

High mortality and annual fecundity in a free-ranging basal placental mammal, *Setifer setosus* (Tenrecidae: Afrosoricida)

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Abstract

The spiny tenrecs, an endemic subfamily of Malagasy insectivores (Tenrecinae), are wide ranging and fairly conspicuous, yet long-term studies on free-ranging populations remain sparse. Basal to most eutherian mammals, they share many ecological and morphological traits with proposed eutherian ancestors. Understanding of their unusual life histories is therefore important to the understanding of mammalian evolution. Here we present the results of a 3-year study on a population of *Setifer setosus* in the dry deciduous forest of Western Madagascar. The annual activity cycle of this species includes a 5–7-month hibernation period, during the dry season, and a dramatic increase in body mass during the active season. Females, observed giving birth to up to three litters in a single season, entered hibernation later than males, after weaning their last litter. Short intervals between parturition dates and simultaneous gestation and lactation provide evidence of post-partum oestrus, previously observed in only one other species of tenrec (*Geogale aurita*, subfamily: Geogalinae). High levels of mortality, primarily by snakes and ground predators, were also observed and likely contribute, along with the unpredictability of Madagascar's climate, to the unusually fast life history of these mammals.

Introduction

Unpredictable and highly variable climatic conditions, as well as an isolated island environment, have led to high levels of endemism on the island of Madagascar (Goodman & Benstead, 2003; Dewar & Richard, 2007). The life-history characteristics of the island's endemic mammals are often unusual, falling on either the extreme 'slow' or 'fast' side of the life-history continuum (Stearns, 1983; Wright, 1999; Dewar & Richard, 2007). One of most speciose groups of endemic mammals, the Tenrecidae (Superorder: Afrotheria) is a highly diverse grouping of insectivorous mammals. Although much is known about the distribution, habitat use and phylogeny of these species (Eisenberg & Gould, 1969; Olson & Goodman, 2003; Muldoon & Goodman, 2010; Soarimalala, 2011), long-term studies on the natural history of free-ranging populations are rare.

The reproductive characteristics of tenrecs are highly varied, and can be found on both the fast (early reproduction, large litters in the spiny tenrecs: Tenrecinae) and slow (late maturing, small litters in the shrew tenrecs: Geogalinae and Oryzorictinae) side of the life-history continuum (Eisenberg & Gould, 1969; Stephenson & Racey, 1995; Racey & Stephenson, 1996; Symonds, 1999). The hedgehog tenrecs (*Echinops telfairi* and *Setifer setosus*) fall somewhere in the middle, maturing early but producing smaller litters (mean of

5.7 and 3.5, respectively) than the larger Tenrecinae (15.5 for *Tenrec ecaudatus*, Symonds, 1999). The reproduction and life history of the Tenrecinae has been well studied in captivity (Eisenberg & Muckenhirn, 1968; Eisenberg, 1975; Stephenson, Racey & Rakotondraparany, 1994) and it is known that they can be preyed on by boid snakes and a number of native and introduced Carnivora (Eisenberg & Gould, 1969; Hawkins & Racey, 2008). However, little information is available on either the life history or the rates of mortality in free-ranging populations (Dewar & Richard, 2007).

Baseline data on the life histories of the Tenrecinae from a wide variety of habitats are necessary to understand the evolution of these unique species. For example, because of the basal phylogenetic position of tenrecs, these data would greatly assist in reconstructing the characteristics of the ancestral placental mammal (Lovegrove, 2012), which was also insectivorous and probably similar in ecology (O'Leary *et al.*, 2013). It has been suggested that tenrecs may retain certain plesiomorphic characteristics of Late Cretaceous mammals (Lovegrove, 2012), which allowed the ancestral mammal to survive the asteroid impact at the Cretaceous-Paleogene boundary (Robertson *et al.*, 2004).

As part of a study on the physiology and temperature regulation in *S. setosus*, a free-ranging population inhabiting the dry deciduous woodlands of Western Madagascar was moni-

tored and individuals were followed for three rainy seasons. We present findings on the body condition, reproduction, phenology and causes of mortality in this species.

