

## Home range and use of diurnal shelters by the Etendeka Round-eared Sengi, a newly discovered Namibian endemic desert mammal

Galen B Rathbun, John P Dumbacher

To understand habitat use by the newly described Etendeka round-eared sengi (*Macroscolides 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). 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.

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3  
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13

**14 Abstract**

15 To understand habitat use by the newly described Etendeka round-eared sengi (*Macroscelides*  
16 *micus*) in northwestern Namibia, we radio-tracked five individuals for nearly a month. Home  
17 ranges (100% convex polygons) in the rocky desert habitat were remarkably large (mean 14.9  
18 ha) when compared to sengi species in more mesic habitats (< 1.5 ha). The activity pattern of *M.*  
19 *micus* was strictly nocturnal, which contrasts to the normal diurnal or crepuscular activity of  
20 other sengis. The day shelters of *M. micus* were under single rocks and they likely were  
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22 average, only 7% of the day shelters were used more than once by the five tagged sengis. The  
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26 solar radiation is probably an important aspect of *M. micus* thermal ecology, similar to other  
27 sengis. Compared to published data on other sengis, *M. micus* generally conforms to the unique  
28 sengi adaptive syndrome, but with modifications related to its hyper-arid habitat.

29

**30 Introduction**

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

44 From the earliest studies of sengis (Sauer, 1973; Rathbun, 1979), it was recognized that  
45 their combined life history traits formed a unique adaptive syndrome, not seen in any other  
46 mammals in other biogeographic regions of the world. The syndrome blends life history  
47 strategies usually associated with ant-eaters and some antelopes, including a diet of invertebrates  
48 with an associated long nose and tongue and small mouth, highly cursorial locomotion, small  
49 precocial litters, absentee maternal care, lack of nest-use (Macroscelidinae only), and social  
50 monogamy. These traits do not vary greatly among the species so far studied, despite the  
51 considerable variation in their size and habitats (Rathbun, 1979; 2009).

52 When it was found that some sengis were socially monogamous (Rathbun, 1979), which  
53 is unusual in mammals (Komer & Brotherton, 1997), additional studies were completed to better  
54 understand the evolution of this social organization (FitzGibbon, 1995; Ribble & Perrin, 2005;  
55 Rathbun & Rathbun, 2006; Schubert et al., 2009; Oxenham & Perrin, 2009). One of the main  
56 focuses of these studies has been home range characteristics, but other aspects of their life  
57 history have been documented incidentally, such as the unusual sheltering habits among the  
58 Macroscelidinae.

59 Although Rathbun (2009) reviewed sengi taxonomy and life history traits, recent

60 taxonomic revisions have resulted in new taxa being recognized (Rovero et al., 2008; Smit et al.,  
61 2008; Dumbacher et al., 2012). The Etendeka round-eared sengi (*Macroscelides micus*  
62 Dumbacher & Rathbun, 2014) was discovered in 2006 and is the newest species to be described  
63 (Dumbacher et al., 2014). It is the smallest sengi and only occurs in a small remote hyper-arid  
64 area in northwestern Namibia, sandwiched between the coastal Namib Desert and the inland  
65 escarpment (Swart & Marais, 2009; Rathbun, Osborne & Coals, 2015).

66 The objective of our research on *M. micus* was to gather the first basic information on  
67 habitat and shelter use to determine the similarity of these and other life history traits to those of  
68 previously studied sengis, especially the Macroscelidinae.

69

## 70 **Materials and Methods**

71 Our study site (latitude -21.32338, longitude 14.32738) was in northwestern Namibia, within the  
72 eastern edge of the Namib Desert, and the lower eastern slope of the Goboboseb Mountains,  
73 which are part of the Etendeka geological formation that was created by lava flood events about  
74 132 million years ago (Swart & Marais, 2009; Fig. 1). The study site was about 580 m above sea  
75 level, on the lower slopes of a 900 m high mountain. The slopes (average = 13.4°, range = 3-29°,  
76 N = 48) were composed of rust-colored compact gravel with an estimated 40-95% of the surface  
77 covered with fist to building-block sized rocks (Fig. 1). The closest town was Uis (population  
78 about 4,000), about 60 km to the east. The study site was about 55 km inland from the cold  
79 Benguela ocean current, which resulted in wet coastal fogs at our site on about a quarter of the  
80 nights. The fog left moisture on rock surfaces, but both completely dissipated by midmorning.  
81 Based on our interpolation of weather data from Henties Bay and Uis, we estimate the average  
82 yearly rainfall at the study site is 10 mm. During our fieldwork, the average overnight low  
83 temperature at our study site was 9.6° C (range = 3.9-18.7° C), and the average maximum  
84 (afternoon) temperature was 27.8° C (22.0-30.0° C). On many afternoons, winds blew up to 13.5  
85 m/sec (48 km/h). Full moon occurred on 7 October, and sunrise and sunset was at about 0630  
86 and 1905 hrs respectively.

87 Our study spanned from 30 September through 26 October 2014, and we trapped (H.B.  
88 Sherman Traps, Tallahassee, Florida; model LFA, 7.6 x 8.9 x 22.9 cm) and tagged sengis on 13  
89 days during the first two weeks. We set about 200 traps per night at 10-20 m intervals on  
90 transects within about 50 ha of likely *M. micus* habitat, and traps were moved to new transects  
91 every 1-4 days. We baited traps with a dry mixture of rolled oats, peanut butter, and Marmite (a  
92 yeast paste or spread), opened the traps at dusk, and checked and closed them at dawn. Trapped  
93 sengis (we only captured *M. micus*) were immediately tagged and released at the capture site. At  
94 the end of our study, the sengis were recaptured at their day shelters by hand or flushed into mist  
95 nets (DTX 36 mm stretch mesh), all radios and tags were removed, and the sengis were released.

