

Effects of Sex and Age on Heterothermy in Goodman’s Mouse Lemur (*Microcebus lehilahytsara*)

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Abstract All habitats of Madagascar go through a dry season from April to September each year, resulting in a period of fruit scarcity lasting up to 6 months and creating selection pressure for adaptation to fluctuations in resources. Some Cheirogaleid lemurs, including mouse lemurs (*Microcebus*), use daily torpor and long-term hibernation during this period, saving energy through inactivity. Capture–recapture studies in some mouse lemur populations have suggested a pattern of biased sex ratio throughout the winter as a result of females hibernating while most males remain active. We studied winter activity in a captive population of *Microcebus lehilahytsara*, Goodman’s mouse lemur, in a large enclosure at Zoo Zürich, Switzerland using capture–recapture methods to determine how this behavior varies with sex and age, and what this pattern suggests about the ultimate cause of torpor use in this clade. Our results suggest that Goodman’s mouse lemurs use torpor to avoid seasonal food shortage, even though they experience less extreme seasonal variability of food availability than western dry forest mouse lemurs. Male and female Goodman’s mouse lemurs are equally capable of winter torpor, and most remaining active individuals are young that have not sufficiently fattened. This suggests that the “ideal” winter behavior for both males and females is torpor, which ultimately avoids periods of seasonal food scarcity.

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Introduction

The severe and unpredictable climate of Madagascar has created strong selective pressure for energy-conserving adaptations in its inhabitants (Gould *et al.* 1999). All habitats of Madagascar go through a dry season during the austral winter from April to September each year, resulting in a period of fruit scarcity lasting up to 6 months in both dry deciduous and rain forest areas (Wright 1999; Wright and Martin 1995). Members of the small-bodied, polygynous, sexually monomorphic, nocturnal lemur family Cheirogaleidae possess an unusual adaptation for energy conservation found in no other primate group: some species within the Cheirogaleidae go into torpor daily and use hibernation for extended periods of time during the dry austral winter (Dausmann *et al.* 2000, 2004; Schülke and Ostner 2007). Both hibernation and torpor are characterized by a regulated period of lower metabolic rate, which results in body temperature approaching ambient temperature (Geiser 2004). Ventilation, heart rate, transcription, translation, protein synthesis, ATP production, and cellular proliferation are all reduced (Heldmaier *et al.* 2004). Daily torpor lasts only a few hours at a time, and is usually synched to the rest period of an individual's circadian rhythm, while hibernation lasts for days to months and is generally controlled by an endogenous circannual rhythm (Geiser and Ruf 1995). Interestingly, the use of daily torpor and hibernation during the winter in Cheirogaleid lemurs varies greatly among genera, species, populations, and sexes within populations.

Differences in energy-conservation behavior between the sexes within a species are of particular interest, as they indicate differential selection on energy conservation in males and females. In some Cheirogaleid species, most females appear to be inactive, either in short-term torpor or long-term hibernation, during the resource-poor winter season, whereas males remain active (Schülke and Ostner 2007). Remaining active during the winter should be a risky behavior, as predators are still active and food and water are in short supply. However, although male gray mouse lemurs (*Microcebus murinus*) living in the western dry deciduous forests of Madagascar remain active during the winter while females hibernate, males and females have equal rates of survival during this period (Schmid and Kappeler 1998). Male winter activity does not appear to be significantly risky, but is likely to be the result of some differential selective pressure. Schülke and Ostner (2007) propose that researchers can use differences in hibernation between the sexes within a population to evaluate hypotheses about the ultimate causes of hibernation in this genus. Four major hypotheses emerge from this review: the seasonal food shortage hypothesis (Schülke and Ostner 2007), the seasonal water shortage hypothesis (Schmid and Speakman 2000), the mate competition hypothesis (Schmid and Kappeler 1998), and the predation avoidance hypothesis (Schmid 1999).

The seasonal food shortage hypothesis states that mouse lemurs hibernate because this behavior allows them to avoid and survive the period of food shortage during the winter. During the winter, a period of sexual quiescence in both sexes, food shortage is likely to affect both sexes equally. However, differential fat accumulation seems to

result in differential hibernation (Atsalis 1999; Kobbe *et al.* 2011; Schmid 1999), so females, which are dominant to males and can inhibit male fattening (Génin 2003; Génin *et al.* 2005), may hibernate because it is easier for them to fatten. Some males have been observed to fatten and hibernate (Kobbe *et al.* 2011). Food supplementation experiments on prehibernation gray mouse lemurs in captivity as well as in the wild shows that they may delay hibernation when food is abundant (Vuarin and Henry 2014; Vuarin *et al.* 2013, 2015), suggesting that winter torpor is a proximate response to food shortage in western dry forest mouse lemur species.