Materials and methods

Study site, capture and surgical methods

The study was conducted over three rainy seasons, from January 2010 to February 2012, in the Jardin Botanique A research area in Ankarafantsika National Park (16°19'S, 46°48'E). The site is characterized by large seasonal variations in rainfall with a distinct dry season during the austral winter (April–November) with little or no rainfall, and around 1000–1500 mm of rain falling primarily during the remaining months (data from the Durrell Wildlife Conservation Trust, Ampijoroa 1997–2012, Fig. 1). A detailed description of the study site and methods are provided in Levesque, Rakotondravony & Lovegrove (2012).

All animals were caught by hand, by walking the established trails at night with local guides and transported back to the research camp. Capture effort was fairly constant, averaging 4–6 h, five to six nights per week between January 2010 and November 2011. The time of night varied from immediately after sunset (18:00 h) to midnight (0:00 h). Research activity during the 0:00–06:00 h period by other members of the research team resulted in the occasional opportunistic capture. Animals were housed in plastic containers lined with paper towel and provided with live insects and sardines. At initial capture, all animals were anaesthetized using isoflurane in oxygen (induction, 1–2%; maintenance, 0.5%) and various morphometric measurements were taken. Each animal was marked with a small distinctive clip in the ear and injected with a transponder (Trovan® Small Animal Marking System, David Tweddell and Associates, Pretoria, South Africa) to allow for identification at recapture.

A subset of the population (individuals larger than 180 g) was implanted with radio-transmitters for subsequent tracking and relocation. They were kept for a maximum of 5 days before surgery to allow for the collection of metabolic data

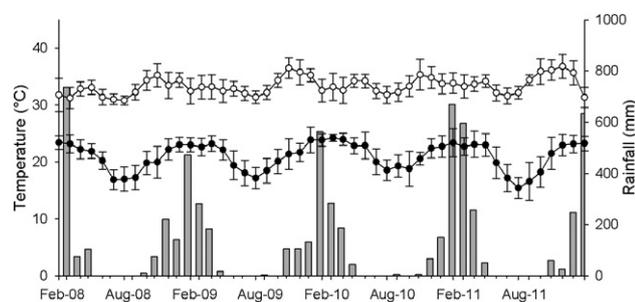


Figure 1 The total rainfall (mm – grey bars) and the average maximum (clear circles) and minimum (black circles) ambient temperature recorded by the Durrell Wildlife Conservation Trust at the Ampijoroa Cheilonian Breeding Centre, for the period of the study.

for a concurrent study. The radio-transmitters (two-stage VHF collar-mounted transmitters, Merlin Systems Inc, Boise, ID, USA) were modified and encapsulated in surgical wax (Paramat Extra-Merck KGaA, Darmstadt, Germany) together with Thermocron iButtons (Dallas Semiconductor, Dallas, TX, USA), and implanted via a ventral midline laparotomy (Levesque *et al.*, 2012). 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, within a range of weight shown to have no adverse effects on locomotory behaviour (Rojas, Koertner & Geiser, 2010). The animals were kept for 1 day of post-operative observations, released at the site of capture, and recaptured within a week of surgery to confirm that the incision had healed.

Collection of life-history data

Females with radio-transmitters were captured once a week to monitor reproductive status (evaluated by observing changes in mass, shape of the stomach and condition of the nipples) and males once every 2 or 3 weeks to assess body condition. The rest sites of the females were located every day (as repeated use of a single nest site indicates parturition – Levesque *et al.*, 2012) and males every couple of days. On occasion, animals without implants were opportunistically recaptured and their mass and reproductive statuses were recorded. If visual contact was possible, the size and number of juveniles were recorded. Due to the lack of external testes, it is not possible to determine the reproductive condition of the males (Petter & Petter-Rousseaux, 1963).

Statistical analysis

All statistics were performed using R version 2.15.2 (R Development Core Team, 2011). Sexual dimorphism in morphometric measurements was assessed using *t*-tests, or Mann–Whitney *U*-tests, and resultant probability values were compared to an α -value of 0.05. Body mass was analyzed using mixed-effects models in the R package 'nlme' (Pinheiro *et al.*, 2013). Pregnant females and animals from the first season were excluded from the analyses as reproductive status and date to parturition were not always known and could not be controlled for in the analyses. To standardize changes in mass between animals of different body size, body condition index (BCI – the ratio of mass to forearm length) was used. To control for time of year, as mass increased dramatically from the time of emergence in October to start of hibernation, a factor 'day' was created with 1 September as 'day' 0. Both BCI and 'day' were logarithmically transformed to control for unequal variances in the different groupings. Females were split into two groups; non-reproductive females, usually only found in the first few months of the season (day 0–100), and lactating or post-pregnant females.

