

Body Mass and Tail Girth Predict Hibernation Expression in Captive Dwarf Lemurs*

Marina B. Blanco^{1,2,†}

Lydia K. Greene^{1,2}

Peter H. Klopfer²

Danielle Lynch¹

Jenna Browning¹

Erin E. Ehmke¹

Anne D. Yoder²

¹Duke Lemur Center, Durham, North Carolina 27705;

²Department of Biology, Duke University, Durham,
North Carolina 27708

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ABSTRACT

Hibernation, a metabolic strategy, allows individuals to reduce energetic demands in times of energetic deficits. Hibernation is pervasive in nature, occurring in all major mammalian lineages and geographical regions; however, its expression is variable across species, populations, and individuals, suggesting that trade-offs are at play. Whereas hibernation reduces energy expenditure, energetically expensive arousals may impose physiological burdens. The torpor optimization hypothesis posits that hibernation should be expressed according to energy availability. The greater the energy surplus, the lower the hibernation output. The thrifty female hypothesis, a variation of the torpor optimization hypothesis, states that females should conserve more energy because of their more substantial reproductive costs. Contrarily, if hibernation's benefits offset its costs, hibernation may be maximized rather than optimized (e.g., hibernators with greater fat reserves could afford to hibernate longer). We assessed torpor expression in captive dwarf lemurs, primates that are obligate, seasonal, and tropical hibernators. Across 4.5 mo in winter, we subjected eight individuals at the Duke Lemur Center to conditions conducive to hibernation, recorded estimates of skin temperature hourly (a proxy for torpor), and determined body mass and tail fat reserves bimonthly. Across and between consecutive weigh-ins, heavier dwarf lemurs spent less time in torpor and lost more body mass.

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†Corresponding author; email: marina.blanco@duke.edu.

At equivalent body mass, females spent more time torpid and better conserved energy than did males. Although preliminary, our results support the torpor optimization and thrifty female hypotheses, suggesting that individuals optimize rather than maximize torpor according to body mass. These patterns are consistent with hibernation phenology in Madagascar, where dwarf lemurs hibernate longer in more seasonal habitats.

Keywords: Duke Lemur Center, *Cheirogaleus*, primate, torpor, tropical, Madagascar.

Introduction

Hibernation is a metabolic strategy found in all major mammalian lineages (Carey et al. 2003). Its prevalence speaks to its evolutionary significance: hibernating animals can survive prolonged periods of energetic deficits by depressing metabolism (Geiser 2004, 2013). Energetic savings, however, may come at a cost: hibernation can impose a physiological burden associated to acute metabolic stress as individuals remain metabolically depressed for long periods or transition from torpor to arousal (Nowack et al. 2019). For instance, while undergoing torpor bouts, individuals may be immunocompromised and unable to fight infections (Bouma et al. 2010); while undergoing arousals, individuals may be subjected to considerable increases in cellular oxidative stress (Orr et al. 2009). The trade-off between energy conservation and physiological costs has been formalized under the torpor optimization hypothesis, which states that hibernation is optimized by adjusting torpor expression in relation to energy availability (Humphries et al. 2003). Simply put, hibernation should be minimized when there is an energy surplus.

Alternatively, hibernation has been linked to cellular resilience and greater survivability (Lyman et al. 1981; Turbill et al. 2011; Wu and Storey 2016; Al-attar and Storey 2020). Physiologically, hibernators may have evolved not only the mechanisms to depress metabolism but also those to cope with the cellular stress incurred during arousals (Al-attar and Storey 2020). These mechanisms could, potentially, delay senescence (Wu and Storey 2016). Ecologically, hibernators may avoid predation by hiding and, in doing so, increase their chances for survival (Turbill et al. 2011). Myriad benefits of hibernation may lead to its maximization according to

available resources (e.g., greater fat storage would lead to longer hibernation). In the context of this article, “optimization” refers to hibernation use that is negatively associated to energy surplus, whereas “maximization” refers to hibernation use that is positively correlated to energy reserves.