96 We attached a reflective ear-tag inside the distal margin of a pinna – right ears of males,  
97 and left ears of females. The tags were constructed of two 5-mm-diameter disks of reflective  
98 silver-colored plastic (Reflexite FD 1430 marine adhesive tape), which only reflected when a  
99 light source was aligned closely with the spotter's eyes, thus eliminating the likelihood of  
100 increased predation on the ear-tagged sengis on moon-lit nights. The disks were attached to an  
101 ear with a nylon stud (monofilament fishing line) through holes previously melted in the centers  
102 of the two disks and a hole pierced through the pinna (Fig. 2A; see Rathbun, 1979; Rathbun &  
103 Rathbun, 2006 for further details). Because the sengis were nocturnal (see results), we used  
104 bright (275 Lumen) narrow-beamed light-emitting diode (LED) headlamps (Princeton Tec model  
105 Apex, and Fenix model HP15) to spot the ear-tagged sengis, often with the aid of binoculars.

106 The ear tags were visible up to 100 m away, but fog, dust, and rocks often reduced visibility to  
107 much lower distances. Vegetation was sparse or lacking and did not hinder visibility (Fig. 1).

108 We also attached radio-collars (Holohil Systems, Carp, Ontario, Canada; transmitter  
109 model BD-2C, frequencies in 164 MHz band, weight about 1.5 g) to seven of the eight captured  
110 sengis. The transmitter whip antennae were incorporated into Tygon tubing collars, leaving  
111 about 8 cm extending from the top of the collars, and the transmitters hung from the bottom of  
112 the collars.

113 We located the radio-tagged sengis by homing (Kenward, 2001) using receivers  
114 (Communications Specialist, Orange, Calif., model R-1000; Wildlife Materials International,  
115 Murphysboro, Illinois, model TRX-1000S) attached to two-element Yagi directional receiving  
116 antennae (Telonics, Mesa, Arizona). Upon approaching a sengi, the ear-tag was easily spotted,  
117 when we made a mental note of a prominent landscape feature at the sengi's location, and took  
118 GPS coordinates there. If the sengi was sheltering under a rock, we took the coordinates of the  
119 shelter. At night, one of us radio-tracked from about 2100 hrs to 0100 hrs, and the other from  
120 about 0200 hrs to 0600 hrs. Combining our effort, each sengi was located between two and six  
121 times per night, in arbitrary order. During the day, we located sheltering animals in the morning  
122 or midday, and again at dusk when we monitored the departure of selected sengis from their day  
123 shelters. We determined universal transverse Mercator (UTM) coordinates with the GPS  
124 functions on a Motorola MotoG (2013 model) mobile phone and a Samsung Galaxy Player 4.  
125 Both receivers used the Android operating systems with the LOCUS MAPS navigation  
126 application (version 3.4.0) for entering, storing, plotting, and exporting location coordinates and  
127 associated data. In the field, locations were based on 1 sec intervals averaged during 15-60 sec.  
128 We tested the accuracy of the receivers at the field site, and they were within a diameter of 5 m  
129 (MotoG) and 10 m (Galaxy).

130 To determine home range areas, we used RANGES 9 software (Anatrack Ltd., Wareham,  
131 Dorset, UK). We ran several different analyses (Kenward, 2001) in order to compare home  
132 range size estimates with published values. We included the object restricted-edge polygon  
133 (OREP) analysis (Anatarack, 2015) because this and the concave polygon analysis may be useful  
134 for future comparisons. For the analyses, we used a censored data set that included capture  
135 localities (except for the OREP analysis), all radio and sighting records, all day and night shelter  
136 locations, and the final capture (or death) location for each individual. We eliminated records  
137 that were obviously incorrect due to observer error. Because we have not analyzed the data for  
138 differential use of home range areas, and the sengis were remarkably active and swift during the  
139 night, we did not censor the data set for location and time auto-correlations. For all home range  
140 analyses, the units of measure were meters with the resolution set at 1 m, and we used the 'curve  
141 and polygon' option in RANGES 9. To keep our home range estimates comparable to published  
142 estimates, we only used the 'buffer tracking resolution' option for the concave polygon and  
143 OREP analyses. For the convex polygon (= minimum convex polygon or MCP) analysis we  
144 used 95% and 100% 'cores' based on 'arithmetic mean centers'. For the concave polygon analysis  
145 we used the 'selected edge restriction' option with a value of 0.4. For the OREP analysis we used  
146 the '> 5% distribution distance' and 'KED and Strip' options. We used all the default settings for  
147 the 95% core kernel analysis, which were fixed kernel, location density contours, fixed  
148 smoothing multiplier, and 40 matrix cells set to rescale to fit matrix.

149 While radio-tacking sengis after dawn, we located, flagged and recorded GPS coordinates  
150 for the day shelter used by each sengi, and then rechecked shelters arbitrarily during the  
151 remainder of the day for continued occupancy. The last and most focused check started at about

152 sunset, when one of us sat inconspicuously among rocks or boulders about 5-10 m from an  
153 occupied shelter, and watched for sengi movement and listened for variations in radio signal  
154 pitch, strength, and direction, which indicated an active sengi. Once the animal was active, we  
155 briefly searched the area around the shelter with binoculars and headlamp for an ear-tag  
156 reflection, thus further confirming that the sengi was active and had departed its shelter for the  
157 night.

