Home range and habitat use by the Etendeka Round-eared Sengi, a Namibian endemic desert mammal

Comment [JDS1]: I suggest changing the title to

Home range and use of diurnal shelter by the Etendeka Round-eared Sengi, a Namibian endemic desert mammal

because you haven't really quantified habitat use other than looking at diurnal shelter sites

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Abstract

To understand habitat use by the newly described Etendeka round-eared sengi (*Macroscelides micus*) in northwestern Namibia, we radio-tracked five individuals for nearly a month. Home ranges (100% convex polygons) in the rocky desert habitat were remarkably large (mean 14.9 ha) when compared to sengi species in more mesic habitats (< 1.5 ha). These comparisons suggest that low abundance of invertebrate prey in the desert may be an important factor in determining home range characteristics. The activity pattern of *M. micus* was strictly nocturnal, which contrasts to the normal diurnal or crepuscular activity of other sengis. The day shelters of *M. micus* were under single rocks and they likely were occupied by single sengis. One tagged sengi used 22 different day shelters during the study. On average, only 7% of the day shelters were used more than once by the five tagged sengis. The shelters were also unusual for a small mammal in that they were unmodified in terms of excavation or nesting material. Shelter entrances were significantly oriented to face south by south west (average 193°), away from the angle of the prevailing midday sun. This suggests that solar radiation is probably an important aspect of *M. micus* thermal ecology, similar to other sengis. Compared to published data on other sengis, *M. micus* generally conforms to the unique sengi adaptive syndrome, but with modifications related to its hyper-arid habitat.

Comment [JDS2]: In the absence of data on invertebrate abundance and an appropriate analysis the data don't suggest this. It's just a hypothesis.

Subjects: Behavioral ecology, Zoology,

Keywords: Elephant-shrew, Home Range, Shelter, Namib Desert, Namibia

Introduction

The sengis or elephant-shrews (Order Macroscelidea) are a well-defined monophyletic clade of mammals that are endemic to Africa, not closely related to other clades in the supercohort Afrotheria (Seiffert, 2007). There are only 19 extant species, which are divided into the subfamilies Rhynchocyoninae and Macroscelidinae (Corbet & Hanks, 1968). The four species of *Rhynchocyon* in the first subfamily are forest dwellers in central and eastern Africa and weigh between 300 and 750 g (Rovero et al., 2008). The genera *Petrodromus*, *Elephantulus*, and *Macroscelides* are in the second subfamily. *Petrodromus* is monospecific, weighs about 200 g, and occupies thickets, dense woodlands, and forests of central and eastern Africa (Jennings & Rathbun, 2001). The 12 species of *Elephantulus* (Smit et al., 2008) weigh from 45 to 60 g, occupy habitats that include grasslands, bushlands, and open woodlands throughout much of Africa, with the exception of the Sahara Desert and western Africa (Rathbun, 2015). The three species of *Macroscelides* occur in the deserts of southwestern Africa, and weigh only 25-45 g (Dumbacher et al., 2014).

From the earliest studies of sengis (Sauer, 1973; Rathbun, 1979), it was recognized that their combined life history traits formed a unique adaptive syndrome, not seen in any other mammals in other biogeographic regions of the world. The syndrome blends life history strategies usually associated with ant-eaters and some antelopes, including on one hand a diet of invertebrates with an associated long nose and tongue and small mouth, and on the other hand highly cursorial locomotion, small precocial litters, absentee maternal care, lack of nest-use (Macroscelidinae only), and social monogamy. These traits do not vary greatly among the species so far studied, despite the considerable variation in their size and habitats (Rathbun, 1979; 2009). When it was found that some sengis were socially monogamous (Rathbun, 1979), which is unusual in mammals (Komer & Brotherton, 1997), additional studies were completed to better understand the evolution of this social organization (FitzGibbon, 1995; Ribble & Perrin, 2005; Rathbun & Rathbun, 2006; Schubert et al., 2009; Oxenham & Perrin, 2009). One of the main focuses of these studies has been home range characteristics, but other aspects of their life history have been documented incidentally, such as the unusual sheltering habits among the Macroscelidinae. Although Rathbun (2009) reviewed sengi taxonomy and life history traits, recent taxonomic revisions have resulted in new taxa being recognized (Rovero et al., 2008; Smit et al., 2008; Dumbacher et al., 2012). The Etendeka round-eared sengi (*Macroscelides micus* J. P. Dumbacher & G. B. Rathbun, 2014) is the newest species to be described (Dumbacher et al., 2014) and is of particular interest because it is the smallest sengi and it only occurs in a small hyper-arid area in northwestern Namibia, sandwiched between the coastal Namib Desert and the inland escarpment (Swart & Marais, 2009; Rathbun, Osborne & Coals, 2015).

The objective of our research on *M. micus* was to determine how closely its life history traits fit the adaptive syndrome seen in other sengis, especially the Macroscelidinae. We focused on habitat use in its desert habitat by gathering data on home range characteristics and sheltering habits.

Comment [JDS3]: Given this objective I would suggest beginning the introduction more generally, perhaps introducing the concept of adaptive syndrome and explaining what it means ecologically.

From there, you, you can talk about sengis, as you have done, but then could not you derive some predictions about the life history traits of the new species based on the adaptive syndrome seen in other sengis?

I think this would make a stronger introduction

Materials and Methods

Our study site (latitude -21.32338, longitude 14.32738) was in northwestern Namibia, within the eastern edge of the Namib Desert, and the lower eastern slope of the Goboboseb Mountains, which are part of the Etendeka geological formation that was created by lava flood events about 132 million years ago (Swart & Marais, 2009; Fig. 1). The study site was about 580 m above sea level, on the lower slopes of a 900 m high mountain. The slopes (average = 13.4^{o}, range = $3 – 29^{o}$, N = 48) were composed of rust-colored compact gravel with an estimated 40-95% of the surface covered with fist to cinder-block sized rocks, which made walking difficult (Fig. 1). The closest town was Uis (population ca. 4,000), about 60 km to the east and about a 1.5 hour drive by four-wheel drive vehicle on poor roads and tracks. The study site was about 55 km inland from the cold Benguela ocean current, which resulted in wet coastal fogs at our site on about a quarter of the nights. The fog left moisture on rock

Comment [JDS4]: What is a cinder block? (I'm Australian) surfaces, but fog and moisture completely disappeared by mid-morning. Based on our interpolation of weather data from Henties Bay and Uis, we estimate the average yearly rainfall at the study site is 10 mm. During our field work, the average overnight low temperature at our study site was 9.6^{o} C (range = 3.9-18.7^{o} C), and the average maximum (afternoon) temperature was 27.8^{o} C (22.0-30.0^{o} C). On many afternoons, winds up to 13.5 m/sec (30 mi/h) occurred. Full moon occurred on 7 October, and sunrise and sunset was at about 0630 and 1905 hrs.

Our study spanned from 30 September through 26 October 2014, and we trapped (H.B. Sherman Traps, Tallahassee, Florida; model LFA, 3 x 3.5 x 9 inches) and tagged sengis on 13 days during the first two weeks. We set about 200 traps per night at 10-20 m intervals on transects within likely *M. micus* habitat, and traps were moved to new transects every 1-4 days. We baited traps with a dry mixture of rolled oats, peanut butter, and Marmite (a yeast paste or spread), opened the traps at dusk, and checked and closed them at dawn. Trapped sengis (we only captured *M. micus*) were immediately tagged and released at the capture site. At the end of our study, the sengis were recaptured at their day shelters by hand or flushed into mist nets (DTX 36 mm stretch mesh), all radios and tags were removed, and the sengis were released.

Comment [JDS5]: It's not clear to me how large the area was where the trapping took place. Several hectares? Can you include this info please.

