Big Is Beautiful—Fat Storage and Hibernation as a Strategy to Cope with Marked Seasonality in the Fat-Tailed Dwarf Lemur (Cheirogaleus medius)

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TROPICAL AND SEASONAL: THE CLIMATE OF THE MALAGASY WEST COAST

Organisms of the ecosystems of the dry forests along the Malagasy west coast show distinct adaptations to the marked seasonality of this region. All plants and animals occurring here need to cope with the long and relatively cold dry season during the austral winter, with virtually no precipitation and no open water available from April through October (Figure 1). The dry season alternates with the rainy season, which lasts from mid-November to mid-March, with most rain

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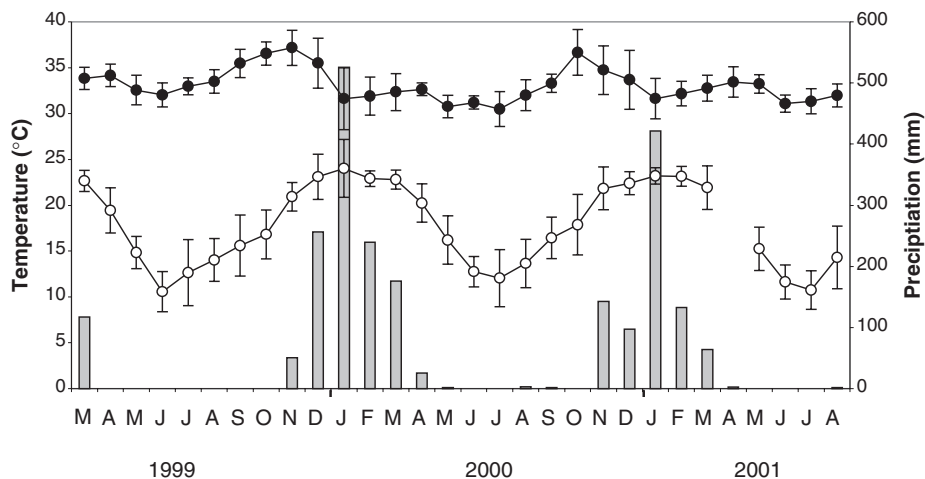
Figure 1. Climate of the Kirindy forest. Shown are data from March 1999 to August 2001, taken at a standard location in the field camp. Temperature is given as monthly mean ± standard deviation. For precipitation cumulative data per month are shown. (●) Daily maximum temperature; (○) daily minimum temperature. Data on daily minimum temperature are not available for April 2001. Note the interannual variation in climate, especially in the timing and amount of precipitation.

falling during the hottest months between December and February. Mean annual precipitation is 800 mm (range 390 – 1511 mm; Ganzhorn and Sorg, 1996).

   While average daily maximum temperature is comparable between dry and rainy season (around 32°C; Table 1), average daily minimum temperature differs dramatically between the two seasons, with ambient temperature dropping to about 13°C at night during the dry season, but only to about 23°C during the rainy season. The average amplitude of daily temperature fluctuations is therefore about twice as great during the dry season (about 19°C) than during the rainy season (about 10°C; Table 1). The coldest months are June and July, with ambient temperature dropping below 10°C at night (Figure 1).

   Concomitant with these climatic changes, variations in the availability of food resources like fruits and insects occur. Even though fruits are produced throughout the year, the percentage of fleshy fruits decreases dramatically during the dry season (Bollen et al., 2005). Insect abundance is positively correlated with rainfall and leafing of the trees, and therefore insects are also less abundant during the dry season (Hladik et al., 1980).

   The austral winter in the dry deciduous forest of western Madagascar thus represents a bottleneck of energy and water supply, combined with energetically disadvantageous low ambient temperature. However, the occurrence of this period of scarcity is very predictable, giving organisms inhabiting these ecosystems the opportunity to take measures to master these challenges.