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

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

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

175

## 176 **Results**

### 177 Capture and radio-tracking

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

187

### 188 Home range

189 The average home range sizes of the five radio-collared sengis, as determined by the different  
190 methods of analyses, were highly variable (Table 2), spanning from 7.2 to 22.8 ha. The average  
191 maximum length of the home ranges, calculated using the 100% convex polygon method, was  
192 705 m. However, this was greatly influenced by #4254M that had a remarkably large oblong-  
193 shaped home range (Figs. 3 & 4). The average distance between the arithmetic mean centers of  
194 overlapping 100% convex home ranges was 425 m, range 256-608 m, which is a useful  
195 comparative measure of sengi dispersion (see interpretation of *M. flavicaudatus* home range  
196 estimates in Discussion). Because of our small sample size and uncertainty that all resident  
197 sengis in the study area were captured, we have not presented detailed overlap analyses.

198 The home range size (Table 2) and shape (Figs. 3 & 4) of #4254M was odd compared to  
199 the other four sengis. We located this male mostly at each end of his oblong-shaped home range,  
200 which spanned over 1.5 km (Table 2). He moved from end-to-end of his home range 11 times,  
201 making the journey so quickly that we were only able to roughly track his path once, when he  
202 traveled the length of his home range (about 1.5km and over 80 m in elevation) within 60 min,  
203 presumably in a relatively straight course with few pauses. The area between the ends of his  
204 home range was atypical habitat for *M. micus*, being a slightly sloping alluvial fan composed of  
205 softer and lighter-colored gravels and fewer rocks than on the surrounding higher slopes (Fig. 3).  
206 The only other home range that was not completely located on rust-colored Etendeka volcanic  
207 substrates was that of #4020F, with about 0.73 ha at the southern edge falling on the lowest  
208 alluvial flats in the study area, which were composed of finer and lighter colored gravels with  
209 few rocks on the surface (Figs. 1 & 3). The home range areas of all the sengis tended to fall  
210 below the steeper areas of the Etendeka formation that had huge boulders and rock faces (Fig. 3).

211 We closely followed #4020F on her home range twice during the night of 1 October 2014  
212 by keeping sight of her reflective ear-tag. Starting at 2152 hrs, she covered about 219 m in 10  
213 min (1.3 km/hr) and her route (based on the GPS-determined track of the observer) was a large  
214 circle that did not quite meet the starting point. The second track started at 2217 hrs, and  
215 covered 89 m in 3 min (1.6 km/hr) in roughly a straight line. The sengi easily kept ahead of us  
216 as it bounded from rock to rock, obviously following a familiar route. During our study, we  
217 found no worn sengi paths across the substrate, but nevertheless they appeared to follow familiar  
218 routes, as demonstrated when we spotted a lone unmarked sengi (became #4585M) within the  
219 home range of #4856F. The sengi appeared unfamiliar with the area because he continually  
220 stumbled over and bumped into rocks as he clumsily fled, which allowed us to chase and hand-  
221 capture him while keeping him in the beam of our headlamp (no physical or visual impairments  
222 were noted when collared and released). It was impossible to similarly capture our tagged sengis  
223 because they were too agile and swift.

224 After we radio-collared #4585M, we only located him once the next day, even though we  
225 searched widely (several km) in areas adjacent to our study area on several days. Because our  
226 transmitters had a line-of-sight range of about 1 km, it seems unlikely that we lost the signal. It  
227 is possible that the transmitter failed, but we never spotted any male ear-tagged sengis without an  
228 associated radio signal. Sengi #4585M possibly became prey of a Cape fox (*Vulpes chama* A.  
229 Smith 1833) that we saw in our study site on several nights. This was probably also the fate of  
230 #4612F, given that we found her shed and functioning transmitter with tooth damage (Table 1).

231 The areas (100% convex polygons) encompassing all day shelters for each of the five  
232 radio-tagged sengis averaged 36.8% of their respective home range (Table 2). The distribution  
233 of day shelters within a home range showed no obvious pattern, other than the sengis used  
234 locations with suitable rock shelters and tended to be well inside the home range boundaries (Fig.  
235 4).

### 236 237 Shelter characteristics

238 We examined a sample of day shelters used by the five collared sengis (#4020F n = 13, #4254M  
239 n = 9, #4612F n = 5, #4856F n = 11, #4947M n = 11). The ground surrounding the shelters was  
240 always rock and boulder strewn, averaging 52% coverage (range 40%-95%). Aspect and slope  
241 varied by animal, but showed no overall trend that differed from the surrounding habitat in each  
242 home range. Shelters were typically under a single rock with a horizontal crevice (Fig. 2B) with  
243 an average height of 6.6 cm (range 3-12 cm). No shelters showed any obvious signs of

244 alteration, such as excavation, digging, or collected bedding. Three of 49 shelters had some  
245 windblown grasses or plant matter, but it was never noticeably arranged or manipulated, and  
246 seemed typical of the surrounding boulder fields. Interior substrates of dust, sand, or gravel  
247 more or less matched the surrounding substrate. Only one shelter of 49 contained feces (3  
248 pellets), and none of the shelters had partially eaten food or scraps. The entrances to shelters  
249 showed significant directionality (Raleigh's Z test,  $n = 41$ ,  $z = 3.66$ ,  $p < 0.05$ ) with an average  
250 compass direction of  $193^\circ$  south by southwest, despite the fact that slope aspect varied among  
251 individuals and showed no overall directionality (Raleigh's Z test,  $n = 49$ ,  $z = 0.35$ ,  $P > 0.2$ ).

