermore, under unfavourable environmental conditions associated with cold temperatures and low food abundance, it employs torpor to overcome long-term energetic shortfalls (Lovegrove et al. 1999).

Reproduction occurs throughout the year, but there is a decline in pregnancies during early winter in Mar.–May (Bernard et al. 1996). Females have a post-partum oestrus, which is reported to be 1 d (Sauer & Sauer 1971). The precocial pups, normally twins, are born after a gestation period of 61 d (Olbricht et al. 2006). Maternal care is characterized by an absentee system, i.e. maternal care is restricted to short nursing bouts every 24 h (Sauer 1973). Additionally, dependent pups are fed solid food via mouth-to-mouth feeding by the mother (Sauer 1973). To date, there is no evidence that male round-eared sengis engage in direct parental care (Sauer & Sauer 1971; Sauer 1973). Young sengis are weaned at approx. 4 wk of age, and both sexes leave the natal territory thereafter (Sauer 1973). Females become sexually mature at 4–9 mo, whereas males reach maturity at 3 mo (Olbricht et al. 2006).

Trapping

Systematic capture–recapture was carried out continuously from Sep. 2005 to Apr. 2006, Jul. 2006–Apr. 2007 and Jul. 2007–Oct. 2007, four to seven times a week. Round-eared sengis were trapped using locally produced metal traps (26 × 9 × 9 cm, similar to Sherman traps), which were baited with a mixture of peanut butter, oats, marmite and sunflower oil. Trapping was performed between 18:00–22:00 and 04:00–07:00. Traps were checked every 1.5–2 h. In winter, traps were provided with cotton wool to avoid trap deaths. Individuals were weighed by placing them in a plastic box, which was situated on top of a kitchen scale (capacity 500 g, accuracy 0.1 g). Sexes could be easily distinguished because males have an abdominal penis. However, we could not assess breeding status of young sengis, because males have intra-abdominal testes (Woodall 1995) and females have no true vagina (van der Horst 1946). Late-stage pregnant females could be confidently identified because of a body mass increase during pregnancy of approx. 20 g. The average female body mass was 48.0 g (± 4.1 SD) 1 d after birth, 64.3 g (± 5.5 SD) 1 wk before birth, 59.0 g (± 5.1 SD) 2 wk before birth and 52.8 g (± 3.4 SD) 3 wk before parturition (n = 11). All individuals were marked using hair dye (Inecto Rapid, South Africa) and ear tags (National Band and Tag Co., USA). The total number of round-eared sengis trapped during the 2.5 yr project comprised of 65 males and 62 females (young and adults combined). During radio-tracking periods (see below), all adult individuals trapped at the study site were equipped with a radio-collar.

Radio-Tracking

A total of 47 different adult individuals (24 females and 23 males) were used for radio-tracking studies. A total of six males and eight females were radio-tracked in September/October (= breeding season (BS), see results) 2005, 11 males and 10 females in March/April (= non-breeding season (NBS), see results) 2006, seven males and six females in the 2006 breeding season, and five males and five females in the 2007 breeding season. Eleven (five females and six males) individuals were radio-tracked twice: one time in the

non-breeding season and one time in the subsequent or the previous breeding season. Of these animals, nine individuals were radio-tracked in the same location and two in a neighbouring area (see Results). In the 2007 non-breeding season, no individuals were radio-tracked due to low population density resulting from high mortality rates, which may have been caused by increased predation rates as a result of the radio-collars and radio-tracking (Webster & Brooks 1980).

Sengis were equipped with a MD-2C radio-collar (Holohil Systems Ltd, Carp, Ontario, Canada) for a continuous period of approx. 2 mo. Before attaching the radio-collar around the neck, individuals were briefly anaesthetized with ether. The duration of the whole procedure from capturing, anaesthetizing the individuals, attaching the collar, and finally releasing them at the point of capture was 2–3 h. Radio-collars weighed 2.5 g, which was less than 10% of the adult body mass. Radio-tracking was performed using a Telonics TR-4 receiver (Telonics Inc., Mesa, AZ, USA) and an H-antenna.

Data were collected using the homing-in method: sengis were approached until they were seen or known to be hidden in a particular hiding spot, like shrubs or burrows. Locations were recorded with a GPS receiver (eTrex venture, Garmin International Inc., Olathe, KS, USA), which had an accuracy of ±5 m. To determine space use, individual locations were determined every 2 h five times a day. Two hours was chosen to avoid inter-fix autocorrelations and provide enough time for the individual to travel within the area. Radio-tracking was performed from 16:00 to 0:00 for 5 d in the 2005, 2006 and 2007 breeding seasons and in the 2006 non-breeding season. A $\bar{x}$ of 24.6 (±1.5 SD) fixes were obtained for each individual. After termination of home range data collection, individuals were radio-tracked once every day to check their location and status for another 6 wk.

Data Analyses

Population density was estimated using the capture-recapture method as 'minimum number known to be alive' (MNA, Krebs 1966). Young sengis were excluded from density calculations because both sexes disperse before sexual maturity. The adult sex ratio was determined from the MNA and calculated as the proportion of adult males and females in the population. A binominal test was used to determine whether the number of males vs. the number of females deviated from a 1:1 ratio.

A reproductive synchrony index (SI) was determined after Kempenaers (1993):

$$SI = \frac{1}{F} \sum_{p=1}^{F} f_{i,p} \left[\frac{\sum_{i=t}^{t_p} f_{i,p}}{t_p(F-1)} \right] \cdot 100$$

where F = the total number of breeding females in the population; $f_{i,p}$ = the number of fertile female individuals in the population on day i, excluding female p; t_p = the number fertility days for female p.

Data collection on male mate guarding during female post-partum oestrus (M. Schubert, unpublished data) revealed that females are probably fertile for approx. 24 h, which is in accordance with the results of Sauer & Sauer (1971). The reproductive synchrony index was determined for 2006 and 2007. At the start of this study in 2005, we were not able to identify all the females which prevented us from calculating a reproductive index for 2005.