Table 1. Climate of the Kirindy forest

		T_{max} (°C)	T_{min} (°C)	Daily amplitude (°C)	N	Precipitation (mm)	First heavy rain	Last heavy rain
Rainy	1998/99					803.3	15.02.99	09.03.99
Dry	1999	32.8 ± 1.4	13.0 ± 3.0	19.8 ± 3.0	118			
Rainy	1999/00	33.5 ± 3.4	22.8 ± 1.8	10.6 ± 4.1	109	1274.4	08.12.99	06.03.00
Dry	2000	31.1 ± 1.5	13.6 ± 3.0	17.5 ± 3.5	112			
Rainy	2000/01	32.6 ± 2.5	23.1 ± 1.5	10.0 ± 2.9	72	915.9	21.11.00	31.01.01
Dry	2001	31.8 ± 1.4	12.5 ± 2.9	19.3 ± 2.7	88			

Dry season (*Dry*): May – August. Rainy season (*Rainy*): mid-November – mid-March. *Precipitation*: total rainy season. *N* gives the number of days within the respective season included in the analysis. T_{max}: maximum daily temperature; T_{min}: minimum daily temperature. *Heavy rain* is defined as > 50 mm precipitation. Temperature data are not available for the rainy season 1998/1999.

The fat-tailed dwarf lemur (*Cheirogaleus medius*) occurs throughout the western dry-deciduous forest and has adapted to this marked seasonality and resource limitation in a particularly intriguing manner. During the unfavorable dry season these lemurs suspend their activities and hibernate for up to 7 months (Petter, 1978; Dausmann et al., 2004, 2005).

In the following section we will give insight into the ecological, behavioral, and physiological adaptations of *C. medius* to the described climatic challenges and resource restrictions, that we have gained during a long-term (1995–2005) field study on this species conducted in the Kirindy forest, western Madagascar. Demographic data were achieved by capture-recapture and individual marking (Fietz, 1999a). Behavioral and nutritional data were recorded during nightly follows of radio-collared individuals (Fietz and Ganzhorn, 1999; Fietz et al., 2000). Physiological measurements were performed with the help of temperature-sensitive collar transmitters (Dausmann et al., 2004, 2005), portable gas analyzers (Dausmann et al., 2000, submitted), and fat biopsies (Fietz et al., 2003).

CHEIROGALEUS MEDIUS—A PRIMATE WITH AN EXCEPTIONAL LIFE HISTORY

C. medius are small-bodied (130 g; Fietz, 1999a) nocturnal lemurs that live in small family groups consisting of the reproducing male–female pair and the offspring from one or more breeding seasons (Fietz, 1999a; Müller, 1999). Males and females live in lifelong pair bonds and usually separate only when one partner dies. Even though yearlings or older offspring may remain in their family group when new offspring is born, they do not help raising their kin. Members of one family inhabit a common territory of 1–2 ha, and use the same tree holes as sleeping sites (Fietz, 1999a; Fietz et al., 2000). Territories are defended and olfactorily

marked by the adult male–female pair, especially along the territory borders (Müller, 1998; Fietz, 1999a,b; Wiedemann, unpublished data). Depending on climatic conditions, adults mate during November or December (Hladik et al., 1980; Fietz, 1999a) and females give birth to one or two infants after a gestation period of 61–64 days (Figure 2). Remarkably, both sexes take extensive care of their offspring (Fietz, 1999a; Fietz et al., 2000). During the first 2 weeks after birth, infants remain in the nest holes, and parents take turns caring for them. As soon as infants start to leave their nest holes, either the male or the female accompanies them on their excursions (Fietz, 1999a). The participation of males seems to be crucial for the survival of the newborns, as females without paternal help were not able to raise their offspring successfully and infants died shortly after birth. Surprisingly, especially in view of the high investment of infant care by males in this species, genetic parentage analyses revealed an extraordinarily high incidence (44%) of extra-pair young (Fietz et al., 2000).

BODY MASS ALMOST DOUBLES BEFORE HIBERNATION

During hibernation *C. medius* do not feed and rely entirely on their endogenous fat reserves. Typical for a hibernating species, they exhibit remarkable prehibernation fattening during the period of food abundance from March until May (Figure 3) and adults may double their body mass during this time (from about 130 g to over 250 g; Fietz and Ganzhorn, 1999; Fietz et al., 2003). Part of the fat is stored within the tail, which swells from 10 ml to approximately 50 ml in volume, giving the fat-tailed dwarf lemur its name (Petter et al., 1977; Hladik et al., 1980).

