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NEWS AND PERSPECTIVES

Evidence of prolonged torpor in Goodman's mouse lemurs at Ankafobe forest, central Madagascar

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Abstract The small-bodied mouse lemurs of Madagascar (*Microcebus*) are capable of heterothermy (i.e., torpor or hibernation). The expression of these energy-saving strategies has been physiologically demonstrated in three species: *M. berthae*, the pygmy mouse lemur (daily torpor), *M. murinus*, the gray mouse lemur (daily torpor and hibernation), and *M. griseorufus*, the reddish-gray mouse lemur (daily, prolonged torpor and hibernation). Additional evidence, based on radiotracking and seasonal body mass changes, indicated that mouse lemur capabilities for heterothermy extended to *M. lehilahytsara*, the Goodman's mouse lemur. In this study, we confirm the use of hibernation in Goodman's mouse lemurs at a new location, a high-plateau forest fragment in Ankafobe, central Madagascar. Our evidence is based on sleeping site monitoring of radiocollared individuals and the retrieval of three mouse lemurs from inside a tree hole, all of which displayed a lethargic state. Though our data are preliminary and scant, we show that hibernation occurs in high-plateau mouse lemurs, and suggest that a buffered environment (i.e., tree holes instead of nests) may be crucial to avoiding potentially extreme ambient temperatures.

Keywords *Microcebus lehilahytsara* · Hibernation · High plateau · Madagascar

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Introduction

The mouse lemurs of Madagascar (genus *Microcebus*) are one of the most speciose groups of lemurs, with 24 species described thus far (Hotaling et al. 2016). They are, as a group, the most pervasive in Madagascar's forests, and can be found even in degraded and fragmented habitats close to human habitation. The ability of mouse lemurs to survive erratic climate patterns and high resource seasonality in their habitats stems from their ecological flexibility. They are opportunistic omnivores and rely on a wide range of food resources, including gums, arthropods, reptiles, fruits, and flowers (Thorén et al. 2011). Mouse lemurs also display unusual physiological plasticity, one example being the use of daily/prolonged torpor or hibernation (i.e., heterothermy) by some individuals, populations, and species (Schülke and Ostner 2007; Schmid and Ganzhorn 2009; Kobbe et al. 2011).

Daily torpor (i.e., controlled reductions in body temperature and metabolic rates for periods of less than 24 h) has previously been physiologically demonstrated in two mouse lemur species, *M. berthae* (one of the smallest species, referred to as *M. myoxinus* in the original study) and *M. murinus* (the gray mouse lemur) at Kirindy, a dry deciduous forest in western Madagascar (Ortmann et al. 1997; Schmid 2001). Prolonged torpor and hibernation—controlled reductions in temperature and metabolic rates for up to a couple of days (in the former) or several weeks at a time (in the latter)—have been indisputably reported in two species: the gray mouse lemur from the littoral southeastern forests, and *M. griseorufus* (the reddish-gray mouse lemur) from spiny southern forests (Schmid and Ganzhorn 2009; Kobbe et al. 2011). Skin temperature profiles, used as a proxy for metabolic rates, showed that a subset of mouse lemurs were able to passively track the ambient temperature over periods of several days up to several weeks.

Indirect evidence of heterothermy, as ascertained by the lack of nocturnal sightings during active phases and/or observations of fat accumulation in captured individuals (i.e., tail fattening in preparation for prolonged torpor or hibernation), was reported for gray mouse lemurs in dry deciduous western forests and *M. rufus* (brown mouse lemurs) from montane rainforests (Atsalis 1999; Schmid 2000). Radiotracking observations and body-mass data from *M. lehilahytsara* (Goodman's mouse lemurs, referred to as *M. rufus* in the original study) at Mantadia, an eastern rainforest, showed that a portion of the mouse lemur population remained inactive during the winter (Randrianambinina et al. 2003). Mouse lemurs that were heavier were more likely to experience seasonal torpor, confirming the association between body mass and hibernation. At Tsinjoarivo forest, a high-elevation rainforest in central-eastern Madagascar, several Goodman's mouse lemurs captured at the end of the reproductive season (February–March) also showed significant tail fattening, so prolonged torpor/hibernation was suspected at this site (Blanco 2010). More recently, studies conducted under semi-natural conditions at the Zoo Zürich, Switzerland, showed that most Goodman's mouse lemurs stopped visiting feeding stations during the winter and were, presumably, hibernating (Karanewsky et al. 2015).