Model selection was used starting with a base model of 'reproductive status', 'season' and 'day', as well as interaction effects between the three factors. The model residuals were assessed graphically and no heterogeneity was observed. Model selection identified 'day' and 'animal' and their inter-

action (in the form ~‘day/animal’) as the optimal structure for random effects. The optimal fixed structure included ‘reproductive status’, ‘day’ and a ‘day–season’ interaction effect. Differences within the significant categorical factors were determined using a Tukey *post hoc* test using the package ‘multcomp’ (Hothorn, Bretz & Westfall, 2008).

Results

Population levels and rate of capture

The fates of individuals with implants from the first and second seasons are described in Levesque *et al.* (2012), but are included below as additional information on these individuals is presented. Despite similar capture effort, the number of new individuals captured in each season, or recaptured for the first time in subsequent seasons, varied dramatically (Fig. 2). The first season (January–April 2010), was a preliminary study in which eight individuals (three males, five females) were implanted and followed until hibernation commenced in March–April. An additional 13 individuals were captured over the same time period but did not receive implants for various reasons: too small, pregnant or lactating, or caught before the surgical equipment was available. The second study period was longer (September 2010–April 2011), and resulted in the capture and radio-tracking of 14 individuals (eight males, six females). An additional 30 individuals (9 females, 16 males and 5 juveniles) were captured and released without receiving implants, either because of low mass or reproductive status.

By the third study period (September 2011–February 2012), the rate of new captures decreased and only 14 individuals (five females, six males and three juveniles) were captured over

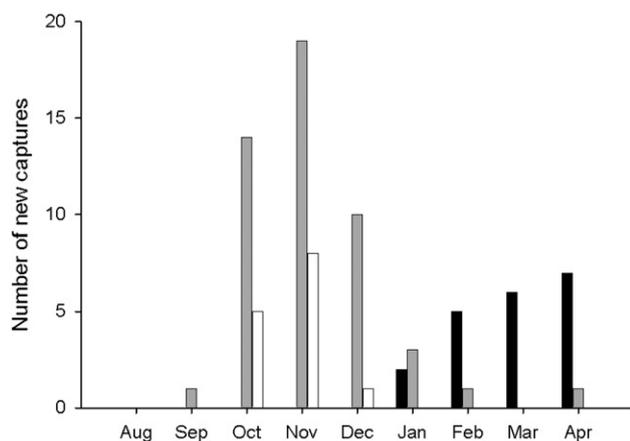


Figure 2 Number of new *Setifer setosus* captured each month in Ankarafantsika National Park. Black bars are from the first season (January–May 2010), light grey the second season (September 2010–April 2011) and clear from the final season (September 2011–January 2012). The data from the second and third season include the first date of recapture for that season. Similar sampling effort was made from January 2010 to January 2012.

the entire study period. All animals with the exception of two heavily pregnant females and one male caught near the end of the study, received implants.

Morphometrics and changes in body mass

The morphometric measurements of *S. setosus* in this study (Table 1) equal those previously reported for this species in other parts of its range (Soarimalala & Goodman, 2011), as well as for Ankarafantsika (Randrianjafy, 2003). Repeated measures obtained from individuals captured over multiple seasons showed little differences, with the exception of a few individuals who were likely to have been yearlings at date of first capture (data not shown). There were no differences between the sexes in any of the measurements ($P < 0.05$).

Mass varied widely between individuals and over time (Fig. 3). The animals were lightest after emergence from hibernation and heaviest immediately prior to hibernation or during pregnancy. This increase in mass was consistent between seasons and there were no overall differences found between the seasons ($F_{1,53} = 1.25$, $P = 0.27$). Model selection indicated that only reproductive status ($F_{2,53} = 28.34$, $P < 0.001$), day ($F_{1,53} = 76.30$, $P < 0.001$) and the interaction effect between day and season ($F_{1,53} = 13.43$, $P < 0.001$) were significant. Non-reproductive females had significantly smaller masses than post-reproductive females ($Z = -2.39$, $P = 0.04$) and no differences were found between males and either class of female ($P = 0.52$ and $P = 0.14$).