In order to accumulate these fat deposits, different strategies are feasible, by which either energy intake is maximized, or energy expenditure minimized. *C. medius* seem to employ both methods. They feed generally on flowers, nectar, fruits, gum, seeds, insects, and spiders. The proportion of animal prey varies seasonally, depending on availability, and comprises about one-fifth of the diet. During the period of extreme fat accumulation before the onset of hibernation,
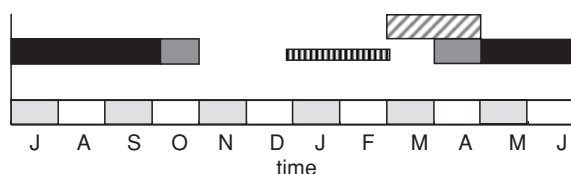

Figure 2. Seasonal temporal patterns in adult *Cheirogaleus medius* in Kirindy forest. *Black bars*: time of hibernation; *dark gray bars*: variability of immergence and emergence, and occurrence of daily torpor; *hatched bar*: prehibernation fattening period; *striped bar*: time of birth (variability between years).
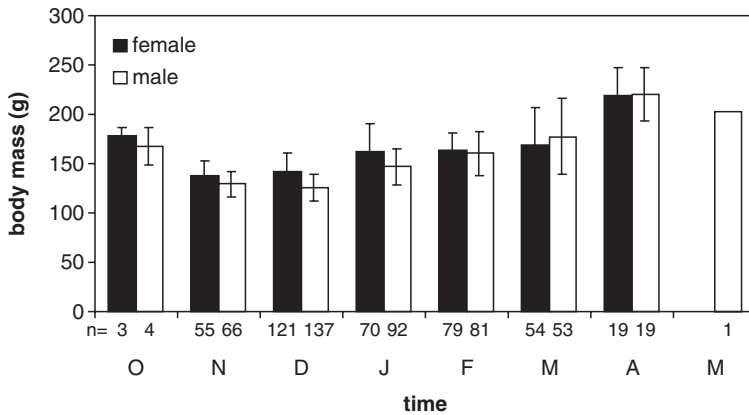
Figure 3. Seasonal variations of body mass in adult male and female *Cheirogaleus medius* of Kirindy forest. Given are mean and SD; data are pooled over the whole study period; body mass of each individual was included maximally once per month of a certain year.

berries with high sugar content are the staple food, and seem to be preferred to fruit items with low sugar content (Petter, 1978; Hladik et al., 1980; Petter-Rousseaux and Hladik, 1980; Fietz and Ganzhorn, 1999). In addition to seasonal variations in diet, the fat-tailed dwarf lemur also shows seasonal changes in loco-motor activity. After emergence from hibernation in November, nightly travel distances increase until February. Between February and April, which is shortly before the onset of hibernation (Figure 2), locomotor activity is extremely reduced and nightly travel distances are halved (Fietz and Ganzhorn, 1999). Thus, during the prehibernation fattening *C. medius* accumulate fat stores for winter by eating high-energy, sugary fruits, as well as by drastically reducing their locomotor activity.

In hibernating species, the quantity of fat stored before the onset of hibernation is believed to influence winter mortality, as only individuals with sufficient energy stores are able to survive (Geiser and Kenagy, 1993; Florant, 1998). Furthermore, body condition at emergence, which again is dependent on levels of prehibernation fat storage, was shown to critically influence fecundity and reproductive success in the following reproductive period in several hibernating species (Barnes, 1984; Kenagy, 1985; Kenagy and Barnes, 1988; Hackländer and Arnold, 1999; Millesi et al., 1999). In mammals, females generally incur higher reproductive costs than males, due to pregnancy and lactation (Clutton-Brock and Harvey, 1978; Clutton-Brock et al., 1989). Nevertheless, in species exhibiting male parental care, high reproductive costs should be anticipated for both sexes. This is the case for *C. medius*. Here not only do females incur considerable energetic costs through reproduction, but also males through infant care, resulting in reduced fat stores and body condition in both sexes in comparison to nonreproducing individuals before

the onset of hibernation (Fietz and Dausmann, 2003). The effects of such energy expenditure on winter survival and future fecundity are so far unknown. Nevertheless, in Kirindy forest *C. medius* exhibit a biannual fluctuation of reproduction, which is synchronized within the population (Fietz, 1999b). Factors causing such fluctuations remain speculative, but resource depletion during one reproductive year might reduce reproductive activity in the following year. This assumption fails to explain why nonreproductive years are synchronized on a population level, but higher survival rates of offspring due to density-dependent advantages are conceivable.