Goodman's mouse lemurs are considered highland specialists. This species is regularly exposed to cold temperatures during the winter/dry season, and is therefore the best candidate to employ hibernation in the wild (Radespiel et al. 2012). Torpor use can be more energetically profitable in colder habitats because it allows individuals to reduce body temperature, and consequently metabolic demands, to a greater degree.

Here we present evidence of prolonged torpor in Goodman's mouse lemurs at Ankafobe Forest, a tiny forest fragment enclaved in the high plateau of central Madagascar. Ankafobe seems particularly relevant to the study of torpor/hibernation in mouse lemurs because, unlike other lower-elevation rainforests harboring Goodman's mouse lemurs (such as Mantadia), absolute temperature minima can drop significantly on occasion, increasing the risks of freezing. Thus, selection for buffered environments (e.g., sleeping sites and/or hibernacula) may be strong at this site. In this preliminary survey, we begin to answer basic ecological questions such as the prevalence of hibernation among mouse lemurs at Ankafobe and the preferences for particular hibernacula.

Methods

Study site

We used capture/mark/recapture techniques between February 5 and 13, 2016 at a forest fragment in Ankafobe, central Madagascar (S18°06′23.1″ E47°11′13.2″, 1472 m). Climate profiles from a nearby site (Ambohitantely) characterize it as subhumid, with the highest average temperatures observed during November and the lowest in August (Birkinshaw et al. 2009). At Ankafobe, temperature minima can drop below 0 °C on rare occasions (pers. obs.).

Sherman traps were set at ~1.5 m high along a single trail, in pairs, baited with pieces of fresh banana. Traps were set at 16:00 and checked at 5:00 the following morning. We set up to 29 Sherman traps daily for 9 nights, resulting in a total of 243 trap nights. Captured mouse lemurs were brought back to the campsite, marked with a microchip, weighed, measured, and fitted with small transmitters (1.5 g, Advance Telemetry Systems, Isanti, MN, USA). We employed telemetry to locate sleeping sites and monitor nocturnal activity. Between February 6 and March 10, 2016 we conducted sleeping site monitoring daily. During a second short expedition to the site, from May 16–20, 2016, we monitored sleeping sites four times a day to document sleeping site occupancy during day and night.

Study animals

A total of six mouse lemurs were captured and radiocollared in February. Two of the collars were retrieved from mouse lemurs at the beginning of March. During the May expedition, we detected signals from three individuals. We suspected hibernation expression in one of the radiocollared mouse lemurs based on: (a) clear evidence of body and tail fattening during the February capture, (b) absence of nocturnal activity for two nights during the May expedition, and (c) a change to a more thermally stable (buffered) sleeping site, a tree hole as opposed to a nest. In order to confirm hibernation, we proceeded to retrieve the radiocollared individual from the sleeping site location. Retrieval procedures are described below. A total of three individuals were found inside the tree hole. All three mouse lemurs were brought back to the campsite and weighed. Once fully aroused from hibernation, they were released at the capture location around 19:00.

Results

Captured mouse lemurs

Despite our small sample size, captured mouse lemurs displayed a range of body masses and tail fattening conditions. Table 1 shows body mass and tail base circumference measurements. The individual “Bet” was the heaviest, displaying significant tail fattening in early February (Fig. 1). Reproductive observations showed she was an adult female, though there was no evidence of recent lactation. A second adult female captured the same day displayed no tail fattening but swollen nipples, suggestive of active lactation. A third female, estimated to be around a year old, showed no evidence of reproductive activity and almost no tail fattening at the time of capture (Table 1).

Sleeping site monitoring

Between February 6 and March 10, we documented a minimum of 11 and a maximum of 19 sleeping site observations per mouse lemur (Table 2). During this period, all six radiocollared mouse lemurs occupied nest-like structures as sleeping sites (Table 3). During May 16–18, we observed that one of the three radiocollared individuals (the adult female) was using a tree hole, whereas the two remaining males were occupying nest-like structures (Table 4). The individual female occupying the tree hole remained at this site during all telemetry checks, whereas two individual males occupying nests were absent from their sleeping sites during at least a portion of the night, i.e., the active phase. In order to confirm that the tree hole was used as a hibernaculum, we proceeded to retrieve the individual from this location.