Across mammals inhabiting temperate, predictable, and seasonal environments, hibernation expression increases with latitude and is generally proportional to the duration of unfavorable periods (i.e., low ambient temperature and low productivity; Ruf and Geiser 2015; Geiser 2020). Hibernation phenology (i.e., timing and duration) within species covering large geographic ranges also generally tracks elevational and latitudinal gradients. For example, prairie dogs (*Cynomys ludovicianus* and *Cynomys parvidens*) spend more time in torpor at higher elevations (Lehmer and Biggins 2005). Woodchuck populations (*Marmota monax*) in the northern range (Maine) spend twice as much time hibernating compared with those in the southern range (South Carolina; Zervanos et al. 2010). Under colder conditions, woodchucks display longer torpor bouts and shorter arousals. Interestingly, the percentage of body mass loss across their geographic range is similar, 31%–33%, suggesting that individuals from different populations deposit comparable amounts of fat but deplete depots faster under warmer conditions. Zervanos et al. (2010) also showed that different woodchuck populations spend comparable time in euthermia across their geographic range while modulating the time spent in torpor.

Energetic net benefits of hibernation depend on the arousal-incurred costs set against torpor-induced savings. Although arousals are metabolically expensive in cold environments because of the greater thermal differentials between ambient and body temperatures (Song et al. 2000; Karpovich et al. 2009; Németh et al. 2009), overall metabolic deficits accrued during torpor bouts are lessened at lower temperatures because metabolism is more deeply depressed (Geiser and Kenagy 1988). Thus, overall, longer torpor bouts at higher latitudes incur greater energy savings.

Hibernation profiles vary both between species and among individuals within the same population according to energetic demands. In some bats (e.g., *Nyctophilus bifax*), heavier individuals expressed more torpor than did leaner individuals (Stawski and Geiser 2010); in others (e.g., *Myotis lucifugus*), females depleted fat stores at a slower pace than did males (i.e., spent less energy during hibernation; Jonasson and Willis 2011). Considering that reproductive costs vary by sex, for many fat-storing females, reproductive success depends on whether they have leftover fat reserves after emergence from hibernation (Kunz et al. 1998). Fat depots can offset the high energetic costs of pregnancy and lactation before food resources become available after emergence from hibernation (Humphries et al. 2003). The thrifty female hypothesis, a variation of the torpor optimization hypothesis, states that females conserve more energy than do males because of their more substantial reproductive burden (Jonasson and Willis 2011). Females can save more energy than males by undergoing longer torpor bouts or shorter arousals or hibernating at colder ambient temperatures (Jonasson and Willis 2011, 2012; Czenze et al. 2017). The thrifty female hypothesis has received support from studies on the little brown bat (*M.*

lucifugus) of widespread temperate distribution (Jonasson and Willis 2011; Czenze et al. 2017).

In subtropical or tropical environments, the energetic benefits of hibernation may be less defined and more difficult to assess. Individuals are subjected to warmer ambient temperatures but often to less predictable conditions (Nowack et al. 2020). In particular, the duration of the unfavorable period may vary from month to month because energy availability is less certain throughout the year (Nowack et al. 2017). Moreover, water deficiencies may impose an additional energetic burden (Lehmer et al. 2006; Geiser and Brigham 2012). Species that evolved in habitats with unpredictable climate and rainfall patterns tend to display lower metabolic rates and thermolabile tendencies and are prone to use both torpor and hibernation, though they show less strict seasonality in their expression (Lovegrove 1996, 2000; Nowack et al. 2020). Opportunistic use of torpor is common in many tropical and subtropical species throughout the year when individuals are exposed to short-term energetic bottlenecks: sugar gliders (*Petaurus breviceps*) use torpor to overcome adverse weather events like storms, and echidnas (*Tachyglossus aculeatus*) can use torpor to mitigate adverse effects of fires on food availability (Nowack et al. 2015, 2020). When echidnas hibernate, they undergo shorter hibernation periods in mild climatic zones compared with colder climatic zones (Nicol and Andersen 2002). Pygmy possums (*Cercartetus nanus*) that live in relatively mild climates in eastern Australia preferred to use torpor in warmer temperatures under experimental conditions (Song et al. 2000). The preference for milder temperatures allowed pygmy possums to undergo shallow torpor bouts and to rewarm from torpor faster, which may be beneficial for sporadic foraging. However, as metabolic rates increase with ambient temperature, it also means that pygmy possums may be optimizing torpor rather than maximizing energy savings (Song et al. 2000).

