

Home range and shelter site selection in the greater hedgehog tenrec in the dry deciduous forest of Western Madagascar

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Introduction

The island of Madagascar has one of the highest levels of endemism in the world (Goodman & Benstead, 2003; Harper *et al.*, 2007). One of the most speciose endemic mammal families is the Tenrecidae (Superorder: Afrotheria). Since their colonization of Madagascar *c.* 37 mya, tenrecs have diversified, spanning wide ranges in body size, morphology and life histories (Douady *et al.*, 2002; Olson & Goodman, 2003). One of the largest species of tenrec, the greater hedgehog tenrec (*Setifer setosus*), is also one of most widespread, and yet it remains poorly studied (Goodman, Ganzhorn & Rakotondravony, 2003). They are a cryptic, strictly nocturnal, insectivorous species with a relatively low rate of trap success (Randrianjafy, 2003). Field and laboratory studies undertaken in the 1960s showed that they nest in shallow holes in the ground or in tree cavities during the day, often out of visual range (Gould & Eisenberg, 1966; Eisenberg & Gould, 1969). In the more seasonal parts of the country, they are notably absent during the dry periods and are therefore likely to hibernate (Eisenberg & Gould, 1969; Stephenson, 1994; Randrianjafy, 2003).

The vast majority of data available on this species is restricted to that obtained through general surveys on small mammal populations (Stephenson, 1993; Randrianjafy, 2003). There have been few in-depth studies, and baseline data

Abstract

Information on the spatial distribution and habitat use of the Tenrecidae (Supraorder: Afrotheria) of Madagascar are severely lacking. Here, we present the first data available on home range size, as well as further data on population distribution and rest site selection of a large tenrec, the greater hedgehog tenrec (*Setifer setosus*). Data were collected over two rainy seasons in the dry deciduous woodland of Western Madagascar, in Ankarafantsika National Park. Home ranges were surprisingly large for a 200–300-g animal: males had an average home range (95% minimum convex polygon) of 13.7 ± 4.9 ha ($n = 5$), and females of 6.7 ± 2.0 ha ($n = 5$). A high overlap between multiple individuals of the opposite sex supports a promiscuous mating system for this species. Daytime shelter sites proved to be highly variable and differed between sex and reproductive status.

on the animal in its natural habitat are lacking (Eisenberg & Gould, 1969; Randrianjafy, 2003; Randrianjafy & Goodman, 2008). Information on the distribution, home range and shelter sites can provide invaluable insights into the basic ecology of a species and how it will respond to various environmental stressors (Burt, 1943; Brown & Orians, 1970; Komers & Brotherton, 1997; Wilkinson, Grigg & Beard, 1998). This is especially important in Madagascar where rates of deforestation and forest fragmentation are high (Ganzhorn *et al.*, 1990; Green & Sussman, 1990; Smith, Horning & Moore, 1997; Agarwal *et al.*, 2005; Harper *et al.*, 2007).

Here, we present data on the home ranges, distribution and rest site selection of a population of *S. setosus* in a segment of the western deciduous forest in Madagascar. This constitutes the first study to successfully follow multiple *S. setosus* for an extended period of time, and provides baseline data on the spatial distribution and habitat use of this species.

Materials and methods

The study took place over two rainy seasons. The first, from January to April 2010, was a preliminary study in which eight individuals (three males, five females) were followed until hibernation commenced in March–April. The second study period was longer, from September 2010 to April 2011, and

resulted in the capture and radio-tracking of 14 individuals (eight males, six females).

Study site

All animals were trapped in the Jardin Botanique A (JBA) research area adjacent to the Ampijoroa Forestry Station in Ankarafantsika National Park (16°19'S, 46°48'E), one of the largest remaining sections of dry deciduous woodland in Madagascar (Alonso *et al.*, 2002). The habitat consists of dry forest situated on sandy soils. The JBA research area used in this study includes undisturbed forest habitat as well as once-burnt forest as described in Chouteau, Fenosoa & Rakotoarimanana (2004). Both forest types are composed primarily of trees less than 5 cm in diameter with only 8.4% of the trees in the unburnt forest reaching a diameter of greater than 10 cm (Chouteau *et al.*, 2004). The site is characterized by large seasonal variation in rainfall with a distinct dry season during the Austral winter, from April to November with little or no rainfall, with the 1000–1500 mm of rain falling primarily during the remaining months (data from Durrell Wildlife Conservation Trust, Ampijoroa 1997–2010). Previous work indicated that *S. setosus* activity is limited during the dry season, indicating the potential for seasonal heterothermy (hibernation) during this time (Randrianjafy, 2003).