Retrieval procedure and description of the tree hole

The sleeping site/hibernaculum of individual “Bet” was identified as a cavity in an *Aphloia theiformis* tree, about 9 m high. We observed several tree holes along the trunk but the radio signal was strongest when an antenna was directed to one specific hole, located about 5 m high. The external aperture of the hole was about 4 cm wide and 5 cm long. Due to its small size, the hole had to be widened before we could manually retrieve the radiocollared individual. This procedure took about 40 min, during which no vocalizations were heard from within the tree cavity. The first visible individual was a mouse lemur wearing a collar (later identified as “Bet”). Upon removal of this mouse lemur, two additional individuals were found. All three individuals were unresponsive when removed from the tree hole and cold to the touch. Body temperature was too low to be detected by a standard digital thermometer. Inspection of the hole after the removal of the three individuals showed humus-like soil and *Aphloia theiformis* leaves (Fig. 2). The internal dimensions of the hole were approximately 42.5 cm (height) by 6.5 cm (depth). The enlarged hole was later boarded with wood to close up the entrance to approximate the original entrance size.

Table 1 Body masses and tail base circumferences of the captured mouse lemurs

ID	Capture date	Sex	Age	Body mass (g)	Tail base circumference (mm)	Observations
Cl	2/5/16	Male	~1 year old	38.5	16	Testes completely regressed
Be	2/8/16	Male	~1 year old	39	18	Testes completely regressed
Dy	10/1/15	Male	Adult	47	14	Unpublished data
Dy	2/9/16	Male	Adult	49	17	Testes regressing
Bet	2/11/16	Female	Adult	73	27	Developed nipples but no evidence of recent lactation—evidence of fattening in tail and body
Bet	5/18/16			56.5	26	Hibernating
Ja	2/11/16	Female	Adult	59	14	Swollen nipples, lactating, no evidence of fattening
Ja	2/27/16			50	17	Collar was removed
Bea	9/30/15	Female	Juvenile	42	16	Unpublished data
Bea	2/11/16	Female	~1 year old	52	18	Developed nipples but no evidence of recent lactation—little evidence of fattening
Bea	3/1/16			59	20	Collar was removed

Note the body mass of the female “Bet” in early February

Fig. 1 Adult female "Bet," showing tail fattening

Table 2 Sleeping site monitoring during the February–March study period

ID	#SS	MNI	#Obs
Cl	11	4	18
Bea	3	2	11
Be	6	3	16
Bet	4	2	19
Dy	6	1	8
Ja	3	2 (uncollared)	11

ID individual mouse lemur, *#SS* number of sleeping sites, *MNI* minimum number of individuals sharing the sleeping site with the targeted mouse lemur, *#Obs* number of observations

Discussion

Goodman's mouse lemurs may be better characterized as highland specialists rather than rainforest mouse lemurs (Radespiel et al. 2012). By virtue of occupying higher-elevation habitats, Goodman's mouse lemurs are consistently exposed to low ambient temperatures during the winter. Exposure to cold increases the energetic demands associated with maintaining a high body temperature (i.e., remaining normothermic); thus, high-plateau habitats should favor the expression of hibernation. Heterothermic responses can be predicted on the basis of body mass and habitat characteristics, such as temperature minima and degree of resource seasonality (Schülke and Ostner 2007); however, more ecophysiological studies are warranted to test these predictions. The paucity of ecophysiological data on mouse lemurs stems in part from the technical difficulties involved in fitting individuals with light radiocollars or devices (weighing less than 5% of their body mass) that can measure temperature and, simultaneously, provide a radio signal to detect the individual's location. Thus far, with rare exceptions (Schmid 2001, for torpor use), researchers have mainly confirmed that mouse lemurs hibernate without pinpointing hibernation locations (Schmid and Ganzhorn 2009; Kobbe et al. 2011). Here, we have identified a potential hibernaculum but had to disturb the site in order to confirm that the subject was heterothermic.

