

Hibernation Patterns of Dwarf Lemurs in the High Altitude Forest of Eastern Madagascar

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Introduction

The unusual ecophysiology of dwarf lemurs (*Cheirogaleus* spp.), the only obligatory hibernators among primates, was first documented both in captivity and in the wild between 1962 and 1980 (Petter 1962; Petter et al. 1977; Hladik et al. 1980; Petter-Rousseaux 1980). Petter (1962) described dwarf lemur hibernacula as well as aspects of their hibernation behavior and ecology. Yet, the ecophysiology of these tropical hibernators remained poorly known until after the turn of the century, when researchers supplemented ecological and behavioral data with records of body temperature and metabolic measurements of hibernating and nonhibernating individuals in the wild (Dausmann et al. 2004, 2005, 2009; Dausmann 2005). A population of the western dwarf lemur, *C. medius*, at Kirindy (a low altitude western dry deciduous forest near the coastal city of Toliara) was the object of almost all of this research; thus, for an extended period of time, virtually all that was known about the ecophysiology of hibernation in dwarf lemurs was derived from studies conducted at a single locality. A combination of high seasonality, low annual rainfall, and high fluctuation in daily ambient temperature makes Kirindy forest unique, and it is likely that the hibernation patterns found there are uncharacteristic of hibernation patterns manifested in other dwarf lemur species, most of which live in moister, less seasonal habitats, and some of which live in cold, high-altitude forests.

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Today, the high-altitude rainforests of Madagascar stretch along the peaks of the escarpment that forms the eastern border of the central high plateau. Although they were originally part of a forested “corridor” extending north–south from Mantadia to Ranomafana, and likely east–west across part of the Vakinakaratra region of the Antananarivo district, deforestation and habitat disturbance have broken the corridor’s continuity and high-altitude plant and animal communities have become increasingly isolated. One of the few remaining high-altitude forests is Tsinjoarivo, located about 80 km to the southeast of the capital Antananarivo. Tsinjoarivo forest is comprised of a domain of primary forest toward the eastern half and of forest fragments with different levels of anthropogenic disturbance on its western side, just to the east of the central high plateau. The latter extends far to the west of this north–south corridor, decreasing gently in elevation from east to west so that, at its westernmost boundary, it rises only a few hundred meters above sea level. The west-to-east profile of the escarpment at Tsinjoarivo also represents an altitudinal gradient, ranging between 1,700 to 1,300 m. Effectively, Tsinjoarivo sits atop the escarpment that separates the central highlands from the eastern lowland forests (Irwin 2008) (Fig. 1).

We argue that it was in habitats like this, in the cold and relatively high-altitude forests of Madagascar, that obligatory hibernation evolved. Because all species of the genus *Cheirogaleus* (but no other cheirogaleids) are obligatory hibernators, we assume that obligatory hibernation was a derived feature of their common ancestor. Recent molecular genetic research (Groeneveld et al. 2010) has affirmed that *C. sibreei*, the only dwarf lemur species apparently restricted to high-altitude habitats today, holds a basal position in the *Cheirogaleus* clade. It may retain the

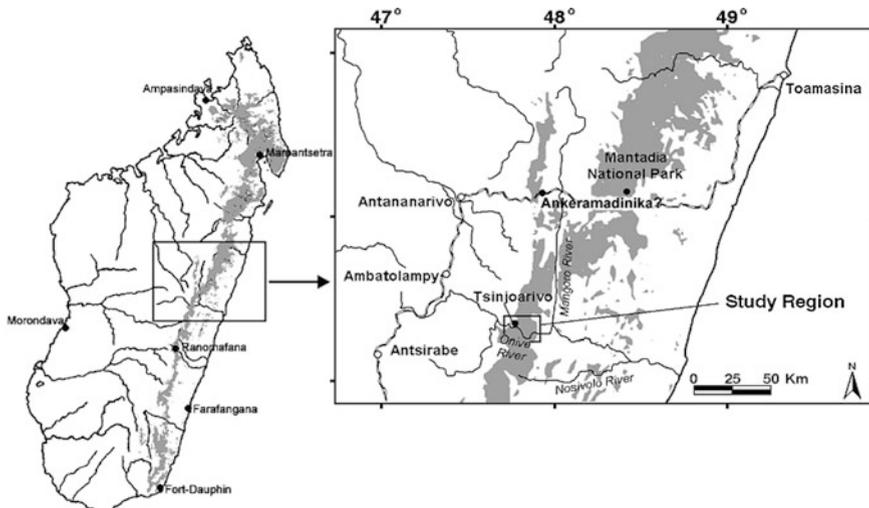


Fig. 1 Map of our main study area (*Tsinjoarivo*) and reference to other sites mentioned in this chapter. Map courtesy of Mitchell T. Irwin

ancestral dwarf-lemur condition for a number of traits. In some ways, the *low* altitude, smallest-bodied, western dwarf lemurs (*C. medius*) are the most specialized. Whereas individuals belonging to all species of *Cheirogaleus* accumulate fat in their tails to sustain them through prolonged hibernation, no eastern species does this to the extreme manifested in the western dwarf lemurs (who therefore have been dubbed the “fat-tailed” dwarf lemurs).