Trapping and transmitter implantation

Initial attempts were made to capture animals using Tomahawk-style and Sherman live traps baited with sardines or dried fish and open pitfall traps (consisting of a 10-L plastic bucket placed in the ground with drainage holes). However, neither technique had any success after a month of trapping. Trapping was abandoned in favor of catching individuals by hand. Hand catching consisted of walking the established trails in the area at night with local guides, locating individuals by sight or by sound, chasing and catching them and then transporting them back to the research camp. Animals were housed in plastic containers lined with paper towel and provided with live insects and sardines. They were kept for a maximum of 5 days before surgery to allow for collection of metabolic data for a concurrent study.

After several failed attempts to place external radio transmitters both as collars (made impossible by the lack of clearly defined neck) or glued to the spines on the back (complicated by the animals' ability to pass through the smallest cracks), the radio transmitters (two-stage collar transmitter, Merlin Systems Inc, Boise, ID, USA) were modified for implantation. This coincided with a concurrent study on long-term body temperatures in this species (Levesque and Lovegrove, unpubl. data) so the telemeters were encapsulated in surgical wax (Paramat Extra-Merck KGaA, Darmstadt, Germany) alongside two miniaturized DS1922L Thermocron iButtons (Dallas Semiconductor, Dallas, TX, USA) as outlined in Lovegrove (2009). The telemeter package weighed around 13.0 g (mean 13.0 g, range 11.7–13.5 g) constituting around 5–8% of the animal's body mass. Surgery was undertaken under sterile conditions in an enclosed laboratory site at the research camp.

Oxygen and vaporized anesthetic (isoflurane) were delivered to the animal through a mask at a rate of 700 mL min⁻¹. Anesthesia was induced at 1–2% isoflurane and maintained at 0.5%. The telemeter package was inserted via an incision in the peritoneal cavity which was then sutured using 3/0 catgut and sealed with Vetbond™ tissue adhesive (3 m, London, ON, Canada). An intramuscular injection of antibiotics (1 µL/10 g of Duplocillin) was given to prevent postoperative infection. The animals were kept for 1 day of post-surgery observations and were released at the site of capture. Implanted animals were recaptured within a week of surgery to ensure proper recovery or corrective suturing, if needed. Subsequent locations of the animal were made using either the R-1000 Telemetry Receiver (Communications Specialists, Orange, CA, USA) or the IC-R10 Communications Receiver (ICOM, Tokyo, Japan) connected to an RA-23K 'H' antenna (Telonics, Mesa, AZ, USA) or a standard 150-MHz Yagi antenna (manufactured by Cliff Dearden, Pietermaritzburg, KZN, South Africa) and a 150-MHz power booster (Merlin Systems Inc). Females were captured once a week to determine reproductive status and males once every 2 or 3 weeks to assess body condition. The animals were recaptured and the transmitter package explanted after emergence from hibernation in September 2011.

Data collection

Rest site selection

Setifer setosus is strictly nocturnal (Rand, 1935; Randrianjafy, 2003) and can therefore be expected to stay stationary throughout the day. This allowed the easy identification of their day/rest shelter sites by locating them between dawn and dusk. Females were located every day (as repeated use of a single nest site would indicate parturition) and males every couple of days. Using only the handheld radio receivers (without an aerial), it was possible to locate them to within a few centimeters of their precise location, usually in a tree. Their geographic location was recorded using a handheld global positioning system (GPS) unit (accurate to 3 m) and included in the home range analysis. Various characteristics [height from the ground, cover and diameter at breast height (DBH) of the tree] of their shelter site were also recorded.