252 We regressed shelter temperature against the shelter rock thickness and recovered a  
253 significant negative relationship ( $n = 47$ ,  $R^2 = 0.396$ ,  $p < 0.01$ , Fig. 5A), thus confirming that  
254 thicker rocks may provide more stable temperature environments and protection from wide  
255 temperature fluctuations. Because we measured shelters on different days, we additionally  
256 sought to control for differences in midday temperature by subtracting shelter temperature from  
257 local ambient air temperature. We again found a significant positive relationship, suggesting that  
258 thicker rocks were cooler relative to air temperature (general linear regression,  $n = 47$ ,  $R^2 =$   
259  $0.4117$ ,  $p < 0.01$ , Fig. 5B). Despite confirming the potential benefit of thicker shelter rocks to  
260 protect from extreme temperatures or wide fluctuations, we cannot confirm whether sengis are  
261 actually choosing shelters to take advantage of these benefits. In fact, most shelters were under  
262 rocks with smaller thicknesses (Fig. 5), but it is not clear whether this is due to an active choice  
263 on the part of sengis, or whether they are constrained by availability.

264

#### 265 Shelter use

266 The collared sengis were strictly nocturnal. Once sheltered at night, usually near dawn, they  
267 normally remained in the same shelters throughout the day, and were very reluctant to leave. For  
268 example, we checked 33 occupied shelters twice during the day between 13 and 5.5 hours prior  
269 to sunset, and in only two cases did a sengi change shelters. In one case (#4947M) the distance  
270 between shelters was about 3 m, and in the second case (#4612F) it was about 30 m. On three  
271 days we checked #4020F four different times during daylight, and on one day three times, and  
272 #4856F at four different times on one day. Neither of these sengis shifted shelters during the  
273 day. When we recaptured the four remaining radio-tagged sengis at the end of the study on 26  
274 October 2014, between 1000 hrs and 1145 hrs, we had to dislodge or remove the shelter boulders  
275 to get the animals to flee into the capture nets, which further demonstrated their reluctance to  
276 leave their day shelters.

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

283 We determined whether collared sengis used different shelters during late night (usually  
284 just before dawn) compared to the following day. In 26 of the 31 cases, switching did not occur,  
285 indicating that the sengis often sheltered for the day well before first light. Related to this  
286 pattern, we extracted location data for four sengis (those with the most robust overall data sets:  
287 #4020F, #4254M, #4856F, #4947M) and determined whether we found them in a night shelter or  
288 not during two periods: between 2100 and 0100 hrs (early night), and between 0200 and 0600  
289 hrs (late night). In the early period, there were 130 pooled observations, with 14 in night shelters

290 (10.8%). During the late period, we had 117 observations with 37 (31.6%) in night shelters.  
291 These data support our subjective assessment that the animals were more active early in the night  
292 compared to late at night. This pattern made it nearly impossible for us to determine when  
293 animals retreated to shelters for the day, compared to when they left their day shelters for a night  
294 of activity. We monitored 40 day shelters starting at about sunset and the average departure time  
295 was 1938 hrs, with a range of 1913 to 1959 hrs. In two additional cases a sengi (#4254M) had  
296 not left the day shelter by 2010 and 2015 hrs, when we terminated observations.

297 Even though the sengis rarely switched shelters within a day, they readily switched  
298 shelters from day to day, rarely using a site more than once (Table 3). Pooling individuals, we  
299 monitored 85 day shelters and 93% were used once, 5% twice, and 1% each for three and four  
300 times. The average interval between using the same shelter was 3.2 days, with a range of 1-9  
301 days. We found no evidence that different individuals used the same shelter, nor that more than  
302 one sengi occupied a shelter at the same time, although it is remotely possible that untagged  
303 sengis paired with our collared animals.

304 Twice we located sengis under low bushes at night — a 1 m high *Commiphora* bush and  
305 a 2 m high *Boscia* bush (Fig. 1). Bushes in this size range only numbered 2 or 3 individuals in  
306 each home range. While under the canopy of these bushes, the sengis were “nervous” and easily  
307 disturbed by our movement, running to the opposite side of the bush from the observer on  
308 several occasions, but they did not flush into the open nor did they foot drum. While we were  
309 about 5 m from the animals, we observed them for about 15 min while they groomed and rested  
310 (Fig. 2A) on the surface of the gravel substrate. They were always alert with their eyes open and  
311 ready to flee. These observations were terminated after they bounded off into the night.

312

## 313 Discussion

314 We were unsure what to expect in a first study of the behavioral ecology of a newly discovered  
315 species found only in a hyper-arid desert, especially in a group of mammals already known for  
316 several unusual traits (see introduction and Rathbun, 2009). Soon after starting our field work,  
317 we realized that densities were disappointingly low, and in conjunction with the difficult logistics  
318 associated with large home ranges, we knew our data would be limited. Faced with interpreting  
319 our findings, we realized that few insights could be gained in terms of general home range  
320 information and theory. However, some of our findings provided ample opportunity to compare  
321 some features among different sengi species, and thereby gain some interesting insights into the  
322 behavioral ecology of this group. Below, we discuss our findings in the context of sengi life  
323 history traits that lead to further insights into the sengi adaptive syndrome.

324

### 325 Home ranges

326 The estimated home range sizes of the five sengis we collared are dependent on the method of  
327 analysis. Both convex polygon and kernel methods incorporate areas that were rarely if ever  
328 used, but we have included both metrics to allow comparison with published data. Our limited  
329 data suggest that a more conservative representation of the home ranges of our tagged sengis is  
330 obtained with the relatively new OREP method, especially for #4254M (Table 2, Figs. 3 and 4).  
331 Unfortunately, no previous sengi studies have used this method, as is the case with the concave  
332 polygon technique. We nevertheless have included both with the hope that future studies will  
333 also find that they are a useful alternative to convex polygon estimates because they may provide  
334 better insights into space use by sengis.