ECTOTHERMIC PATTERN OF BODY TEMPERATURE REGULATION DURING HIBERNATION

Besides reproduction another important energy expenditure in endotherms is the maintenance of their relatively high body temperature, especially when ambient temperature is low. Hibernation is the most powerful means for endotherms to reduce this cost (Heldmaier et al., 2004) and is therefore seen as an important adaptation to survive predictably unfavorable periods. It is usually defined by a controlled reduction of metabolic rate down to a fraction of the euthermic level, and a substantial decrease of body temperature down to the level of ambient temperature (Lyman et al., 1982; Heldmaier, 1989; Geiser and Ruf, 1995). Temperate animals, however, cannot enjoy several months of continuous hibernation, but must awaken regularly to experience phases of euthermic body temperature for one to several days. The function of these so-called arousals remains an unsolved mystery, but they are presumably necessary for the maintenance of vital body functions during hibernation with otherwise permanently low body temperature.

The tropical *C. medius* show a fascinatingly different thermal behavior during hibernation compared to that of their temperate counterparts. The hibernation phase of *C. medius* can be divided into 5 months of deep hibernation (May – September) and 2 months of transition (April and October; Figure 2). Before the entrance into deep hibernation, lemurs leave their tree holes occasionally, and therefore do not yet have to rely exclusively on their endogenous fat reserves during this time. During the coldest hours of the night, they employ short bouts of torpor, which means that their body temperature drops to almost ambient values for some hours during the early morning, but reaches euthermic levels again the next night (Dausmann et al., 2005). Combined with their decreased locomotor activity, this allows them additional fat storage during the last weeks before hibernation. From May onward, the adult animals retreat into tree holes and engage in continuous hibernation. Juveniles remain active for a few more weeks, but also suspend their activities by the end of May (Figure 2).

The pattern of body temperature and metabolic rate during hibernation in *C. medius* is astonishingly flexible for a mammal, and depends on the insulation capacities of the tree hole used during hibernation (hibernaculum). The lemurs

adjust their body temperature to the prevailing ambient temperature in the tree holes, and their thermal behavior resembles an ectothermic pattern, as observed in reptiles (Figure 4; Dausmann et al. 2004, 2005).

Whenever a tree hole has relatively thin walls or the sleeping chamber is very close to the entrance, the sleeping chamber is then poorly insulated against the strong daily fluctuations of ambient temperature. *C. medius* using these kinds of tree holes passively heat and cool during hibernation, closely tracking the daily fluctuations of ambient temperature with its diurnal increase and nocturnal fall. This results in strong daily fluctuations of body temperature of up to 20°C
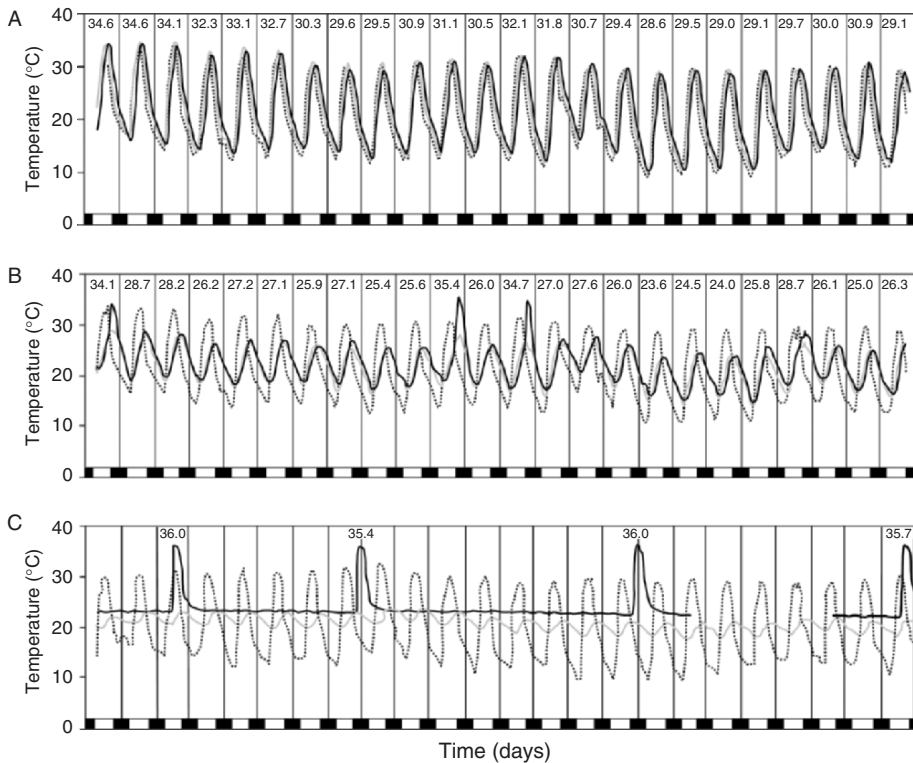