Collection of spatial data

Only the daytime (rest-phase) locations, as described above, were collected during the first season. The second season also included the collection of night (active-phase) locations. Night locations were made from either 1800–000 or 000–0600. To avoid serial autocorrelation, each individual was located once per night in a randomized order (Swihart & Slade, 1985). On occasion, visual contact was made with the animal in which case its location was recorded directly into the handheld GPS. If visual contact was not possible, the animal was triangulated by recording the angle at which the signal was strongest from three to four different locations at least 10 m apart. Estimated

locations from the triangulation data were obtained using Locate III (Pacer Computing, Tatamagouche, NS, Canada). All points were entered into MapSource (Garmin, Olathe, KS, USA), and the latitude and longitude data were transformed into Universal Transverse Mercator coordinates for analysis.

Data analysis

Statistical analysis

All statistics were performed using either the base program in R (R Development Core Team, 2011), or using MYSTAT or Sigma Stat 3.0.1 (Systat Software, Inc, Chicago, IL, USA). Resultant probability values were compared to an α -value of 0.05, unless otherwise stated.

Rest site selection

The height of the rest sites were placed into distinct categories (<0, 0–0.5, 0.5–1, 1–1.5, 1.5–2 and >2 m) and then analyzed using a chi-squared test (or Fisher's exact test for non-normal data), between the sexes and among the different reproductive statuses. Similar analyses were performed on the level of cover provided by the rest site (classed as closed, open, partially open and unclear) as well as the DBH (DBH in m binned as follows: 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.4, 0.4–0.5, >0.5) of the tree in which they were resting.

Home range analysis

Home ranges sizes were calculated in R using the 'adehabitatHR' package (Calenge, 2006). With the exception of lactating females, rest sites changed daily and therefore rest-phase locations were included in all home range analyses. To account for the high variance in calculated home ranges (see Wauters *et al.*, 2007 for more details), multiple estimators were used. We used the minimum convex polygon (MCP) method as it is the most robust, in order to compare data from this study to that from other home range studies. The use of 95% MCP was supported by a preliminary analysis in R (using the `mcp.area` function) indicating that excluding the most extreme 5% of the distribution points for each animal did not affect the calculated values.

However, the MCP method has been widely criticized in that it often overestimates home range size (Worton, 1989). Home ranges were therefore also calculated using fixed kernel density estimation (KDE) with three different smoothing vectors: KDE with h_{ref} (KDE_{h_{ref}}), the least squares cross-validation (KDE_{LSCV}) and h_{adj} (KDE_{adj}). This last value was proposed by Wauters *et al.* (2007) as a means of decreasing the overestimation of home range size in a small mammal. The smoothing vector, h_{adj} , was calculated by multiplying h_{ref} by the average ratio of h_{LSCV}/h_{ref} (0.4 in this study). The 'kerneloverlap' function in 'adehabitatHR' was used to calculate the percentage of range overlap between individuals. The individuals followed exclusively between January and April 2010 were excluded from this analysis to ensure that the recorded overlaps were temporal as well as spatial.

Rest-phase locations are, in general, easier to collect and more accurate, and these were the only locations that were available from animals from the first season (with the exception of a few active-phase locations). It was also of interest, and ease of future study, to determine how accurate rest-phase data were as a predictor of overall home range size. Home range size analyses were also performed on the daytime locations only and were compared to home ranges calculated including the night locations. Differences between home range estimates and sex were calculated using a two-way repeated-measures analysis of variance (ANOVA). After visually observing home range size based on the number of locations, home ranges of individuals with less than 30 locations were considered incomplete. Although they are reported, they were excluded from the calculation of the means and the statistical analyses. The reciprocal of the data was used to satisfy the assumptions of the ANOVA. Differences among categories were determined using Holm-Sidak all pairwise multiple comparison procedures as a post hoc test.

Results

Of the eight individuals followed (SF01–SF08) in the first year, only three (SF02, SF04 and SF07) were active long enough to collect more than 30 locations (Table 1). The others either died (predation or unknown cause) or commenced hibernation shortly after implantation (early March 2010). An individual was considered to be hibernating when it remained