To determine sexual dimorphism, only body mass data from individuals in the non-breeding season were included in the analysis. This was done to avoid bias of the increase in body mass during pregnancy.

Space use was estimated using the minimum convex polygon (MCP) analysis. This method describes the area boundary containing all positional fixes of an individual (Mohr 1947). For the determination of kernel home ranges, we used 95% MCP to exclude fixes outside of the activity centre. The software RANGES 6 (Kenward et al. 2002) was used to analyse spatial areas. For the home range analyses, data were available for 45 individuals; two round-eared sengis (one male, one female) were predated upon shortly after starting with the collection of home range data. To determine the amount of overlap between neighbouring home ranges, we included all fixes (100%) in the analyses. Data were available for 41 individuals; in two cases data for neighbouring individuals could not be collected, and two round-eared sengis had only a widowed male neighbour, whose female had disappeared 2 d after starting to collect radio-tracking data.

Statistical Analyses

All statistical analyses were done with R version 2.8.1 (R Development Core Team 2008). Mixed-effects models were fitted with the package lme4

with the Laplace approximation of the likelihood function (Bates 2005). p-Values were calculated by likelihood-ratio tests based on changes in deviance (using maximum likelihood estimates) when each term was dropped from the full (main effects) model. Interactions were tested by considering the changes when these were added to the model (Faraway 2006).

In all tests, possible interactions between the main effects were tested, but interactions are only reported when significant results were obtained. Residuals were tested for normality visually by checking normal probability plots and with the Shapiro–Wilk test. Data are reported as $\bar{x} \pm$ SD, except for home range overlap data, which are presented as median (first and third interquartile ranges).

We included year as a three-level fixed factor and also tested for all two-way interactions with the other predictor variables. There were no significant effects of year or interactions with year (p > 0.10); therefore year was removed from the models and p-values of the other predictor variables were recalculated.

Home range size

Home range size was determined for the breeding and the non-breeding seasons. Home range data were log transformed before testing. We calculated a linear mixed-effects model (LMM) with home range size as the response variable and included sex (male or female) as two-level factors, and body mass as a covariate. Population density was also added as a covariate for home range sizes in the breeding season. Pair identity was entered as a random factor in the model for the non-breeding and the breeding season. Individual identity was entered in the model when comparing home range sizes between the 2006 breeding and the 2006 non-breeding seasons.

Number of neighbouring individuals

The number of neighbours was determined in the breeding and the non-breeding seasons. The relationship between the number of neighbouring males (NM) (response variable) and sex was analysed using a LMM. By adding the covariates of population density (only for breeding season), home range size and the random factor of pair identity into the model, different possible effects were determined with regard to the number of neighbouring males. Individual identity was included in the model when

comparing the number of neighbouring males between the 2006 breeding and the 2006 non-breeding seasons. The same procedure was used for the number of neighbouring females (NF).

Home range overlap

To determine home range overlap with neighbouring individuals, one mean for adjacent males and neighbouring females was calculated for each individual. Home range overlap data were transformed with $[x^{0.4}]$. Firstly, the overlap of an individual with its 'pair mate' was compared with the amount of overlap with neighbouring animals of both sexes in the breeding and non-breeding seasons, using repeated measurements ANOVA. Secondly, to determine the effects of different variables on the amount of overlap in breeding season with the mate, neighbouring females and neighbouring males (response variables), an LMM was used, which included sex (two-level factor), home range size and population density (covariates), and pair identity (random factor). A similar model was used for testing for effects on overlap with individuals in the non-breeding season, but population density (covariate) was excluded from the analysis.

Results

Population Demography

Population density varied during the study period, with a peak at the beginning of data collection in 2005 (Table 1). During the course of the study, population density declined from 1.59 individuals/ha to 0.35 individuals/ha.

Pregnant females and young individuals (below 26 g) were only observed from July to January indicating that reproduction was seasonal. Young were trapped between August and January; pregnant females were caught from July to December.

Table 1: Size of the study area, and the proportion of males and females in round-eared sengis during three breeding seasons (BS) and one non-breeding season (NBS)

Season and year	Study site (ha)	Sengis (ha)	Males (%)	Females (%)	p
BS 2005	11.93	1.59	45	55	0.597
BS 2006	26.80	0.63	51	49	0.999
BS 2007	36.70	0.35	41	59	0.523
NBS 2006	31.29	0.89	53	47	0.567

Statistics: Sex ratio between males and females: Binominal test.

Females had an inter-litter interval of 61 d (n = 2). Reproduction was not highly synchronized, with a reproductive synchrony index of 0.0% in 2006 and 2007, indicating no overlap in the fertile periods of females. The inter-birth interval between neighbouring females was 11.0 d ($\pm$ 3.0 SD) in 2006 and 11.9 d ($\pm$ 4.3 SD) in 2007.

Adult Sex Ratio

The adult population sex ratio did not deviate from the expected 1:1 ratio during the entire study period (Table 1). On average, the population consisted of 47.5% ($\pm$ 5.5 SD) adult males and of 52.3% ($\pm$5.9 SD) adult females.

Sexual Dimorphism in Body Mass

The mean body mass during the non-breeding season was 42.6 g ($\pm$ 4.1 SD) for males and 43.3 g ($\pm$ 3.3 SD) for females. There was no evidence of sexual dimorphism of body mass in male and female sengis (t-test for independent samples: n_{males} = 33, $n_{females}$ = 28, df = 59, t = -0.770, p = 0.440).

Do Individuals Live in Pairs?

Throughout the entire study, females maintained exclusive areas with only little overlap between neighbouring females. Individuals overlapped significantly more with one sengi of the opposite sex in comparison to intra- and inter-sexual overlap with other neighbouring individuals in the breeding (BS) and non-breeding seasons (NBS) (BS – repeated measurements ANOVA: n = 32, F = 179.65, df = 2, p < 0.001, Fig. 1a, NBS – repeated measurements ANOVA: n = 20, F = 7.46, df = 2, p = 0.006, Fig. 1b). Individuals that shared a common home range, i.e. their home ranges largely overlapped, are defined as mates hereafter. Paired males and females were spatially faithful, because when individuals were radio-tracked again after 4–5 mo, they maintained home ranges that overlapped 62.5–87.0% (min, max) with their 'old' home range (n = 9).