Here we review what is known about the ecology, behavior, and ecophysiology of hibernation of eastern dwarf lemurs, with an emphasis on the two species living in the high-altitude forests of Tsinjoarivo—*C. sibreei* and *C. crossleyi*—and with comparisons to western dwarf lemurs. We explore that variation within the context of the environments in which they live, and ask whether and how altitude affects the biology and behavior of dwarf lemurs. Does body size vary with altitude, as might be expected under Bergmann’s rule, or is some other factor such as primary productivity the main driver of body size variation in eastern dwarf lemurs? Do sleeping sites and hibernacula preferences vary with altitude? Does the duration of hibernation vary with altitude? Finally, on the basis of these data, as well as the broader context of paleoecological data, we offer some thoughts on the evolution of hibernation in the genus *Cheirogaleus* and the hypothetical relevance that altitude may have had in their evolutionary history.

Dwarf Lemur Distributions

There are four recognized living species of dwarf lemurs, two of which live in sympatry at Tsinjoarivo forest, central-eastern Madagascar: *Cheirogaleus sibreei* and *C. crossleyi*. Tsinjoarivo harbors the only living population of *C. sibreei* studied to date. This species is found today exclusively on the western side, at elevations between 1,400 and 1,700 m. It may occur as well at Ranomafana (southeastern rainforest) where an individual similar to *C. sibreei* was captured at a high-altitude location (at 1,474 m, on the top of Mt. Maharira, the highest mountain in Ranomafana National Park); this report warrants further confirmation (Wright et al. 2012). Additional evidence in support of this argument can be garnered from the accounts of Forsyth Major (1896), who collected the type specimen of *C. sibreei* at Ankeramadinika, a locality situated in the central high plateau. Although Forsyth Major failed to report the exact location (he gave a vague reference, “one day’s journey east of Antananarivo”), the altitude of this town was documented by his contemporaries at over 1,400 m (see Groeneveld et al. 2010).

Unlike Sibree’s dwarf lemurs, *C. crossleyi* is also found at low, middle, and high altitude forests, from northern to southern Madagascar, including sites along the eastern edge of the central plateau (Blanco et al. 2009; Groeneveld et al. 2009, 2011; Groves 2000; Hapke et al. 2005). Whereas it does not occur in the dry forests of the west or south, it does tolerate a wide range of habitats, differing in

both temperature and mean annual rainfall. Tsinjoarivo may be the high elevation limit for *C. crossleyi*.

The third species of “eastern” dwarf lemur is *C. major*, which also has been found in eastern littoral to high-altitude, escarpment forests. It had a broad geographic range from the eastern lowland forest to the middle of the central plateau, well to the west of the eastern escarpment. The skull of a very large individual, likely *C. major*, was found at a subfossil site Ampasambazimba (Standing 1908) located at 1,036 m near Lake Itasy. This site lies in the middle of the Itasy District of the Antananarivo Province of the central highlands (18°56'S, 46°39'43"E), approximately halfway between Antananarivo (to its east) and Tsiroanomandidy (to its west). The dwarf lemur specimen has not been dated but radiocarbon dates for other specimens from subfossil sites in the central highlands range from around 1,400 Cal B.P. to 9,000 Cal B.P. (Crowley 2010).

Petter et al. (1977) described *C. major* as still living today in the central highlands—indeed further west, in an “eastern-like,” isolated forest called Bongolava (now Ambohijanahary Special Reserve). This forest, between 800 and 1,600 m in elevation, is located near the western border of the Central Plateau just east of the Bemaraha tsingy massif and northwest of Tsiroanomandidy (Bongolava District of the Antananarivo Province) (see also Ausilio and Raveloanrinoro 1998; Thalmann 2000; Thalmann and Rakotoarison 1994). Thalmann (2000) published a photograph of an adult. Whereas this individual was considerably smaller than the adult *Cheirogaleus* photographed beside it, and not nearly as large as that described by Standing (1908) from the subfossil site, Ampasambazimba, mentioned above, the individual was nevertheless significantly larger than adult western dwarf lemurs. Groeneveld et al. (2011) tentatively identify the dwarf lemur from Bongolava as *Cheirogaleus crossleyi*. If this is correct, then the range of *C. crossleyi* extends broadly across the central highlands.

The fourth species, *C. medius*, is found primarily along the western dry deciduous forests, from Ankarana in the north to Tabiky in the south, but its range extends to the northeastern rainforest of Sambava and the southeastern littoral forest of Mandena and St. Luce. The highest altitudinal record for a *C. medius* site is 590 m, from an unnamed locality 170 km east of Toliara (Groeneveld et al. 2009). No *Cheirogaleus* is found in the southernmost spiny forests, between the western dry deciduous forests and the southeastern littoral forests.