Table 1 Height of day site location, percent distribution by sex, and reproductive status

| Height category (m) | All data % | Males % | Females % | Females | | |
|---------------------|------------|---------|-----------|------------|-------------|---------|
| | | | | Pregnant % | Lactating % | Other % |
| <i>N</i> | 325 | 141 | 178 | 74 | 27 | 78 |
| <0 | 7.4 | 8.5 | 6.5 | 0 | 3.7 | 13.3 |
| 0–0.5 | 38.8 | 32.6 | 43.5 | 43.2 | 22.2 | 50.6 |
| 0.5–1 | 10.2 | 7.1 | 12.5 | 16.2 | 14.8 | 8.4 |
| 1–1.5 | 6.5 | 7.8 | 5.4 | 9.5 | 0 | 3.6 |
| 1.5–2 | 12.9 | 19.9 | 7.6 | 12.2 | 3.7 | 4.8 |
| >2 | 24.3 | 24.1 | 24.5 | 18.9 | 55.6 | 19.3 |

'Other' refers to all females of undetermined reproductive status. Significant differences were found between sexes and between reproductive statuses in females.

in the same day site, and no nocturnal activity was observed, for more than 1 week. All individuals had entered hibernation by the end of April 2010. Problems with the transmitters and possible predation or dispersal meant that none of the animals from the first season, with the exception of one female (SF07), were recovered post-hibernation (September 2010). However, the transmitters of two individuals (one male and one female), who had not changed rest sites since March, continued to work until the beginning of September. Unfortunately, the transmitters stopped working just as the animals started relocating, and they were both lost to the study. The one female to be recaptured (SF07) was fitted with a new transmitter, and the recorded locations span the two seasons.

Of the 14 individuals implanted during the second season, only 10 were followed long enough to obtain more than 10 accurate geographic locations. One male had a transmitter malfunction within a day of release and a female was killed by an unknown terrestrial predator within a week of capture. These data were excluded from all analyses. Another animal died while entering a small tree cavity (SF11) and, whereas her data are included in the tables, they were excluded from statistical analyses since only 14 locations were collected before her death. A total of six individuals, three males (SF09, SF15, SF17) and three females (SF13, SF14 and SF21), were eaten by boas (either *Acrantophis madagascariensis* or *Boa manditra*). However, complete home ranges were calculated for two of these individuals (SF13 and SF14) prior to their deaths.

The activity patterns of *S. setosus* observed in this study were highly seasonal, restricted from late September to early March for the males and to the end of April for the females. The breeding season began shortly after emergence from hibernation until just before reentry. The first heavily pregnant females were observed in late October 2010 and at no point between that time and April 2011 were any of the females nonreproductive. Females in late lactation (30–40 days) were also found to be gestating. Due to the lack of external testes, it was not possible to determine the reproductive condition of the males (Petter & Petter-Rousseaux, 1963). Body mass was highly seasonal, fluctuating from the lowest values just after emergence from hibernation in 2010 (120–160 g) and reaching as high as 327 g for a male 1 week before hibernation commenced in 2011. Females tended to be smaller than the males but reached similar weights (>350 g) during late gestation.

Rest site selection

All individuals, with the exception of lactating females, changed rest sites daily, rarely retuning to the same area. Lactating females (four observed in this study) would remain stationary for approximately 20–25 days before the young were large enough to move. The mother would forage at night and return to the same day location throughout this time. On occasion, individuals were found in locations where they had previously been observed and even occasionally on the exact nest site where another individual had been located. On a single occasion, in the breeding season in December, a male and a female shared a single rest location for a few days. Activity was restricted to nighttime and in no case was an individual found in a different location at dusk than at dawn.

Common rest sites included hollows found in either live or dead trees and, only very occasionally, underground. Resting in underground or hillside holes was much more common in individuals found closer to the valley area surrounding the JBA forest site. The sandy soil of the JBA area made underground holes rare. Differences in all nest-site characteristics were found between both males and females (chi-square tests resulting in $P < 0.001$, Tables 1, 2 and 3) and between reproductive and nonreproductive females. Pregnant and lactating females were generally found higher up than nonreproductive females and pregnant females were more often found in closed nest sites.

Home range calculations

Home range size varied widely according to the estimation used. KDE_{href} produced the largest values, and KDE_{adj} and MCP produced the smallest, whereas K_{LSCV} estimates had the highest interindividual variability (Fig. 1, Table 4). Males had significantly larger home ranges than females, regardless of the estimate used ($F_{1,38} = 14.82$, $P = 0.005$). Home range sizes estimated by KDE_{href} were significantly higher than those calculated by any other estimate ($F_{3,38} = 13.98$, $P < 0.001$). Individual home ranges had a high degree of overlap with individuals of both sexes (Table 5, Fig. 2). In general, the males overlapped with a higher number of individuals than females. Home range sizes were normally distributed when calculated using 95% MCP and KDE_{adj} but non-normally distributed when K_{LSCV} or KDE_{href} was used. In all cases, the coefficient of variation between individuals was high.