Figure 4. Patterns of body temperature during hibernation in *Cheirogaleus medius* (A) in a poorly insulated tree hole. Body temperature passively follows tree hole temperature in amplitude and slope and the lemur does not show arousals. (B) In a moderately insulated tree hole. Body temperature fluctuates with tree hole temperature, but is sometimes actively increased to euthermic levels. (C) In a well-insulated tree hole. Body temperature fluctuates little and the lemur shows regular arousals with euthermic body temperature. *Inserted numbers* give the daily maximum of body temperature (A, B) and the maximum body temperature during arousals (C). *Vertical lines* indicate midnight. *Black horizontal bars* show the dark phase. *Black line*: body temperature; *gray line*: tree hole temperature; *dotted line*: ambient temperature. Modified from Dausmann et al. (2004, 2005).

between about 10°C and 30°C (Figure 4A). Lemurs using these kinds of tree holes as hibernaculum do not interrupt hibernation by spontaneous arousals, as temperate hibernators have to, but show this pattern of passively fluctuating body temperature over many weeks or even months. However, the observations of predator attacks and other disturbances have proven that, contrary to reptiles, the ability for thermoregulation persists during hibernation. The lemurs are therefore at all times able to actuate the endogenous regulation of body temperature whenever they need to.

Some lemurs hibernate in large trees with thick walls, which provide better thermal insulation. Their body temperature fluctuates only by a few degrees (around 25°C), but contrary to the body temperature profile described above they exhibit regular arousals, similar to temperate hibernators (Figure 4C).

All transitions between completely passively fluctuating body temperature with high daily amplitude, and barely fluctuating body temperature with regular wake-up phases can occur during hibernation of *C. medius* (Figure 4B; Dausmann et al., 2004, 2005). Considering how meticulously body temperature is usually adjusted within a narrow range in mammals and birds, it is truly astounding how *C. medius* tolerate high daily fluctuations of body temperature and various patterns of thermoregulation, that can be changed from one day to the next.

ENERGY SAVINGS DURING TROPICAL HIBERNATION AMOUNTS TO 70%

The pattern of metabolic rate follows the pattern of body temperature. Therefore, as is the case for body temperature, the pattern of metabolic rate and the extent of its daily fluctuations are exogenously determined by the pattern of hibernaculum temperature and thus the properties of the tree hole used as hibernaculum. However, in lemurs that hibernate in well-insulated tree holes, the high costs of increased metabolic rate during the regular arousals seem to be balanced-out by an otherwise steady, relatively low metabolic rate. Surprisingly, therefore, the choice of hibernaculum seems to be of relatively little energetic relevance, despite the great implications with respect to the pattern of thermoregulation for the lemurs.

Due to the overall higher levels of body temperature in the tropical hibernator *C. medius*, mass specific metabolic rate is about tenfold higher than that of temperate hibernators, which hibernate at body temperature close to the freezing point. This corresponds to the finding that overall energetic savings of tropical hibernation do not reach the high levels of temperate hibernation (over 90%), but rather lie within the range of temperate daily torpor. Nevertheless, overall energetic savings of tropical hibernation in *C. medius* amounts to about 70% (Dausmann et al., submitted).

Temperate hibernators increase their body weight by about 40–50% before hibernation (Humphries et al., 2003), compared to about 90% in *C. medius* (Fietz

and Ganzhorn, 1999). Based on the measurement of metabolic rates, 0.77 g body lipids are consumed by *C. medius* on average per day during the hibernation period. Given 5 months of deep hibernation (à 30 days), this means that they should have at least 115.5 g lipid at their disposal during hibernation. This corresponds to the observed increase in body mass before hibernation of about 120 g. However, it also shows that the energy supply of *C. medius* is fairly limited, clearly restricting the extension of the hibernation phase (Dausmann et al., submitted).

