



Underground hibernation in a primate

Marina B. Blanco^{1,2}, Kathrin H. Dausmann², Jean F. Ranaivoarisoa³ & Anne D. Yoder^{1,4}

SUBJECT AREAS:

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¹Duke Lemur Center, 27705 Durham, USA, ²Department of Animal Ecology and Conservation, University of Hamburg, 20146 Hamburg, Germany, ³Department of Biological Anthropology and Paleontology, University of Antananarivo, 101 Antananarivo, Madagascar, ⁴Department of Biology, Duke University, 27708 Durham, USA.

Hibernation in mammals is a remarkable state of heterothermy wherein metabolic rates are reduced, core body temperatures reach ambient levels, and key physiological functions are suspended. Typically, hibernation is observed in cold-adapted mammals, though it has also been documented in tropical species and even primates, such as the dwarf lemurs of Madagascar. Western fat-tailed dwarf lemurs are known to hibernate for seven months per year inside tree holes. Here, we report for the first time the observation that eastern dwarf lemurs also hibernate, though in self-made underground hibernacula. Hence, we show evidence that a clawless primate is able to bury itself below ground. Our findings that dwarf lemurs can hibernate underground in tropical forests draw unforeseen parallels to mammalian temperate hibernation. We expect that this work will illuminate fundamental information about the influence of temperature, resource limitation and use of insulated hibernacula on the evolution of hibernation.

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Correspondence and
requests for materials
should be addressed to
M.B.B. (marina.
blanco@duke.edu)

The dwarf lemurs of Madagascar (*Cheirogaleus*) are the only obligate hibernators within the Primates^{1–3}. In western dry deciduous forests, fat-tailed dwarf lemurs (*C. medius*) are exposed to drastic daily temperature fluctuations throughout the year, especially during the winter (changing up to 30 °C per day)^{1,2,4}. During hibernation, individuals occupying poorly-insulated tree holes can passively raise body temperature above 30 °C, as is necessary to achieve physiological homeostasis. Hence, they do not need to undergo energetically expensive periodic arousals^{1–3,5,6}. Intrinsic arousal bouts are obligatory for all other known mammalian hibernators with the exception of bears, which hibernate while maintaining body temperature above 30 °C⁷. The ability of hibernating lemurs to withstand high ambient temperatures while maintaining suspended homeothermy further demonstrates that cold weather is not a precondition for hibernation¹.

The fact that dwarf lemurs undergo a period of seasonal lethargy has been suspected for decades^{8–10}, but it was not until the use of radiotelemetry that temperature profiles and hibernacula locations could be documented for western dwarf lemurs^{1,2}. *C. medius* hibernates for 7 months inside tree holes with varying degrees of insulation. Those inside highly-insulated hibernacula maintain stable body temperature and undergo regular active arousals; those inside poorly-insulated tree holes track ambient temperature and avoid arousals by passively reaching 30 °C during the hottest time of the day^{1,2,6}. No systematic investigation exists for eastern species. The only references to hibernacula preferences of eastern dwarf lemurs stem from anecdotal accounts primarily gathered in the 1960s and 1970s. Petter⁸ and Petter et al.⁹ mention that *C. major* (an eastern dwarf lemur) can be found buried at the base or underneath rotten trees during periods of lethargy. More recently, Wright and Martin¹¹ refer to an observation of a ring-tailed mongoose preying on a live *C. major* that had been taken from the base of a tree. Since the mid-1990s, there has been no published documentation of hibernacula preferences of eastern dwarf lemur species¹².

The underlying mechanisms and environmental triggers of tropical hibernation have yet to be elucidated, though it is likely that a number of factors are at play. Madagascan habitats are ecologically heterogeneous and thus resident species face different physiological challenges depending upon their geographic location. Whereas western dwarf lemurs face extreme dry conditions for up to 8 months during the winter^{3,6}, eastern dwarf lemurs that inhabit high-altitude environments have to cope with stronger thermoregulatory pressures due to cold weather, albeit for a shorter period^{12,13}. Unlike the western *C. medius*, eastern dwarf lemur species (*C. sibreei*, *C. crossleyi*, and *C. major*) occupy rainforest environments, which are generally less seasonal – and more humid – than western habitats¹². Nonetheless, eastern forests are also subject to climate stochasticity¹⁴, and high-quality fruits, which are critical food sources in dwarf lemur diets, are scarce during the austral winter^{6,8,15,16}. Of particular importance for studies of lemur hibernation are rainforests located in the “highlands” of Madagascar (i.e., high plateau, 1600–1700 m) which represent the island’s coldest habitats. In the highland rainforests, ambient temperature drops consistently to nearly 5 °C during the winter (and even below 0 °C on occasion) and never exceeds 30 °C during the day^{12,13}.