Table 2 Level of cover of day site location of *Setifer setosus*

| Level of cover | All data% | Males % | Females % | Females | | |
|----------------|-----------|---------|-----------|------------|-------------|--------|
| | | | | Pregnant % | Lactating % | Other% |
| <i>N</i> | 319 | 140 | 179 | 74 | 27 | 78 |
| Closed | 52.4 | 58.6 | 47.5 | 62.8 | 36.5 | 33.3 |
| Open | 21 | 10 | 29.6 | 26.9 | 33.8 | 25.9 |
| Partially open | 12.2 | 13.6 | 11.2 | 6.4 | 16.2 | 11.1 |
| Unclear | 14.4 | 17.9 | 11.7 | 3.8 | 13.5 | 29.6 |

Level of cover refers to the portion of the animal visible to the observer. Closed, the animal could not be seen when the nest site was located; Open, the animal was fully visible; Partially open, the animal was partially visible; Unclear, when the nest site was too high to be evaluated by the observer. Significant differences were found between sexes and reproductive status.

Table 3 Frequency distribution (%) of diameter at breast height (DBH in m) of trees housing the rest sites of *Setifer setosus*

| DBH (m) | All data % | Males % | Females % | Females | |
|----------|------------|---------|-----------|----------------|--------------------|
| | | | | Reproductive % | Non-reproductive % |
| <i>N</i> | 208 | 113 | 95 | 73 | 22 |
| 0–0.1 | 13.5 | 13.3 | 13.7 | 12.3 | 18.2 |
| 0.1–0.2 | 37 | 41.6 | 31.6 | 27.4 | 45.5 |
| 0.2–0.3 | 22.6 | 23 | 22.1 | 24.7 | 13.6 |
| 0.3–0.4 | 13.5 | 12.4 | 14.7 | 17.8 | 4.5 |
| 0.4–0.5 | 9.1 | 5.3 | 13.7 | 12.3 | 18.2 |
| >0.5 | 4.3 | 4.4 | 4.2 | 5.5 | 0 |

Differences presented according to sex, and female reproductive status. Pregnant and lactating females were combined ease in statistical analysis.

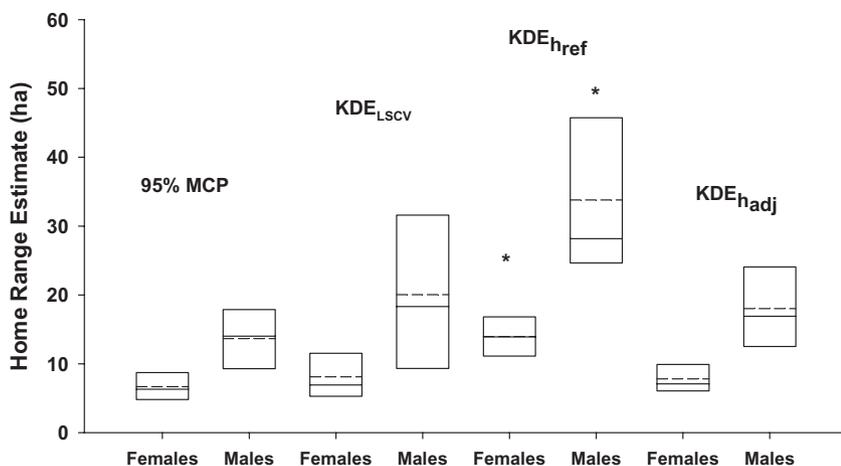


Figure 1 A comparison, by sex, of the various home range estimates. Boxplots show the mean and median values (dotted and solid line, respectively), minimum and maximum values (lower and upper ends of boxes). * indicates a significant difference in home range size between estimate type. MCP, minimum convex polygon.