A small percentage of tropical heterotherms are strict seasonal hibernators: among them are the small-bodied dwarf lemurs of Madagascar (*Cheirogaleus* spp.; Blanco et al. 2018; Nowack et al. 2020). Dwarf lemurs are obligate hibernators in the wild and store large fat reserves in their tails (Fietz and Dausmann 2006). In Madagascar, there are as many species of dwarf lemur as there are habitat types (Blanco et al. 2018). At least nine species are distributed across the island, in variably seasonal habitats that range from dry deciduous forests to lowland littoral and moist forests (McLain et al. 2018). Across Madagascar, hibernation phenology shifts according to habitat type: species inhabiting more seasonal environments (e.g., dry deciduous and high-elevation forests) hibernate longer than do those in lower-elevation and moist forests (Dausmann 2014; Dausmann and Blanco 2016; Blanco et al. 2018). Differences in hibernation profiles can be detected even in closely related species. For instance, fat-tailed dwarf lemurs (*Cheirogaleus medius*) in the western dry forests hibernate for up to 7 mo a year compared with 5 mo of hibernation in *Cheirogaleus thomasi* (formerly listed as *C. medius*) inhabiting the southeast littoral forests (Lahann and Dausmann 2011). Differences in hibernation phenology are attributed to a wider window of food availability in lowland moist habitats (Blanco et al. 2018). Dwarf lemur females have priority of access to food compared with males, which may allow females to achieve maximum fattening earlier (Blanco and

Godfrey 2014). Whereas females were reported to hibernate longer than males in some dwarf lemur species (Blanco and Godfrey 2014), no sex differences were found in others (Lahann and Dausmann 2011).

In sum, at a species level, hibernation expression in wild dwarf lemurs seems to vary according to seasonality and energy availability in different environments, thus supporting the torpor optimization hypothesis. At the individual level, anecdotal data from eastern species (*Cheirogaleus sibreei* and *Cheirogaleus crossleyi*) support the claim that heavier individuals (e.g., adult females) may hibernate longer than leaner individuals (Blanco and Godfrey 2014). These data are consistent with both the thrifty female hypothesis (females conserve more energy) and the torpor maximization hypothesis (fatter individuals hibernate longer). Unfortunately, we lack the resolution from field studies to address torpor expression in relation to energy availability at the individual level. To overcome this challenge, we investigated torpor expression in captive dwarf lemurs that vary in body mass and sex but are maintained under identical environmental conditions.

The Duke Lemur Center (DLC), North Carolina, houses a population of fat-tailed dwarf lemurs whose ancestors can be traced to the western dry deciduous forests in Madagascar (Blanco et al. 2021). Like their wild counterparts, DLC dwarf lemurs increase body mass seasonally, mainly as an accumulation of fat tissue deposited in their tails. When subjected to cold temperature and food restriction protocols, captive dwarf lemurs display multiday torpor bouts for about 4.5 mo a year. The changes in body mass throughout hibernation are largely due to the depletion of fat stores (Blanco et al. 2021). Preliminary data showed that females, overall, displayed longer torpor bouts and lost relatively less fat than did males, while males ate food more often and stayed more active during the hibernation season. We recently conducted a follow-up study on torpor expression by DLC dwarf lemurs.

To ascertain whether dwarf lemurs behave like hibernation optimizers or hibernation maximizers, we investigate the expression of torpor according to individuals' body mass and fat reserves under varying temperature and food-provisioning conditions. We predict that under the torpor optimization hypothesis, heavier dwarf lemurs would use less torpor; under the thrifty female hypothesis, regardless of starting body mass, females would save more energy than males; and under the maximization hypothesis, heavier dwarf lemurs, regardless of sex, would spend more time in torpor.

Methods

Study Subjects

Eight dwarf lemurs, four females (three adults, one juvenile) and four males (four adults), were selected for the hibernation study and transferred to temperature-controlled rooms on October 16, 2020. The individuals were kept in separate enclosures, with one exception: individuals Sa and My (mother and daughter) had access to each other's enclosures. Despite her young age, juvenile My had achieved adult body size and mass before study onset: she was among the heavier subjects entering the hibernation season.

For details on the enclosures, see Blanco et al. (2021). All individuals were fitted with radio collars (M1550, 3.5 g, Advanced Telemetry Systems, Isanti, MN; collar size/body mass ratio of <4%). These external transmitters changed their pulse rates according to the collars' surface temperature, and when in tight contact with dwarf lemurs' necks, they provided a reliable estimation of dwarf lemurs' skin temperature (T_{ske}). Because the implantation of devices for temperature data recording is not permitted in these endangered primates, we used T_{ske} as proxy for body temperature, with the understanding that temperature recordings were most reliable when individuals were hibernating (i.e., in the curl-up position). These methods have been successfully employed in previous studies (Dausmann 2005; Blanco et al. 2021). Pulse rates from individual transmitters were automatically converted to temperature values ($^{\circ}\text{C}$) and stored hourly by a receiver with data logger (R4500, Advanced Telemetry Systems).