335 The three species of *Macroselides* occupy very arid habitats (Dumbacher et al., 2012;

336 Dumbacher et al., 2014) compared to other sengis, thus ecological insights may be gained from  
337 these and other sengi species. Schubert et al. (2009) provides quantitative home range data for  
338 the Karoo round-eared sengi (*Macroscelides proboscideus* Shaw 1800) near Springbok, South  
339 Africa, based on radio-tracking methods. Using direct observations, Franz Sauer (1973) with his  
340 wife Elinore report home ranges of about 1 sq km for the Namib round-eared sengi  
341 (*Macroscelides flavicaudatus* Lundholm 1955) in the Namib Desert southeast of Walvis Bay,  
342 Namibia, which is over 80 times larger than what Schubert et al. (2009) found (Table 4). As  
343 additional home range data for other species were published (Table 4), sengi home ranges of a  
344 square kilometer seemed almost unbelievable.

345 To better understand the Sauer (1973) home range estimate, we closely examined his  
346 definitions of space use, which are different than what is typically used. For example, Sauer  
347 (1973, pages 74 and 94 among others) states that *M. flavicaudatus* had an average home range of  
348 a square kilometer, but he also indicates that this was in fact a crude calculation of density based  
349 on his 20 sq km study area. On the other hand, based on his descriptions, it is almost certain that  
350 his sengis had home ranges that were larger than other small sengis, which are less than 2 ha  
351 (Table 4). To obtain a crude home range estimate that more closely conforms to the more widely  
352 accepted definition of Burt (1943), we used the 300 m mode of the average distances between  
353 the main shelters used by two closest neighbors on adjacent home ranges (Sauer, 1973, pg 71,  
354 Table 1, Fig. 7, pg 95). If we assume that the length of each of two adjacent sides of a  
355 hypothetical home range is thus 300 m, and adjoining home ranges were in relatively  
356 homogeneous habitats (Ibid.), we obtain an estimated home range area of about 9 ha, which is  
357 over an order of magnitude smaller than the density of 100 ha/sengi that he called a “home  
358 range”. This re-estimation of home range size (*sensu* Burt, 1943) reconciles the seemingly small  
359 modal average distances between shelters on adjacent home ranges of 300 m and an estimate of  
360 home range areas of 1 sq km. Lastly, 300 m is not very different than our similar metric of 425  
361 m for *M. micus* (Table 4). Even through our home range estimate for *M. flavicaudatus* is not  
362 strictly comparable with other sengi home range estimates, it probably is sufficient for our  
363 discussion.

364 The literature related to mammalian home ranges is large, including attempts to relate the  
365 sizes of home ranges with physiological factors such as trophic level (calorie sources), body size  
366 (calories needs), metabolic rate (rate that calories are used), social structure (group versus  
367 individual needs), and phylogeny (McNab, 2002 pages 335-336). These factors are highly  
368 variable across a wide range of mammals, making comparisons difficult, except for the sengis,  
369 which share a very tightly defined adaptive syndrome with very similar phylogeny, metabolic  
370 rate, morphology, diet, reproduction, locomotion, social structure, etc. (Rathbun, 1979; 2009). In  
371 contrast, the variation in the body size and habitats occupied by sengis stands out (Rathbun 2009,  
372 see Introduction).

373 Although body weight data for sengis are available (Table 4), there are several metrics  
374 that might be used to quantify the habitats used by sengis. Given the life history traits of sengis,  
375 we believe that prey abundance is particularly important. Unfortunately, prey abundance is not  
376 easily measured or available from most sengi study sites (but see Rathbun, 1979; FitzGibbon,  
377 1995), however rainfall is probably a reasonable proxy, and these data are available (Table 4).  
378 When sengi home range sizes are plotted against rainfall, the points for *M. flavicaudatus* and *M.*  
379 *micus* are far removed from the rest of the sengis in the plot (Fig. 6A), despite our using  
380 conservative estimates for these two species (see discussion of Sauer above, and Table 2).  
381 Although *M. proboscideus* occupies a low-rainfall habitat similar to its congeners, it clusters

382 with the other smaller sengis (Fig. 6A), which suggests that low rainfall habitats do not fully  
383 explain home range size for similarly sized sengis (keeping in mind their very similar adaptive  
384 syndrome). The Succulent Karoo, where the data for *M. proboscideus* were gathered (Schubert  
385 et al., 2009; Schubert 2011), is a relatively small area between the very low and concentrated  
386 winter rainfall regime of the Namib Desert to the north, and the low summer rainfall regime of  
387 the Mediterranean climate to the south. Although the Succulent Karoo is arid, the rainfall is  
388 spread across both winter and summer months (Desmet & Cowling, 1999). This rainfall pattern  
389 results in a richer vegetation (Cowling & Hilton-Taylor, 1999) and invertebrate fauna (Vernon,  
390 1999) than might be expected based only on total average rainfall. Thus, the home range area of  
391 *M. proboscideus* clusters closer to the other small sengis than with *M. flavicaudatus* and *M.*  
392 *micus* (Fig. 6A). The general positive relationship of mammalian body weight and home range  
393 size (McNab, 2002) is supported by syntopic *Petrodromus* and *Rhynchocyon* in a coastal forest  
394 in Kenya (FitzGibbon, 1995; Table 4; Fig. 6B), but is overshadowed by the *Macroselides*  
395 species, especially the two in the Namib Desert (Fig. 6B). Based on our analysis, we  
396 hypothesize that prey availability may have the greatest influence on the home range sizes of  
397 sengis, but unfortunately data on prey availability are lacking for most sengis.