Here we report the results of a study of two sympatric dwarf lemur species from Tsinjoarivo, a high-altitude forest of central-eastern Madagascar. Sibley's dwarf lemur (*C. sibleyi*) is only found on the western half of Tsinjoarivo forest and may be a high-altitude specialist^{12,17,18}. Furthermore, genetic analysis places this species as the basal member of the genus, and thus, it may retain the ancestral condition¹⁸. Crossley's dwarf lemur (*C. crossleyi*) occupies a variety of low to high-altitude rainforests, including forest fragments and continuous forest at Tsinjoarivo^{14,17,18}. The two species also differ in body mass (250 g vs. 350 g respectively), fur coloration and genital morphology¹⁷. Preliminary data indicate that dwarf lemurs in high-altitude forests display shorter hibernation periods than their western counterparts¹⁴. We document, for the first time, hibernacula preferences and temperature hibernation profiles of eastern dwarf lemurs inhabiting high-altitude forests in Madagascar.

We hypothesize that dwarf lemurs living at Tsinjoarivo will resemble other non-primate temperate/arctic hibernators which employ well-insulated underground locations or caves during the hibernation period. We predict differences in hibernacula selection between Tsinjoarivo dwarf lemurs and their close relatives in western Madagascar because: 1-rewarming above 30 °C cannot be achieved passively in the high-altitude forests of Tsinjoarivo; 2-exposure to low ambient temperature (e.g., risk of freezing) in the highlands of Madagascar may threaten survival of individuals occupying poorly insulated hibernacula; 3-maintaining stable body temperature during hibernation may be more energetically-efficient and/or physiologically advantageous in colder habitats, i.e., when passive rewarming is not an option.

Results

Skin temperature recordings confirmed heterothermy in all studied dwarf lemurs to varying degrees between April and September. At Tsinjoarivo, *C. sibleyi* and *C. crossleyi* hibernated between 3 and 6 months each year. Body temperature during hibernation approximated the temperature of the hibernacula in a fashion analogous to

that of arctic/temperate hibernators, though predictably, ambient temperatures were higher at Tsinjoarivo than in temperate or arctic environments (i.e., ~15 °C vs. ~0 °C or colder respectively¹⁹). All studied dwarf lemurs used underground hibernacula. Prior to the prolonged hibernation season, however, four of seven Crossley's dwarf lemurs in our study passively tracked ambient temperature for more than 24 hours (short hibernation bouts) while occupying poorly insulated nests, indicating their ability to also hibernate under variable ambient temperature conditions (Fig. 1). These individuals eventually entered underground hibernacula within two months of the first recorded hibernation bouts.

In order to confirm underground hibernation and accurately document placement and position of hibernating dwarf lemurs, we excavated the hibernacula of 6 individuals (2 *C. sibleyi* and 4 *C. crossleyi*) (Videos 1, 2). Dwarf lemurs were found buried below ground between 10–40 cm deep, under a spongy layer comprised of secondary roots and root hairs, humus and leaf matter (Fig. 2). Burrows were not necessarily associated with root systems at the base of large trees. No internal galleries or chambers were found in connection with burrows. However, we observed small crevices and openings in the ground around hibernacula locations that may serve as entry/exit points. Dwarf lemurs always hibernated individually and rarely changed hibernacula, occupying 1–2 locations per season, with rare exceptions.

Discussion

In retrospect, the presence of underground hibernacula in the tropics is not surprising. Burrows are the type of hibernaculum most often preferred by temperate and arctic hibernating mammals²⁰. Underground shelters provide effective insulation during cold winters, when the ground is frozen or covered by a thick layer of snow. In Madagascar's eastern forests, burrows provide more insulation –i.e., more stable hibernaculum temperature than tree holes or nests– given that soil temperature is generally lower than ambient temperature during the day but higher during the night. Hibernating in