Besides the amount of fat accumulated before hibernation, the composition of the fatty acids seems to be equally important to the hibernation ability and quality in temperate hibernators (Frank, 1991; Geiser, 1993). During the prehibernation fattening period, temperate hibernators selectively store polyunsaturated, essential fatty acids in their white adipose tissue (Armitage, 1979; Geiser and Kenagy, 1987). This is thought to represent an adaptation to low body temperature during hibernation (Frank, 1991; Geiser, 1993). Considering the relatively high and diurnally fluctuating body temperature of *C. medius* during tropical hibernation, polyunsaturated fatty acids would not be expected to play a key role under these conditions. Indeed, *C. medius* have an unusually low content (<3%) of essential fatty acids in their white adipose tissue compared to 35–45% found in temperate hibernators (Geiser and Kenagy, 1987) before the onset of hibernation (Fietz et al., 2003).

The changes in thermoregulation and energy expenditure compared to the activity period show that tropical hibernation in *C. medius* is an important, well-regulated adaptive response to survive the unfavorable dry season.

IS TROPICAL HIBERNATION AN ADAPTATION TO WATER SHORTAGE?

In temperate hibernators the occurrence of hibernation is interpreted as an adaptation to the combination of low ambient temperature and food scarcity. Accordingly, temperate hibernators show physiological and behavioral adaptations to low ambient and consequently low body temperature during hibernation like the fatty acid pattern of the fatty tissue or the location of their hibernacula. Due to climatic differences between temperate zones and the tropics, the intriguing question remains, which are the driving factors for the evolution of hibernation in a tropical species like *C. medius*? Is the occurrence of hibernation in *C. medius* ultimately an adaptation to food scarcity, or to water shortage? Water is definitely a scarce resource during the long dry season. It is therefore conceivable that *C. medius* does not only need its fat stores for energy reserves, but additionally for the extraction of metabolic water, especially as it does not hibernate in water-saturated burrows as do its temperate counterparts, but in tree holes with comparatively low humidity (Dausmann et al., 2005). This hypothesis is supported by the finding that the closely related mouse lemur (*Microcebus murinus*) saves notable amounts of water by entering daily torpor (Schmid and Speakman, 2000).

Therefore, tropical hibernation could possibly also be considered as a measure to cope with water shortage.

Ultimately, hibernation in *C. medius* is a successful adaptation to both food scarcity and water shortage, taking energetic advantage of the cool nighttime temperatures of the dry season.

HOW ARE BIOLOGICAL RHYTHMS INDUCED?

In many hibernators circannual cycles of reproductivity, body mass, and hibernation are known to be generated by an endogenous program either independently or synchronized by environmental cues such as photoperiod or ambient temperature (*Spermophilus lateralis*: Kenagy, 1980; *Eutamias* ssp.: Kenagy, 1981; *Marmota*: Davis and Finnie, 1975). Least chipmunks (*Eutamias minimus*), for example, have strong internal programming and emerge from hibernation with year-to-year precision, irrespective of environmental conditions (Kenagy, 1981). In other species, emergence dates correlate with changes in temperature of the air or soil, and snow cover (Michener, 1977; Bronson, 1980; Murie and Harris, 1982; Kenagy, 1985; French and Forand, 2000). In the tropical mouse lemurs (*Microcebus murinus*), the prehibernation fattening phase was found to be dependent on photoperiod (Genin and Perret, 2000). The occurrence of daily torpor, on the other hand, seems to be a rapid response to food restriction, whatever the photoperiod, but enhanced by short photoperiod and low ambient temperature (Genin and Perret, 2003).

In *C. medius*, circannual cycles of reproduction, body mass, and body temperature depend on the variations of the photoperiod (Pages and Petter-Rousseaux, 1980; Petter-Rousseaux, 1980). Day length is a very reliable cue for such predictable seasonal changes as occurring in Kirindy forest. Indeed, the mean dates of entrance into hibernation do not change greatly between the years, despite differences in the progression of the vegetation period and thus the availability of food resources, due to differences in amount and timing of precipitation during the rainy season (Table 1, Figure 1). Taking the last change of tree hole before hibernation as an indicator of when hibernation starts, the mean date varied only little more than a week between the years 1999 and 2001. Within one year, however, the range is much greater, with the first animals occupying their hibernation tree holes at the end of March, and the last at the end of May (Figure 2). The opposite pattern is true for birth dates. The population is highly synchronized within one year, with all females giving birth within a tight time frame of about 2 weeks. Between the years, however, variation is high, and birth may occur any time between December and February (Figure 2). The cause for such flexibility remains unknown, but climatic conditions or food availability after the emergence from hibernation when mating takes place seem plausible. Thus, these seasonal patterns seem to be flexible up to a certain degree within the individual, as well as on the population level.