Tsinjoarivo Dwarf Lemurs

Study Sites

One of us (MBB) has conducted research at Tsinjoarivo since 2006, at locations previously selected by Mitchell Irwin and collaborators for the study of diademed sifakas, *Propithecus diadema* (Irwin 2006, 2008; Irwin et al. 2010). Blanco and her collaborators conducted surveys and trapped cheirogaleids (mouse and dwarf

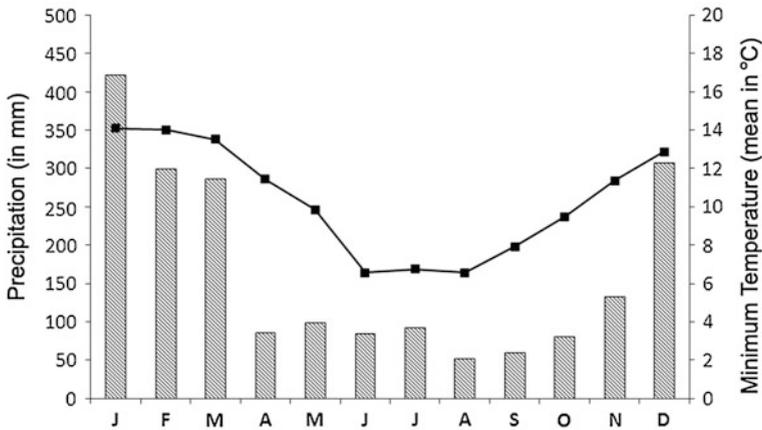


Fig. 2 Precipitation and mean minimum temperature data from the forest fragment at Tsinjoarivo forest. Data are compiled from >5 years between 2002 and 2008

lemurs) at three study sites: in one of the western forest fragments, Andasivodihazo (~225 ha, 1,600–1,700 m); an intermediate location (Ankadivory 1,400 m); and a site within continuous forest about 10 km to the southeast of Andasivodihazo (Vatateza 1,300 m). Climate is seasonal at Tsinjoarivo. A “rainy” season extends from December to March, but rain falls during the “dry” season as well, albeit to a lesser degree. Annual rainfall is generally higher in the continuous forest toward the east (~2,500 mm) than in the western fragments (~2,000 mm). Temperatures are highest in December and January (Irwin 2008). The monthly mean temperature minimum at Tsinjoarivo ranges between 6 and 14°C in the forest fragment of Andasivodihazo (Fig. 2) which is much lower than values recorded for low altitude forests such as the western dry deciduous forest at Kirindy (11.7–23.6°C) or the littoral southeastern forest at Mandena (16.3–23.8°C) (Lahann and Dausmann 2011). Unlike Kirindy, where maximum temperatures in the coldest months (June and July) exceed 30°C during the day (Dausmann et al. 2009), maximum temperatures at Tsinjoarivo during the same 2 months do not reach 30°C and average 19°C (Irwin 2006). Tsinjoarivo is indubitably one of the more extreme environments in Madagascar. As one of the coldest forests in Madagascar, it offers ideal conditions for the study of the metabolic strategies of hibernating species.

Measurements

At Tsinjoarivo, dwarf lemurs were live-trapped using Tomahawk traps set between 3–10 m along trails and baited with small pieces of banana. Traps were set around 17:00 and checked at 4:00 the following morning. All captured dwarf lemurs were brought to the campsite, marked with microchips (AVID Identification Systems,

Inc., CA, USA), weighed, and measured. All individuals were released at the site of capture at dusk on the same day. Measurements used in this study include: head and body length (cm), measured dorsally, from the tip of the rhinarium to the cranial margin of the first caudal vertebra; tail length (cm), ventrally, from the base of the anus to the distal end of the last caudal vertebra; head length (mm), maximum length of the head from the most projecting margin of the rhinarium to the back of the braincase; head width (mm), maximum bizygomatic breadth; ear (or pinna) length (mm), maximum length between the base of the tragus and the tip of the pinna.

For studies of hibernation, a subset of captured individuals was fitted with external transmitters with temperature sensors that recorded skin temperature every 15 min (Advanced Telemetry Systems, Isanti, MN, ~10 g). Data loggers were used (Thermoworks, Lindon, UT) to collect hibernacula and ambient temperature. Hibernation periods were defined as skin temperature below 25 °C for a minimum of 2 days.

Does Altitude Correlate with Variation in the Morphometrics of Dwarf Lemurs?

Under Bergmann's rule, body mass is predicted to increase in colder environments (e.g., at higher latitude or altitude). Simply put, larger animals reduce heat loss to the environment by decreasing their surface-to-volume ratio. Although this principle was initially proposed to explain intraspecific size variation in endotherms (Blackburn et al. 1999; Mayr 1956; Roberts 1953), it has been applied to a variety of organisms and across species since its inception (Huston and Wolverson 2011; Lahann et al. 2006; Lin et al. 2008; Taylor et al. 1985).

A second possibility is that body size varies in accord with resource productivity; low productivity limits available energy and favors selection for small body size. Accordingly, body size should be positively correlated with rainfall, assuming that the latter acts as a good proxy for resource productivity. Resource productivity, seasonality, and quality may interact with body size in important (albeit not necessarily obvious) ways. Thus, for example, small-bodied species living in resource-poor habitats may experience a shortfall in food availability that becomes increasingly taxing (due to thermoregulatory stress) in habitats that are also cold. Reducing body size may be one way to cope with energy deficits; reducing body temperature and metabolic rate may be another. If the supply of food is limiting, rainfall may better predict body size than temperature or altitude. Large body size might be favored in resource-rich but cold environments, while small body size might be favored in resource-poor but equally cold or even colder environments (Ellison et al. 1993).