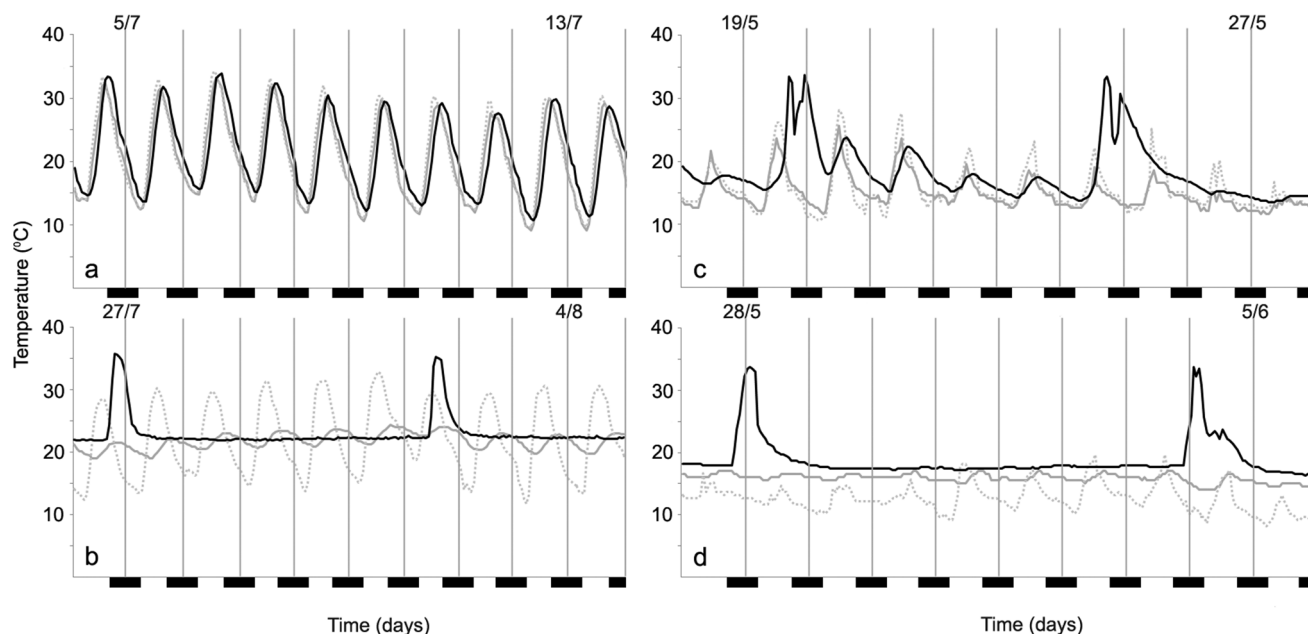


Figure 1 | Temperature profiles for *C. medius* (a, b) and *C. crossleyi* (c, d) occupying poorly-insulated (a, c) or highly-insulated (b, d) hibernacula. For *C. medius*: skin (solid black), tree hole (solid grey) and ambient (dotted) temperatures; for *C. crossleyi*: skin (solid black), nest or underground (solid grey) and ambient (dotted) temperature. Note *C. crossleyi* is not exposed to temperatures above 30 °C while occupying nests (c) and displays low skin temperature when occupying underground hibernacula (d) compared to *C. medius* hibernating inside highly-insulated tree holes (b). Vertical lines, midnight; black bars, dark phase. Data for *C. medius* (Dausmann, unpubl.) were collected in July and August at Kirindy CFPE; data for *C. crossleyi* (this study) were gathered between May and June 2012 at Tsinjoarivo (starting and ending dates are indicated by numbers above vertical lines).



Figure 2 | Eastern dwarf lemur (*C. sibreei*) hibernating underground at Tsinjoarivo forest. Top layer of soil has been removed.

more insulated locations may be more thermally adequate during the hibernation period as it reduces the potential risk of freezing and the exposure to drastic temperature changes during the day. Maintaining a stable body temperature may be of critical importance for surviving the winter, if rewarming above 30 °C cannot be achieved passively and frequent arousals entirely driven by active endogenous heat production are too expensive. Moreover, fluctuating body temperatures might generally be more challenging for tissues and organisms, e. g. due to perfusion problems²¹.