We attached a reflective ear-tag inside the distal margin of the pinna of each sengi - right ears of males, and left ears of females. The tags were constructed of two 5-mm-diameter disks of highly reflective silver-colored plastic (Reflexite FD 1430 marine adhesive tape), which only reflected when a light source was aligned closely with the spotter's eyes, thus eliminating the likelihood of increased predation on the ear-tagged sengis on moon-lit nights. The disks were secured to the ear with a nylon stud (monofiliment fishing line) that passed through holes previously melted in the centers of the two disks and a hole pierced through the pinna (Fig. 2A; see Rathbun, 1979; Rathbun & Rathbun, 2006 for further details). Because the sengis were nocturnal (see results), we used bright (275 Lumen) narrow-beamed light-emitting diode (LED) headlamps (Princeton Tec model Apex, and Fenix model HP15) to spot the ear-tagged sengis. We also used binoculars to aid in spotting and observing the sengis. The ear tags were easily visible from 100 m or greater with our headlamps, but poor visibility (fog and wind-blown dust) and obstructing rocks often reduced our ability to spot ear-tagged sengis. Vegetation was sparse or lacking and did not hinder visibility.

We also attached radio-collars (Holohil Systems, Carp, Ontario, Canada; transmitter model BD-2C, frequencies in 164 MHz band, weight ca. 1.5 g) to seven of the eight captured sengis. The transmitter whip antennae were incorporated into Tygon tubing collars, leaving only about 8 cm extending from the top of the collars, and the transmitters hung from the bottom of the collars. This transmitter attachment method is recommended by Holohil for small mammals, and has been successfully used on sengis in the past (Rathbun & Rathbun 2006). Individual identification numbers were assigned based on radio-frequency and sex (e.g., #4020F was a female with radio frequency 164.020 MHz).

We located the tagged sengis by first homing on the radio-signal (Kenward 2001) using receivers (Communications Specialist, Orange, Calif., model R-1000; Wildlife Materials International, Murphysboro, Illinois, model TRX-1000S) attached to two-element Yagi directional receiving antennae (Telonics, Mesa, Arizona). When approaching a collared sengi, we visually scanned in the direction of the signal with our headlamps, thus easily spotting their reflective ear-tags if they were active above ground. If the spotted sengi was active, we made a mental note of a prominent feature in the landscape at the location where we first sighted the sengi, and then walked to the spot and took GPS coordinates (see below). If the sengi was sheltering under a rock, and thus not active or visible, we radio-located the specific rock and took the coordinates of the shelter. At night, one of us radio-tracked from ca. 2100 hrs to 0100 hrs, and the other from ca. 0200 hrs to 0600 hrs. During the day, we located sheltering animals in the morning or mid-day, and again at dusk when we monitored the departure of selected sengis from their day shelters.

We determined the location of the collared sengis using GPS functions on a Motorola MotoG

(2013 model) mobile phone and a Samsung Galaxy Player 4, and we recorded locations in universal transverse Mercator (UTM) coordinates. Both receivers used the Android operating systems with the LOCUS MAPS navigation application (version 3.4.0) for entering, storing, plotting, and exporting location coordinates and associated data. In the field, we took 1-second-averaged coordinates during 15-60 second periods for locations. We tested the accuracy of both receivers at the field camp during arbitrary times during the day and night on 22-24 October 2014. For the test, we recorded the 60-second average location (1-sec intervals). We accumulated 15 and 11 locations with the receivers (MotoG and Galaxy4, respectively) and calculated the minimum convex polygon area of the locations and the arithmetic mean of the center of each area, which differed by 1.4 m for the two receivers. The average distance from the center of each area to the contributing locations was also calculated (MotoG = 2.3 m, range 0.5-4.2 m; Galaxy4 = 4.6 m, 1.0-8.6 m).

To determine home range areas, we used RANGES 9 software (Anatrack Ltd., Wareham, Dorset, UK). We ran several different analyses (Kenward, 2001) in order to compare home range size estimates with published values. We also including the object restricted-edge polygon (OREP) analysis (Anatarack, 2015) because it may produce a better estimate of the “true” home range areas (Burt, 1943; Powell and Mitchell, 2012). We also included estimates based on a concave polygon analysis because they were remarkably similar to the OREP results, and may be useful for future comparisons. For the analyses, we used a censored data set that included capture localities (except for the OREP analysis), all radio and sighting records, all day and night shelter locations, and the final death (or capture) location for each individual. We eliminated records that were obviously incorrect due to observer error. Because we have not analyzed the data for differential use of home range areas, and the sengis were remarkably active and swift during the night, we did not censor the data set for location and time auto-correlations. For all home range analyses, the units of measure were meters with the resolution set at one meter, and we used the 'curve and polygon' option in RANGES 9. To keep our home range estimates comparable to published estimates, we only used the 'buffer tracking resolution' option for the concave polygon and OREP analyses. For the convex polygon (= minimum convex polygon or MCP) analysis we used 95% and 100% 'cores' based on 'arithmetic mean centers'. For the concave polygon analysis we used the 'selected edge restriction' option with a value of 0.4. For the OREP analysis we used the '>5% distribution distance' and 'KED and Strip' options. We used all the default setting for the 95% core kernel analysis, which were fixed kernel, location density contours, fixed smoothing multiplier, and 40 matrix cells set to rescale to fit matrix.

Comment [JDS6]: This ref is not in the list at the back

Check for other too

While radio-tacking sengis after dawn, we located, flagged and recorded GPS coordinates for the day shelter used by each sengi. We checked shelters arbitrarily during the remainder of the day for continued occupancy, with the last and most focused effort starting at about sunset (ca. 1900 hrs). At sunset, one of us sat inconspicuously among rocks or boulders about 5-10 m from an occupied shelter, and watched for sengi movement and listened for variations in radio signal pitch, strength, and direction, which indicated an active sengi. Once the animal was active, we briefly searched the area around the shelter with binoculars and headlamp for an ear-tag reflection, thus further confirming that the sengi was active and had departed its shelter for the night.

Near the end of the field study, we sampled sengi day shelters and took a set of standardized metrics, which included the orientation of the rock shelter entrance, gross habitat characteristics (aspect, slope, ground cover), midday temperature of ambient air, temperature inside the shelter, and temperature on the top surface (facing the sun) of the shelter rock. We also measured the dimensions of the rock above the shelter (approximate length, width, and vertical thickness). We then carefully removed and then replaced the shelter rock to record the substrate inside the shelter (gravel, sand, dust), and looked for evidence of occupation (excavation, presence of bedding, or feces).

We recorded the various temperatures because the dark rust-colored rocks heat up from direct solar radiation based largely upon the area of rock that is exposed to the sun (length and width of rock). The thermal inertia of the rock will be approximately linearly related to the thickness of the rock (or mass of the rock divided by the surface area exposed to the sun). We therefore regressed measures of shelter temperature against the shelter rock thickness to test whether thicker rocks provide more stable temperature environments and protection from the heat.

Results

Capture and Radio-tracking

We accumulated 2742 trap-nights, capturing 3 rodent individuals (one each of *Gerbillurus*, *Petromyscus*, *Petromus*; 0.11% trap success) and 7 *M. micus* individuals (0.26%). To try to capture all the sengi individuals at the study site, we often set trap transects across areas where we had already captured sengis, in addition to adjacent areas. Remarkably, we only recaptured one of our tagged sengis (#4612F), and only once. We captured an eigth sengi by hand at night (#4585M), but of the total captured sengis, we radio collared seven (Table 1); a single young female was only ear-tagged. Both #4427F and #4585M disappeared soon after collaring, and provided no data. For any particular analysis, a subset of only relevant data were used, thus sample sizes did not always conform to the overall totals shown in Table 1.