A recent treatment of size variation among lemurs has demonstrated that neither Bergmann's rule nor the productivity hypothesis explains size differences (Kamilar et al. 2012). However, Kamilar et al. (2012) did not test intraspecific

variation. We tested these hypotheses specifically for Crossley's dwarf lemurs, using means for four variables (head length, head width, head and body length, and tail length) at six sites that vary in altitude and mean annual rainfall (Table 1). There is no correlation between altitude and rainfall across these six sites; thus, we are able to test competing hypotheses regarding size variation. Our data came from several sources, including our own collected at two Tsinjoarivo forests (a higher-altitude, disturbed fragment, and a somewhat lower-altitude primary forest) and at Ranomafana National Park. Hapke et al. (2005) reported measurements of a small set of individuals captured at various locations (mostly lowland) in southeastern Madagascar, including humid and littoral forests. Thalmann (2000) reported measurements taken on a single wild-caught adult female at Bongolava and another at Andasibe. Because we lack body mass data for individuals from southeastern Madagascar, and because body mass fluctuates tremendously in single individuals, we did not use body mass to test Bergmann's rule or the productivity hypothesis.

Our data do not support Bergmann's rule. Across the six sites, none of our size metrics is significantly correlated with altitude (CORRELATION: Pearson's r ranges from -0.20 to 0.16 ; P ranges from 0.71 to 0.81); even the signs of the correlation coefficients vary. Crossley's dwarf lemurs at Tsinjoarivo are smaller than conspecifics at Ranomafana (captured at $1,000$ m altitude) (Blanco et al. 2009); however, they are larger than *C. crossleyi* from lower altitude littoral and humid eastern forests (Hapke et al. 2005). The productivity hypothesis fares somewhat better as a predictor of body size. Each of our body size metrics correlates weakly positively with rainfall in Crossley's dwarf lemurs (CORRELATION: Pearson's r ranges from 0.36 to 0.91). The compound probability of finding this consistent a result is $P < 0.001$. Ranomafana has the highest rainfall ($>4,000$ mm per year) and generally the largest individuals; Tsinjoarivo (with $\sim 2,000$ mm annual rainfall) is next, and individuals from the humid and littoral forests in the south ($\sim 1,325$ mm rain at the range midpoint) as well as forests in the central highlands such as Bongolava ($\sim 1,500$ mm rain) are small.

We also compared ear (or pinna) length at each of our six sites (Table 1). The classic explanation for variation in pinna length is Allen's rule, which holds that the relative size of exposed body parts should decrease as temperature decreases in order to conserve heat. Allen's rule thus predicts negative correlations of pinna length with altitude and latitude. However, thermoregulation should not be expected to influence ear length in primates, as primates lack a carotid rete and therefore do not exploit counter-current heat exchange mechanisms for brain cooling. In rabbits, carnivores, elephants, and bovids (animals that do in fact exploit counter-current heat exchange mechanisms; Parmeggiani et al. 1998), pinna size varies with both external temperature and activity levels. But even here, species that occupy a wide altitude range can violate the expectations of Allen's rule (e.g., Liao et al. 2007, on the lagomorph *Ochotona daurica* in northern China, which ranges over altitudes of 400 – $4,000$ m above sea level). Generally, among primates, there is no correlation between ear size and ambient temperature (see, for example, Herskovitz 1977, on marmosets and tamarins).

Table 1 Body mass and morphometrics of *C. crossleyi* inhabiting high to low altitude forests

Location	Tsinjoarivo- FRAG	Tsinjoarivo- PRIM	Ranomafana	Fort Dauphin region	Bongolava	Andasibe
<i>Altitude (m)</i>	1,600	1,300	1,000	500	1,200	1,075
<i>Mean annual rainfall (mm)</i>	2,000	2,500	>4,000	1,425	1,500	1,700
<i>Body mass (g)</i>						
Mean	394.84	335.69	368.36	–	302	383
SD	54.31	55.03	44.44			
Range	321–461	282–456	312–472			
<i>n</i>	9	13	14	–	1	1
<i>Head and Body length (mm)</i>						
Mean	260.16	256.85	261.82	264.00	250	240
SD	15.22	9.73	12.83	6.00		
Range	235.9–287.5	243.7–274.7	245.5–286.7	255–270		
<i>n</i>	9	13	14	6	1	1
<i>Tail length (mm)</i>						
Mean	258.97	252.15	277.07	246.70	240	240
SD	13.88	10.06	13.04	14.30		
Range	240–276	235–267	255–300	229–270		
<i>n</i>	9	13	14	6	1	1
<i>Head length (mm)</i>						
Mean	57.90	56.58	58.73	53.20	44	48
SD	1.74	1.08	1.50	0.50		
Range	54.8–60.9	54.1–58.1	56.6–61.3	52.5–53.7		
<i>n</i>	9	13	14	6	1	1
<i>Head width (mm)</i>						
Mean	35.99	33.53	35.90	33.30	29	32
SD	0.88	1.12	1.51	0.30		
Range	34.6–37.2	32–35.6	33.8–39	32.7–33.6		
<i>n</i>	9	13	14	6	1	1
<i>Ear length (mm)</i>						
Mean	22.53	22.13	19.06	23.68	22	23
SD	1.72	1.47	4.26	1.94		
Range	18.5–24.2	18.9–24.1	11.9–26.5	20.9–26.4		
<i>n</i>	9	13	14	6	1	1