OTHER CHEIROGALEIDS IN KIRINDY FOREST

Although hibernation and daily torpor occur in nearly all mammalian orders and all over the world (Lyman et al., 1982; Carey et al., 2003; Heldmaier et al., 2004), among primates the occurrence of torpid states is so far only known in cheirogaleids. It is interesting to see how the different Cheirogaleidae species of the Kirindy forest have evolved different ways to cope with the marked seasonality of their habitat. As shown above, *C. medius* is capable of prolonged hibernation over many months. *Microcebus berthae*, at 30 g the smallest known primate (Schmid and Kappeler, 1994), shows short bouts of metabolic depression over a few hours (daily torpor) during the cold nights of the dry season (Schmid et al., 2000). Presumably this species is too small to undergo prolonged hibernation, as body size limits the amount of body fat that can be accumulated to fuel hibernation. *Microcebus murinus* (60 g), the second species of the *Microcebus* genera in Kirindy forest, seems to show a mixed strategy of staying active, showing daily torpor or going into hibernation for several days, depending on ambient temperature, body weight, and sex (Schmid and Kappeler, 1998; Schmid, 1999). No physiological parameters are yet known of *Mirza coquereli* (300 g). But as this lemur is found curled up and cold to the touch in traps after cold nights of the dry season, there is no doubt that it is capable of showing torpid stages at least occasionally. *Phaner furcifer* (330 g), the last of the Cheirogaleidae family in the Kirindy forest, is found active throughout the night until dawn all year long (Hladik et al., 1980; Schülke and Kappeler, 2003); it is not assumed to show stages of hypometabolism. Indeed, this lemur has a very specialized diet, feeding mainly on tree exudates that are self-maintained, and is therefore largely independent of seasonal environmental changes.

All lemur species occurring sympatrically with *C. medius* on the west coast have to cope with the strong seasonality of their habitat. Even though hibernation seems to be a very elegant method to survive this period of scarcity, only *C. medius* exhibits obligate hibernation. Life history parameters such as body size and feeding ecology, as well as phylogenetic constraints, may explain the occurrence or absence of hibernation and daily torpor of the lemurs living in the dry deciduous forest of western Madagascar.

REFERENCES

Armitage, K. B. (1979). Food selectivity by yellow-bellied marmots. *Journal of Mammalogy* 60:628–629.

Barnes, B. M. (1984). Influence of energy stores on activation of reproductive function in male golden-mantled ground squirrels. *Journal of Comparative Physiology B* 154:421–425.

Bollen, A., Donati, G., Fietz, J., Schwab, D., Ramanamanjato, J.-B., Randrihasipara, L., Van Elsacker, L., and Ganzhorn, J. (2005). An intersite comparison on fruit characteristics in Madagascar: Evidence for selection pressure through abiotic constraints rather

than through co-evolution. In Dew, J., and Boubli, J. (eds.), *Fruits and Frugivores: The Search for Strong Interactors*. New York, Kluwer Academic Press, pp. 92–118.

Bronson, M. T. (1980). Altitudinal variation in emergence time in golden-mantled ground squirrels (*Spermophilus lateralis*). *Journal of Mammalogy* 61:124–126.

Carey, H. V., Andrews, M. T., and Martin, S. L. (2003). Mammalian hibernation: Cellular and molecular responses to depressed metabolism and low temperature. *Physiological Review* 83:1153–1181.

Clutton-Brock, T. H., and Harvey, P. H. (1978). Mammals, resources and reproductive strategies. *Nature* 273:191–195.

Clutton-Brock, T. H., Albon, S. D., and Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature* 337:260–262.

Dausmann, K. H., Glos, J., and Heldmaier, G. (submitted). Energetics of tropical hibernation.

Dausmann, K. H., Ganzhorn, J. U., and Heldmaier, G. (2000). Body temperature and metabolic rate of a hibernating primate in Madagascar: Preliminary results from the field study. In Heldmaier, G., and Klingenspor, M. (eds.), *Life in the Cold: Eleventh International Hibernation Symposium*. Heidelberg, Springer, pp. 41–47.

Dausmann, K. H., Glos, J., Ganzhorn, J. U., and Heldmaier, G. (2004). Hibernation in a tropical primate. *Nature* 429:825–826.

Dausmann, K. H., Glos, J., Ganzhorn, J. U., and Heldmaier, G. (2005). Hibernation in the tropics: Lessons from a primate. *Journal of Comparative Physiology B* 175:147–155.