398 In most sengi home range studies, a male will occasionally attempt to overlap with more  
399 than one female, often resulting in an exceptionally large and oblong home range. However, this  
400 configuration is not stable due to the would-be polygamous male retreating when a new male  
401 appears to associate with (and mate-guard) one of the females (Komer & Brotherton, 1997;  
402 references in Table 4). We speculate that the large hour-glass-shaped home range of #4254M  
403 represented a similar attempt at polygamy (although we did not trap the northwestern end of his  
404 home range to determine if there was a female in that area).

405 Male-female sengi pairs exhibit few pair-bond behaviors and spend relatively little time  
406 together (except during brief periods of estrus), yet some species have home ranges that are  
407 virtually congruent (Rathbun, 1979), while in others the ranges only partially overlap (all other  
408 references in Table 4, Fig. 3). One hypothesis to explain this variation is that the degree of  
409 overlap is density dependent. In habitats where sengis essentially occupy all suitable space and  
410 thus are dense, male and female home ranges are nearly congruent and intra-sex overlaps are rare  
411 because the areas are defended sex-specifically, whereas when sengis are more dispersed, the  
412 home range overlap within male-female pairs is reduced (Rathbun & Rathbun, 2006). At our  
413 Namibia study site, we were unable to capture and radio-track as many sengis as we had hoped,  
414 and we could not document that all resident sengis were radio-tagged. However, based on our  
415 intensive trapping effort and extensive radio-tracking and observation activities on the study site,  
416 it is unlikely that many if any resident sengis escaped our notice. We speculate that the home  
417 range configurations that we documented (Fig. 3) are consistent with the density dependent home  
418 range overlap model. We again hypothesize that prey availability may be the most important  
419 underlying factor in determining sengi density, and thus many home range characteristics.  
420 However, multiple factors may be involved (Di Stefano et al., 2011), including mate availability.  
421 Sauer (1973) suggested that shelters may have been limiting for *M. flavicaudatus*, although we  
422 doubt this was the case at our study site (Fig. 1).

#### 423 424 Sheltering

425 There were two noteworthy findings regarding shelters. First, was the lack of a central or home  
426 burrow or shelter, as found in many other small mammals. Second, was how unremarkable the  
427 shelters were; there was no sign of bedding, excavation or alteration, and every shelter seemed to

428 simply be a small space or crevice under a rock where sengis hid during the day. Both findings  
429 are similar to the sheltering habits of other Macroscelidinae (Rathbun, 2009). It is difficult to  
430 determine which factors were motivating the use of rock shelters by *M. micus* because of the  
431 large number of possible factors, including sengi behavior, predation threat, weather,  
432 environmental conditions, and shelter availability. We believe the most important two factors  
433 were the thermal traits of the shelters and predation threat.

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

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

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

465 Predation is often difficult to document, but one of our collared sengis was preyed upon,  
466 possibly by a Cape Fox, suggesting that avoiding predation may be challenging. Thus, one  
467 important feature of shelters is likely the availability of refuges that provide adequate protection  
468 from predators. Perhaps just as important are the use of multiple shelters with a very low rate of  
469 return to any single shelter, and the lack of feces accumulation in the shelters. These behaviors  
470 may be related to reducing visual or olfactory cues that predators use to find sengis. Related  
471 explanations were proposed for the similar spatial and temporal traits of sheltering sites of  
472 *Elephantulus intufi* (Rathbun & Rathbun, 2006), and also the nesting traits of *Rhynchocyon*  
473 (Rathbun, 1979). Additionally, at our study site there was little cover other than under rocks.

474 This may explain the strictly nocturnal behavior of *M. micus*, which effectively would avoid  
475 predation by the numerous diurnal predators, including several raptors and bustards.

476  
477 Sengi adaptive syndrome

478 We found that *M. micus* largely conformed to the life history features characteristic of other  
479 sengi species, especially the Macroscelidinae, including swift and agile cursorial locomotion,  
480 relatively exposed multiple sheltering sites, and possibly spatial organization. Additionally, *M.*  
481 *micus* has small litters of precocial young (Dumbacher et al., 2014). However, we were unable to  
482 confirm whether *M. micus* has a female absentee maternal care system, and whether its diet was  
483 composed mainly of small invertebrates, as it almost surely does based on the near absence of  
484 any other visible food at our study site and its morphology, which is very similar to other sengis  
485 that are known to prey on invertebrates (Rathbun, 2009).

486 There are several behavioral features that are worth discussing for future comparative  
487 studies, but may only be peripheral to the adaptive syndrome. We failed to find any indication  
488 that *M. micus* created trails on the substrate, as do other sengis (Rathbun, 1979), including *M.*  
489 *flavicaudatus* (Sauer, 1973). We suspect that *M. micus* used familiar travel routes, but paths did  
490 not form because the substrate was dominated by rock. If sengis traveled mainly on familiar  
491 routes, we probably only trapped them when a route coincided with a trap location, which might  
492 explain our low capture rate. We also failed to see or hear foot drumming during stressful  
493 situations, including while in live traps, which is also characteristic of other sengis (Rathbun,  
494 1979; Faurie, Dempster & Perrin, 1996). Neither distinctive latrines of dung pellets (Rathbun  
495 1979), nor scent-marking behaviors (Rathbun, 1979; Faurie & Perrin, 1995) were observed  
496 during our study, despite *M. micus* having a very large subcaudal scent gland (Dumbacher et al.,  
497 2014). Daily torpor, which is an energy conservation strategy in *M. proboscideus* (Lovegrove,  
498 Lawe, Roxburgh, 1999), may be used by *M. micus*, based on our observation of a torpid  
499 individual.