Range midpoints provided for altitude and rainfall when not available for specific capture sites

Other variables that might influence external ear morphology in primates include habitat structure (because of its influence on acoustics) and sexual selection. Predation risk can vary with habitat structure, which in turn may relate to rainfall, temperature, and disturbance. If predation pressure increases in more open habitats, and if large ears enhance the ability to detect predators, then large ears may be advantageous in open habitats. With regard to acoustics, however, the selective advantage of large or small ears depends on the range of sound frequencies that are of value to the species. A larger external ear can effectively

amplify (and act as a directional receiver for) a broader range of sound frequencies. In particular, increasing pinna size should lower the frequency threshold of concentrated sounds because then the pinna can only effectively block or concentrate sounds with a larger wavelength. It is not clear that ear size matters to species relying on ultrasonic wavelengths.

Our data on pinna length variation in *C. crossleyi* demonstrate a pattern distinctly different from that seen in other morphometric traits. There is no correlation with altitude (CORRELATION: Pearson's $r = -0.16$, $P = 0.77$); thus, unsurprisingly, Allen's rule is not supported. However, in contrast with all other morphometric variables measured, pinna length is significantly *inversely* (not positively) correlated with rainfall (CORRELATION: Pearson's $r = -0.92$, $P < 0.01$). Crossley's dwarf lemurs living in more open habitats have the longer ears (both relatively and absolutely), and those living in dense forests have the shortest. Ear length is smallest at mid-altitude Ranomafana (where rainfall is highest), and greatest at low-altitude Fort Dauphin (where rainfall is the lowest) as well as high-altitude forests with relatively low rainfall. The same contrast is manifested at Tsinjoarivo, where ear length is greater in the higher-altitude fragment (with lower rainfall and higher daily temperature fluctuation) than in the somewhat lower-altitude primary forest.

Hibernation in Dwarf Lemurs

New Results on C. sibreei and C. crossleyi

At the forest fragment of Tsinjoarivo, we recorded daytime sleeping site information for 15 dwarf lemurs and hibernacula preferences for 6 individuals wearing radio collars. *C. sibreei* was observed using tree holes exclusively as sleeping site locations during the active season (three individuals in March, four individuals in October–November 2011, one individual in March 2012). During hibernation (between April and September), individuals occupy underground hibernacula. One of four individuals chose the inside of a dead tree stump as hibernaculum but switched to an underground location later in the same year. The remaining three individuals all used underground hibernacula during the entire hibernation period (Blanco, unpubl.). Unlike Sibree's dwarf lemurs, *C. crossleyi* alternated between tree holes and nest-like structures as sleeping sites during the active season, although some individuals only slept in nest-like structures during our study period (two individuals in April 2009, one individual in March 2011, four individuals in October–November 2011 and two in March 2012). Nest-like structures ranged from simple rearrangements of dried leaves (mostly bamboo) resembling open bird nests to more complex structures—"ball-like"—built with leaves of different tree species, a small opening on the side and inconspicuously located inside the tree crown (Blanco, unpubl.).



Fig. 3 Adult female *C. sibreei* wearing radio collar with a sensor to record skin temperature

Behavioral (focal) observations and skin temperature recordings from radio-collared individuals confirm that dwarf lemurs occupying tree holes and nest-like structures are able to maintain euthermy and remain active at night. Nest use by *C. crossleyi* is not restricted to the reproductive season; nests are also used by adult females preparing for hibernation (presumably after their infants have been weaned) and by adult males who were observed foraging and sleeping alone, which suggests that nest construction is not simply linked to parental care activities. Like Sibree's dwarf lemurs, Crossley's individuals ($n = 3$) hibernated underground.

During the hibernation period, skin temperature was recorded for a total of 6 individuals (3 *C. crossleyi* and 3 *C. sibreei*) between March and September in 2009 and 2011 (Fig. 3). Hibernation periods varied between species and individuals and ranged from 2 to 13 days. Figure 4 shows skin, ambient, and hibernacula temperature during hibernation in a *C. sibreei* adult male recorded between June 27 and July 16, 2011. Skin temperature remained below 20°C for almost 13 days

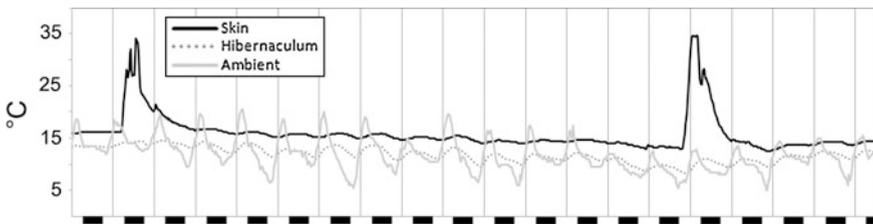


Fig. 4 Records of skin (solid black), ambient (solid gray), and hibernacula (dotted) temperature during hibernation in a *C. sibreei* adult male recorded between June 27 and July 16, 2011

between periods of arousal. The temperature within the hibernaculum was generally 2°–3° lower than the individual's skin temperature, although this may be the result of the data logger being more superficially situated than the individual's hibernaculum. Underground hibernation provides good insulation against daily ambient temperature fluctuation. Similar hibernation profiles were observed in *C. crossleyi* individuals.