Home range

The average home range sizes of the five radio-collared sengis, as determined by the different methods of analyses, were highly variable (Table 2), spanning from 7.2 to 22.8 ha. The average maximum length of the home ranges, calculated using the 100% convex polygon method, was 705 m. However, this was greatly influenced by #4254M that had a remarkably large oblong-shaped home range (Figs. 3 & 4). The average distance between the centers of home ranges (100% convex polygons, Table 3) that overlapped (Table 4) was 425 m, which is a useful comparative measure of sengi dispersion (see Discussion). As with the home range areas, the amount of overlap between individuals depended greatly on the method of calculating the areas, but it varied for our five collared sengis between 0% and nearly 50.5% (Table 4). Unfortunately, our sample size is too small to make any conclusive statements with regard to overlap between males and females.

Comment [JDS7]: Table 3 contains such few data that you could probably just put it in the text. Perhaps a mean and a range would suffice.

Comment [JDS8]: Well, your sample size is probably too small to make any conclusive statements about any of the variables you measured.

Comment [JDS9]: % overlap may not mean much if you didn't catch the majority of individuals living in the area. And given the low recapture rate you possibly didn't.

The home range size (Table 2) and shape (Figs. 3 & 4) of #4254M was odd compared to the other four sengis. We located this male mostly at each end of his oblong-shaped home range, which spanned over 1.5 km (Table 2). He moved from end-to-end of his home range 11 times, making the journey so quickly that we were only able to roughly track his path once, when he made the journey from about 570 m elevation to 650 m in less than 60 minutes, presumably in a relatively straight course with few pauses. The area between the ends of his home range was atypical habitat for *M. micus*, being a slightly sloping alluvial fan composed of softer and lighter gravels and fewer rocks than on the surrounding higher slopes (Fig. 3). The only other home range that was not completely located on rust-colored Etendeka volcanic substrates was that of #4020F, with about 0.73 ha at the southern edge falling on the lowest alluvial flats in the study area, which were composed of finer and lighter colored gravels with virtually no rocks on the surface (Figs. 1 & 3). The home range areas of all the sengis tended to fall below the steeper areas of the Etendeka formation that had huge bounders and large rock faces (Fig. 3).

Comment [JDS10]: Which is presumably why he didn't spend any time there. Is this bit discussion material rather than results?

We closely followed #4020F on her home range twice during the night of 1 October 2014 by keeping sight of her reflective ear-tag. Starting at 2152 hrs., she covered about 219 m in 10 min (1.3 km/hr) and her route (based on the GPS-determined track of the observer) was a large circle that did not quite meet the starting point. The second track started at 2217 hrs, and covered 89 m in 3 min (1.6 km/hr) in roughly a straight line. The sengi easily kept ahead of us as it bounded from rock to rock, obviously following a familiar route. During our study, we found no worn sengi paths across the substrate, because the sengis mainly bounded from rock to rock, but nevertheless they appeared to easily follow familiar routes, as demonstrated when we spotted a lone unmarked sengi (became #4585M) within the home range of #4856F. The sengi was obviously unfamiliar with the area because

Comment [JDS11]: I love the phrase 'bounded from rock to rock' but to me it sounds a bit odd appearing twice here so close together he continually stumbled over and bumped into rocks as he clumsily fled. He was so slow in his attempt to escape that we were able to chase and hand-capture him while keeping him in the beam of our headlamp. It was impossible to similarly capture our tagged sengis because they were too agile and swift. If sengis largely restricted their normal movements to familiar routes, then we probably only trapped them when a sengi route coincided with a trap location, which may have contributed to our low capture rate.

Comment [JDS12]: Paints a great picture…

Comment [JDS13]: Discussion?

After we radio-collared #4585M, we only located him once the next day, even though we searched widely (several km) in areas adjacent to our study area on several days. Because our transmitters had a line-of-sight range of about one kilometer, it seems unlikely that we lost the signal. It is possible that the transmitter failed, but we never spotted any male ear-tagged sengis without an associated radio signal. Sengi #4585M possibly became prey of the Cape fox (*Vulpes chama* A. Smith 1833) that we saw in our study site on several nights. This was probably also the fate of #4612F, given that we found her shed and functioning transmitter with tooth damage (Table 1).

The areas encompassing all day shelters (100% convex polygon) for each of the five radio-tagged sengis averaged 36.8% of each home ranges (Table 2). The distribution of day shelters within a home range showed no obvious pattern other than the sengis used locations with suitable rock shelters and tended to be well inside the home range boundaries (Fig. 4).

Shelter characteristics

We examined a sample of day shelters used by the five tagged sengis with the greatest available data (#4020 n= 13, #4254 n=9, #4612 n=5, #4856 n=11, #4947 n=11). The ground surrounding the shelters was always boulder strewn, with 52% average rock coverage (range 40% - 95%). Aspect and slope varied by animal, but showed no overall trend that differed from the surrounding habitat in each home range. Shelters were typically a crevice under a single rock with an average opening of 6.6 cm (range 3-12 cm). No shelters showed any obvious signs of alteration such as excavation, digging, or collected bedding. Three of 49 shelters had some windblown grasses or plant matter, but it was never noticeably arranged or manipulated, and seemed typical of the surrounding boulder fields. Interior substrate varied from dusty to sandy to gravelly, but more or less matched the surrounding substrate. Only one shelter of 49 contained feces (3 pellets), and none had partially eaten food or scraps. The entrances to shelters showed a significant directionality (Raleigh's Z test, $n=41$, $z=3.66$, $p<0.05$) with an average compass direction of 193° south by southwest, despite the fact that slope aspect varied among individuals and showed no overall directionality (Raleigh's Z test, $n=49$, $z=0.35$, $P>0.2$).

We regressed shelter temperature against the shelter rock thickness and recovered a significant negative relationship ($n=47$, $R^2=0.396$, $p<0.01$, Fig. 5A), thus confirming that thicker rocks may provide more stable temperature environments and protection from wide temperature fluctuations. Because we measured shelters on different days, we additionally sought to control for differences in midday temperature by subtracting shelter temperature from local ambient air temperature. We again found a significant positive relationship, suggesting thicker rocks were relatively cooler relative to air temperature (general linear regression, $n=47$, $R^2=0.4117$, $p<0.01$, Fig. 5B). Despite confirming the potential benefit of thicker shelter rocks to protect from the heat or wide temperature fluctuations, we cannot confirm whether sengis are actually choosing shelters to take advantage of these benefits, in fact most shelters were under rocks with smaller thicknesses (Fig. 5). It is not clear whether this is due to an active choice on the part of sengis, or whether they are constrained by availability.

Comment [JDS14]: It would have been nice to compare the characteristics used shelter sites to available shelter sites – but I guess you don't have data about the characteristics of available shelter sites

Shelter use

The radio collared sengis were strictly nocturnal. Once sheltered at night, usually near dawn, they normally remained in the same shelters throughout the day, and were very reluctant to leave. For example, we checked 33 occupied shelters twice during the day between 5.5 to 13 hrs prior to sunset (1900 hrs), and in only two cases did a sengi change shelters during the daylight. In one case (#4947M) the distance between shelters was about 3 m, and in the second case (#4612F) it was about 30 m. On three days we checked #4020F four different times during daylight, and on one day three times, and #4856F at four different times on one day. Neither of these sengis shifted shelters during the day. When we recaptured the four remaining radio-tagged sengis at the end of the study on 26 October 2014, between 1000 hrs and 1145 hrs., we had to dislodge or remove the shelter boulders to get the animals to flee into the capture nets, which further demonstrated their reluctance to leave their day shelters.

We never observed or radio-tracked any day-time sengi movements, and they all were active on every night with one exception. During the night of 8 October, #4020F did not leave her day shelter, and when we checked her after dawn she was torpid in her shelter. We thought she might have entangled a forefoot in her collar, but upon capture we found no problems. She quickly came out of torpor and after her release her activity pattern did not change again.