Seasonal activity patterns and reproduction

All members of this population restricted activity patterns to between sunset and sunrise (Levesque *et al.*, 2012). Additional observations performed over the course of the study showed that individuals commenced night-time activity after sunset (range 18:45–21:20 h, mean 19:31 h, $n = 13$) and ceased activity before dawn (range 2:30–05:36 h, mean 4:30 h, $n = 7$).

Seasonal patterns of activity showed little change between years, although the start date for hibernation had a high level of variability both between sexes and between individuals (Table 2). Males entered into hibernation earlier than females: as early as 18 February by a first season male, and as late as 2 April by two males in the second season. Females were observed to enter hibernation anytime from April to May with gestating females observed as late as 17 April 2010. Similar to two individuals from the first season (reported in Levesque *et al.*, 2012), a male from the second season remained in a single nest throughout the dry season (19 March–2 September

Table 1 Summary of morphometric measurements for adult *Setifer setosus*

Body length (mm)	188.2 ± 12.1 (39)
Head length (mm)	46.2 ± 3.4 (38)
Head width (mm)	23.1 ± 2.8 (38)
Tibia length (mm)	36.0 ± 2.2 (39)
Forearm length	30.1 ± 2.1 (39)

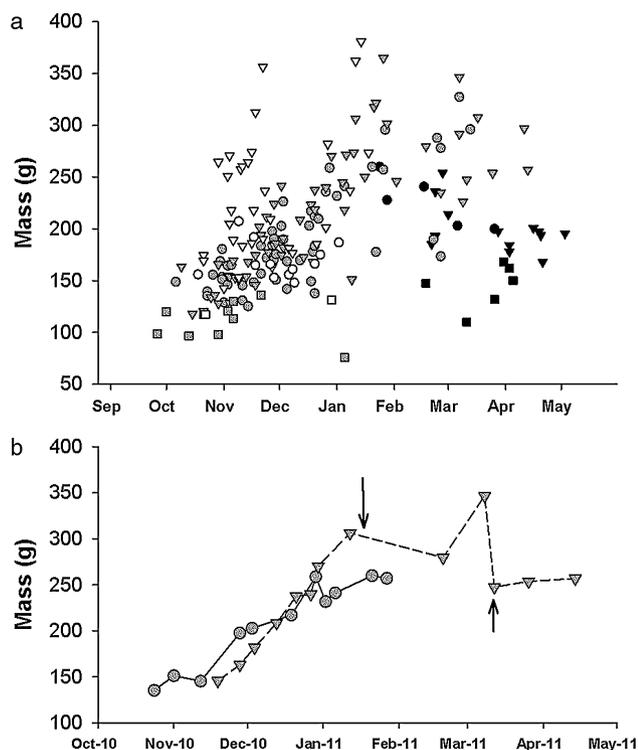


Figure 3 (a) Annual changes in body mass of male (circles), female (triangles) and juvenile (squares) *Setifer setosus* over the three study seasons (first – black, second – light grey, third – clear). Data from females include gestating and lactating females (November–March) and multiple measures per individual are also included. (b) Representative change in body mass of a male (circles) and female (triangles) during the second season. The female gave birth on 16 January and on 10 March (arrows). The male entered into hibernation on 2 April, and the female on 26 April.

2011). Overwintering body temperature recordings were obtained from a single female and body temperature closely tracked ambient temperature, indicating that hibernation continued from the end of April until the end of October (data shown in Lovegrove *et al.*, 2014).

Gestating females were observed shortly after emergence from hibernation (Table 3). Using the published gestation length of this species of ~60 days (Eisenberg & Muckenhirn, 1968; Eisenberg, 1975), the earliest estimated dates for insemination fall around mid-October. Females with implants were observed to have up to three litters per season. However, litter survival rates were low. Of the six litters followed, four were lost, and only two litters, with one pup and three pups, were observed until weaning (~34 days). Reduced levels of activity were occasionally observed in lactating females and one female in the second season remained at a single nest site, without evidence of nocturnal activity, for a month.

Mortality

As presented in Levesque *et al.* (2012), mortality among adults in this population is high (25% in the first season, 58% in the

second season and 100% in the third, Table 4). Boid snakes (*Acranthophis madagascariensis* and *Boa manditra*) were the most common predators, although a large proportion of individuals in the third season (3/7) were killed by an unknown ground predator. In addition, one individual whose home range covered an area transected by a busy road (Route National 4) was run over by a vehicle.