Housing Protocols: Photoperiod, Room Temperature, and Food Restriction Regimes

Dwarf lemurs were subjected to reversed alternating light/dark cycles that approximate the natural photoperiod of North Carolina. Room temperature was set at different temperatures during the study period: during the acclimatization period between October 16 and 26, room temperature was set at 21°C ; from October 26 to December 7, the first phase of the study, room temperature was lowered to 15°C ; from December 7 to January 19, the temperature was set at 11°C ; and from January 19 to March 4, the last phase of the study, room temperature was set 14°C . Different temperature settings during the hibernation season reflected, to some degree, seasonal temperature variation in the wild. These protocols are tested in the context of renaturalization efforts at the DLC to maintain the well-being of the captive population. Temperature settings are within the natural ranges that this species would experience in Madagascar (Dausmann et al. 2016). Rooms were subjected to unintended temperature variation around set points as a result of external fluctuations. Deviations from the set point were about 2°C during the study and up to 4°C during two warm days.

Although wild dwarf lemurs do not eat or drink for up to 7 mo a year, DLC dwarf lemurs had to be provisioned food according to institutional animal care regulations. Starting October 26, we implemented a food restriction protocol based on the accumulation of euthermic hours, as described in Blanco et al. (2021). Every morning, if applicable, food bowls were removed and inspected for leftovers, and data were reported as "food eaten" if any or all the food was consumed or "food uneaten" if food was left in full (Blanco et al. 2021).

Data Collection and Analysis

Data collection began on October 26, 2020, when room temperatures were lowered to 15°C and food restriction protocols were in place. For the next 2 wk, however, we observed that some dwarf lemurs stayed euthermic and active despite a decrease in food provisioning, leading to a disproportionate loss of body mass. To

avoid introducing an artifact (i.e., body mass lost related to unusual behaviors), we considered body mass from November 9 as the “onset of hibernation” and from March 3 as the “end of hibernation.” The dwarf lemurs were weighed approximately every other week, though when possible, we timed weighing sessions with natural arousals to avoid inducing artificial arousals. In addition to assessing body mass, we measured tail base circumference and middle tail circumference with a measuring tape (mm). We calculated tail girth as the average between tail base and middle base circumferences.

To determine whether dwarf lemurs were torpid, we calculated individual T_{ske} thresholds. These thresholds varied throughout the study to account for changes in room temperature settings and were calculated as 8°C above the minimum T_{ske} at each period, that is, when room temperature was set at 15°C, 11°C, and 14°C. The 8°C mark based on room temperature ranges and visual inspection of T_{ske} data ensured that torpor expression was not overestimated as a result of possible ambient temperature interference in T_{ske} recordings. This may be the case when the transmitter is not tightly pressed against the dwarf lemurs’ neck, which occurs when individuals are not torpid and moving around.

For statistical tests, we ran nonparametric Mann-Whitney tests and linear regressions in GraphPad Prism (ver. 9.1.2). We further implemented linear mixed models (LMMs) using the glmmADMB package (ver. 0.8.3.3; Skaug et al. 2016) and R software program (ver. 4.0.2; R Development Core Team 2020) in Rstudio (ver. 1.3.959; RStudio Team 2020). We set the significance threshold to $P < 0.05$.

We determined whether there was a sex difference in body mass or tail girth at the onset of the hibernation season using Mann-Whitney tests and compared body mass at the study onset with the total percentage of time spent in torpor per individual via linear regression. We compared body mass loss and tail girth loss with body mass at bimonthly weigh-ins and sampling periods by sex using linear regressions. We further ran three sets of LMMs.

In our first LMM, we examined the relationships between body mass, torpor expression, and sex between consecutive weigh-ins. We included lemur sex (two categories: male or female) and bimonthly body mass (g; continuous variable) as the explanatory variables, lemur ID as a random variable, and the time spent in torpor (mean h/d) until the next weigh-in as the dependent variable. We determined that a Gaussian model best fit these data.