We accumulated 31 cases where we determined whether a sengi switched shelters from one used at night and the day shelter (after dawn at ca. 0600 hrs). In 26 of the 31 cases switching did not occur, indicating that the sengis often sheltered for the day well before first light. Related to this pattern, we extracted location data for four sengis (those with the most robust overall data sets; #4020F, #4254M, #4856F, #4947M) and determined whether we found them in a night shelter or not during two periods: between 2100 and 0100 hrs (early night), and between 0200 and 0600 hrs (late night). In the early period, there were 130 pooled observations, with 14 in night shelters (10.8%). During the late period, we had 117 observations with 37 (31.6%) in night shelters. These data support our subjective assessment that the animals were more active early in the night compared to late at night. This pattern made it nearly impossible for us to determine when animals retreated to shelters for the day, compared to when they left their day shelters for a night of activity. We monitored 40 day shelters starting at about 1900 hours (sunset) and the average departure time was 19:38 hrs, with a range of 19:13 to 19:59 hrs. In two additional cases a sengi (#4254M) had not left the day shelter by 2010 and 2015 hrs, when we terminated observations.

Even though the sengis were very reluctant to switch shelters within a day, they readily switched shelters from day to day, rarely using a site more than once (Table 5). Pooling individuals, we monitored 85 day shelters and 93% were used once, 5% twice, and 1% each for three and four times. The average interval between using the same shelter was 3.2 days, with a range of 1-9 days. We found no evidence that more than one sengi occupied a shelter at the same time, although it is possible that untagged sengis might have paired with our collared animals.

During our night radio-tracking, on two occasions we located sengis sheltered under low bushes, a 1 m high *Commiphora* bush and a 2 m high *Boscia* bush (Fig. 1). Bushes in this size range only numbered 2 or 3 individuals in each home range. While under the canopy of these bushes, the sengis were "nervous" and easily disturbed, running to the opposite side of the bush from the observer on several occasions, but they did not flush into the open nor did they foot drum. While we were about 5 m from the animals, we observed them for about 15 minutes while they groomed and rested (Fig. 2A) on the surface of the gravel substrate. They were always alert with their eyes open and ready to flee. These observations were terminated after they bounded off into the night.

Discussion

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Home Ranges

The estimated home range sizes of the five sengis we collared were~~are~~ greatly dependent on the method of analysis. There is little doubt that both convex polygon and kernel methods incorporate large areas that are rarely if ever used, but we have included both metrics to allow comparison with published data. We believe that the most accurate representation of the home ranges of our tagged sengis is obtained with the relatively new OREP method, but unfortunately no previous studies have used this method, as is the case with the concave polygon technique. We nevertheless have included both, with the hope that

Comment [JDS15]: I find this difficult to understand – can you rewrite more clearly?

Comment [JDS16]: Did different individuals have their own shelters, or did individuals happily use shelters that other sengis had used previously?

If the latter is true, then I assume some shelters were used more than others. If this was the case, is it possible to link shelter use to shelter characteristics? I'm thinking something like poisson regression with the number of times a shelter was used as the response variable and measured shelter characteristics as predictor variables.

Comment [JDS17]: I suggest beginning the discussion with a more general statement reiterating the theme and general importance of your research.

future studies will also find that they closely represent actual home range areas, and thus allow a better ecological understanding of sengis.

The three species of *Macroscelides* occupy very arid habitats (Dumbacher et al., 2012; Dumbacher et al., 2014) compared to other sengis, thus ecological insights may be gained from intra- and inter-generic comparisons. Schubert et al. (2009) provides quantitative home range data for the Karoo round-eared sengi (*Macroscelides proboscideus* Shaw 1800) near Springbok, South Africa, based on radio-tracking methods. Franz Sauer (1973) with his wife Elinore used only direct observations to determine home ranges of Namib round-eared sengis (*Macroscelides flavicaudatus* Lundholm 1955) in the Namib Desert southeast of Walvis Bay, Namibia, which they claim were about one sq km. As additional home range data were published (Table 6), sengi home ranges this large seemed almost unbelievable. Adding to the skepticism was that Sauer (1973) did not mark the sengis he studied, and thus it is not clear how reliably sengis were individually distinguished, which is a basic foundation of modern behavioral ecology research. In addition, Sauer apparently provisioned the sengis with a commercial pet food (Cornelias Coetzee, pers. comm.), with unreported and unknown influences on his results. However, the Sauers were obviously careful and insightful observers (Sauer, 1972; 1973; Sauer & Sauer, 1971; 1972). With the insights from our results on *M. micus*, it seems likely that the remarkably large home range areas reported by Sauer (1973) can be better evaluated, understood, and interpreted to allow more meaningful comparisons with other sengi results.

Sauer (1973) uses terms to describe the use of space without clear definitions, and his usage is different than what is currently used (translation does not seem to have altered meanings). For example, Sauer (1973, pages 74 and 94 among others) states that *M. flavicaudatus* had an average home range of a square kilometer, but he also indicates that this was in fact a crude calculation of density within his 20 sq km study area. Home ranges this large are also contradicted by figures and data in Sauer (1973, Figs. 7 and 9), which focus on intense observations of a “pair” of sengis and their twins. Sauer (1973) indicates that some of his sengis traveled one km or more along their well-defined paths, and he indicates this supports his estimate of a square kilometer home range. Our radio-tracking data on *M. micus* indicate that routine linear movements of a kilometer were undertaken, but this does not equate to a square kilometer home range (defined by Burt, 1943, as an area used in routine daily activities). Because Sauer (1973) was a keen and accurate qualitative observer, we can use some of his published information to reinterpret his “home range” estimate to more closely conform to the more widely accepted definition (Burt, 1943). The mode of the average distances between the main shelters used by individual sengis on adjacent home ranges was 300 m (Sauer, 1973, pg 71, Table 1, Fig. 7, pg 95). If we use this datum as the length of each of two adjacent sides of an approximately square home range, and adjoining home ranges were in relatively homogeneous habitats (Ibid.), we obtain an estimated home range area of about 9 ha, which is nearly an order of magnitude smaller than the density of 100 ha/sengi that he called a “home range”. We believe that our home range estimate, albeit crude, is more consistent with the descriptions, illustrations, and photographs in Sauer (1973), and probably more closely fits the more widely accepted definition of home range.

The literature related to mammalian home ranges is large, including attempts to relate the sizes of home ranges with physiological factors such as trophic level of food (calorie sources), body size (calories needs), metabolic rate (rate that calories are used), social structure (group versus individual needs), and phylogeny (McNab, 2002). These factors are highly variable across a wide range of mammals, making comparisons difficult, except for the sengis, which share a very tightly defined adaptive syndrome with very similar phylogeny, metabolic rate, morphology, diet, reproduction, locomotion, social structure, etc. (Rathbun, 1979; 2009). The variation in the body size and habitats occupied by sengis stands out in the context to their similar adaptive syndrome (Rathbun 2009, see Introduction).