Discussion

The abundance of *S. setosus* in Ankarafantsika National Park has always been considered low (Rakotondravony, Randrianjafy & Goodman, 2002; Randrianjafy, 2003) and appears to have decreased over the course of this study. Despite similar trapping efforts, capture rates decreased during the third season. Low capture rates coincided with a decrease in the number of *T. ecaudatus* (K. D. Lobban, pers. comm.; D. L. Levesque, pers. obs.), a species whose low abundance in the study area has been attributed to high levels of hunting for human consumption (Andriatsarafara, 1981). Although *S. setosus* is generally not consumed locally (Randrianjafy, 2003), reduced populations of *T. ecaudatus* could lead to higher natural predation pressure on *S. setosus*. Both species constitute a large proportion of the diet of the fossa, *Cryptoprocta ferox* (Hawkins & Racey, 2008) at another site in the Western dry forest. Remains have been also found in fossa scat in Ankarafantsika (Dollar, Ganzhorn & Goodman, 2007), albeit in smaller proportions as the latter study was conducted primarily during the hibernation season. Any mortalities attributed to ‘unknown ground predator’ in Table 4, could have been by fossa, however, it is equally likely to have been one of the more abundant introduced predators found at the study site, such as small Indian civets (*Viverricula indica*), African wild cats (*Felis silvestris*) and feral dogs (*Canis lupus familiaris*, Dollar *et al.*, 2007). In the spiny forests of Southwest Madagascar, mortality by introduced dogs and wild cats is on the rise in diurnal lemurs (Brockman *et al.*, 2008) and might equally pose a problem for the spiny tenrecs, especially since dogs are used to hunt these species (Eisenberg & Gould, 1969; Andriatsarafara, 1981). Our research group observed a feral dog killing a female *T. ecaudatus* (D. L. Levesque & K. D. Lobban, pers. obs.); however, it is not known if *S. setosus* is common prey.

In addition to the data presented in Levesque *et al.* (2012), this study provides further conclusive evidence that *S. setosus* hibernates, at least in the Western dry forest. Sex differences in the timing of entrance into hibernation are similar to those found in *T. ecaudatus* (Andriatsarafara, 1981), where females entered hibernation later, attributed to the need for additional time to fatten after weaning their litter. However, the lack of difference in body condition between males and females in this study suggest that it is maternal care itself, and not its effect on body condition, that delays entry into hibernation. Not enough information is available to compare emergence dates between the sexes.

Environmental conditions appeared to vary between seasons; the first season in particular was preceded by one of driest rainy seasons in recent history (Fig. 1). No evidence of

Table 2 Confirmed hibernation start and end dates for *Setifer setosus* in the Western dry forest (Ankarafantsika National Park) over two dry seasons (season 1: September 2010–May 2011; season 2: September 2011–February 2012)

Animal	Sex	Date of capture	Season	Hibernation start	Hibernation end
SF01	M	17-Feb-10	1	19-Feb-10	Approx. 14-Sep-10
SF02	F	19-Feb-10	1	After 18-May-10	Lost to study
SF05	M	7-Mar-10	1	14-Mar-10	Lost to study
SF07	F	29-Mar-10	1	After 5-May-11	Before 19-Nov-11
SF08	F	17-Apr-10	1	28-Apr-10	Lost to study
SF18	M	23-Oct-10	2	2-Apr-11	Before 19-Oct-11
SF07	F	19-Nov-10	2	26-Apr-11	22-Oct-11
SF16	M	22-Nov-10	2	8-Mar-11	Lost to study
SF20	M	6-Dec-10	2	2-Apr-11	Before 29-Nov-11
SF19	M	29-Jan-11	2	19-Mar-11	2-Sep-11

Table 3 Length of gestation and lactation of *Setifer setosus* in Ankarafantsika National Park