All pairs were stable, with a duration that could exceed two breeding seasons. Pairs only terminated when one of the pair mates disappeared or died. Death and disappearance most likely resulted from predation. During the entire study period, no pairs or single members of the pair were evicted by intruding conspecifics and no paired individual dispersed and left its mate.
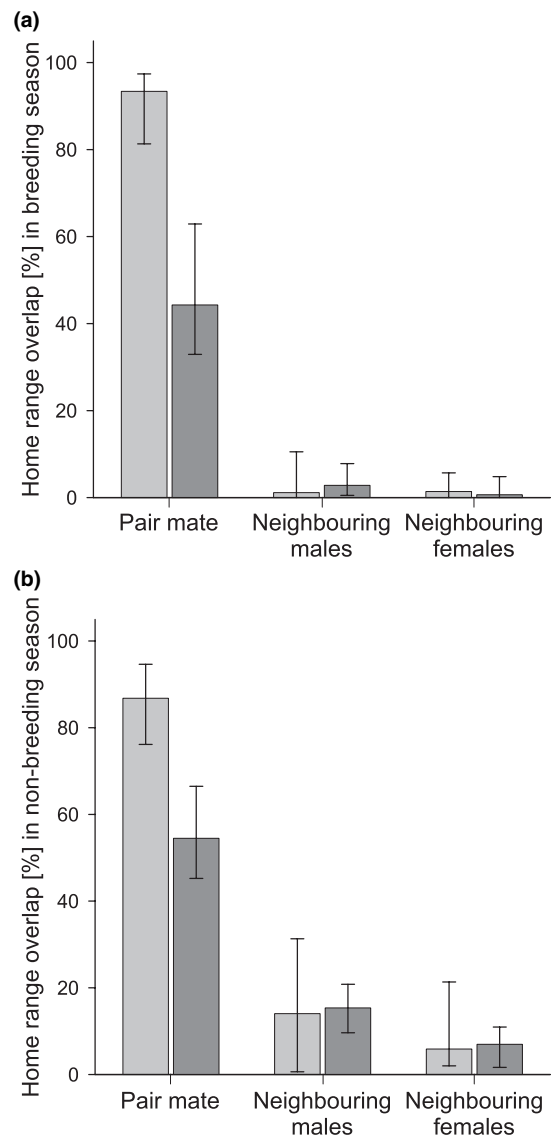

Fig. 1: Overlap of home ranges of male and female round-eared sengis with the pair mate, neighbouring males and neighbouring females in the (a) breeding and (b) non-breeding seasons. Overlap data are reported as median (first and third interquartile ranges), and are presented in light grey for females and in dark grey for males.

Widowed females

Ten females lost their mate, probably due to predation, and became widows. In one case, a neighbouring male–female pair intruded into the widowed female's home range, resulting in a polygynous situation, which lasted for 5–6 wk until one of the females died. The second widow shifted her home range into a neighbouring area to partner with a single male and became socially monogamous again. The other eight widows formed pairs in their original

home range with previously unpaired males. Five of these males originated from neighbouring home ranges, which they abandoned. In the remaining three cases, the new males immigrated from outside the study area. The duration until a new male entered the area of the widowed female was 2.0 d ($\pm$ 0.7 SD).

In three cases, already paired neighbouring males expanded their home ranges to encompass a widowed female's home range along with that of their original female mate. At the same time, a new unpaired male intruded into the widow's area. However all paired males returned to their original home range configuration and female mate after 2–3 d.

The average body mass was 45.1 g ($\pm$ 2.4 SD) for former residents, i.e. males that disappeared, 42.9 g ($\pm$ 4.8 SD) for new resident males and 48.2 g ($\pm$ 5.1 SD) for the heaviest neighbouring male. There was a significant difference regarding the body mass for the three different male categories (LMM: n = 8, df = 2, χ^2 = 7.91, p = 0.019): new residents were lighter than the heaviest male neighbour, although not statistically significant after Bonferroni adjustment (t = −2.41, df = 7, p = 0.047). There was no difference regarding the body mass between former and new residents (t = 1.39, df = 7, p = 0.209) and former residents compared to the heaviest neighbouring male (t = −1.36, df = 7, p = 0.216). In the three observed cases, in which already paired neighbouring males intruded into the area at the same time as the new un-paired males, all neighbours were assigned to be the heaviest neighbouring male of the widowed female.

Male widowers

Six males lost their mate, probably due to predation, and became widowers. Four of these males left their home ranges to take over a single female in a neighbouring area and thus became pair-living again. Widowed males did not immediately leave their home ranges; instead they waited 8.5 wk ($\pm$ 5.2 SD) and then abandoned their original home ranges to take-over a widowed neighbouring female. Of the remaining two widowers, one remained solitary in his home range for approx. 4 mo, after which he wandered around and then took over a new female approx. 0.5 km away from his original home range. The sixth widower did not leave his home range, but a female emigrated from outside the study area into his home range and he became socially monogamous again.

Table 2: Linear mixed models testing for the effects of sex, population density and individual body mass of the home range owner in the breeding season (n = 32) and non-breeding season (n = 20)

Parameter	Breeding season			Non-breeding season		
	χ^2	df	p	χ^2	df	p
Sex (S)	11.90	1	**<0.001**	19.70	1	**<0.001**
Density (D)	7.81	1	0.005			
Body mass (BM)	1.24	1	0.264	0.27	1	0.606
S × D	7.65	1	**0.006**			

The random factor in both models was pair identity; the covariate, density, was not included in the analysis for home ranges in non-breeding season. Significant effects are given in bold.