500  
501 **Conclusions**

502 The home range pattern that emerged from our study was similar to the findings for other sengis,  
503 except that the areas of *M. micus* were exceptionally large. Their size was likely the result of  
504 low rainfall, sparse vegetation, and low densities of invertebrate prey. The home range  
505 characteristics that we found are similar to those of socially monogamous sengis, suggesting that  
506 *M. micus* may also be socially monogamous, although the highly dispersed individuals made this  
507 difficult to establish. In nearly all aspects, *M. micus* conformed to the sengi adaptive syndrome,  
508 although with some variation to accommodate desert conditions, such as sheltering habits to  
509 buffer desert temperatures. Their sheltering patterns also may have evolved to prevent the  
510 accumulation of olfactory and visual cues used by predators. Their nocturnal activity may also  
511 be related to predator avoidance in a desert with little plant cover.

512  
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524

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**Table 1** (on next page)

Data associated with Etendeka round-eared sengis captured at the study site in the Goboboseb Mountains, Namibia.

Only those sengis with an \* in last column were used for home range analyses.

1

ID	Sex	Age	Wt (g)	Initial Capt Date	Fate at end of study	Fate Date	Total days radio-tracked
4020	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*

2

**Table 2** (on next page)

Home range areas (ha) of five radio-collared sengis (see Table 1) at the Goboboseb Mountains study site in Namibia.

Column headings: Obs No = number of locations used in home range analyses, CP = 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 CP 100% home range in meters, % day shelter area = proportion of shelter area to home range area based on 100% convex polygon estimates.

1

Sengi ID	Obs No	CP 100%	CP 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

2

**Table 3** (on next page)

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.

1

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	--	--

2

**Table 4**(on next page)

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 study site mean yearly rainfall and mean body weight (Fig. 6). See methods section for explanation of inter-home-range distances.

1

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

2

## 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 *Macroscelides 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** (on next page)

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.

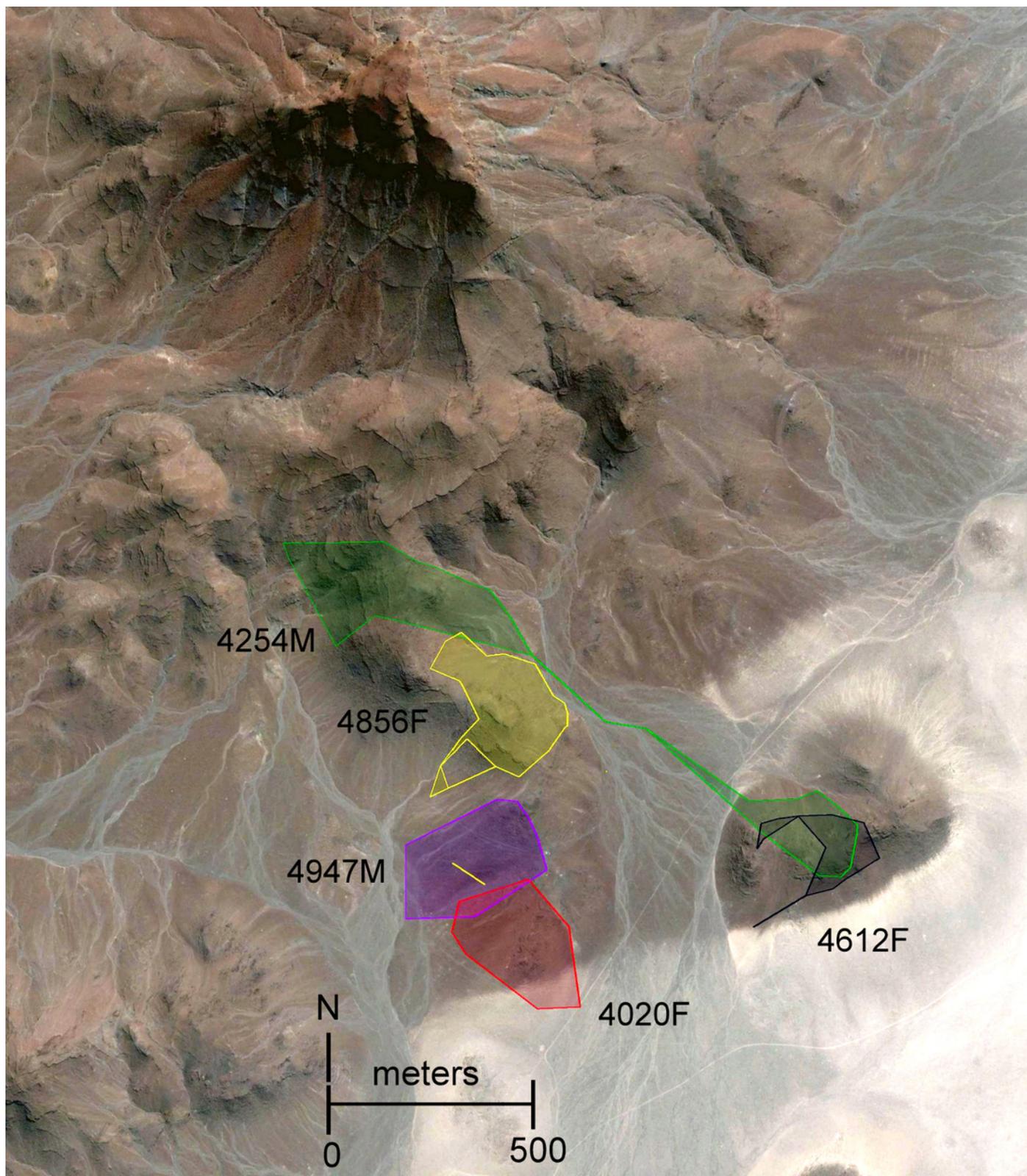
Radio collar is completely hidden by fur. B) Sengi #4947M at the opening of a typical rock shelter on 25 Oct 2014 at 2351 hrs. Photos by GBR.