Second, to examine relationships between body mass loss (g/d) and tail girth loss (mm/d) and absolute body mass between consecutive weigh-ins, we included lemur sex and bimonthly body mass as the explanatory variables, lemur ID as a random variable, and rate of body mass or tail girth loss until the next weigh-in as the dependent variable. The Gaussian distribution best fit these data. To visualize patterns relative to time, we graphed rates of body mass and tail girth loss relative to study period.

Third, we identified contributory factors underlying observed patterns of torpor expression. In these LMMs, we included the duration (h) of individual arousal bouts and torpor bouts as the response variables; food intake during the current or preceding arousal bout (categorical variable: yes or no), sex (categorical variable: female or male), and room temperature (categorical

variable: 15°C, 11°C, 14°C) as explanatory variables; and dwarf lemur ID as a random variable. We determined that a log-transformed Gaussian distribution best fit our data.

Research protocols used in this study were approved by the Duke University Institutional Animal Care and Use Committee under protocols A263-17-12 and A213-20-11. These protocols followed guidelines established by the *Guide for the Care and Use of Laboratory Animals* of the National Institutes of Health.

Results

There were no differences between males and females at the onset of the study in body mass (Mann-Whitney $U = 5, P = 0.429$) or tail girth (Mann-Whitney $U = 6, P = 0.657$; fig. 1). Across the entire hibernation season, body mass at the onset predicted the total percentage of time spent in torpor, with heavier individuals spending less time in torpor ($R^2 = 0.68, P = 0.012$, fitted regression equation: $y = -0.2047x + 131.8$; fig. 2A).

Between subsequent weigh-ins, the average hours per day spent in torpor was predicted both by sex and by body mass (for females: $R^2 = 0.46, P < 0.0001, y = -0.05218x + 31.08$; for males: $R^2 = 0.51, P < 0.0001, y = -0.06099x + 31.26$; fig. 2B), such that males spent significantly less time torpid than did females (LMM: $z = 3.39, P < 0.0001$), and leaner weights were associated with more hours in torpor (LMM: $z = 7.58, P < 0.0001$).

The rate of body mass loss (g/d; fig. 3A) was positively correlated with individuals’ weights (for females: $R^2 = 0.29, P = 0.0014, y = 0.007820x - 1.159$; for males: $R^2 = 0.43, P < 0.0001, y = 0.0087x - 1.095$), with heavier individuals losing more body mass between bimonthly periods than did leaner individuals (LMM: $z = 7.26, P < 0.0001$). The rate of body mass loss did not significantly differ between sexes (LMM: $z = 1.77, P = 0.077$). The rate of tail girth loss (mm/d; fig. 3B) was negatively correlated with individuals’ weights (for females: $R^2 = 0.18, P = 0.0152, y = -0.001832x + 0.4927$; for males: $R^2 = 0.11, P = 0.0582, y = -0.001787x + 0.5636$). Tail girth loss was significant by sex, with leaner individuals

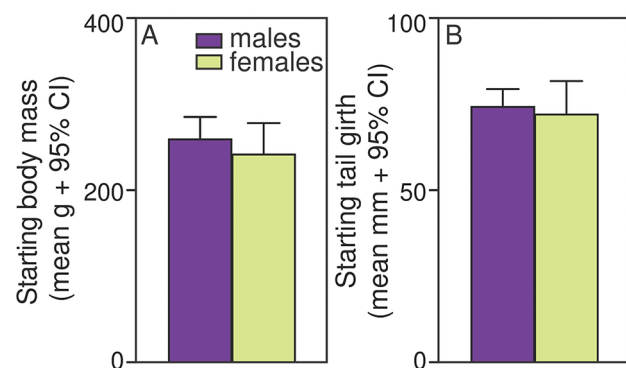


Figure 1. Measurements at the beginning of the study. Shown here are body mass (g; A) and tail girth (mm; B) in male and female fat-tailed dwarf lemurs (*Cheirogaleus medius*). No significant differences were found between sexes in body mass ($P = 0.429$) or tail girth ($P = 0.657$). CI = confidence interval.