Space Use of Male and Female Round-Eared Sengis

Home range

During breeding season, the average home range size was 1.7 ha ($\pm$ 1.1 SD) for males and 0.8 ha ($\pm$ 0.3 SD) for female round-eared sengis, and home range sizes differed significantly between the sexes (Table 2). However, there was also a significant interaction between sex and population density with regard to home range sizes in the breeding season (Table 2). When considering the two sexes separately, male home range size was significantly affected by population density (post-hoc: LM:F = 12.40, df = 1, p = 0.004; Fig. 2). With increasing population density, the differences between home range sizes of male and female round-eared sengis declined. In contrast, no
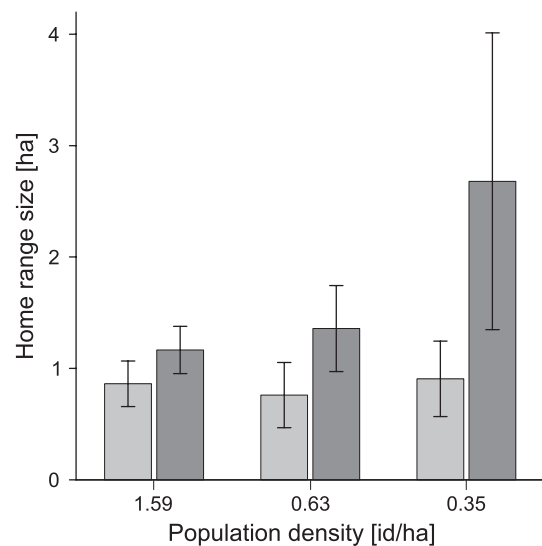

Fig. 2: Effect of population density on home range size of male and female round-eared sengis in the breeding season. x̄ $\pm$ SD are reported for females in light grey and for males in dark grey.

relationship between home range size and population density was found for females (post-hoc: LM:F = 0.72, df = 1, p = 0.412; Fig. 2). During the breeding season, individual body mass did not significantly influence sengi home range sizes (Table 2).

Home range size did not differ between the 2006 breeding season and the 2006 non-breeding season (LMM: n = 30, χ^2 = 0.38, df = 1, p = 0.542). During the 2006 breeding season, the average home range size was 1.4 ha ($\pm$0.4 SD) for males and 0.8 ha ($\pm$ 0.3 SD) for females. Home range size was 1.0 ha ($\pm$ 0.3 SD) for males and 0.7 ha ($\pm$0.2 SD) for females in the non-breeding season. Male round-eared sengis maintained significantly larger home ranges in the non-breeding season compared to the home ranges used by their female mates (Table 2). Body mass did not affect home range sizes in the non-breeding season (Table 2).

Neighbouring Individuals

During the breeding season, male home ranges bordered with significantly more neighbouring males and females than home ranges of their female mate (Table 3). There were 1.5 ($\pm$ 0.7 SD) neighbouring males per male vs. only 0.8 ($\pm$ 0.6 SD) neighbouring males per female, and 0.9 ($\pm$ 0.7 SD) neighbouring females per male vs. 0.7 ($\pm$ 0.6 SD) neighbouring females per female. Population density and home range size did not significantly affect the number of adjacent males and females for round-eared sengis (Table 3). The number of neighbouring males did not differ between the 2006 breeding season and the 2006 non-breeding season (LMM: n = 30, χ^2 = 0.09, df = 1, p = 0.775). The same was found for the number of neighbouring females (LMM: n = 28, χ^2 = 0.22, df = 1, p = 0.639). In the non-breeding season, the number of neighbouring

males (NM) and females (NF) was not affected by sex (NM—LMM: n = 20, χ^2 = 0.73, df = 1, p = 0.392, NF—LMM: n = 18, χ^2 = 0.01, df = 1, p = 0.925) and home range size (NM–LMM: n = 20, χ^2 = 0.19, df = 1, p = 0.666, NF–LMM: n = 18, χ^2 = 0.33, df = 1, p = 0.567). On average, 1.4 ($\pm$1.0 SD) neighbouring males and 1.1 ($\pm$ 0.9 SD) neighbouring females bordered with male home ranges in the non-breeding season. Female home ranges bordered with 1.2 ($\pm$ 1.2 SD) neighbouring males and 1.0 ($\pm$ .7) neighbouring females.

Overlap with Partner

Sex influenced the overlap with the mate in the breeding season, and there was also an interaction between sex and density (Table 4). When considering the two sexes separately, male overlap was significantly positively affected by population density (post-hoc – LM:F = 9.84, df = 1, p = 0.008; Fig. 3). In contrast, female overlap with her mate was negatively influenced by population density (post-hoc – LM:F = 7.30, df = 1, p = 0.018; Fig. 3). Home range size affected the overlap with the partner for both sexes (Table 4).

The overlap with the mate did not differ in the 2006 breeding season compared to the 2006 non-breeding season (LMM: n = 30, χ^2 = 0.04, df = 1, p = 0.844). In the 2006 non-breeding season, overlap with the pair mate was affected by sex (LMM: n = 20, χ^2 = 11.29, df = 1, p < 0.001; Fig. 1b) and slightly by home range size (LMM: n = 20, χ^2 = 3.72, df = 1, p = 0.053).

Overlap with Neighbouring Individuals

In the breeding season, male and female sengis showed overlap with neighbouring individuals of

Table 3: Linear mixed models testing for effects of sex and breeding season, and the covariates density and home range size on the number of adjacent males and females in round-eared sengis in the breeding season (n = 32)

Parameter	Number of neighbouring males			Number of neighbouring females		
	χ^2	df	p	χ^2	df	p
Sex	6.69	1	**0.010**	3.65	1	**0.056**
Density	1.80	1	0.180	2.11	1	0.146
Home range size	0.09	1	0.760	2.51	1	0.114

Pair identity was included as a random factor. Significant effects and p-values just outside significance are presented in bold.