Although body weight data for sengis are available, there are several factors that might be used to quantify the habitats used by sengis. Given the life history traits of sengis, we believe that prey abundance is particularly important. Unfortunately, prey numbers are not easily measured or available from most sengi study sites (but see Rathbun, 1979; FitzGibbon, 1995), however rainfall is probably a reasonable proxy, and these data are available. When sengi home range sizes are plotted against rainfall, the points for *M*. *flavicaudatus* and *M*. *micus* are far removed from the rest of the sengis in the plot (Fig. 6A), and we have used the most conservative data for these two species (see discussion of Sauer above, and Table 2). Although *M*. *proboscideus* occupies a low-rainfall habitat similar to its congeners, it clusters with the other smaller sengis (Fig. 6A), which suggests that low rainfall habitats do not fully explain home range size for similarly sized sengis (keeping in mind their very similar adaptive syndrome). The Succulent Karoo, where the data for *M*. *proboscideus* were gathered (Schubert et al., 2009; Schubert 2011), is a relatively small area between the very low and concentrated winter rainfall regime of the Namib Desert to the north, and the low summer rainfall regime of the Mediterranean climate to the south. Although the Succulent Karoo is arid, the rainfall is spread across both winter and summer months (Desmet & Cowling, 1999). This rainfall pattern results in a richer vegetation (Cowling & Hilton-Taylor, 1999) and invertebrate fauna (Vernon, 1999) than might be expected based only on total average rainfall. Thus, the home range area of *M*. *proboscideus* clusters closer to the other small sengis than with *M. flavicaudatus and M. micus* (Fig. 6A), overshadowing the general positive relationship of mammalian body weight and home range size (McNab, 2002). However, this latter relationship is supported by syntopic *Petrodromus* and *Rhynchocyon* in a coastal forest in Kenya (FitzGibbon, 1995; Table 6B). Based on our analysis, we hypothesize that prey availability may have the greatest influence on the home range sizes of sengis, but unfortunately this metric is lacking for most sengis.

In almost all studies of sengi home ranges, a male will occasionally attempt to overlap with more than one female, often resulting in an exceptionally large and oblong home range. However, this configuration is not stable due to the would-be polygamous male retreating when a new male appears to associate with (and mate-guard) one of the females (Komer & Brotherton, 1997; references in Table 6). We speculate that the large hour-glass-shaped home range of #4254M represented a similar temporary attempt at polygamy (although we did not trap the northwestern end of his home range to determine if there was a female in that area).

Male-female sengi pairs exhibit few pair-bond behaviors and spend relatively little time together (except during brief periods of estrus), yet some species have home ranges that are virtually congruent (Rathbun, 1979), while in others the ranges only partially overlap (all other references in Table 6). One hypothesis to explain this curious variation is that the degree of overlap is density dependent. In habitats where sengis essentially occupy all suitable space and thus are dense, male and female home ranges are nearly congruent and intra-sex overlaps are rare because the areas are defended sex-specifically, whereas when sengis are more dispersed, the home range overlap within male-female pairs is reduced (Rathbun & Rathbun, 2006). At our Namibia study site, we were unable to capture and radio-track as many sengis as we had hoped, and our study period was relatively short, but our findings are consistent with the density dependent model to explain overlap between sexes. We again hypothesize that prey availability may be the most important underlying factor in determining sengi density and thus many home range characteristics. However, other resources also may be factors, such as shelter availability, as vaguely suggested by Sauer (1973) for *M*. *flavicaudatus*.

Comment [JDS18]: Potentially, the combination of multiple resources might be important – see one of my papers:

Di Stefano, J., Coulson, G., Greenfield, A., Swan, M., 2011. Resource heterogeneity influences home range area in the swamp wallaby *Wallabia bicolor*. Ecography 34, 469-479.

<u>Sheltering</u>

There were two noteworthy findings regarding shelters. First, was the lack of a central or home burrow or shelter, as found in many if not most other small mammals. Second, was how unremarkable the shelters were; there was no sign of bedding, excavation or alteration, and every shelter seemed to simply be a small space or crevice under a rock where sengis hid during the day. Both findings are similar to the sheltering habits of other Macroscelidinae (Rathbun, 2009). It is difficult to determine which factors were motivating the use of rock shelters by *M*. *micus* because of the large number of possible factors, including sengi behavior, predation threat, weather, environmental conditions, and shelter availability. We believe the most important two factors were the thermal traits of the shelters and predation threat.

We found that midday temperatures of shelter rocks were inversely related to rock thickness (confirming the ability of thicker rocks to resist temperature fluctuations), and we found that shelter openings were significantly orientated toward 193° south. We suspect that these two features have related consequences for sheltering sengis. Like many deserts, the Namib is characterized by frequent high and low temperature extremes (Seely, 2004). Thus, the size and orientation of a shelter rock may allow *M. micus* to passively (behaviorally) avoid temperature extremes and thus reduce energy needed for thermoregulation (McNab, 2002), which is likely important for such a small-bodied desert dweller. For example, the sengis might chose shelters in order to take advantage of the thermal inertia of rock to buffer day and night temperature extremes. In western Namibia, the prevailing winds come primarily from the south (Mendelsohn et al., 2002). Winds often blew hard (we measure up to 13.5 m/sec or 30 mi/h) during the midday and afternoon. Thus, south-facing shelter entrances may be more exposed to cooling breezes during the heat of the day. In addition, the south side of a shelter corresponds with the shady and thus cooler side of the rock during the heat of mid-day because the sun is slightly angled toward the north during this time of year.

Lovegrove, Lawe, & Roxburgh (1999) documented daily torpor in *M. proboscideus*, which is likely a physiological strategy that sengis use under conditions of limited food availability and low temperatures to conserve energy (Mzilikazi, Lovegrove, Ribble, 2002). It is possible that the torpid sengi we encountered (#4020F) was implementing this strategy in this hyper-arid study site with a hypothesized low abundance of prey. However, more research is needed to further explore the relationships between shelter traits, shelter choice, and sengi behavior.

Sauer (1973) also believed that thermoregulation was an important feature of the shelters that were used by *M. flavicaudatus*. However, shelters were less abundant at Sauer's study site compared to our site, as clearly illustrated by his numerous photographs (Ibid). Low shelter availability may also partially explain why *M. flavicaudatus* either uses abandoned rodent burrows, or excavates shallow shelters in the gravel substrates (Sauer, 1973). The only hint that *M. micus* might excavate shallow shelters was the use of two shallow holes (9 and 22 cm deep) by the two young sengis that we captured. We had no direct evidence that sengis fashioned these sites, so they may have been abandoned rodent burrows, although rodents were even less common than sengis at our study site.

Predation is often difficult to document, but one of our collared sengis was depredated, possibly by a Cape Fox, suggesting that avoiding predation may be challenging. The availability of space under a rock that could provide adequate protection is one important feature of shelters. Perhaps just as important is the use of multiple shelters with a very low rate of return to any single shelter, and the lack of feces accumulation in the shelters. Each of these behaviors may be related to avoiding visual or olfactory cues that predators use to develop search images for shelters. This explanation is related to those proposed for the similar spatial and temporal traits of sheltering sites of *Elephantulus intufi* (Rathbun & Rathbun, 2006), and also the nesting traits of *Rhynchocyon* (Rathbun, 1979). Additionally, at our study site there was little cover other than relatively small rocks. This may explain the strictly nocturnal behaviour of *M. micus*, which effectively would avoid predation by the numerous diurnal predators, including several raptors and bustards.

Comment [JDS19]: Is this the right word?

<u>Sengi Adaptive Syndrome</u>

We found that *M. micus* largely conformed to the life history features characteristic of other sengi species, especially the Macroscelidinae, including swift and agile cursorial locomotion, relatively exposed multiple sheltering sites, and possibly spatial organization. Additionally, *M. micus* has small litters of precocial young (Dumbacher et al., 2014). However, we were unable to confirm whether *M. micus* has a female absentee maternal care system, and whether its diet was composed of small invertebrates, as it almost surely does based on its morphology, and the near absence of any other visible food at our study site.

There are several behavioral features that are worth discussing for future comparative studies, but may only be peripheral to the adaptive syndrome. We failed to find any indication that *M. micus* created trails on the substrate, as do other sengis (Rathbun, 1979), including *M. flavicaudatus* (Sauer, 1973). We suspect this is due to the substrate at our study site being dominated by rock. We also failed to see or hear foot drumming during stressful situations, including while in live traps, which is also characteristic of other sengis (Rathbun, 1979; Faurie, Dempster & Perrin, 1996). Neither distinctive latrines of dung pellets (Rathbun 1979), nor scent-marking behaviors (Rathbun, 1979; Faurie & Perrin, 1995) were observed during our study, despite *M. micus* having a very large subcaudal scent gland (Dumbacher et al., 2014). Daily torpor, which is an energy conservation strategy in *M. proboscideus* (Lovegrove, Lawe, Roxburgh, 1999), may be used by *M. micus*, based on our observations.