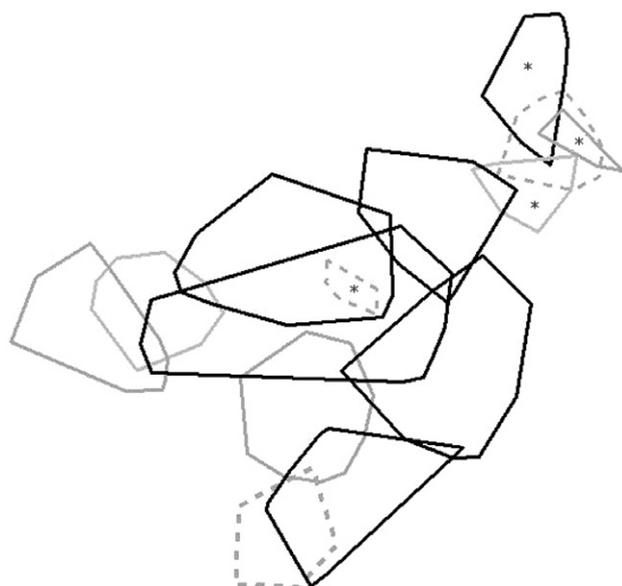
Table 4 Home ranges estimates of *Setifer setosus* in Ankarafantsika National Park using both day and night locations

| Animal | Sex | Mass (g) | <i>N</i> | 95% MCP (ha) | K_{Lscv} (ha) | K_{Href} (ha) | K_{Hadj} (ha) |
|--------------------|-----|--------------------|--------------|--------------|-----------------|-----------------|-----------------|
| SF02 ^a | F | 198 | 33 | 5.29 | 12.85 | 13.92 | 7.09 |
| SF04 ^a | F | 221.7 | 33 | 4.33 | 4.86 | 11.61 | 5.16 |
| SF07 | F | 181.8 | 95 | 6.32 | 5.72 | 10.64 | 6.97 |
| SF08 ^{ab} | F | 199.4 | 14 | 0.90 | 0.37 | 4.99 | 1.83 |
| SF09 ^b | M | 148.9 ^c | 29 | 4.89 | 5.26 | 17.87 | 8.37 |
| SF11 ^b | F | 165.6 ^c | 14 | 2.96 | 0.37 | 12.75 | 5.57 |
| SF13 | F | 154.0 ^c | 107 | 9.17 | 6.93 | 16.59 | 10.49 |
| SF14 | F | 158.5 ^c | 78 | 8.29 | 10.22 | 17.07 | 9.33 |
| SF16 | M | 183.7 ^c | 83 | 14.02 | 18.32 | 28.18 | 16.92 |
| SF17 | M | 183.9 | 36 | 14.66 | 42.97 | 37.61 | 21.22 |
| SF18 | M | 256.5 | 67 | 21.10 | 11.07 | 53.87 | 26.93 |
| SF19 | M | 295.7 | 50 | 9.52 | 20.25 | 24.59 | 12.46 |
| SF20 | M | 142.0 | 30 | 9.06 | 7.60 | 24.73 | 12.58 |
| SF21 ^b | F | 235.0 | 12 | 1.07 | 1.15 | 4.46 | 3.38 |
| Mean | | 194.6 ± 44.3 | 58.3 ± 28.8 | 9.70 ± 5.09 | 13.28 ± 11.11 | 23.33 ± 12.90 | 12.50 ± 6.70 |
| CV | | 22.8 | 49.4 | 52.5 | 83.7 | 55.3 | 53.6 |
| Mean | M | 201.8 ± 61.4 | 53.2 ± 21.9 | 13.67 ± 4.87 | 20.04 ± 13.82 | 33.80 ± 12.41 | 18.02 ± 6.15 |
| Mean | F | 189.3 ± 28.6 | 69.2 ± 34.62 | 6.68 ± 2.02 | 8.12 ± 3.34 | 13.97 ± 2.88 | 7.81 ± 2.11 |

The mean (± SD) and coefficient of variation (CV) are for all individuals excluding those marked with a ^bwhich had insufficient data to provide accurate estimates. Significant differences were found between males and females using all estimates. ^aindicates individuals followed during the first season (Jan–Apr 2010 only). Reported masses are from the date the animal was implanted, ^cindicates that the surgery occurred within the first two months post-hibernation when the animal was at lower than average mass.