The seasonal water shortage hypothesis states that mouse lemurs use torpor primarily because of its water-saving benefits during the dry winter period. Water turnover is significantly reduced during daily torpor in both sexes (Schmid and Speakman 2000). As daily torpor and hibernation occur in June, July, and August, which in the wild is the driest part of the year [as little as 25 mm of rain in the rain forest (Wright *et al.* 2005)] it is likely that mouse lemurs would need to conserve water.

The mate competition hypothesis states that males remain active during the winter because this behavior confers a competitive advantage during the following reproductive season. In polygynous species such as mouse lemurs, males should engage in more risky behavior as a result of weaker selection for longevity and strong selection for traits that confer advantages in intrasexual competition (Clutton-Brock and Isvaran 2007; Trivers 1972). During the mating season, male gray mouse lemurs roam throughout their range to find receptive females, and use contest competition with other males (Andres *et al.* 2001; Eberle and Kappeler 2004; Schmelting *et al.* 2007). Males may spend the winter locating females and gaining fat to increase their chances of monopolizing fertile females during the short mating season. Older males are able to establish dominance over younger males easily (Aujard and Perret 1998) and may be able to become inactive for longer periods of time during the winter without jeopardizing their competitiveness. In any case, males cannot develop their testes while in hibernation (Fietz *et al.* 2004; Perret and Aujard 2001) as testicular tissue is only functional and spermatogenic when the animal is normothermic (Barnes *et al.* 1986), so they must emerge from hibernation before females to be fertile in time for the breeding season (Michener 1992).

The predation avoidance hypothesis states that remaining inactive in a tree hole decreases predation risk and increases survival probability (Schmid 1999). Mouse lemurs are small, and so have many predators, including snakes, at least two species of carnivores (*Galidea elegans*, the ring-tailed mongoose, and *Cryptoprocta ferox*, the fossa), and seven species of hawks and eagles (Deppe 2011; Karpanty 2003, 2006; Karpanty and Goodman 1999, Karpanty and Wright 2007; Wright 1998). Mammalian predators check tree holes when searching for prey, and will even dig up hibernating dwarf lemurs (Wright and Martin 1995), so although remaining hidden may protect mouse lemurs from some of their major predators, such as owls (Goodman 2003), this behavior does not confer total protection to hibernators (Kraus *et al.* 2008).

Mouse lemur species adapted to different environments may use flexible heterothermy differently, and it is important to study multiple mouse lemur species to evaluate how this phenotype and the diversity of its expression evolved. Although all habitats in Madagascar experience a cold, dry season every year, the extent of seasonal limitation of food and water, and the severity of predation, vary greatly between different habitat types, creating different selective pressures and different expression

patterns of the hibernation phenotype. Gray mouse lemurs living in dry forests in western Madagascar have been studied extensively in the wild and in captivity, and the physiological and environmental factors governing their use of hibernation are well understood. Mouse lemurs living in rain forests in eastern Madagascar have been the subjects of ecological studies, but fine-scale studies of individual animals and their winter activity patterns have not been possible. The existence of long-term, high-resolution activity data on a population of Goodman's mouse lemurs (*Microcebus lehilahytsara*) at Zoo Zürich presented an opportunity to evaluate these hypotheses in eastern rain forest mouse lemurs. Food and water are consistently available on trees and at feeding stations throughout the Masoala Rainforest greenhouse ecosystem year-round (Bauert *et al.* 2007), and therefore the hibernation patterns of the free-roaming mouse lemurs in this exhibit are free from proximate constraints on fattening. If seasonal food shortage is the ultimate evolutionary cause of hibernation in mouse lemurs, then we predict that in an area with unlimited food, either all individuals should fatten and hibernate in anticipation of later food shortage, or all individuals should remain active because hibernation will be unnecessary. If the mate competition hypothesis explains why many male mouse lemurs remain active during the winter while most females and some males hibernate, then we predict that few males, except some older males, should hibernate in any habitat, but may use daily torpor during resting periods. Females should always hibernate, as their reproductive success is not improved by staying active. Regardless of the cause of winter inactivity in this species, we predict that males will emerge from hibernation before females to allow testicular development and territory marking. We do not evaluate the two other hypotheses proposed by Schülke and Ostner (2007). Dry forest gray mouse lemurs save more water than wet forest mouse lemurs through daily torpor (Schmid and Speakman 2009), which suggests that water conservation is an important adaptive benefit of torpor in the dry forest, but less so in the wet forest. Thus water conservation is therefore unlikely to explain differential hibernation in rain forest mouse lemurs. A very large long-term dataset would be required to detect the likely small survivorship advantage conferred by predator avoidance through dry season hibernation, so do not evaluate the predation avoidance hypothesis.