	Pregnancy number	Estimated start of gestation ^a	Parturition date	Gestation length (days)	Lactation		Estimated length of lactation (days)	Result
					Start lactation	End lactation		
SF13	1	21-Oct-10	1-Dec-10	>41	2-Dec-10	7-Dec-10	5	Lost litter
	2	13-Dec-10	23-Jan-11	41–53	23-Jan-11	8-Mar-11	44	Unknown
	3	8-Mar-11	Deceased 23-Mar-11	n/a	n/a	n/a	n/a	n/a
SF14	1	25-Oct-10	5-Dec-10	>41	5-Dec-10	8-Jan-11	34	1 juvenile weaned
	2	13-Dec-10	12-Feb-11	61–69	12-Feb-11	Deceased 19-Feb-11	n/a	n/a
SF07	1	6-Dec-10	16-Jan-11	>41	16-Jan-11	11-Feb-11	26	Lost litter (snake)
	2	16-Jan-11	10-Mar-11	~53	10-Mar-11	13-Apr-11	34	3 juveniles weaned
SF22	1	19-Oct-11	Unknown	n/a	Unknown	28-Dec-11	n/a	Moved out of range of study
	2	28-Dec-11	Deceased 17-Jan-12	n/a	n/a	n/a	n/a	n/a
SF23	1	14-Oct-11	24-Nov-11	>41	25-Nov-11	Deceased 8-Dec-11	n/a	n/a
SF24	1	14-Oct-11	2-Dec-11	>49	3-Dec-11	16-Dec-11	13	Possible lost litter
	2	16-Dec-11	Deceased 26-Jan-11	n/a	n/a	n/a	n/a	n/a
SB01	1	26-Oct-11	6-Dec-11	>41	6-Dec-11	Lost to study 9-Dec-11	n/a	n/a

^aStart of gestation was taken either from the first day that the individuals were visibly pregnant, or taken as the parturition date from the last pregnancy.

this was reflected in either hibernation start times or end times or patterns of body condition, although any existing patterns might have been obscured by small sample sizes in the first and third seasons. More data would be necessary to draw any further conclusions.

The animals studied showed a remarkable ability to increase body mass throughout the active season (Fig. 3). Although partially omnivorous, especially in urban areas (Petter & Petter-Rousseaux, 1963; Eisenberg & Gould, 1969), *S. setosus* are primarily insectivorous, and insect abundance increases dramatically during the rainy season coinciding with their activity periods (Nicoll, 1985; Rakotoarivelo *et al.*, 2007; Dammhahn & Kappeler, 2008). High levels of easily assimilated energy (Bell, 1990) and relatively low thermoregulatory costs (Levesque & Lovegrove, unpublished data) for this time of year assist in rapid mass increases. Seasonal fattening is also seen in other Malagasy hibernators such as the fat-tailed dwarf lemur (*Cheirogaleus medius*), which remain more sedentary during fattening but also make use of high levels of sugar in fruit instead of protein in insects (Fietz & Ganzhorn, 1999).

Gestation did not preclude mass gain in females. Despite giving birth to multiple litters, they had similar body conditions to males later in the season (Fig. 3b). Similar gains in mass during gestation have been observed in captive *E. telfairi* (Poppitt, Speakman & Racey, 1994), as well as in other non-hibernating mammals where mass stores accumulated during gestation are believed to be important for lactation (Humphries & Boutin, 1999). No juveniles were caught both pre- and post-hibernation, and therefore, the effects of date of birth, usually a strong predictor of overwinter survival, could not be assessed.

Similar to observations on captive populations of both species of hedgehog tenrecs (Mallinson, 1974; Eisenberg, 1975; Künzle, Nautrup & Schwarzenberger, 2007), gestation lengths were highly variable. The shortest amount time between subsequent parturition dates for a single individual in this study was around 53 days. This is much shorter than the 60-day average reported in comparative studies (Eisenberg & Gould, 1969; Symonds, 1999), but is similar to observations from a captive population held at higher-than-usual ambient temperatures (Mallinson, 1974). This short inter-birth interval

Table 4 Causes of mortality in *Setifer setosus* over the three study seasons

Animal	Sex	Date of capture	Date of death	Cause of death
SF03	F	23-Feb-10	14-Mar-10	Unknown ground predator
SF06	M	27-Mar-10	Unknown	Undetermined boa species
SF09	M	7-Oct-10	2-Feb-11	<i>Boa manditra</i>
SF10	F	10-Oct-10	20-Oct-10	Unknown ground predator
SF13	F	5-Nov-10	23-Mar-11	<i>Boa manditra</i>
SF14	F	5-Nov-10	19-Feb-11	<i>Boa manditra</i>
SF15	M	19-Nov-10	16-Dec-11	<i>Acranthophis madagascariensis</i>
SF17	M	22-Dec-10	1-Feb-11	<i>Acranthophis madagascariensis</i>
SF18	M	29-Dec-10	27-Oct-11	Unknown ground predator
SF20	M	24-Feb-11	12-Dec-11	Undetermined boa species
SF21	F	26-Feb-11	6-Mar-11	Undetermined boa species
SF22	F	19-Oct-11	17-Jan-12	<i>Boa manditra</i>
SF23	F	19-Oct-11	8-Dec-11	Unknown ground predator
SF24	F	2-Nov-11	26-Jan-12	Unknown ground predator
SF25	M	19-Nov-11	17-Jan-12	Unknown ground predator
SF26	M	28-Nov-11	26-Dec-11	Hit by vehicle on RN 4