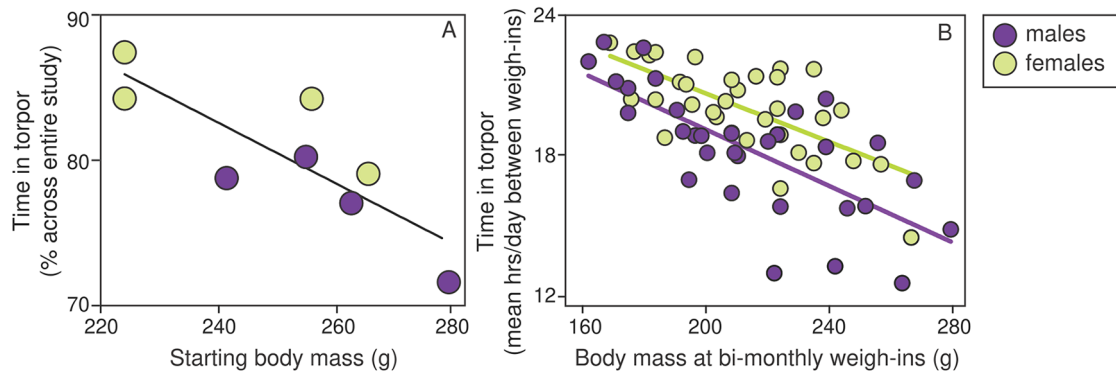


Figure 2. Body mass relative to torpor expression in captive fat-tailed dwarf lemurs, including males and females. Shown here are the total time spent in torpor across the entire hibernation season relative to starting body mass (g; A) and the hours per day spent in torpor relative to body mass between bimonthly weigh-ins (B). Lines represent regression lines across all animals (A) or within sexes (B). Correlation was significant between body mass and total time in torpor ($P = 0.012$; A), and body mass and sex significantly predicted time in torpor within bimonthly periods ($P < 0.0001$ in both cases; see text for details; B).

losing more tail fat than heavier individuals (LMM: $z = 3.23$, $P = 0.0012$) but with males losing more tail fat than females (LMM: $z = 2.24$, $P = 0.0248$). In fact, when body mass loss and tail girth loss are plotted against time, rates of body mass loss are higher at the beginning of the hibernation period than at the end (for females: $R^2 = 0.30$, $P < 0.0012$, $y = -0.08548x + 0.8815$; for males: $R^2 = 0.55$, $P < 0.0001$, $y = -0.1347x + 1.366$;

fig. 3C), whereas tail girth loss is greater at the end of the season (i.e., tail fat deposits are the latest to be depleted; for females: $R^2 = 0.14$, $P = 0.0372$, $y = 0.01723x + 0.02714$; for males: $R^2 = 0.23$, $P = 0.0055$, $y = 0.03458x + 0.02688$; fig. 3D). Males lose comparably more body mass than females, though toward the end of the season both sexes converge as they approximate low body mass status.