Materials and Methods

Captive Goodman's mouse lemurs lived in the Masoala Rainforest greenhouse exosystem enclosure at Zoo Zürich in Zürich, Switzerland. The exhibit, which replicates conditions in Masoala National Park in Madagascar, covers almost 11,000 m², with a ceiling reaching 35 m high, and has housed >45 animal species and 35,000 plants since 2003 (Bauert *et al.* 2007; Jürges *et al.* 2013). Visitors to the Zoo travel along marked paths during the day, but do not disturb the interior forest and are usually not present at night. Temperatures vary within the enclosure due to natural and artificial heating and cooling; during the night, the greenhouse may cool to 18°C, and during the day it reaches a minimum of 24°C, with temperatures rising above 24°C because of outside solar radiation. Long-term temperature data unfortunately are not available for the study period. Humidity remains between 70 % and 100 %, and rain falls occasionally within the exhibit.

Microchip scanners mounted in feeding boxes scattered throughout the enclosure collected data on the activity patterns of mouse lemurs living in Masoala Rainforest at Zoo Zürich. Zoo Zürich veterinarians subdermally inserted Trovan identifying microchips into mouse lemurs in the exhibit during their first capture after birth or before introduction into the exhibit. Zoo Zürich microchipped and tracked 58 mouse lemurs (27 female, 28 male, 2 unknown sex) between 2005 and 2010. An individual with a microchip entering a feeding box triggered the microchip reader automatically, and a computer recorded the time, date, and identification number. Although some fruiting trees within the enclosure are a possible source of food, most mouse lemurs used the feeding stations every night (Fig. 1), and we assume that a period during the winter during which very few or no mouse lemurs are seen active in the exhibit or observed using the feeding stations indicates population-wide hibernation. Volunteers also recorded some body masses in 2008 from video recordings of mouse lemurs stepping onto a scale inside a feeding box.

Data Analysis

Zoo Zürich veterinarians microchipped every mouse lemur within a few months of its birth. The last scan at a feeding station in the year of birth is an individual's first estimated date of immergence into hibernation: immergence at age 0. When that individual emerged the following year and a feeding station scanner scanned the individual for the first time, we assigned that date as their age 1 emergence date. We assigned each individual an estimated age in this manner for each year of life, with the

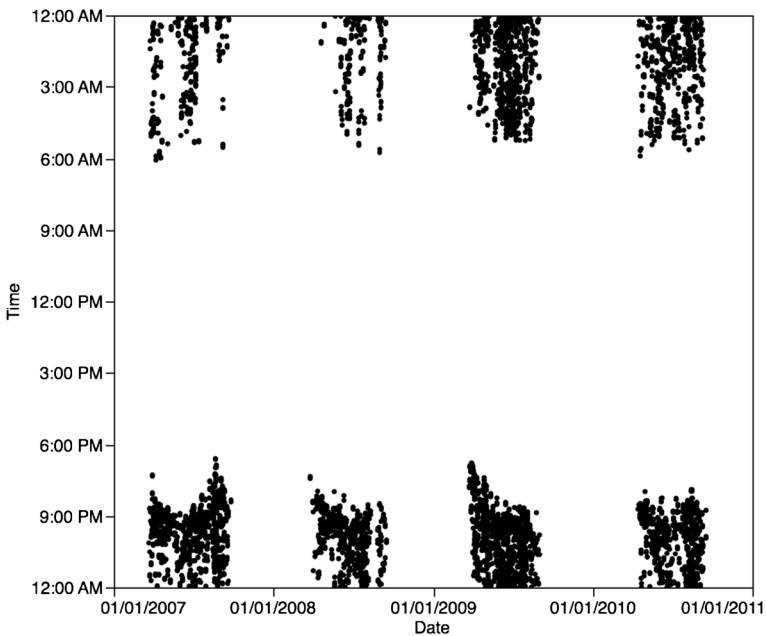


Fig. 1 Example plot of 4 full years of microchip scans at nest boxes collected on one individual *Microcebus lehilahysara* in the Masoala Hall at Zoo Zürich. The individual is male ID# 68337, born at Zoo Zürich in 2006. Each dot represents one scan. The inactivity period is defined as the period when no scans were recorded, indicating no use of feeding stations.