For some individuals, there was clear evidence of predation by boas (transmitters found along with undigested spines) but the species was not confirmed. Ground predators could not be determined (deaths not witnessed).

would indicate a period of overlap between lactation and gestation. It is therefore likely that *S. setosus* is capable of post-partum oestrus, previously thought to be unique to the large-eared tenrec *Geogale aurita* (Stephenson, 1993; Racey & Stephenson, 1996). The observation, on two separate occasions, one reported in Levesque *et al.* (2012), the other from this study, of males sharing a nest site with lactating females further supports this.

In this population, in the Western deciduous forest, breeding occurred throughout the active season, and parturition dates were not synchronized. In contrast, females from a population studied in the Eastern rainforest gave birth in October, and no pregnancies were observed after that date (Eisenberg & Gould, 1969). Similarly flexible breeding schedules were observed in *T. ecaudatus* introduced to the Seychelles (Nicoll & Racey, 1985), where peak reproduction coincided with peak food availability. The capacity to give birth to multiple litters during a single season (max of 3 observed in this study), dramatically increases the annual fecundity of this species, especially when compared to previously reported values which only considered a single litter per year (Eisenberg & Gould, 1969; Symonds, 1999). In combination with the capacity for fast sexual maturation, as early as 74 days for a captive individual (Eisenberg, 1975), high annual fecundity places *S. setosus* further towards the 'fast' end of the mammalian life history continuum showing more similarities with the extreme reproduction observed in *T. ecaudatus*.

Symonds (2005) posited that it is unclear if the high rate of reproduction and overall reproductive flexibility observed in the Tenrecinae relative to other insectivores is by-product of Madagascar's environment, or of their phylogeny, as little is known about the life histories of the other members of the Afrosoricida; the otter shrews (family: Tenrecidae; subfamily: Potamogalinae) and the golden moles (family: Chrysochloridae). However, similar flexibility is also seen in

the life-history traits of other endemic Malagasy mammals, especially the cheirogaleid lemurs (Lahann, Schmid & Ganzhorn, 2006; Dewar & Richard, 2007; Lahann & Dausmann, 2011; Canale *et al.*, 2012). Therefore, it is likely that the environment does play a large role in shaping the life histories of these species (Wright, 1999; Dewar & Richard, 2007). In addition to environmental conditions, mortality is one of the primary drivers of the 'rate' of life histories, with high rates of predation leading to high birth rates (Read & Harvey, 1989). The high mortality rates observed in *S. setosus* support this hypothesis.

This study presents aspects of the natural history of a free-ranging tenrec and illustrates the importance of long-term studies across a species' range. Both the level of mortality as well as reproductive activity in this species were significantly higher than what has been reported in previous studies. The opportunistic nature of the data collection and the cryptic nocturnal character of the species precluded accurate estimations of certain population parameters (population size, juvenile growth rates, lifespan, etc.), but other aspects of the life history of *S. setosus*, which were hitherto unknown, have been made clear. The study was greatly limited by the inability to follow single individuals over multiple seasons. It would be of interest to quantify rates of survival of the different juvenile cohorts to determine if there are any advantages to the synchronous reproduction observed in the eastern rainforests (Eisenberg & Gould, 1969) over the multiple litters observed in this western population. In addition, hibernation has been shown to increase the probability of overwinter survival, and is believed to lead to slow life histories (Turbill, Bieber & Ruf, 2011). As a slow life history is not the case for this species, at least not in the habitat studied here, a comparison of the rates of mortality and the rates of reproduction with populations, which are active year round, could help to interpret this exception. Greater understanding of the reproduction,

phenology and rates of mortality of these basal mammals could help shed light on the evolution of mammalian life histories.

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