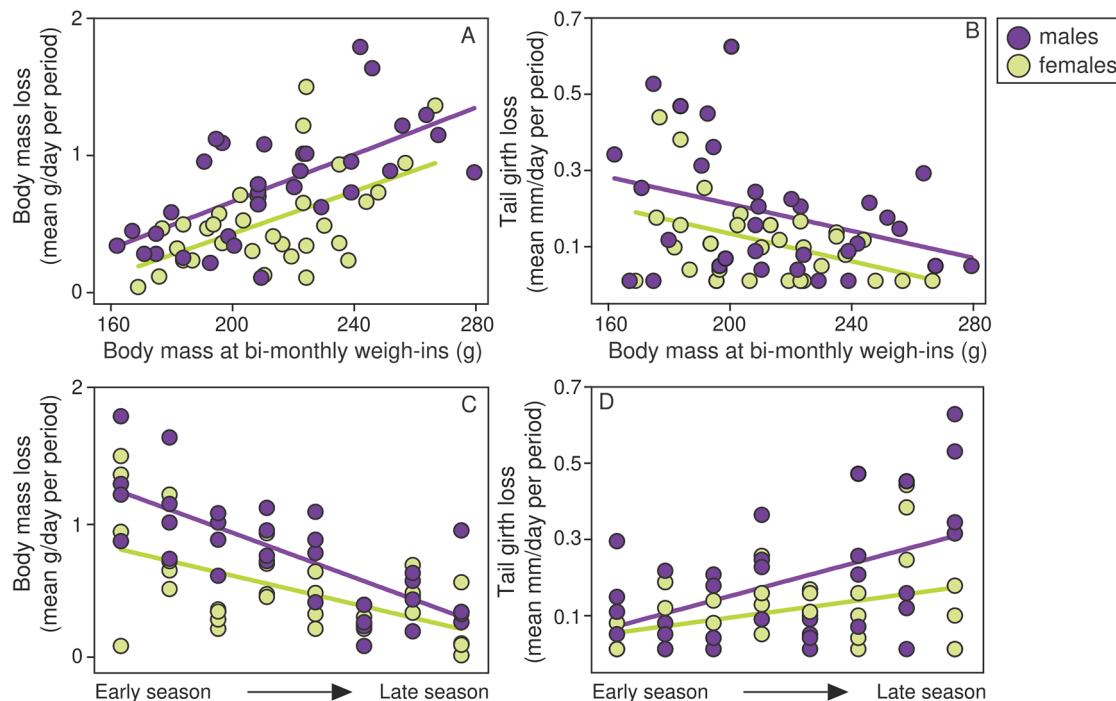


Figure 3. Rates of body mass loss (g/d/period) and tail girth loss (mm/d/period) relative to starting body mass and time. Shown here are body mass loss (A, C) and tail girth loss (B, D) graphed against body mass measured at consecutive weigh-ins (A, B) and against study period (C, D). Lines represent regression lines for males and females. There was a significant positive correlation between body mass loss and body mass at onset of weigh-in periods (for females: $P = 0.0014$; for males: $P < 0.0001$) and a significant negative correlation in females between tail girth loss and body mass at onset of weigh-in periods (for females: $P = 0.0142$; for males: $P = 0.0535$). Sex was not predictive of body mass loss, but it was predictive of tail girth loss when running linear mixed models (see text for details).

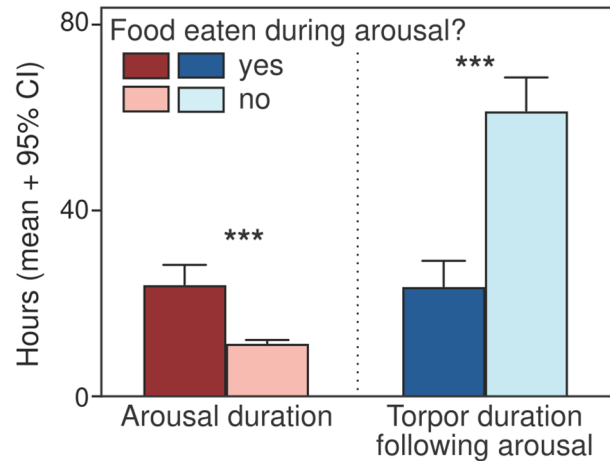


Figure 4. Duration (h) of arousal and torpor bouts relative to whether food was eaten or not eaten during the current or preceding arousal. Food intake significantly affected the arousal duration and torpor bout duration following the arousal. Asterisks indicate $P < 0.0001$. CI = confidence interval.

Overall, torpor bouts were significantly shorter at the warmest room temperature set point (15°C vs. 11°C ; LMM: $z = 9.06$, $P < 0.0001$) and when food was eaten during the preceding arousal (LMM: $z = 8.51$, $P < 0.0001$; fig 4). There was no significant difference between sexes in the duration of torpor bouts (LMM: $z = 1.78$, $P = 0.076$). Arousals were significantly shorter at the warmest temperature set point (less differential between T_{ske} and ambient temperature; LMM: $z = 2.23$, $P = 0.026$) but significantly longer when food was eaten during the arousal (LMM: $z = 10.97$, $P < 0.0001$). There was a significant sex difference, with males showing longer arousals and spending more time euthermic than females (LMM: $z = 2.07$, $P = 0.038$).

Discussion

By inducing hibernation in captive dwarf lemurs, we demonstrate how body mass, fat reserves, and sex can modulate the expression of torpor within and across the hibernation season. Overall, heavier dwarf lemurs spent less time in torpor than did leaner individuals, supporting the torpor optimization hypothesis. Moreover, females spent relatively more time in torpor, less time euthermic, and proportionally lost less body mass than did males even at comparable body mass, consistent with the thrifty female hypothesis. Thus, we did not find evidence that heavier individuals, regardless of sex hibernated longer than leaner individuals, contrary to expectations of the maximization hypothesis. Our results suggest that individual lemurs optimize rather than maximize their use of hibernation. Our small sample sizes, however, render our findings tentative, warranting further testing.