Do Sleeping Sites and Hibernacula Preferences Vary with Altitude?

Altitude does not correlate in a simple fashion with variation in preferences for different types of hibernacula or sleeping sites. Descriptions of sleeping sites and hibernacula preferences for *C. crossleyi* in middle and low altitude forests are very sparse. Petter (1962) and Petter et al. (1977) referred anecdotally to the use of tree holes as well as nests by “*C. major*” in forests like Ranomafana during the active season and underground locations “enterré au pied des arbres” as hibernacula. Note that *C. crossleyi* was considered a subspecies of *C. major* in the 1960s and 1970s. More recent reports at Ranomafana document nest construction by female dwarf lemurs during the birth season (Wright and Martin 1995); the authors also indicate that individuals may hibernate underground at this location. It is worth noting that Wright and Martin (1995) believed they were describing *C. major*, but later genetic analysis of *Cheirogaleus* at this study site identified it as *C. crossleyi* (Groeneveld et al. 2010). *C. major* at Mandena prefer tree holes as sleeping sites and no references to nest construction have been made (Lahann 2007).

Interestingly, no underground hibernation has been described for *C. medius*, which shows strict preference for sleeping and hibernating in tree holes or hollow tree trunks. Petter (1962) reports that fat-tailed dwarf lemurs were never observed in nests and always chose tree holes as sleeping sites and hibernacula. Furthermore, Petter et al. (1977) mentioned the use of live trees (instead of dead tree stumps) and presence of debris (e.g., humus) inside tree hollows to maintain a humid environment, which may be of critical importance in the hot and dry deciduous forests of western Madagascar. This further supports the notion that the common ancestor of all species belonging to the genus *Cheirogaleus* evolved in a humid environment.

Does the Duration of Hibernation Vary with Altitude?

Lahann and Dausmann (2011) argue that seasonality (and not temperature) correlates with the duration of hibernation in dwarf lemurs; seasonality is hypothesized to be important because of its effect on food and water availability. These

authors compared *C. medius* inhabiting low altitude forests in western and southeastern Madagascar. Fat-tailed dwarf lemurs at the highly seasonal Kirindy forest in the west hibernated 6–7 months a year whereas their southeastern counterparts in the more humid and less seasonal Mandena forest hibernated for only 4–5 months. Time of emergence at Mandena was ~ 2 months earlier (at the beginning of September) than in the west (early November).

Our preliminary data on eastern dwarf lemurs offer some support for an association between duration of hibernation and seasonality, and little for altitude *per se*. All eastern dwarf lemurs live in habitats that are less seasonal than Kirindy (this is particularly the case for eastern lowland sites), and none exhibits hibernation periods as long as that seen in Kirindy *Cheirogaleus*. Eastern dwarf lemurs do not show the degree of variability manifested in western dwarf lemurs. *C. sibreei* have hibernation periods (~ 5 months) that are roughly similar to those of eastern dwarf lemurs living in lower altitude rainforests. Indirect evidence of hibernation (lack of sightings during censuses) in *C. crossleyi* at mid-altitude Ranomafana suggests that these dwarf lemurs hibernate for a maximum of 5 months (Wright and Martin 1995); this needs confirmation. A comparable hibernation period was reported for the similarly sized *C. major* at the low-altitude forest of Mandena (Lahann 2007). Better records for sympatric *C. crossleyi* and *C. sibreei* at Tsinjoarivo suggest shorter hibernation time for the former (3–3½ months) than the latter (4–5 months) (Blanco and Rahalinarivo 2010, Blanco, unpubl.) (Table 2). In fact, hibernation in *C. sibreei* may be longer than 5 months at Tsinjoarivo. Furthermore, there may be a difference between sexes, with adult females beginning hibernation earlier than males. No adult females of this species were trapped in March 2009, 2011, or 2012 and a single adult female was observed already hibernating in mid-March 2008 (pers. obs.). More samples per year and across years will be necessary to determine whether these interspecific and intraspecific differences hold.

If indeed *C. sibreei* hibernates longer than any of the other eastern dwarf lemurs, and if indeed *C. sibreei* is limited to high altitude forests, then a case might be made that increasing the duration of hibernation is adaptive in extreme environments, be they very cold and somewhat seasonal (as at Tsinjoarivo) or very dry and highly seasonal (as at Kirindy). If it is also true that female *C. sibreei* hibernate longer than males, it behooves us to explore how the duration of hibernation may or may not relate to female dominance and access to preferred food resources. In this regard, it is of interest to note that females of *C. sibreei* and *C. medius* both have masculinized genitals (Blanco et al. 2009), whereas *C. crossleyi* and *C. major* do not (Fig. 5). Certain other lemur species exhibit the same phenomenon (see Drea and Weil 2008, on *Lemur catta*), as do some other mammals in Madagascar and beyond (Hawkins et al. 2002). The functional significance of masculinized genitals in females is poorly understood, but this phenomenon has been related to female dominance (Ostner et al. 2003), specifically to the notion that masculinization confers higher fitness to females. If it helps females attain greater access to preferred food, there is a reason to expect greater expression in the harshest environments where such foods may be limited. In the cold forests of Tsinjoarivo,