Individuals selecting underground hibernacula in the cold forests of Madagascar can maintain low fairly constant body temperatures (~15 °C) for over 10 days before undergoing energetically expensive arousals. In doing so, they avoid (passively) increasing metabolic rates if body temperature were to increase during the day. Indeed, maintaining a stable body temperature may be the physiological “default”. For instance, hibernating tropical bats also occupy well-insulated roosts to keep body temperature stable during hibernation as fluctuation in ambient temperature may curtail their ability to undergo multiday torpor²². It can also be hypothesized that at Tsinjoarivo, hibernating in poorly insulated tree holes could actually be life-threatening if ambient temperature decreases near the freezing point during cold winters. It is unknown whether dwarf lemurs are capable of initiating active thermoregulation and defend a minimum temperature or would perish in the attempt.

The use of underground hibernacula may indeed have thermal advantages, yet it shows a significant behavioural deviation from that of the active period, as these arboreal primates generally occupy the higher portion of the canopy to forage and find shelter during the non-hibernating period. Whether or not dwarf lemurs have to face higher predatory risks while occupying underground burials is unknown. During the non-hibernation period, large predatory birds were observed flying by tree holes used as sleeping sites and at least two study animals were killed by avian predators early in the morning, just prior to or around the time of return to their tree holes. On the other hand, no evidence of predation has been recorded in hibernating dwarf lemurs at Tsinjoarivo, but, as mentioned before, Wright and Martin¹¹ referred to the observation of a mongoose preying on the lemur removed from the base of a tree at Ranomafana, southeastern Madagascar. The hibernacula locations that we identified at Tsinjoarivo were inconspicuous and may be deep enough to prevent smell tracking by terrestrial predators. It is possible that individuals may be “safer” in underground settings if most predation events occur while animals are entering or exiting resting locations

because dwarf lemurs remain in the same hibernacula for several weeks at a time.

Given the possible thermal advantages of underground hibernacula in the eastern high-altitude forests of Madagascar, why do western dwarf lemurs not hibernate underground? The answer may come down to local ecological constraints: hard and dry soils in western Madagascar (opposed to spongy, moist and soft soils of eastern rainforests) may not allow clawless lemurs to bury themselves safely. Indeed, other Malagasy hibernating mammals, such as tenrecs, have been observed hibernating/resting with dwarf lemurs inside tree holes at Kirindy CFPF, a deciduous dry forest in western Madagascar, but can be found underground in other forests²³. Paradoxically, substrate-dependent reliance on tree holes as hibernacula in western Madagascar may have brought about fortuitous consequences: poorly-insulated tree holes may allow fat-tailed dwarf lemurs living in the driest forests of Madagascar to rewarm their bodies passively and thus avoid the energetically expensive periodic arousals that are typical of temperate hibernators³.

Observations of the use of underground locations by dwarf lemurs at Tsinjoarivo during hibernation differ from those recorded during the active, non-hibernating season. During the active season, Crossley’s dwarf lemurs occupy nests or tree holes during their daily resting phase, whereas Sibree’s dwarf lemurs use tree holes exclusively¹². The social system of eastern dwarf lemurs is poorly-known but similarities between western *C. medius* and eastern *C. major* have been observed, e.g., presence of monogamous pairs and presumed offspring sharing sleeping sites and conducting gregarious feeding at night^{24,25}. At Tsinjoarivo, dwarf lemurs of both species show flexible foraging and sleeping group patterns: whereas members of the same social groups are sometimes observed sharing sleeping sites, e.g., adult female-male pairs, siblings, parent-infant or subadult offspring, they frequently occupy sleeping sites individually. Similarly, our data from nocturnal tracking has shown that dwarf lemurs generally forage individually at night, although pairs and multiple individuals of the same group have been observed feeding on the same tree occasionally. We also noted that infant dwarf lemurs at Tsinjoarivo are found actively foraging weeks after adult individuals have already become “inactive”, similar to what has been reported for western dwarf lemurs⁶. During winter, however, all dwarf lemurs hibernate solitarily.

A systematic study of hibernacula preferences among dwarf lemurs across Madagascar will determine whether underground hibernation is the norm rather than the exception. Underground burials in these small-bodied arboreal primates may, in fact, represent the ancestral condition of this genus, and might be ultimately related to the evolution of dwarf lemur hibernation in the highlands of Madagascar. Our findings that dwarf lemurs can hibernate underground in tropical forests draw unforeseen parallels to mammalian temperate hibernation. These findings also highlight a remarkable fact: that a clawless primate is able to bury itself underground in order to escape the energetic challenges of winter in the eastern forests of Madagascar.