hibernation period as the transition from one age class to the next. For statistical analysis, we calculated dates of immergence into and emergence from hibernation for each individual for each year of data collection. We removed first dates of scanning for individuals in their year of birth from analysis because these only reflect when the individual received a microchip. We calculated the duration of hibernation for each individual in each year using these immergence and emergence dates. Immergence and emergence dates are normally distributed within each age group, so we performed two-way ANOVAs to compare male and female immergence and emergence dates between age groups. There were a few mouse lemurs that did not hibernate at all at age 0, and we performed a Fisher's exact test on the sex ratio of these individuals to determine whether this was significantly related to sex. We averaged body masses by month for each individual weighed during the body mass data collection period. Body masses of mouse lemurs during the body mass data collection period were not normally distributed, so nonparametric Mann–Whitney U tests were used to compare male ($N=6$) and female ($N=8$) body masses for each month during the short body mass data collection period in 2008. We performed all statistical analyses using JMP Pro (V11.2, SAS Institute, Cary, NC).

Results

We were able to estimate immergence and emergence dates for 44 individual Zoo Zürich Goodman's mouse lemurs (18 female, 21 male, 5 unknown) for at least 1 yr of life. As a result of loss of individuals due to mortality, sample size decreases as age increases. Only 3 of 31 sexed mouse lemurs, all males, did not hibernate during the first winter after birth. This sex ratio is not significantly different from 1:1 (Fisher's exact test, $P = 0.101$). After the year of birth, all mouse lemurs, including those that did not become inactive in their first year, became inactive for an extended period of time [mean 171.8 days ($N = 59$, $SD = 31.2$)] during each winter. A two-way ANOVA evaluating effects of age and sex on date of immergence into hibernation found no significant effect of sex ($F_{1,99} = 0.128$, $P = 0.721$), but a significant effect of age ($F_{4, 99} = 9.813$, $P < 0.001$), with young individuals immerging later. There was extreme variability in immergence dates in year 0. In years 1, 2, 3, and 4, immergence dates were more clustered (Fig. 2). A two-way ANOVA evaluating effects of age and sex on date of emergence from hibernation in each year of age showed no significant effect of age ($F_{3,93} = 1.510$, $P = 0.217$), but a significant effect of sex ($F_{1,93} = 13.941$, $P < 0.001$) (Fig. 3). Adult males emerged *ca.* 20 days before females, resulting in a mean apparent inactivity time of 167.8 days ($N = 44$, $SD = 39.8$) for adult females and 143.5 days ($N = 45$, $SD = 50.5$) for adult males.

Body masses for both males and females increased over time as mouse lemurs fattened in preparation for hibernation from April to August (Fig. 4). Recorded body masses ranged from a minimum of 35.8 g to a maximum of 88.5 g, with a mean of 51.1 g and a standard deviation of 12.4 g. Body masses from March to September did not differ significantly between males and females. When we separated body masses by month, Mann–Whitney U tests found no difference between male and female body masses in March ($S = 9$, $P = 0.167$), April ($S = 35$, $P = 0.215$), May ($S = 12$, $P = 0.016$), June ($S = 13$, $P = 0.857$), July ($S = 22$, $P = 0.788$), August ($S = 11$, $P = 0.133$) or September ($S = 8$, $P = 0.800$), with Bonferroni correction, $\alpha = 0.007$.