Conclusions

The home range pattern that emerged from our study was similar to the findings for other sengis, except that the areas of *M. micus* were exceptionally large. Their size was likely the result of low rainfall, sparse vegetation, and low densities of invertebrate prey. The home range characteristics that we found are similar to those of socially monogamous sengis, suggesting that *M. micus* may also be socially monogamous, although the highly dispersed individuals made this difficult to establish. In nearly all aspects, *M. micus* conformed to the sengi adaptive syndrome, although with some variation to accommodate desert conditions, such as sheltering habits to buffer desert temperatures. Their sheltering patterns also may have evolved to elude predators, preventing them from developing olfactory and visual search images. Their nocturnal activity may also be related to predator avoidance.

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Additional Information and Declarations

Competing Interests: None

Author Contributions: Galen B. Rathbun and John P. Dumbacher both conceived and designed the project, gathered and analyzed the field data, wrote the paper, prepared figures and tables, and reviewed drafts of the paper.

Animal Ethics: Our study was approved by the Namibia Ministry of Environment and Tourism (permit number 1927/2014), and reviewed by the California Academy of Sciences Institutional Animal Care and Use Committee (approval number 2014-1).

References

Anatrack. 2015. User's guide to Ranges 9. *Available at http://ranges-*

support.anatrack.com/wiki/Review_Of_Home_Range_Analyses (accessed 1 April 2015).

Burt WH. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.

Cowling RM, Hilton-Taylor C. 1999. Plant biogeography, endemism and diversity. In: Richard W, Dean J, Milton SJ, eds. *The Karoo: Ecological Patterns and Processes.* Cambridge, UK: Cambridge University Press, 42-56.

Desmet PG, Cowling RM. 1999. The climate of the karoo - a functional approach. In: Richard W, Dean J, Milton SJ, eds. *The Karoo: Ecological Patterns and Processes.* Cambridge, UK: Cambridge University Press, 3-16.

Dumbacher JP, Rathbun GB, Osborne TO, Griffin M, Eiseb SJ. 2014. A new species of round-eared sengi (genus *Macroscelides*) from Namibia. *Journal of Mammalogy* 95:443-454.

Dumbacher JP, Rathbun GB, Smit HA, Eiseb, SJ. 2012. Phylogeny and taxonomy of the round-eared sengi or elephant-shrew, Genus *Macroscelides* (Mammalia, Afrotheria, Macroscelidea). *PLoS (Public Library of Science) ONE* 7:e32410 (12 + 4 suppl pages).

Faurie AS, Dempster ER, Perrin, MR. 1996. Footdrumming patterns of southern African elephant-shrews. *Mammalia* 60:567-576.

Faurie AS, Perrin MR. 1995. A histological investigation of the structure and distribution of scent glands in four species of elephant-shrews. *Mammal Review* 25:95-96.

FitzGibbon CD. 1995. Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. *Mammal Review* 25**:**19-30.

Jennings MR, Rathbun GB. 2001. Petrodromus tetradactylus. *American Society of Mammalogists, Mammalian Species* 682:1-6.

Kenward RE. 2001. *A Manual for Wildlife Radio Tagging*. London: Academic Press.

Komer PE, Brotherton PNM. 1997. Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London, Series B* 264:1261-1270.

Lovegrove BG, Lawe M.J, Roxburgh, L. 1999. Confirmation of pleisiomorphic daily torpor in mammals: the round-eared elephant shrew *Macroscelides proboscideus* (Macroscelidea). *Journal of Comparative Physiology B* 169:453-460.

Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. 2002. *Atlas of Namibia; A portrait of the Land and its People*. Cape Town, South Africa: David Philip Publishers.

McNab BK. 2002. *The physiological ecology of vertebrates: a view from energetics.* Ithaca, NY: Comstock Publishing Associates (Cornell University Press).

Mzilikazi N, Lovegrove BG, Ribble DO. 2002. Exogenous passive heating during torpor arousal in free-ranging rock elephant shrews, *Elephantulus myurus*. *Oecologia.* 133:307-314.

Olbricht GA, Sliwa A, Abenant NL. 2012. Sengi research in the Free State, South Africa. *Afrotherian Conservation - Newsletter of the IUCN-SCC Afrotheria Specialist Group* 9**:**7-8.

Oxenham KH, Perrin M. 2009. The spatial organization of the four-toed elephant-shrew (*Petrodromus tetradactylus*) in Tembe Elephant Park, KwaZulu-Natal, South Africa. *African Zoology* 44**:**171-180.

Rathbun GB. 1979. The social structure and ecology of elephant-shrews. *Zeitschrift fur Tierpsychologie (Supplement)* 20**:**1-77.

Rathbun GB. 2009. Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology? *African Journal of Ecology* 47**:**1-13.

Rathbun GB. 2015. Distribution maps of sengis. *Available at* http://www.sengis.org/distribution.php (accessed 1 April 2015).

Rathbun GB, Osborne TO, Coals PGR. 2015. Distribution of the Etendeka round-eared sengi (*Macroscelides micus*), a Namibian endemic mammal. *Journal of Namibia Scientific Society* 63:149-153.

Rathbun GB, Rathbun CD. 2006. Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. *Journal of Zoology, London* 269**:**391-399.

Ribble DO, Perrin MR. 2005. Social organization of the eastern rock elephant-shrew (*Elephantulus myurus*): the evidence for mate guarding. *Belgian Journal of Zoology* 135 (Supplement)**:**167-173.

Rovero F, Rathbun GB, Perkin A, Jones T, Ribble D, Leonard C, Mwakisoma RR, Doggart N. 2008. A new species of giant sengi or elephant-shrew (genus Rhynchocyon) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology, London* 274:126-133.

Sauer EGF. 1972. Setzdistanz und Mutterfamilie bei der Kurzohrigen Elefantenspitzmaus. *Mitteilungen der Basler Afrika Bibliographien* 4-6**:**114-134.

Sauer EGF. 1973. Zum sozialverhalten der kurzohrigen elefantenspitzmaus. *Macrocelides proboscideus*. *Zeitschrift fur Saugetierkunde* 38**:**65-97.

Sauer EGF, Sauer EM. 1971. Die kurzohrige Elefantenspitzmaus in der Namib. *Namib und Meer* 2**:**5-43.

Sauer EGF, Sauer EM. 1972. Zur biologie de kurzohrigen elefantenspitzmaus *Macroscelides proboscideus. Zeitschrift des Kolner Zoo* 15**:**119-139.

Schubert M, Pillay N, Ribble N, Schradin C. 2009. The round-eared sengi and the evolution of social monogamy: factors that constrain males to live with single females. *Ethology* 115**:**972-985.

Schubert, M. 2011. A summary of the social system of the round-eared sengi. *Afrotherian Conservation - Newsletter of the IUCN-SCC Afrotheria Specialist Group* 8:12-13.

Seiffert ER. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evolutionary Biology* 7:224:13 pp.

Seely, M. 2004. *The Namib – Natural History of an Ancient Desert.* Windhoek, Namibia: Desert Research Foundation of Namibia.

Smit HA, Robinson TJ, WATSON J, Jansen van Vuuren B. 2008. A new species of elephant-shrew (Afrotheria: Macroscelidea: Elephantulus) from South Africa. *Journal of Mammalogy* 89:1257-1269.

Swart R, Marais C. 2009. *Landshapes, the geomorphology of Namibia.* Windhoek, Namibia: Macmillan Education Namibia Publishers.