## 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.

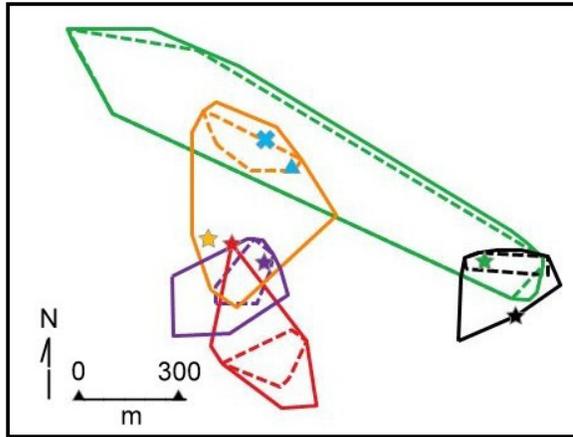


**Figure 4**(on next page)

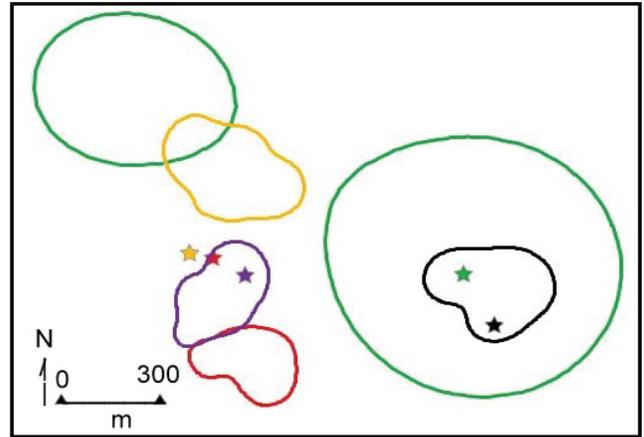
Home range polygons for five radio-collared *Macroscelides micus* at study site in the Goboboseb Mountains, Namibia.

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.

(A)



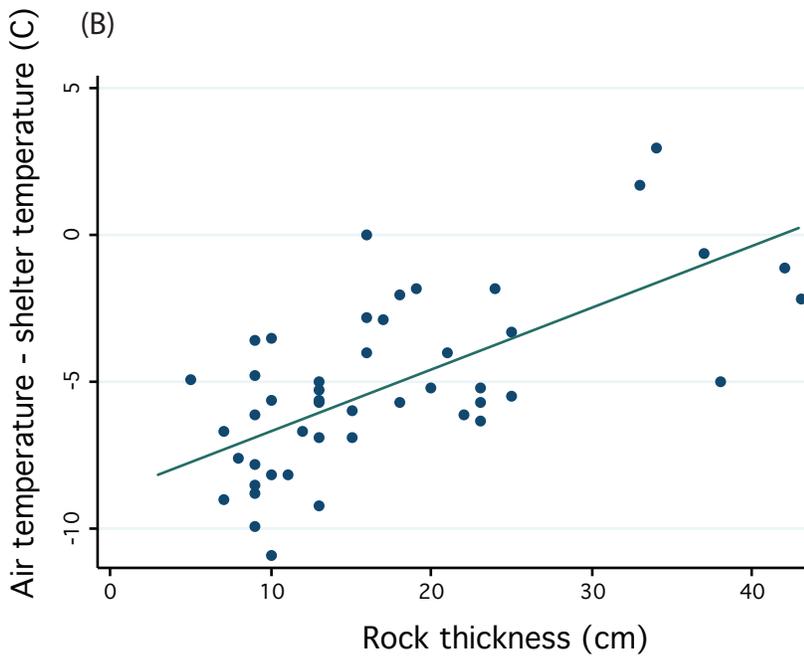
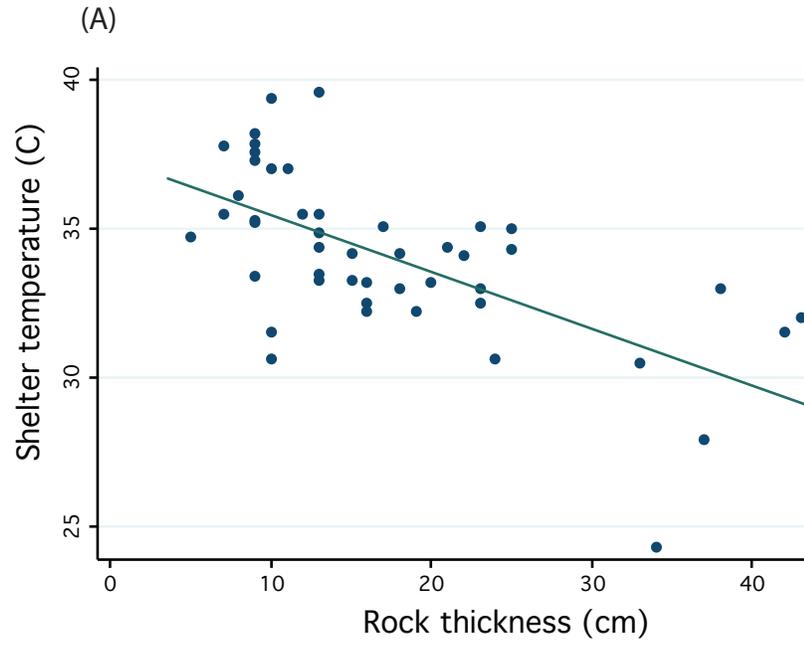
(B)



**Figure 5** (on next page)

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.



**Figure 6** (on next page)

Scatter plots of sengi home range areas against study site rainfall (A) and sengi weights (B). Data from this study and published literature (Table 4).