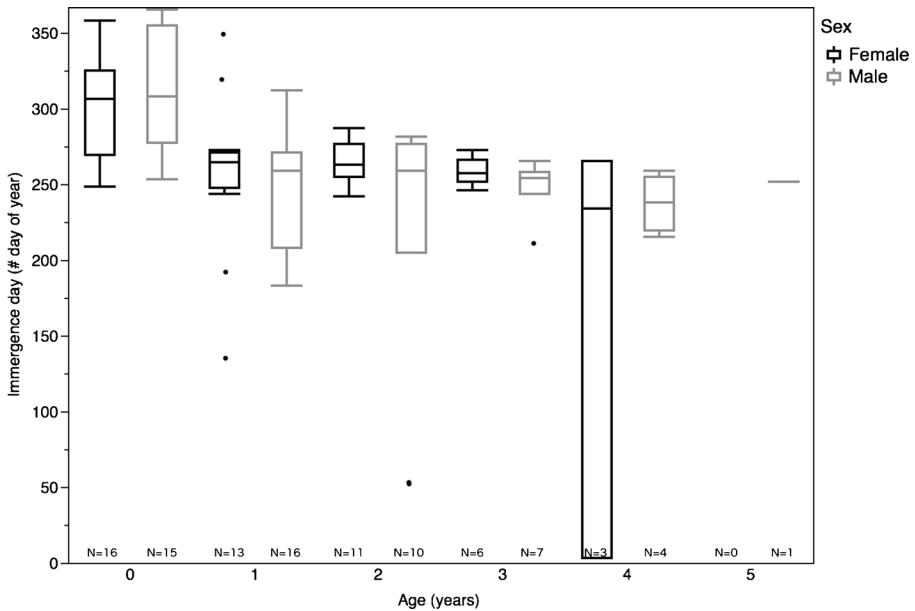


Fig. 2 Emergence dates of captive *Microcebus lehilahytsara* in the Masoala Hall at Zoo Zürich from 2006 to 2011, by sex and age. Boxes show the interquartile range of the data, and horizontal lines represent the median. Whiskers show the highest and lowest non-outlier data points. Black dots are outliers, defined as points below $Q_1 - 1.5 \times IQR$ or above $Q_3 + 1.5 \times IQR$. N gives sample size for each age and sex class. The day of the year is counted from January 1.

Discussion

The results of this study did not support the mate competition hypothesis, which states that male mouse lemurs remain active during the winter, using only occasional daily torpor, to be in optimal condition for the mating season. Male mouse lemurs emerged earlier than females, but still had an extended period of apparent inactivity wherein no feeding station use occurred before emergence. Widespread winter inactivity in this population with unlimited resources supports the seasonal food shortage hypothesis: all individuals fattened and hibernated in preparation for resource scarcity, despite the fact that resource scarcity never occurred. Males did emerge from hibernation before females, as predicted, because they cannot increase their testes size or mark territories while hibernating, but they only needed to emerge *ca.* 20 days before females to prepare for the breeding season.

All nonhibernators observed in this study were males less than a year old. Because there were only three mouse lemurs that did not enter hibernation in this study, it is impossible to determine whether this sexual skew is a product of small sample size or due to a factor unique to males. Schmid (1999) found a similar but more extreme pattern of sex bias in wild gray mouse lemurs, with 73.1 % of females and 18.9 % of males becoming inactive for long periods of time during the winter, but that study made no distinction between young animals and adults >1 yr old. Because a few but not all juvenile males did not hibernate during their first year of life, it may be more difficult, but certainly not impossible, for males to fatten sufficiently for hibernation.