Table 5 Percent overlap of home range for individuals followed between September 2010 and May 2011

| Sex | SF07 (F) | SF09 (M) | SF11 (F) | SF13 (F) | SF14 (F) | SF16 (M) | SF17 (M) | SF18 (M) | SF19 (M) | SF20 (M) | SF21 (F) |
|--------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| SF07 | – | 0 | 0 | 0 | 60 | 0 | 54 | 94 | 0 | 0 | 0 |
| SF09 | 0 | – | 24 | 0 | 0 | 0 | 0 | 0 | 0 | 17 | 25 |
| SF11 | 0 | 33 | – | 0 | 0 | 2 | 5 | 10 | 0 | 55 | 31 |
| SF13 | 0 | 0 | 0 | – | 0 | 22 | 25 | 47 | 49 | 0 | 0 |
| SF14 | 38 | 0 | 0 | 0 | – | 0 | 9 | 68 | 0 | 0 | 0 |
| SF16 | 0 | 0 | 1 | 13 | 0 | – | 27 | 62 | 23 | 25 | 0 |
| SF17 | 15 | 0 | 2 | 11 | 4 | 20 | – | 78 | 0 | 24 | 0 |
| SF18 | 19 | 0 | 2 | 15 | 21 | 33 | 55 | – | 4 | 24 | 0 |
| SF19 | 0 | 0 | 0 | 33 | 0 | 26 | 0 | 9 | – | 0 | 0 |
| SF20 | 0 | 12 | 28 | 0 | 0 | 28 | 37 | 52 | 0 | – | 2 |
| SF21 | 0 | 48 | 42 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | – |
| Number of overlaps | 3 | 3 | 6 | 4 | 3 | 6 | 7 | 8 | 3 | 6 | 3 |

**Figure 2** Minimum convex polygon (95%) home ranges of *Setifer setosus* in the Jardin Botanique A area of Ankarafantsika National Park, Madagascar. Male home ranges are outlined in black, females in grey. Individuals from the first season are indicated by dashed outlines and * indicates that the individual was excluded from statistical analysis.

Differences in home range estimates using day and night locations and those omitting night locations (Table 6) were larger than expected and much larger in males than in females ($F_{1,38} = 10.32$, $P = 0.012$), but did not differ between estimate type ($F_{3,38} = 1.52$, $P = 0.24$). Both day and night locations appear to be necessary to accurately determine home range size.

Discussion

Our study is the first to establish home range size for a terrestrial Malagasy tenrec. We also provide the first conclusive

evidence that *S. setosus* hibernates, at least in the highly seasonal dry deciduous woodland. The success of this study was based on the use of peritoneal implanted radio transmitters. Although implanting reduces the transmission range of the transmitter, it is the only solution for the long-term tracking of free-ranging individuals when external mounts do not work (Pavey, Goodship & Geiser, 2003; Dausmann, 2005). One major disadvantage for this species, at least in the dry forest, is that there is little time during the active season when the females are not either gestating or lactating; they must therefore be caught early in their active season to ensure that their fitness is not impaired. As a result, a number of females caught after October 2010 could not be tracked. Coupled with the highly unreliable trapping technique, this limitation led to part of the population being completely absent from the study. However, enough individuals with overlapping ranges were tracked to allow for some conclusions to be drawn.

Early studies in captivity noted that *S. setosus* was likely to be polygamous and promiscuous (Eisenberg & Gould, 1969). This is supported by the observed distribution patterns. All individuals had range overlaps with multiple individuals of the opposite sex. In addition, one male, SF18, was observed copulating with an unknown female, and later was found in the same nest site as SF14 (300 m away) for a few days. These were the only mating events observed in this study. As only one individual, a female, was tracked over both seasons, it is unknown if the high interannual site fidelity observed was representative of either her sex or the population.