Table 4: Linear mixed models testing for the effects of sex and the covariates population density and individual home range size concerning the amount of intra- and inter-sexual overlap with adjacent individuals in round-eared sengis (n = 32)

Parameter	Mate			Neighbouring males			Neighbouring females		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Sex (S)	27.58	1	**<0.001**	0.36	1	0.551	0.03	1	0.855
Density	0.25	1	0.616	<0.01	1	0.953	<0.01	1	0.988
Home range size	9.82	1	**0.002**	0.43	1	0.513	0.04	1	0.842
S × D	11.09	1	**0.001**						

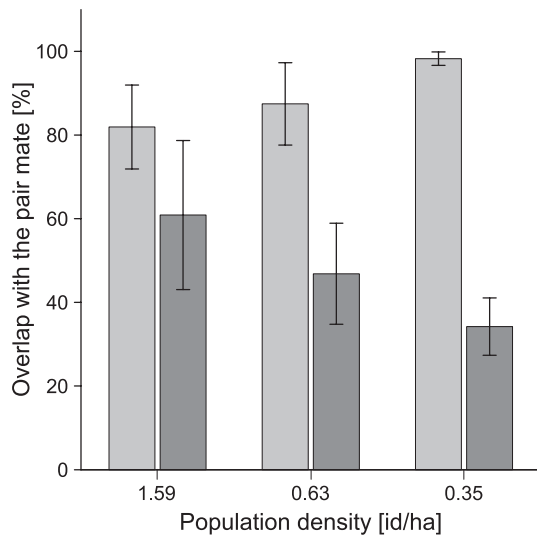Pair identity was included as random factor. Significant effects are given in bold.

Fig. 3: Effect of population density on home range overlap with the pair mate of male and female round-eared sengis in the breeding season. x̄ ± SD are reported for females in light grey and for males in dark grey.

both sexes (Fig. 1a). The degree of overlap with neighbouring males and females was not significantly affected by sex and population density (Table 4).

There was no significant difference regarding the degree of home range overlap with neighbouring individuals of both sexes in the 2006 breeding season compared to the 2006 non-breeding season (NF–LMM: n = 26, χ^2 = 0.08, df = 1, p = 0.784, NM–LMM: n = 28, χ^2 = 2.64, df = 1, p = 0.102), but there was an interaction between overlap with neighbouring males and the sex of the home range owner, just outside a statistical significance (LMM: n = 28, χ^2 = 3.25, df = 1, p = 0.070). For males, the degree of overlap with neighbouring males was higher in the non-breeding than in the breeding season (post-hoc – LM:F = 4.88, df = 1, p = 0.049, 15.4% (11.2, 18.6, first and third interquartile ranges) vs. 1.2% (0.4, 3.3)). This was not found for female sengis (post-hoc – LM:F = 1.69, df = 1, p = 0.221, 14.0% (1.7, 24.4) vs. 5.1% (6.5, 7.7)). In the non-breeding season, the overlap with male neighbours was affected by the sex of the home range owner (LMM: n = 20, χ^2 = 5.02, df = 1, p = 0.025) and by home range size (LMM: n = 20, χ^2 = 4.47, df = 1, p = 0.035). The degree of overlap with female neighbours in the non-breeding season was not significantly affected by sex (LMM: n = 18, χ^2 = 0.02, df = 1, p = 0.894) and home range size (LMM: n = 18, χ^2 = 0.57, df = 1, p = 0.450).

Discussion

We investigated potential ecological and physical parameters affecting the social organization of the round-eared sengis in a semi-desert. Our study population was characterized by a lack of sexual dimorphism in body mass, a population density ranging from 0.35 to 1.59 individuals/ha, and balanced adult sex ratios. Females maintained exclusive home ranges and reproduced asynchronously during a long breeding season. Round-eared sengis lived in perennial pairs and were territorial, as suggested by little overlap with neighbouring individuals of both sexes, which is generally seen as good indicator for territorial behaviour (Powell 2000).

Our results in a semi-desert population contradict the findings of Sauer in the Namib Desert, where round-eared sengis were considered to live solitarily in undefended home ranges (Sauer & Sauer 1971, 1972; Sauer 1973). Female reproductive success is generally limited by access to resources, and resource distribution is considered to be the key factor in female spacing behaviour (Emlen & Oring 1977). Round-eared sengis in our study used a different life history strategy than the sengis from Sauer's studies, even though both populations were characterized by balanced adult sex ratios. In the Namib, the study site was flat and open with scantily distributed shrubs. Food availability was generally low, especially in dry season when round-eared sengis left their home range in order to find a more favourable habitat or changed the size of their home ranges to converge around areas with more favourable food supply; some individuals even died of starvation. Home ranges were maintained by mutual avoidance. Thus the low and uneven distribution of key resources in space and time may have reduced the economic value of establishing a territory in the Namib Desert. Since females maintained very large undefended and overlapping areas that centred on resource 'hot spots' with other individuals, males might have had the opportunity to encounter several females, favouring a roaming tactic for male round-eared sengis in the Namib Desert.

In contrast, our study site in the succulent karoo semi-desert was characterized by relatively denser vegetation, which was distributed along dry riverbeds and rocky outcrops. Population density was much higher than in the Namib Desert (1.59–0.35 individuals per ha vs. one individual per 100 ha), and females maintained exclusive areas that were characterized by little overlap with neighbouring females, thereby probably minimizing feeding

competition with other females (Wrangham 1980). Furthermore, females maintained smaller-sized territories throughout the entire study period, i.e. in the breeding and non-breeding seasons, despite changes in population density. Thus territories of female round-eared sengis may have been minimized for energetic efficiency, because home ranges may allow them to forage sufficiently on the one hand and to reduce predation risk and energy expended on the other hand (Sandell 1989). Although the availability of resources may have been reduced in the dry season (Schradin & Pillay 2005b) leading to a cessation in reproductive activity in round-eared sengis, the abundance of resources may have been still high enough to allow individuals to maintain their territories. Thus a more even distribution of resources in space and time may have favoured year-round territoriality in round-eared sengis from a semi-desert, creating the opportunity for males to become territorial and pair-living.