Methods

Study area. Dwarf lemurs were studied in a forest fragment at Tsinjoarivo, a high-altitude rainforest in central-eastern Madagascar (19°41′15″S, 47°46′25″E, 1660 m). Climate at this forest is seasonal and characterized by a rainy season (December–March) and a dry season (April–November). Rainfall averages 2000 mm per year and temperature is highest between December and January²⁶. Monthly mean temperatures oscillate between 6 °C and 14 °C, and maximum ambient temperatures during the core of the hibernation season (June and July) do not reach 30 °C and average 19 °C¹². Data for June–July 2011 and 2012 combined showed a mean temperature of 13 °C, a maximum value of 22 °C and a minimum value of 5 °C (this study). Tsinjoarivo is one of the coldest environments in Madagascar.

Experimental procedures. All experiments were conducted in the field under natural conditions and using wild animals. Our research complied with the current laws of the country where they were performed (Ministère de l’Environnement et des Forêts of the Malagasy government, research permits N° 46/09/MEFT/SG/DGEF/DSAP/



SLRSE, 015/11, 202/11, 142/12/MEF/SG/DGF/DCB.SAP/SCB) and research protocols complied with those of the Institutional Animal Care and Use Committee in the USA (26-17-03 and 2010-0069, University of Massachusetts, Amherst; 11-06-03, Dartmouth College; A040-12-02, Duke University, submitted by MBB).

Trapping. Animals were live-trapped using Tomahawk traps baited with pieces of banana and set between 3–10 m high and separated by a minimum of 50 m along known trails. Captured individuals were sexed, measured, weighed and individually marked with microchips (AVID Identification Systems, Inc., CA, USA). A selected number of dwarf lemurs captured in April 2009, March 2011 and March 2012 were equipped with external radio transmitters (see below).

Radio-tracking. Hibernacula locations of the radio-collared animals were determined with the use of telemetry equipment (Receiver R410, Advance Telemetry System, Isanti, MN). Transmitters' signals were checked daily in March and April and weekly between May and September. Individuals that were removed from their natural hibernacula were released to the same underground locations after dark, while they were alert, to facilitate their return under safe conditions. Although it was impossible to track study individuals immediately after release (due to the fact that their transmitters with expiring batteries had been removed after capture), we nonetheless opportunistically re-trapped three out of the six study individuals at various time points later in the study, thus indicating their subsequent health and survival.

Temperature measurements. We fitted external radiotransmitters (collars) in 12 individuals (8 *C. crossleyi*, 4 *C. sibreei*). These radio-transmitters possessed archival tags that recorded skin temperature every 60 minutes (ARC 400, 10 g, Advanced Telemetry Systems, Isanti, MN; collar size/body mass ratio of <4%). Radio-transmitters were fitted on dwarf lemurs at the end of the active season, just prior to hibernation, to minimize health risks associated with tightening of collars due to increasing fat deposits. Radio-transmitters were removed from individuals during the hibernation season (July: 1 *C. sibreei* and 5 *C. crossleyi* and September: 1 *C. sibreei*) or after the hibernation period (September: 1 *C. crossleyi* and 1 *C. sibreei* and October: 1 *C. sibreei* and 2 *C. crossleyi*). Temperature recordings were retrieved at the collar production site (Advanced Telemetry Systems, USA). It has been shown that skin temperature accurately reflects body temperature when individuals are curled up during hibernation²⁷. Ambient temperature and temperature of the sleeping sites or hibernacula were recorded by data loggers (Maxim DS1922 iButton, Maxim Integrated Products, Inc., San Jose, CA). If the individual was located inside a tree hole, we placed the data logger close to the entrance of the hole on the interior side (i.e., a u-shape wire was attached to the logger on one side and a long stick (i.e., thin branch) on the other. The stick allowed us to place the logger inside the tree hole without climbing the tree and potentially disturbing the individual. If the individual was inside a nest, a logger was placed in proximity to the nest, within 2–3 m to avoid disturbing the sleeping dwarf lemur. If the individual was hibernating underground, a logger was placed in the soil, about 5 cm under the surface and above the area where strongest signal was recorded by the receiver. Ambient temperature was obtained from a logger placed in a shady area in the forest. Measurements were recorded hourly.

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Author contributions

M.B.B. collected, analysed and wrote the paper; K.H.D. supplemented data, discussed and commented on the manuscript; J.F.R. collected data; A.D.Y. discussed and wrote the paper.

Additional information

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Competing financial interests: The authors declare no competing financial interests.

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