Future investigations into torpor/hibernation in mouse lemurs should provide not only an increased understanding of their ecological flexibility and resilience to habitat degradation or fragmentation, but could also shed light on mouse lemur biogeographic history and the role that hibernation may have played in the diversification and radiation of this group across Madagascar. For example, torpor and/or hibernation strategies may have favored the dispersion of mouse lemurs across the highlands of Madagascar, which may have originally comprised a mosaic of scrublands, grasslands, and forest fragments like Ankafobe (Yoder et al. 2016). Moreover, studies of mouse lemur torpor/hibernation should be carried out in tandem with those on the dwarf lemurs (*Cheirogaleus*), a lemur group closely related to mouse lemurs. Dwarf lemurs occupy many of the same environments as do mouse lemurs, but they are obligatory hibernators, are larger in size (about ten times bigger), and are more ecologically susceptible to disturbance (i.e., they are primarily fruit eaters).

We observed intrapopulation plasticity in the expression of hibernation at Ankafobe. Males captured in February showed no evidence of tail fattening, and remained active in May. Among female mouse lemurs, there was a range of behaviors. Female "Ja" showed evidence of recent lactation and no fat deposits, whereas female "Bet" displayed tail fattening but no evidence of recent reproductive activity. This is consistent with the argument that reproduction seems to be incompatible with hibernation (or fattening to sustain hibernation). Variability in the expression of polyestry (more than one reproductive opportunity per season) and weaning profiles likely influences fattening capacity and eventually the timing of hibernation in females. Though resource availability is severely depressed during the winter time, the inactivity of a portion of the mouse lemur population may ameliorate

Table 3 Description of sleeping sites of radiocollared mouse lemurs

ID	SS	Tree	Tree height	Signal height	DBH	Observations
Cl	Nest	Hasina (*Dracaena reflexa*)	5	5	42	
Cl	Nest	*Elatrangidina (Filicium dicipiens)*	6	6	22	Dead leaves on top of tree crown—shared with Be
Cl	Nest	Andraresina (*Trema orientalis*)	6	6	14.5	Bamboo leaves—shared with Bea and Be
Cl	Nest	Hafotra (*Dombeya*)	12	6	52	Dry leaves/entangled liana branches—shared with Be and Bea
Cl	Nest	Hasina (*Dracaena reflexa*)	9	6	41	Dry bamboo leaves/entangled liana branches
Cl	Nest	*Pandanus spinifer*	10	7	55	Shared with Be
Cl	Nest	*Hazombola (Xylopia)*	7	6	24	Same as Bet
Cl	Nest	Hazondrano (*Ilex mitis*)	10	9	45	Same as Bet
Cl	Nest	*Pandanus spinifer*	7	6	56	Same as Be and Bet
Cl	Nest	*Pandanus spinifer*	9	7	52	Same as Be and Bet
Cl	Nest	*Pandanus spinifer*	9	6	55	Same as Bet
Dy	Nest	*Pandanus spinifer*	7	4	56	
Dy	Nest	*Pandanus spinifer*	7	3	27	
Dy	Nest	Andraresina (*Trema orientalis*)	6	6	15	Bamboo leaves—formerly occupied by Bea, Cl, Be. Shared with Cl
Dy	Nest	Hafotra (*Dombeya*)	12	6	58	Dry leaves/entangled liana branches—shared with Cl
Dy	Nest	Bamboo	6	6	n/a	
Dy	Nest	*Pandanus spinifer*	12	10	81	
Dy	**Nest**	**Rotra** (*Syzygium*)	**9**	**7**	**29**	
Be	Nest	Elatrangidina *(Filicium dicipiens)*	6	6	22	Dead leaves on top of tree crown—shared with Cl
Be	Nest	Andraresina (*Trema orientalis*)	6	6	15	Bamboo leaves—shared with Bea and Cl
Be	Nest	Hafotra (*Dombeya*)	12	6	58	Dry leaves/entangled liana branches—shared with Bea and Cl
Be	Nest	Hazombato (*Homalium*)	6	5	16	
Be	Nest	*Pandanus spinifer*	10	7	55	
Be	Nest	Hazondrano *(Ilex mitis)*	10	9	49	Shared with Cl and Bet
Be	Nest	*Pandanus spinifer*	9	7	52	Shared with Cl and Bet
Be	**Nest**	**Voatsilana** (*Polyscias ornifolia*)	**12**	**10**	**61**	
Be	**Nest**	***Coptosperma***	**8**	**6**	**17**	**Shared with another uncollared individual**
Bet	Nest	Hazombola *(Xylopia)*	7	6	24	
Bet	Nest	Hazondrano (*Ilex mitis*)	10	9	49	Dead leaves—shared with Cl and Be
Bet	Nest	*Pandanus spinifer*	9	7	52	Shared with Be and Cl
Bet	Nest	*Pandanus spinifer*	9	6	55	Shared with Be and Cl
Bet	***Tree hole***	***Aphloia theiformis***	***9***	***5***	***50***	***Hibernating—shared with young female and young male mouse lemurs***
Ja	Nest	Voatsilana (*Polyscias ornifolia*)	12	12	43	Dead leaves/entangled liana branches
Ja	Nest	*Pandanus spinifer*	9	6	55	
Ja	Nest	Hazotokana *(Brachylaena ramiflora)*	10	9	82	Shared with two uncollared individual juveniles
Bea	Nest	Andraresina (*Trema orientalis*)	6	6	15	Bamboo leaves—shared with Be and Cl
Bea	Nest	Hafotra (*Dombeya*)	12	6	58	Dry leaves/entangled liana branches—shared with Be and Cl
Bea	Nest	Hazombato (*Homalium*)	6	5	16	Dry leaves