Vernon CJ. 1999. Biogeography, endemism and diversity of animals in the karoo. In: Richard W, Dean J, Milton SJ, eds. *The Karoo: Ecological Patterns and Processes.* Cambridge, UK: Cambridge University Press, 57-85.

Yarnell RW, Metcalf DJ, Dunstone N, Burnside N, Scott DM. 2008. The impact of fire on habitat use by the short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in North West Province, South Africa. *African Zoology* 43**:**45-52.

Table 1. Data associated with Etendeka round-eared sengis captured at the study site in the Goboboseb Mountains, Namiba. Only those sengis with an * in last column were used for home range analyses.

ID	Sex	Age	Wt (g)	Initial Capt Date	Fate at end of study	Fate Date	Total days radio-tracked
4220	Female	Adult	31.5	30 Sept	Released	26 Oct	27*
4254	Male	Adult	-	8 Oct	Released	26 Oct	17*
4427	Female	Young	16.0	8 Oct	Disappeared	9 Oct	1
Ear tag	Female	Young	16.0	8 Oct	Disappeared	13 Oct	-
4585	Male	Adult	26.5	15 Oct	Disappeared	16 Oct	1
4612	Female	Adult	-	10 Oct	Predation	15 Oct	5*
4856	Female	Adult	34.0	3 Oct	Released	26 Oct	24*
4947	Male	Adult	31.0	3 Oct	Released	26 Oct	24*

Table 2. Home range areas (ha) of five radio-collared sengis (see Table 1) at the Goboboseb Mountains study site in Namibia using different methods of calculating area for comparison with other studies (see Discussion). Column headings: Obs No = number of locations used in home range analyses. MCP = minimum Convex Polygon with 100% and 95% of locations, Kernel with 95% locations, Concave = Concave polygon with 0.4 edge restricted option, OREP = Objective Restricted-edge Polygon (see methods). Max distance = maximum distance across MCP 100% home range in meters. % day shelter area = proportion of 100% minimum convex polygon of shelter area of MCP 100% column.

Comment [JDS20]: I find this difficult to understand

Sengi ID	Obs No	MCP 100%	MCP 95%	Kernel	Concave 0.4	OREP	Max distance	% day shelter area
4020F	102	8.48	5.35	5.64	5.0	6.46	549	25.7
4254M	56	36.21	34.05	82.81	16.0	13.44	1619	90.6
4612F	18	5.5	4.13	8.58	2.4	2.42	371	24.4
4856F	89	17.22	9.44	10.16	10.4	6.49	619	13.3
4947M	92	7.23	5.23	6.6	5.77	7.28	367	30.0
Average	-	14.92	11.64	22.76	7.91	7.21	705	36.8

Table 3. Linear distances (m) between arithmetic mean centers of home ranges among five radio-collared sengis that showed overlap using 100% convex polygon areas (see Table 4).

Sengi ID	4020F	4254M	4856F
4612F	--	494	--
4856F	608	406	--
4947M	256	-	364

Table 4. Percent home range area overlap for five radio-tracked sengis using the 100% (and 95%) convex polygon method of calculating areas.

Sengi ID	4020F	4254M	4612F	4856F	4947M
4020F	100	0 (0)	0 (0)	14.3 (0)	29.9 (0.5)
4254M	0 (0)	100	7.7 (8.2)	17.0 (15.8)	0 (0)
4612F	0 (0)	50.5 (67.2)	100	0 (0)	0 (0)
4856F	7.0 (0)	35.7 (56.8)	0(0)	100	17.4 (0)
4947M	35.1 (0.6)	0 (0)	0 (0)	41.4 (0)	100

Table 5. Day to day shelter use by five radio-tagged sengis at the Goboboseb Mountains study site in Namibia. Columns labeled “used...” are the number of times different day rock shelters were used during the study period by each individual (see text). The “Day intervals” column indicates the number of days between sequential use of the different shelters (separated by a slash). For example, 4020F used three different shelters twice each, and the days between the use of each of these shelters was 1, 6, and 1 days. This same sengi used one shelter four times, with the intervals between each use (separated by commas) being 3, 3, and 1 days. The total number of unique shelters used for each individual is in last column.

Sengi ID	Used x1	Used x2	Used x3	Used x4	Day intervals	Total
4020F	18	3	0	1	1/6/1/3,3,1	22
4254M	16	0	0	0	--	16
4612F	5	0	0	0	--	5
4856F	19	0	1	0	4,1	20
4947M	21	1	0	0	9	22
Total	79	4	1	1	--	--

Table 6. Comparison of home range areas for different sengi species as determined by different methods and reported in the literature. See Fig. 6 for full species names. Mean weight (g) and mean rainfall (mm) column based on data from references, or other literature. The tilde (~) indicates values are not calculated means, but an estimate for various reasons (see text). Mean areas (ha) are presented for sexes combined (C), but if the datum was not provided, then we calculated the mean of the two sexes. Male only (M), and females only (F). Number of individuals used to calculate mean areas for the sexes are in parentheses (M/F). Home range areas in BOLD font are used in comparing mean home range areas for sengis with mean body weight and mean study site yearly rainfall (Fig. 6). See methods section for explanation of inter-home-range distances.

Species	Weight Rainfall	100% convex	95% convex	OREP	95% kernel	Inter-home-range distances	Reference
M. micus	26.9g ~10mm	14.92 C (5)	11.64 C (5)	**7.21** C (5)	22.76	425 m	This study
M. flav	31.5g 24mm	~**9.0** (?)	-	-	-	300 m	Sauer 1973
M. prob	~50g 160mm	**1.25** C 1.7 M 0.8 F (23/24)	-	-	-	-	Schubert 2009
E. intufi	46.0g 293mm	-	**0.47** C 0.61 M 0.34 F (7/7)	-	-	-	Rathbun & Rathbun 2006
E. brachy	~45g 650mm	-	-	-	**0.33** C 0.41 M 0.25 F (4/5)	-	Yarnell 2008
E. myur	60.0g ~730mm	**0.30** C 0.39 M 0.20 F (6/6)	-	-	-	-	Ribble & Perrin 2005
E. myur	~60g 315mm	**1.06** C (4)	-	-	-	-	Olbricht et al. 2012
E. ruf	58g 640mm	**0.34** C (10)	-	-	-	-	Rathbun 1979
P. tetra	~200g ~800mm	**1.2** C (14)	-	-	-	-	FitzGibbon 1995
P. tetra	196g ~700mm	-	**0.95** C 1.2 M 0.7 F (4/6)	-	-	-	Oxenham & Perrin 2009
R. chrsyo	~500g ~1000mm	**4.1** C (28)	-	-	-	-	FitzGibbon 1995
R. chryso	540g 1040mm	**1.7** C (11)	-	-	-	-	Rathbun 1979

Figure 1: Study site in eastern Goboboseb Mountains, northwestern Namibia. View from the northern end of #4947M home range looking south across home range area of #4020F (see Fig. 3). White flagging on top of rock in foreground is a day shelter of #4947M. *Boscia* bush in far middle of image was used as a shelter at night (see results). The alluvial plains between the *Boscia* bush and the sand dunes in far distance, beyond rust-colored rocky *M*acroscelides *micus* habitat in foreground, were rarely used by *M. micus*, but are likely habitat of *M. flavicaudatus*. Wooden handle of radio-tracking antenna on right margin of image is 30 cm long. Photo 23 October 2014 by GBR.

Figure 2: Ear-tagged and radio-collared *M. micus* at study site in Goboboseb Mountains, Namibia. A) Sengi #4856F under *Commiphora* bush on 22 Oct 2014 at 2342 hrs. Visible are the reflective tag on

left ear and transmitter antenna extending from top of neck over back. Radio collar is completely hidden by fur. B) Sengi #4947M in a typical rock shelter on 25 Oct 2014 at 2351 hrs. Photos by GBR.