Female round-eared sengis reproduced asynchronously during a long breeding season, so that males could have adopted a roaming strategy, since it would have provided the opportunity to obtain matings with multiple females (Ims 1987; Ostfeld 1990). However, social systems are rarely attributable to a single factor, and pair-living with one female may still offer higher reproductive benefits than searching widely for female mates (Sandell & Liberg 1992). Roaming may entail high costs such as an increase in predation due to the high mobility of males (Magnhagen 1991). Roaming males may also require adequate information about a female's reproductive state and the area she lives in, and must also encounter other competitors, which can cause injuries and may demand a greater time and energy investment (Schwagmeyer 1988; Michener & McLean 1996), which may increase male mortality rates (Kraus et al. 2008). Unfortunately, there are no data regarding survival probabilities of roaming male round-eared sengis in the Namib Desert. In our study, the oldest male was reported to be over 2.5 yr (Schubert, unpubl. data), which may indicate that pair-living in the semi-desert may serve as risk-adverse strategy (Brotherton & Komers 2003). However, future research investigating benefits and trade-offs of different male strategies in the desert and semi-desert is needed for direct comparison.

Although round-eared sengis were pair-living in the semi-desert, our results also indicate that males had polygynous tendencies, because they maintained much larger areas than females. These larger home ranges may permit males to monitor the reproductive status of neighbouring females and the presence of neighbouring males, as suggested for other sengi species (Rathbun 1979; FitzGibbon 1995, 1997; Ribble & Perrin 2005). In the golden-rumped sengi (*Rhynchocyon chrysopygus*), heavier males maintain larger home ranges (FitzGibbon 1997), which may enhance male reproductive success by searching for extra-pair matings with neighbouring females, as observed in pair-living red foxes, *Vulpes vulpes* (Iossa et al. 2008). In our study, we did not find a correlation between male body mass and territory size. Instead male territory sizes were sensitive to population density and the presence of neighbouring males, and the largest male areas were observed when population density was lowest. At higher densities, males may adjust their ranges by either permitting increased overlap (Ims 1987; Gliwicz 1997) or by confining their movements to smaller areas (Wolff & Cicirello 1990; Lambin & Krebs 1991). Round-eared sengi males used smaller areas at higher densities, but the number of neighbouring males was fairly constant during the whole study period despite changes in population density. Thus, male space use seems to be limited by the presence of adjacent males, and male–male competition may play an important role in shaping the social organization of the round-eared sengi. Consequently, by adjusting range sizes in response to density, male round-eared sengis may reduce the level of male–male competition. Furthermore, overlap between neighbouring males was reduced in the breeding compared to the non-breeding season (1.2% vs. 15.4%). Neighbouring males often present the greatest risk to paternity (Currie & Valkama 2000; Komdeur 2001). Since female round-eared sengis reproduced asynchronously during a long breeding season, males may seek copulations with neighbouring females, thereby enhancing their reproductive success. Thus territorial defence by males may function as a form of mate guarding, preventing competitors from gaining access to females (Emlen & Oring 1977). In addition, higher investment in territorial maintenance during the breeding season may also present a form of indirect paternal investment, because males defend resources for dependent young (Rutberg 1983).

Pair-living males intruded into the areas of widowed females. Whereas only one male was able to achieve polygyny, because his female mate also intruded into the widow's area, the majority of paired males shifted back to their original area and female mate, following the intrusion of another unpaired male into the widow's area at the same

time. Paired males that intruded into the widow's area were the heaviest male neighbour. Although new unpaired males were lighter than the heaviest neighbouring male, the difference between male body mass was generally low (10%) compared to species where one male is able to defend more than one solitary ranging female (e.g. wild cavies, *Cavia aperea* Asher et al. 2008). The reason that a single male cannot defend more than one female territory permanently might be due to a small variation in the resource-holding potential (RHP) between males. The RHP describes the fighting ability of an individual, enabling it to monopolize important resources such as females and is closely correlated with body mass (Schradin 2004; Asher et al. 2008; but see Rödel & von Holst 2009). Generally, when asymmetries in the RHP of contestants are small, fights should be long and intense, which may cause high energetic costs, a decrease in time available for foraging, a high risk of injuries or even death (Neat et al. 1998). Thus a low variance in body mass between round-eared sengi males may reduce the benefits of defending more than one female territory permanently, because temporarily polygynous males suffer substantial costs, such as increased activity and a decrease in body mass as observed in the golden-rumped sengi (FitzGibbon 1997).

Although male sengis may not be able to spatially monopolize two female territories permanently, they may employ a mixed reproductive strategy, i.e. maintaining a pair bond with one female, while seeking extra-pair copulations with neighbouring females (Trivers 1972), as observed in many other socially monogamous mammals, such as the aardwolf (*Proteles cristatus*, Richardson 1987), the alpine marmot (*Marmota marmota*, Goossens et al. 1998), the fat-tailed dwarf lemur (*Cheirogaleus medius*, Fietz et al. 2000) and the red fox (Iossa et al. 2008).

Conclusion

The results from our study and Sauer's study indicate that round-eared sengi populations may be characterized by social flexibility caused by environmental variability, with pair-living occurring in a semi-desert and non-territoriality occurring in the Namib Desert. Whether to defend a single female or to search widely for additional mates will be determined by the trade-off between costs and benefits. In our study, female round-eared sengis maintained exclusive areas, possibly because of female–female competition for critical resources. Although, asyn-

chronous breeding may have provided the opportunity for round-eared sengi males to search for multiple fertile females, males were territorial and lived in perennial pairs, suggesting that pair-living offered higher reproductive benefits for males than roaming. Nevertheless, our results revealed that males have polygynous tendencies, as indicated by the large home ranges used and intrusions into areas of widowed females. While a low variance in male body mass and balanced adult sex ratios may have limited the opportunity for males to monopolize additional females, male round-eared sengis in the semi-desert may maximize their reproductive success by maintaining a pair bond with a single female, while seeking copulations with neighbouring females.