We are also prudent about generalizing our results to wild populations. In Madagascar, adult female dwarf lemurs can hibernate for longer periods than males, though data are inconclusive for some species (Lahann and Dausmann 2011; Blanco and Godfrey 2014). Moreover, females generally achieve greater body masses and fatter tails than do males at the onset of hibernation (Blanco and

Godfrey 2013). In contrast, DLC dwarf lemur females did not significantly differ from males in body mass at the onset of the hibernation season.

Differences in the expression of hibernation between wild and captive individuals can result from altered genetic makeup or developmental history of captive individuals or from exposure to inadequate environmental conditions that facilitate hibernation (Geiser and Ferguson 2001; Blanco et al. 2021). For example, in a resource-limiting environment, female dwarf lemurs may reach greater body mass than males before hibernation because they have priority of access to food; however, in resource-rich environments (e.g., captivity), those differences may be erased.

Dwarf lemur females most likely benefit from leftover fat deposits to sustain imminent reproductive costs following hibernation. In the dry deciduous forests of western Madagascar, fat-tailed dwarf lemurs come out of hibernation before the onset of the rainy season, when food availability is still low (Blanco et al. 2018). In fact, food availability can be highly inconsistent across years because Madagascar's climate is inherently stochastic (Dewar and Richard 2007). Some years are marred with droughts; others have longer rainy seasons. Thus, it is not surprising that female dwarf lemurs in highly seasonal dry forests reproduce every other year (Lahann and Dausmann 2011), suggesting that energetic demands cannot be met consistently and that females that reproduce in any given year may not be able to recruit enough fat stores to sustain the following hibernation and reproductive seasons (Blanco et al. 2018).

Dwarf lemurs are known for their reliance on tail fat to fuel hibernation, but they can also deposit white adipose tissue in other parts of their bodies. We found that tail depots were preferentially retained until body fat was first depleted. Although we did not measure subcutaneous fat deposits except for tail girth, morphological changes showing volumetric reduction along the flanks and back areas were evident in all individuals as the hibernation season progressed. Indeed, across consecutive weigh-ins, heavier dwarf lemurs lost more body mass, whereas leaner individuals lost more tail girth. And when body mass loss and tail girth loss are plotted against time, rates of body mass loss are greater at the beginning of the hibernation period, whereas tail girth loss is greater at the end of the season. In primates and other animals, accumulated ectopic (i.e., in abnormal places) body fat can strain organs, including the heart, liver, and kidneys (Rasouli et al. 2007); accordingly, our observed patterns were consistent with earlier depletion of fats stored outside of their tails.

The fact that food was offered sporadically to DLC dwarf lemurs was also different from wild settings, where dwarf lemurs do not eat or drink for up to 7 mo a year (Dausmann and Blanco 2016; Blanco et al. 2018). In our study, food intake significantly affected arousal and torpor bout durations. The presence of food was also shown to shorten torpor expression in other captive hibernators (e.g., pygmy possums), which aroused from torpor more often when food was not withheld (Song et al. 2000).

Humphries et al. (2003) presented a simple but powerful argument: because energy conservation by hibernation comes at a metabolic cost, hibernating animals modulate hibernation expression according to their internal energy status. Some researchers have argued that hibernation benefits extend beyond

energy conservation (Geiser and Brigham 2012; Siutz et al. 2017), most prominently predator avoidance, and that even in the presence of energy surplus, phenological changes are not always followed by changes in the duration of hibernation (Sheriff et al. 2011). Bieber et al. (2014) argue that heavier dormice hibernated longer but that they underwent more arousals (i.e., spent more time euthermic) and hibernated at higher temperatures than leaner individuals. Thus, there may be different routes to reduce the potential metabolic burden imposed by hibernation without shortening the hibernation season. In fact, survival rates increase in dormice during hibernation (Turbill et al. 2011; Bieber et al. 2012).

We find that captive fat-tailed dwarf lemurs with greater body mass spend less time in torpor than those with lower body mass and that dwarf lemur females deplete fat at slower rates than do males. Although the torpor optimization hypothesis may not be universally supported by empirical data (e.g., several species hibernate up to a year and in the presence of food; Geiser 2020), there is ample evidence from heterothermic species in temperate and tropical environments that energy availability affects torpor patterns (e.g., Vuarin et al. 2013; Bieber et al. 2014). Additional studies in wild dwarf lemur populations are warranted to characterize dwarf lemurs as optimizers or maximizers at the species and individual levels.

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