The shelter site selection observed in this study, for the most part, supported early observations (Eisenberg & Gould, 1969; Randrianjafy, 2003). As mentioned in those studies, the primary rest sites for *S. setosus* are in tree cavities. However, the reliance of previous studies on visual observations, and locating the animal by chance, underrepresented the amount of nest sites found high in the canopy. Whereas nest-site characteristics varied widely, lactating females were more commonly found in high (>2 m), closed nest sites, likely as a means to protect the young from predators. Interestingly, Gould & Eisenberg (1966) observed a level of nest-site fidelity not observed in the present study, which may indicate differences

Table 6 The difference in home range estimates based on calculations including, and excluding active-phase locations

| Animal | Sex | N | 95% MCP (ha) | K _{LSCV} (ha) | K _{Href} (ha) | K _{Hadj} (ha) |
|-----------|-----|----|--------------|------------------------|------------------------|------------------------|
| SF02 | F | 24 | 0.96 | -2.55 | 0.72 | 0.84 |
| SF04 | F | 23 | 0.97 | -9.41 | 0.04 | -0.25 |
| SF07 | F | 57 | 0.48 | 0.60 | -0.65 | -0.10 |
| SF09 | M | 25 | 0.59 | 1.09 | 1.80 | 0.70 |
| SF13 | F | 52 | 1.74 | 3.76 | -0.11 | 2.03 |
| SF14 | F | 39 | 0.98 | 2.27 | -0.53 | 0.35 |
| SF16 | M | 33 | 4.30 | 4.75 | 0.69 | 3.29 |
| SF17 | M | 17 | 2.83 | 4.52 | 0.31 | 2.82 |
| SF18 | M | 33 | 7.76 | 3.98 | -3.71 | 3.42 |
| SF19 | M | 30 | 1.94 | 15.61 | -0.86 | 0.49 |
| Mean ± SD | M | | 3.49 ± 2.75 | 5.99 ± 5.57 | -0.36 ± 2.1 | 2.14 ± 1.43 |
| Mean ± SD | F | | 1.03 ± 0.45 | -1.07 ± 5.22 | -0.11 ± 0.54 | 0.58 ± 0.92 |

Significant differences were found between the sexes.

in nest-site selection across the species geographic range. Only females with dependent young remained in the same site for multiple days, although individuals of both sexes were observed to return to previous nest sites throughout the active season. This behavior was less common in males than in females. In addition to having larger home ranges, males also travelled more, sometimes traversing the entire study grid in one evening.

The home ranges measured in the study were surprisingly large for a 200–300-g animal. Recorded home ranges were 9.8 times larger for males and 4.8 larger for females than that predicted by McNab (1963) for a 300-g animal. There are few similar-sized Malagasy mammals with which to compare these data. The greater dwarf lemur *Cheirogaleus major* (360 g) has a home range of only 4.4 ha for males and 4.0 ha for females (Lahann, 2008). However, *Cheirogaleus* is strictly arboreal, and, therefore, the comparison is likely to be misleading. Interestingly, the terrestrial, 1–1.2 kg, giant jumping rat (*Hypogeomys antimena*) has only 3.1 ha home range (Sommer, 1997), almost exactly the size predicted by McNab (1963). One possible explanation for the large size of their home range is that the possession of body armor (in the form of dorsal spines) allows for a greater freedom of movement, without fear of predation (Lovegrove, 2001). Body armor in tenrecs has been proven to be an effective deterrent against the smaller Malagasy carnivores such as *Galidia elegans* (Eisenberg & Gould, 1969), but clearly not against boas, as evidenced by the present study. They also constitute a small proportion of the diet for fossa *Cryptoprocta ferox* (Dollar, Ganzhorn & Goodman, 2007). In the study area, it is a local taboo to hunt *S. setosus*, but this does not hold throughout the species' range and might prove a threat (Randrianjafy, 2003; Jones, Andriamarivololona & Hockley, 2008).

The high variety of shelter sites and propensity for heterothermy indicate that the species is extremely adaptable and likely to perform fairly well with changing habitat and climates. Ganzhorn *et al.* (1990) came to a similar conclusion on the lesser hedgehog tenrec (*Echinops telferi*), after observing the effects of selective logging on that species. In addition to the Western deciduous forest, *S. setosus* have been observed in a wide variety of habitats including urbanized

habitats, open grassland and the wetter forests of eastern Madagascar (Petter & Petter-Rousseaux, 1963; Gould & Eisenberg, 1966). It would be of interest to obtain comparative data from these habitats to gain a better understanding of how various biotic and abiotic factors influence the distribution and habitat usage in this species.

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