Acknowledgements

Literature Cited

Adamczak, V. G. & Dunbar, R. I. M. 2007: Variation in the mating system of oribi and its ecological determinants. Afr. J. Ecol. **46**, 197—206.

Asher, M., Lippmann, T., Epplen, J. T., Kraus, C., Trillmich, F. & Sachser, N. 2008: Large males dominate: ecology, social organisation and mating system of wild cavies, the ancestors of the guinea pig. Behav. Ecol. Sociobiol. **62**, 1509—1521.

Bates, D. 2005: Fitting linear mixed models in R. R News **5**, 27—39.

Bernard, R. T. F., Kerley, G. I. H., Doubell, T. & Davison, A. 1996: Reproduction in the round-eared elephant

shrew (*Macroscelides proboscideus*) in the Southern Karoo, South Africa. J. Zool. Lond. **241**, 233—243.

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 (Reichard, U. H. & Boesch, C., eds). Cambridge Univ. Press, Cambridge, pp. 42—58.

Brown, J. L. & Orians, G. H. 1970: Spacing patterns in mobile animals. Annu. Rev. Ecol. Syst. **1**, 239—262.

Corbet, G. B. & Hanks, J. 1968: A revision of the elephant-shrews, Family Macroscelididae. Bull. Br. Mus. (Nat. Hist.) Zool. **16**, 1—111.

Cowling, R. M., Esler, K. J. & Rundel, P. W. 1999: Namaqualand, South Africa-an overview of a unique winter-rainfall desert ecosystem. Plant Ecol. **142**, 3—21.

Currie, D. & Valkama, J. 2000: Population density and the intensity of paternity assurance behaviour in a monogamous wader: the Curlew *Numenius arquata*. Ibis **142**, 372—381.

van Deventer, M. & Nel, J. A. J. 2006: Habitat, food and small mammal community structure in Namaqualand. Koedoe **49**, 99—109.

Eberle, M. & Kappeler, P. M. 2004: Sex in the dark: determinants and consequences of mixed male mating tactics in *Microcebus murinus*, a small solitary nocturnal primate. Behav. Ecol. Evol. **57**, 77—90.

Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection, and the evolution of mating systems. Science **197**, 215—223.

Faraway, J. J. 2006: Extending the linear model with R. Generalized linear, mixed effects and nonparametric regression models. Chapman & Hall/CRC Press Company, New York.

Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Danzman, K. H. & Ganzhorn, J. U. 2000: High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. Behav. Ecol. Sociobiol. **49**, 8—17.

FitzGibbon, C. D. 1995: Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. Mamm. 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.

Getz, L. L., McGuire, B. & Carter, S. 2003: Social behavior, reproduction and demography of the prairie vole, *Microtus ochrogaster*. Ethol. Ecol. Evol. **15**, 105—118.

Gliwicz, J. 1997: Space use in the root vole: basic patterns and variability. Ecography **20**, 383—389.

Goossens, B., Laurent, G., Waits, L. P., Farand, E., Magnolon, S., Coulon, J., Bel, M. C., Taberlet, P. & Allainé, D. 1998: Extra-pair paternity in the monoga-

mous Alpine marmot revealed by nuclear DNA microsatellite analysis. Behav. Ecol. Sociobiol. **43**, 281—288.

van der Horst, C. J. 1946: Some remarks on the biology of reproduction in the female of *Elephantulus*, the holy animal of set. T. Roy. Soc. S. Afr. **31**, 181—199.

Ims, R. A. 1987: Male spacing system in microtine rodents. Am. Nat. **130**, 475—484.

Iossa, G., Soulsbury, C. D., Baker, P. J. & Harris, S. 2008: Body mass, territory size and life- history tactics in a socially monogamous canid, the red fox *Vulpes vulpes*. J. Mamm. **89**, 1482—1490.

Joubert, D. F. & Ryan, D. F. 1999: Differences in mammal and bird assemblage between commercial and communal rangelands in the Succulent Karoo, South Africa. J. Arid Environ. **43**, 287—299.

Kempenaers, B. 1993: The use of a breeding synchrony index. Ornis Scand. **24**, 84.

Kenward, R., South, A. & Walls, S. 2002: Ranges 6. Anatrack Ltd, Wareham, Dorset, UK.

Kerley, G. I. H. 1995: The round-eared elephant-shrew *Macroscelides proboscideus* (Macroscelidea) as an omnivore. Mamm. Rev. **25**, 39—44.

Kleiman, D. G. 1977: Monogamy in mammals. Q. Rev. Biol. **52**, 39—69.

Komdeur, J. 2001: Mate guarding in the Seychelles warbler is energetically costly and adjusted to paternity risks. Proc. R. Soc. Lond. B Biol. Sci. **266**, 2075—2081.

Komers, P. E. & Brotherton, P. N. M. 1997: Female space use is the best predictor of monogamy in mammals. Proc. R. Soc. Lond. B Biol. Sci. **264**, 1261—1270.

Kraus, C., Künkele, J. & Trillmich, F. 2003: Spacing behaviour and its implications for the mating system of a small precocial mammal: an almost asocial cavy (*Cavia magna*)? Anim. Behav. **66**, 225—238.

Kraus, C., Eberle, M. & Kappeler, P. M. 2008: The costs of risky male behaviour: sex differences in seasonal survival in a small sexually monomorphic primate. Proc. R. Soc. B, Biol. Sci. **275**, 1635—1644.

Krebs, C. J. 1966: Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. **36**, 239—273.

Lambin, X. & Krebs, C. J. 1991: Spatial organisation and mating system of *Microtus townsendii*. Behav. Ecol. Sociobiol. **28**, 353—363.

Leirs, H., Verhagen, R., Verheyen, W. & Perrin, M. R. 1995: The biology of *Elephantulus brachyrhynchus* in natural *miombo* woodland in Tanzania. Mamm. Rev. **25**, 45—49.