Table 2 Duration of hibernation in radio-collared dwarf lemurs from a forest fragment at Tsinjoarivo

Individual	Species	Sex	Age category	Hibernation started	Hibernation ended	Duration (days)	Years
ID “Me”	<i>C. sibreei</i>	Female	Adult	~ 15-Mar			2009
ID “A”	<i>C. crossleyi</i>	Female	Adult	9-Jun	10-Sep	93	2009
ID “C”	<i>C. crossleyi</i>	Male	Juvenile	2-Jun	11-Sep	101	2009
ID “H”	<i>C. crossleyi</i>	Male	Adult	26-Apr	14-Aug	110	2011
ID “R”	<i>C. sibreei</i>	Male	Adult	23-Apr	20-Aug	119	2011
ID “M” ^a	<i>C. sibreei</i>	Male	Subadult	10-Apr	5-Sep	148	2011
ID “J” ^a	<i>C. sibreei</i>	Male	Subadult	10-Apr	28-Aug	140	2011

^a Likely brothers, shared same tree hole during active season, hibernated individually



Fig. 5 Female genitalia of *C. crossleyi*, *C. sibreei* and *C. medius*, from left to right, respectively. Note “masculinized” clitoris in the last two species. Pictures courtesy of Noel Rowe/ alltheworldsprimates.org (*C. sibreei*) and David Haring (*C. medius*)

preferred access to high quality food sources by females will likely affect the degree and rate at which prehibernation fattening can be achieved.

The Evolutionary Context of Hibernation in Lemurs

The status of hibernation as ancestral versus derived condition in lemurs has been contested for decades and is still debated by primatologists. Although hibernation has been considered a “primitive” condition retained in the cheirogaleid group (Dausmann et al. 2012), it can be argued that hibernation may have evolved in basal cheirogaleids when Madagascar was transitioning to the modern climatic pattern of environmental unpredictability. In this context, the evolution of energy-saving metabolic strategies, particularly in small-bodied primates, could be seen largely as a result of selective environmental forces during major climatic changes in the history of Madagascar. In favor of the traditional position, Nowack et al. (2010)

point out that hibernation is expressed in members of all major mammalian lineages, and that some expression of heterothermy (albeit not true hibernation) has been reported in the sister taxa of lemurs, the galagos and lorises. Heterothermy, according to this view, is a plesiomorphic trait present in the ancestral strepsirrhine (Dausmann et al. 2012).

In support of the alternative hypothesis, that hibernation is a derived condition in the Cheirogaleidae, are multiple lines of evidence (e.g., Masters et al. 2007). Generally, molecular phylogenetic studies of hibernating mammals suggest that all mammals have the developmental capacity for hibernation; making it obligatory may not be difficult especially if selective pressures favor the heterothermic phenotype. Molecular analyses (e.g., see Chap. 4, Groeneveld 2008; Perelman et al. 2011) show that the divergence and diversification of the genus *Cheirogaleus* is deeply embedded in the phylogeny of lemurs (around 22–25 mya) and there is no evidence of heterothermy in any of the “older” noncheirogaleid lineages. Basically, the radiation of all lemur families (extinct and extant, excluding the Daubentonidae which diverged much earlier) began less than 40 mya, with the divergence of three clades in rapid succession (the Lemuridae-Megaladapidae clade, the Indriidae-Palaeopropithecidae-Archaeolemuridae clade, and the Lepilemuridae-Cheirogaleidae clade). The Cheirogaleidae had its origin around 35 mya (Perelman et al. 2011). Its basal member, *Phaner*, does not hibernate (Schülke 2004), and whereas there is evidence of some fattening and facultative torpor in the cheirogaleid clade more closely related to *Cheirogaleus* (i.e., *Allocebus*, *Mirza*, and *Microcebus*; Meier and Albignac 1991; Pastorini et al. 2001; Schülke and Ostner 2007), none of these is an obligate hibernator. Paleoclimate data point to severe climatic events occurring around the time of dwarf lemur diversification, most importantly the establishment of the monsoon climate of southern Asia and surrounding oceans around 23 million years ago (Samonds et al. 2012). Later climatic events may have also played a role in the diversification and distribution of dwarf lemur species. There was a second major cooling at around the time the Tibetan Plateau reached its current elevation (between 14 and 15 mya), associated with an expansion of the East Antarctic ice sheet. The monsoon climate continued to intensify until around 8 mya. Climate fluctuations have been also recorded in the not-too-distant past. Thus, for example, Gasse and Van Campo (1998) documented three exceptionally cold episodes at 40,000–39,000 BP, 37,000–32,400 BP, and 22,700–16,900 BP (the latter being the last glacial maximum). During colder episodes, the species that are today restricted to high altitudes would have had broader geographic distributions. Hence, whereas the central plateau is largely devoid of lemurs today, a subfossil site well to the west of Antananarivo has yielded the skeletal remains of ca. 20 species of lemurs and many other vertebrates at an elevation exceeding 1,000 m (Godfrey et al. 1999).