Bolded examples represent sleeping sites described during the May expedition; bolded/italicized indicates a hibernaculum

SS sleeping site, *DBH* diameter at breast height

Table 4 Monitoring of sleeping sites during the May expedition

ID	Date	Time	SS	Type	At SS
Bet	16-May	14:30	*Aphloia theiformis*	Tree hole	Yes
Bet	16-May	19:30	*Aphloia theiformis*	Tree hole	Yes
Bet	16-May	22:30	*Aphloia theiformis*	Tree hole	Yes
Bet	17-May	2:15	*Aphloia theiformis*	Tree hole	Yes
Bet	17-May	9:10	*Aphloia theiformis*	Tree hole	Yes
Bet	17-May	19:10	*Aphloia theiformis*	Tree hole	Yes
Bet	17-May	22:30	*Aphloia theiformis*	Tree hole	Yes
Bet	18-May	5:40	*Aphloia theiformis*	Tree hole	Yes
Be	16-May	15:30	*Polyscias ornifolia*	Nest	Yes
Be	16-May	19:45	*Polyscias ornifolia*	Nest	No
Be	16-May	22:45	*Polyscias ornifolia*	Nest	No
Be	17-May	2:20	*Polyscias ornifolia*	Nest	No
Be	17-May	9:20	*Polyscias ornifolia*	Nest	Yes
Be	17-May	19:15	*Polyscias ornifolia*	Nest	Yes
Be	17-May	22:45	*Polyscias ornifolia*	Nest	No
Be	18-May	6:10	*Polyscias ornifolia*	Nest	Yes
Be	18-May	14:52	*Polyscias ornifolia*	Nest	Yes
Be	18-May	19:40	*Polyscias ornifolia*	Nest	No
Be	19-May	7:15	Coptosperma	Nest	Yes
Dy	16-May	16:40	*Syzygium*	Nest	Yes
Dy	16-May	20:10	*Syzygium*	Nest	No
Dy	16-May	23:10	*Syzygium*	Nest	No
Dy	17-May	2:35	*Syzygium*	Nest	No
Dy	17-May	18:45	*Syzygium*	Nest	No
Dy	17-May	22:10	*Syzygium*	Nest	No
Dy	18-May	5:20	*Syzygium*	Nest	No

The presence of the female “Bet” at the sleeping site during day and night checks indicated prolonged inactivity

SS sleeping site

intraspecific competition for the remainder of the active population.

Our observations highlight the incredible behavioral flexibility of mouse lemurs from the same population exposed to identical ecological/climatic conditions, but more detailed ecological studies could profitably address ecological flexibility in relation to population dynamics. Future studies should also endeavor to assess differential life-history strategies in populations of mouse lemurs under a variety of environmental conditions. Our findings are only the first tiny step towards those goals. At a minimum, with our study, we extend the previously known range of hibernation for mouse lemurs to one of the coldest habitats in Madagascar.

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Fig. 2 Hole inside tree used as a hibernaculum. Note the accumulation of humus-like soil and leaves

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