Lott, D. F. 1984: Intraspecific variation in the social system of wild vertebrates. Behaviour **28**, 266—325.

Lovegrove, B. G., Laws, M. J. & Roxburgh, L. 1999: Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant-shrew, *Macroscelides*

proboscideus (Macroscelidea). J. Comp. Physiol. **169**, 453—460.

Magnhagen, C. 1991: Predation risk as a cost of reproduction. Trends Ecol. Evol. **6**, 183—186.

Martin, J. K. & Martin, A. A. 2007: Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*: Marsupialia). Oecologica **154**, 227—236.

Michener, G. L. & McLean, I. G. 1996: Reproductive behaviour and operational sex ratio in Richardson's ground squirrels. Anim. Behav. **52**, 743—758.

Mohr, C. O. 1947: Table of equivalent populations of North American small mammals. Am. Midl. Nat. **37**, 223—249.

Mucina, L. & Rutherford, M. C. 2006: The Vegetation of South Africa. Lesotho & Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

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.

Neat, F. C., Taylor, A. C. & Huntingford, F. A. 1998: Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Anim. Behav. **55**, 875—882.

Olbricht, G., Kern, L. & Vakhrusheva, G. 2006: Einige Aspekte der Fortpflanzungsbiologie von Kurzohr-Rüsselspringern (*Macroscelides proboscideus* A. Smith 1829) in Zoologischen Gärten unter besonderer Berücksichtigung von Drillingsgeburten. Der Zoologische Garten **75**, 304—316.

Ostfeld, R. S. 1990: The ecology of territoriality in small mammals. Trends Ecol. Evol. **5**, 411—415.

Powell, R. A. 2000: Animal home ranges and territories and home range estimators. In: Research Techniques in Animal Ecology: Controversies and Consequences (Biotani, L. & Fuller, T. K., eds). Columbia Univ. Press, New York, pp. 65—110.

R Development Core Team 2008: R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Austria, Vienna, ISBN 3-900051-07-0, URL http://www.R-project.org.

Rathbun, G. B. 1979: The social structure and ecology of elephant-shrews. Adv. Ethol. **20**, 1—79.

Rathbun, G. B. & Rathbun, C. D. 2006: Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. J. Zool. Lond. **269**, 391—399.

Ribble, D. O. & Perrin, M. R. 2005: Social organisation of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. Belg. J. Zool. **135**, 167—173.

Richardson, P. R. K. 1987: Aardwolf mating system: overt cuckoldry in an apparently monogamous mammal. S. Afr. Tydskr. Wet. **83**, 405—410.

Rödel, H. G. & von Holst, D. 2009: Features of the early juvenile development predict competitive performance in male European rabbits. Physiol. Behav. **97**, 495—502.

Rösch, H. 2001: The identification and description of the management units of the Goegap Nature Reserve. Koedoe **44**, 17—30.

Rutberg, A. T. 1983: The evolution of monogamy in primates. J. Theor. Biol. **104**, 93—112.

Sandell, M. I. 1989: The mating tactics and spacing patterns of solitary carnivores. In: Carnivore Behaviour, Ecology and Evolution (Gittleman, J. L., ed). Cornell Univ. Press, New York, pp. 164—182.

Sandell, M. I. & Liberg, O. 1992: Roamers or stayers: a model on male mating tactics and mating system. Am. Nat. **139**, 177—189.

Sauer, E. G. F. 1973: Zum Sozialverhalten der kurzohrigen Elefantenspitzmaus, *Macroscelides proboscideus*. Z. Säugetierkd. **38**, 65—97.

Sauer, E. G. F. & Sauer, E. M. 1971: Die kurzohrige Elefantenspitzmaus in der Namib. Namib & Meer **2**, 5—43.

Sauer, E. G. F. & Sauer, E. M. 1972: Zur Biologie der kurzohrige Elefantenspitzmaus, *Macroscelides proboscideus*. Zeitschrift des Kölner Zoos **4**, 119—139.

Schradin, C. 2004: Territorial defense in a group-living solitary forager: who, where, against whom. Behav. Ecol. Sociobiol. **55**, 439—446.

Schradin, C. & Pillay, N. 2005a: Intra-specific variation in the spatial and social organisation of the African striped mouse. J. Mamm. **86**, 99—107.

Schradin, C. & Pillay, N. 2005b: Demography of the striped mouse (*Rhabdomys pumilio*) in the succulent karoo. Mamm. Biol. **70**, 84—92.

Schwagmeyer, P. L. 1988: Scramble-competition polygyny in an asocial mammal: male mobility and mating success. Am. Nat. **131**, 885—892.

Schwagmeyer, P. L. & Woonter, S. J. 1986: Scramble competition polygyny in thirteen-lined ground-squirrels: the relative contribution of overt conflict and competitive mate searching. Behav. Ecol. Sociobiol. **19**, 359—364.

Skinner, J. D. & Smithers, R. H. N. 1990: The Mammals of Southern Africa Subregion, 2nd edn. Univ. of Pretoria, Pretoria.

Trivers, R. L. 1972: Parental investment and sexual selection. In: Sexual Selection and the Descent of Man (Campbell, B., ed). Aldine, Chicago, pp. 136—179.

Watanabe, K. 1981: Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. Primates **22**, 145—160.

Webster, A. B. & Brooks, R. J. 1980: Effects of radiotransmitters on the meadow vole, *Microtus pennsylvanicus*. Can. J. Zool. **58**, 997—1001.

Wolff, J. O. & Cicirello, D. M. 1990: Mobility versus territoriality: alternative reproductive strategies in whitefooted mice. Anim. Behav. **39**, 1222—1224.

Woodall, P. F. 1995: The male reproductive system and the phylogeny of elephant-shrews (Macroscelidea). Mamm. Rev. **25**, 87—93.

Wrangham, R. W. 1980: An ecological model of female-bonded primate groups. Behaviour **11**, 89—102.