The Evolution of Obligatory Hibernation: A Hypothesis

We have argued that temperature does not correlate in a simple fashion with body size, choice of sleeping site or hibernacula, or the duration of hibernation. Yet, we have also argued that the basal *Cheirogaleus* may be restricted to high altitude forests, suggesting that obligatory hibernation may well have evolved in high altitudes. Other data (e.g., the maintenance of humid hibernacula conditions in dwarf lemurs living in dry habitats) suggest that hibernation likely evolved in moist habitats. The question arises, why might life in the moist, high altitude forests of Madagascar favor the establishment of obligatory hibernation? Clearly, species of the genus *Cheirogaleus* have spread to virtually all habitats in Madagascar, and hibernation “works” in all of these environments.

We suggest that seasonal montane environments provide the exact conditions under which selection may favor obligatory hibernation. Low ambient temperatures during the season of scarce resources (indirectly resulting in low temperatures in available sleeping sites) should affect energy expenditure during periods of inactivity. In effect, low ambient temperature should favor heterothermy, which would promote survival at reduced metabolic rates. Indirect estimates of metabolic rates in high-altitude dwarf lemurs, ascertained by calculating oxygen consumption before and during hibernation, should confirm or refute this proposition.

One hypothesis that purports to explain body mass or size variation among populations of single species under different environmental conditions is Bergmann’s rule (Lahann et al. 2006). Bergmann argued that larger animals “conserve” more energy by reducing their surface-to-volume ratio, which in turn decreases heat dissipation to the surrounding environment. Evidence in favor as well as against Bergmann’s rule has been published for a variety of organisms although the rule was originally meant to pertain exclusively to mammalian homeotherms (e.g., Lin et al. 2008; Taylor et al. 1985). The failure of dwarf lemurs to follow Bergmann’s rule contrasts with the pattern reported for *Microcebus murinus*, another cheirogaleid species with a broad geographic distribution; body size variation in *M. murinus* does conform to Bergmann’s rule (Lahann et al. 2006). This difference is not entirely surprising as *Cheirogaleus* spp. are obligatory hibernators (whereas mouse lemurs experience only facultative seasonal torpor), and they remain inactive for most of the season of scarce resources. Heterothermic species such as dwarf lemurs show physiological adaptations that are lacking in homeotherms. Because the latter need to maintain a fairly constant body temperature year round, they may be subject to higher thermic stress.

When animals undergo hibernation, they forego euthermy and adjust their body temperature to approximate the temperature of the hibernacula. By reducing body temperature, their metabolic rates decrease as well, resulting in net energetic savings that do not exist in individuals that must maintain homeothermy in cold climates. Thus, although low ambient temperature is not necessarily a trigger for hibernation, it contributes to its energetic benefits. At Tsinjoarivo, ambient

temperatures during the season of scarce resources fluctuate between 5 to 19°C, and can drop below 0°C. Due to such extreme conditions, dwarf lemurs at Tsinjoarivo, unlike their “low-altitude” counterparts, cannot passively raise body temperature over 30°C by tracking the temperature of hibernacula, and consequently they must experience regular arousals. At the same time, they can consistently maintain body temperatures around 15°C when hibernating underground. These values are lower than those reported for *C. medius*, which hibernate in highly insulated hibernacula and experience regular arousals at Kirindy (Dausmann et al. 2004, 2009).

Our hypothesis, simply put, is as follows: The common ancestor of the *Microecebus-Mirza-Allocebus* clade and *Cheirogaleus* would have shared a tendency to accumulate some fat in anticipation of the season of scarce resources; however, that ancestor would have maintained the flexibility observed in species of mouse lemurs, and would not have accumulated fat to the degree observed in species of *Cheirogaleus*. In environments where ambient temperatures are *always* lower than body temperature (during the day and night), a loss of euthermy during the day—when nocturnal animals are inactive—would result in net energy savings (compared to individuals maintaining euthermy). This, in turn, creates a selective premium for extreme fattening, which is a precondition for prolonged hibernation. On the other hand, low altitude environments, such as Kirindy forest, display great daily temperature fluctuation, with temperatures surpassing 30°C during the day even during the austral winter (the season of scarce resources, and lowest temperature maxima). Under these conditions, a loss of daytime euthermy in some individuals would not have provided much of a metabolic advantage over individuals maintaining homeothermy. In these environments, presumably, selective pressures favoring extreme fattening in anticipation of the austral winter would be relatively low.

This is a grossly simplified scenario; further development of these ideas will require more research on the sister taxa of *Cheirogaleus*. For example, it is known that a portion of the gray mouse lemur population (*M. murinus*) at Kirindy does fatten prior to the season of scarce resources and can save up to 40% of daily energy expenditure by using torpor. Interestingly, mouse lemurs terminate torpor actively when temperature rises over 28°C so that mouse lemurs occupying highly insulated tree holes are able to stay in torpor a little longer than others, thus saving up to 5% additional energy (Schmid 1998). Hence, although torpor saves energy in the highly fluctuating habitat of Kirindy, even subtle changes in the temperature of the sleeping site can affect net daily energy savings.

In the final analysis, the role of altitude in the evolution of obligatory hibernation will remain obscure until direct measurements of oxygen consumption of dwarf lemurs in different habitats are made. Such measurements will shed light on the importance of hibernation to their energetic budgets and whether high altitude dwarf lemurs win the bid for the highest daily energy savings.

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