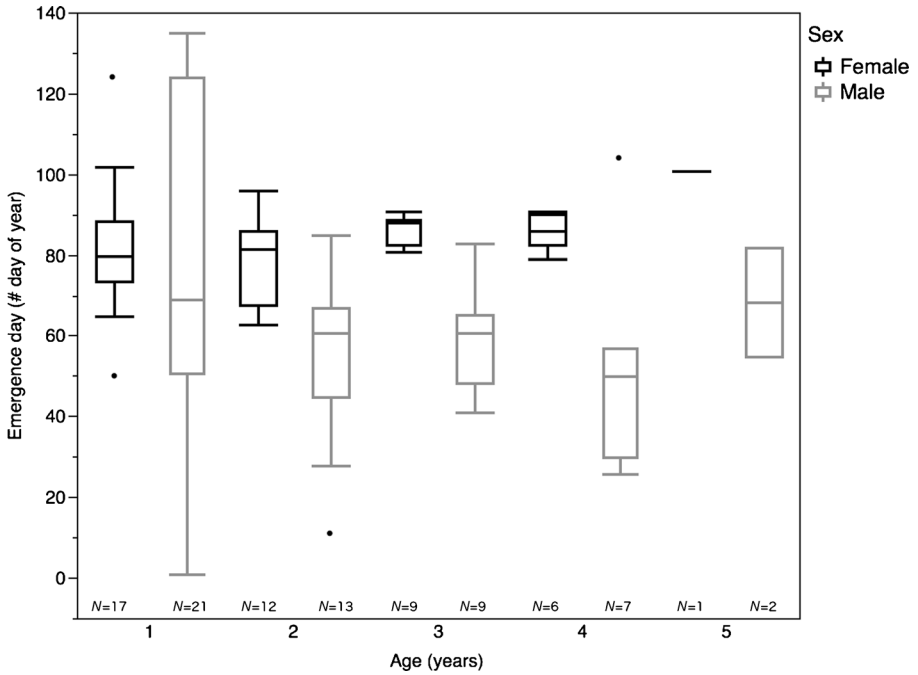


Fig. 3 Emergence dates of captive *Microcebus lehilahytsara* in the Masoala Hall at Zoo Zürich from 2006 to 2011, by sex and age. Boxes show the interquartile range of the data, and horizontal lines represent the median. Whiskers show the highest and lowest non-outlier data points. Black dots are outliers, defined as points below $Q_1 - 1.5 \times IQR$ or above $Q_3 + 1.5 \times IQR$. *N* gives sample size for each age and sex class. The day of the year is counted from January 1.

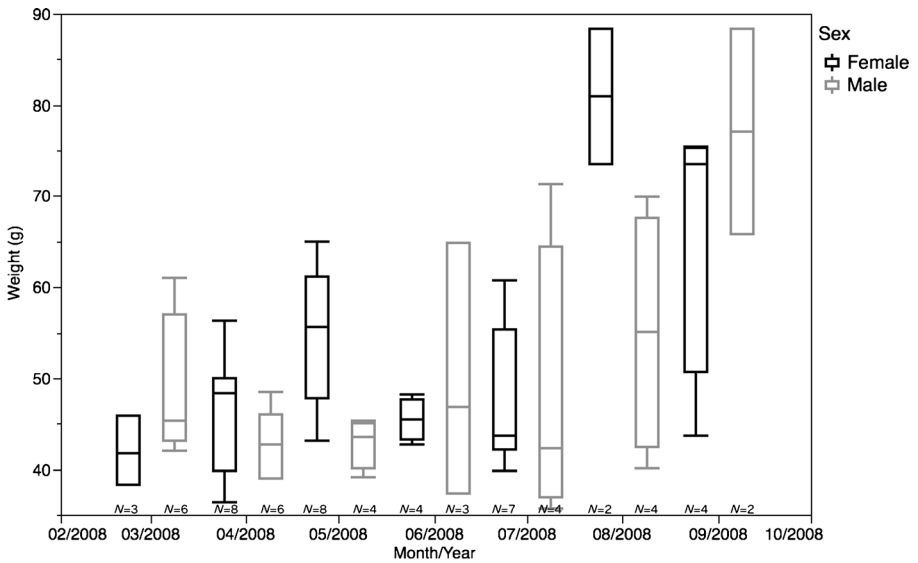


Fig. 4 Body masses of Zoo Zürich mouse lemurs by sex over time in 2008. Boxes show the interquartile range of the data, and horizontal lines represent the median. Whiskers show the highest and lowest data points. *N* gives sample size for each age and sex class.

The results of this study support the seasonal food shortage hypothesis, which states that mouse lemurs use seasonal inactivity to avoid being active during periods of food scarcity. The fact that almost all mouse lemurs in Zoo Zürich hibernated every year is a clear indication that Goodman's mouse lemurs will hibernate throughout the winter if they are able to fatten sufficiently. Some young mouse lemurs less than a year old were able to fatten and hibernate, but many young became inactive after adults, and a few did not become inactive at all during their first year. As these young were born only a few months earlier, it is likely that they were not able to gain sufficient fat as quickly as the adults. An important conclusion that follows from support of the seasonal food shortage hypothesis is that both male and female Goodman's mouse lemurs benefit from conservation of energy and avoidance of periods of food shortage. Males use fat reserves during the breeding season, which immediately follows the hibernation season, during their searching and competing for females (Schmid and Kappeler 1998), and larger males are more likely to secure matings (Schmelting *et al.* 2007). Female mouse lemurs have litters of offspring, and if a female is fat enough she may be able to successfully give birth to and raise two to five offspring (Perret 1990). There is no indication of a sexual skew in the ability or need for hibernation in the captive population studied here. Even this rain forest species, which does not face the extreme dry winters that the western dry forest mouse lemurs face, is adapted to hibernate throughout the winter to avoid resource scarcity. The sexual skew observed in wild populations may be due to proximate barriers to fattening, not sexual selection for different energy use between males and females.