Figure 3: Object restricted-edge polygon (OREP) home range polygons for five radio-collared *Macroscelides micus* at study site in Goboboseb Mountains, Namibia. See Table 2 for home range areas. Note the disjointed home range of #4856F, with two points within the home range of #4947M. Home range polygons (colored for clarity) are concentrated on lower rocky slopes of rust-colored Etendeka volcanic substrate, with the exception of #4254M and #4020F (see results and Fig. 1.). Background satellite image captured on 17 Aug 2004, © 2015 Google Earth, DigitalGlobe.

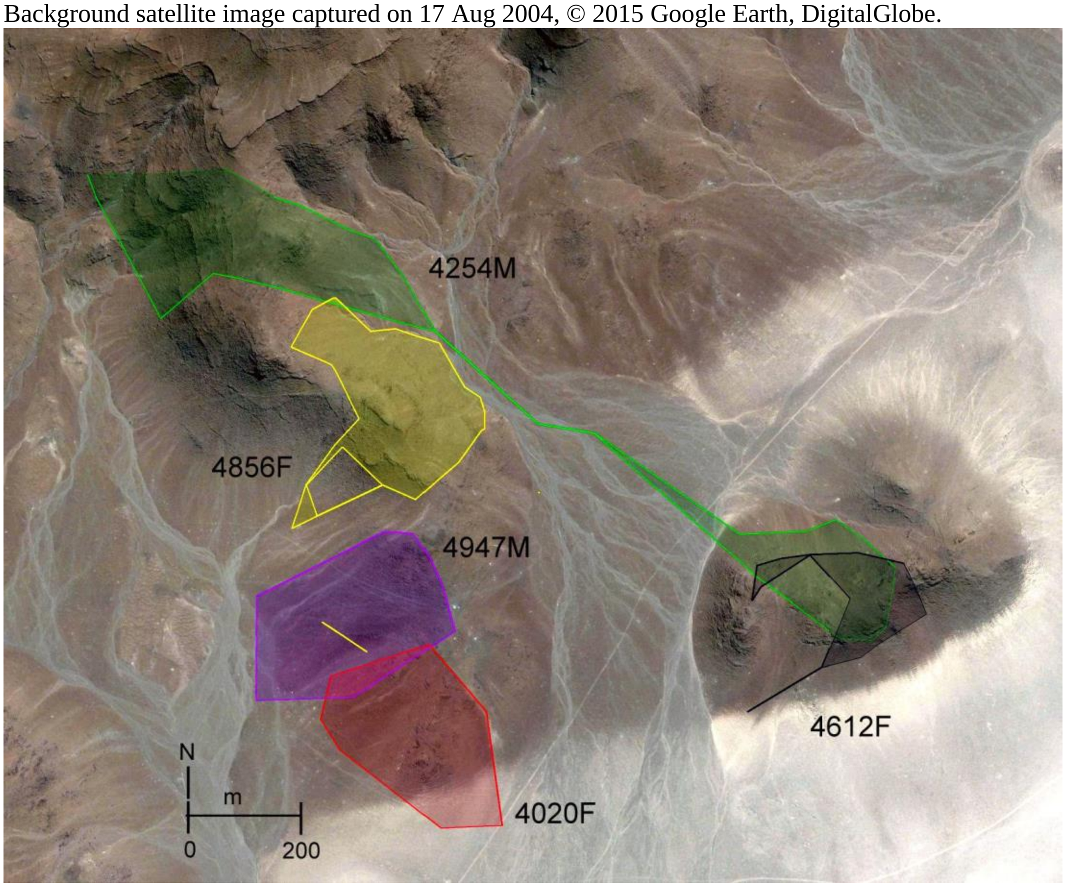
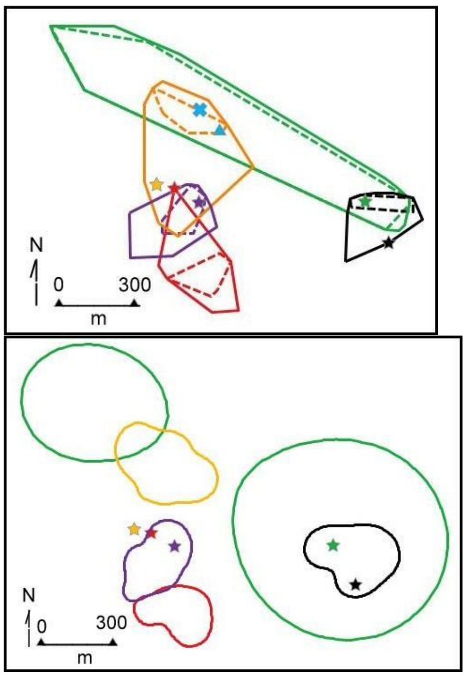


Figure 4: Home range polygons for five radio-collared *Macroscelides micus* at study site in the Goboboseb Mountains, Namibia. Colors and identifications same as Fig. 3, see Table 2 for areas. A) minimum convex polygons for home ranges (solid lines based on 100% of points) and day shelters (dashed lines 100% of shelters). Initial capture locations are shown with a star that match individual home range line colors. Capture locations of young #4427F and ear-tagged female are shown with a blue X, and adult #4585M in a blue triangle (see Table 1). B) Kernel 95% contour home range areas (see Table 1), including stars at initial capture locations.

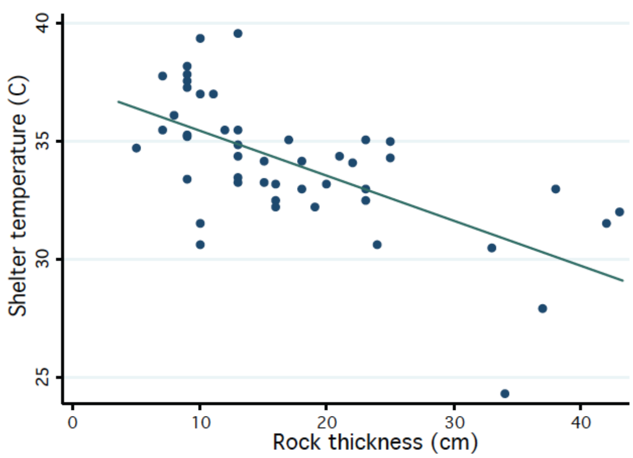


Comment [JDS21]: This fig would look neater if the external black boxes were the same dimensions

Figure 5: Regressions investigating the thermal inertia of *Macroscelides micus* shelter rocks. Graphs illustrate the negative relationship between shelter temperature and the thickness of the shelter rock (A). Because we measured shelters on different days, with different ambient air temperatures, we also plotted (B) the difference between air temperature and shelter temperature and regressed this against rock thickness.

Comment [JDS22]: Please provide some representation of error (eg 95% confidence bands) in these figures.

A.



B.

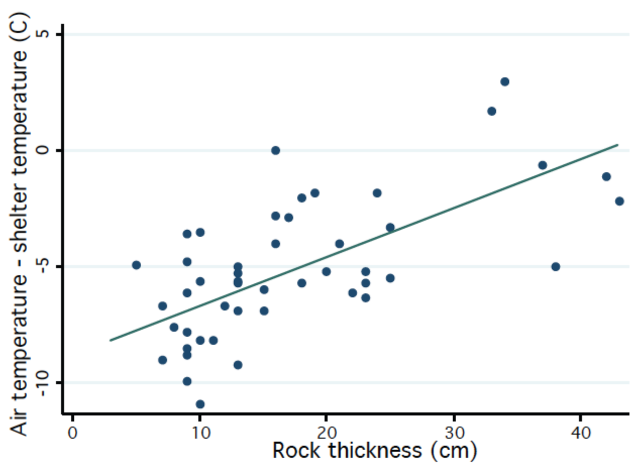


Figure 6: Scatter plots of sengi home range areas against study site rainfall (A) and sengi weights (B). Data from this study and published literature (Table 6).