A radiotracking study in this same Zoo Zürich exhibit of 10 Goodman's mouse lemurs from March to May, just after the inactive period, found that they sleep mostly in unisexual sleeping groups, with stable sleeping groups for females and fission–fusion groups for males. Although researchers have observed many mouse lemur species to use tree holes as sleeping sites, the trees in Masoala Hall are not old enough to have holes in them, and mouse lemurs living in the enclosure were observed to sleep in leaf structures close to the trunks of trees. Sharing sleeping sites may confer thermoregulatory benefits, especially in these relatively unprotected sleeping sites (Jürges *et al.* 2013). It is likely that mouse lemurs undergoing winter torpor also use these sleeping sites, again using other mouse lemurs as additional insulation against fluctuating temperatures. Further radiotracking studies on this population could confirm the period of prolonged inactivity in this population as well as determine where exactly they spend this time.

This study of Goodman's mouse lemurs supports the hypothesis that mouse lemurs hibernate to avoid anticipated seasonal food shortage. Other factors, such as water shortage and preparation for the reproductive season, have surely shaped mouse lemur winter behavior, but based on our data, factors that affect male and female mouse lemurs unequally have been less crucial to the evolution of this trait than those that affect both sexes equally, such as food scarcity. Predator avoidance is another threat to fitness that is particularly intense during the winter, and affects both sexes equally, but winter inactivity cannot provide total protection from predation. Depending on the availability of resources, all mouse lemurs in the population fatten in anticipation of seasonal resource scarcity and begin hibernation prior to the period of extreme scarcity, which suggests that they are spontaneous hibernators rather than facultative hibernators

that hibernate only in response to negative energy balance (Frank 2011). Ancestral lemurs, which have been posited as similar to mouse lemurs of today (Schülke and Ostner 2007), most likely also encountered extreme resource scarcity during the winter in Madagascar, and use of hypometabolism was an effective adaptation to deal with predictably harsh conditions. The presence of this energy-conserving trait in mouse lemur species living in a variety of habitats suggests that winter conditions have been extreme throughout Madagascar's evolutionary history, and these conditions have likely shaped the evolution of the many other endemic species as well (Wright 1999). Still, hibernation is optional in mouse lemurs (Kobbe *et al.* 2011; Schmid and Ganzhorn 2009). This plasticity of hibernation in mouse lemurs is particularly adaptive for the unpredictable nature of Madagascar's climate (Wright 1999; Wright and Martin 1995). Seasonal food shortage as the ultimate cause of hibernation has resulted in conservative but flexible behavior in Goodman's mouse lemurs.

As global climate change causes increased uncertainty in Madagascar's climate overall and increased temperatures and decreased rainfall in the area where these animals live in the wild (Dunham *et al.* 2011; Hannah *et al.* 2008; Wright 2007), such conservative behavior may protect mouse lemurs from resource scarcity during the dry winter, but increased ambient temperatures and anthropogenic habitat disturbance may limit the ability of many populations to hibernate. These compounded effects of climate change and habitat disturbance can in turn lead to a negative impact on reproductive success, as females need energy to produce and feed litters of young and males need fat stores to locate and gain access to females. It is therefore important to attend to shifting patterns of hibernation in populations experiencing changing habitat quality and temperature for the persistence of this seemingly hardy clade. Future research should expand on the comparison of energy conservation adaptations between western dry forest and eastern wet forest lemurs to understand how the different selective regimes of these different habitats have influenced the evolution and divergence of these species over time. This could include methods of closely monitoring winter daily torpor and hibernation patterns in wild eastern rain forest mouse lemurs, such as implanted body temperature loggers, to determine whether torpor depth and length are similar to that which has been reported in western dry forest species (Schmid and Ganzhorn 2009). In addition, researchers should evaluate habitats, including captive habitats, to determine which foods are most critical to the ability of lemurs to hibernate during the winter (Frank 2011), both for a better understanding of the physiology of torpor in this clade and to identify habitats that could limit conservative behavior (Ganzhorn and Schmid 1998). Hibernation in Goodman's mouse lemurs evolved as an adaptation to resource scarcity during the winter in Madagascar, but as habitats change as a result of climate change and anthropogenic disturbance, the ability of mouse lemurs to express this trait may be limited.

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