Davis, W. L., and Finnie, E. P. (1975). Entrainment of circannual rhythm in weight of woodchucks. *Journal of Mammalogy* 56:199–203.

Fietz, J. (1999a). Monogamy as a rule rather than exception in nocturnal lemurs: The case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology* 105:259–272.

Fietz, J. (1999b). Demography and floating males in a population of *Cheirogaleus medius*. In Rakotosamimanana, B., Rasaminanana, H., and Ganzhorn, J. U. (eds.), *New Directions in Lemur Studies*. New York, Kluwer Academic/Plenum, pp. 159–172.

Fietz, J., and Dausmann, K. H. (2003). Costs and potential benefits of parental care in the nocturnal fat-tailed dwarf lemur (*Cheirogaleus medius*). *Folia Primatologica* 74:246–258.

Fietz, J., and Ganzhorn, J. U. (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: How does it get so fat? *Oecologia* 121:157–164.

Fietz, J., Zischler, H., Schwiegk, C., Tomiuk, J., Dausmann, K. H., and Ganzhorn, J. U. (2000). High rates of extra-pair young in the pair-living fat-tailed dwarf lemur, *Cheirogaleus medius*. *Behavioral Ecology and Sociobiology* 49:8–17.

Fietz, J., Tataruch, F., Dausmann, K. H., and Ganzhorn, J. U. (2003). White adipose tissue composition in the free-ranging fat-tailed dwarf lemur (*Cheirogaleus medius*; Primates), a tropical hibernator. *Journal of Comparative Physiology B* 173:1–10.

Florant, G. L. (1998). Lipid metabolism in hibernators: The importance of essential fatty acids. *American Zoologist* 38:331–340.

Frank, C. L. (1991). Adaptations for hibernation in the depot fats of a ground squirrel (*Spermophilus beldingi*). *Canadian Journal of Zoology* 69:2707–2711.

French, A. R., and Forand, S. (2000). Role of soil temperature in timing of emergence from hibernation in the jumping mouse, *Zapus hudsonius*. In Heldmaier, G., and Klingenspor, M. (eds.), *Life in the Cold: Eleventh International Hibernation Symposium*. Heidelberg, Springer, pp. 111–118.

Ganzhorn, J. U., and Sorg, J. P. (1996). Ecology and economy of a tropical dry forest in Madagascar. Primate Report 46-1, Göttingen.

Geiser, F. (1993). Dietary lipids and thermal physiology. In Carey, C., Florant, G. L., Wunder, B. A., and Horwitz, B. (eds.), *Life in the Cold: Ecological, Physiological and Molecular Mechanisms.* Boulder, Westview Press, pp. 141–153.

Geiser, F., and Kenagy, G. J. (1987). Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *American Journal of Physiology* 252:897–901.

Geiser, F., and Kenagy, G. J. (1993). Dietary fats and torpor patterns in hibernating ground squirrels. *Canadian Journal of Zoology* 71:1182–1185.

Geiser, F., and Ruf, T. (1995). Hibernation versus daily torpor in mammals and birds: Physiological variables and classification of torpor patterns. *Physiological Zoology* 68:935–966.

Genin, F., and Perret, M. (2000). Photoperiod-induced changes in energy balance in gray mouse lemurs. *Physiology and Behavior* 71:315–321.

Genin, F., and Perret, M. (2003). Daily hypothermia in captive grey mouse lemurs (*Microcebus murinus*): Effects of photoperiod and food restriction. *Journal of Comparative Physiology B* 136:71–81.

Hackländer, K., and Arnold, W. (1999). Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behavioral Ecology* 10:592–597.

Heldmaier, G. (1989). Seasonal acclimatization of energy requirements in mammals: Functional significance of body weight control, hypothermia, torpor and hibernation. In Wieser, W., and Gnaiger, E. (eds.), *Energy Transformations in Cells and Organisms.* Stuttgart, Thieme Verlag, pp. 130–139.

Heldmaier, G., Ortmann, S., and Elvert, R. (2004). Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory Physiology and Neurobiology* 141:317–329.

Hladik, C. M., Charles-Dominique, P., and Petter, J. J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J. J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour.* New York, Academic Press, pp. 41–73.

Humphries, M. M., Thomas, D. W., and Kramer, D. L. (2003). The role of energy availability in mammalian hibernation: A cost–benefit approach. *Physiological and Biochemical Zoology* 76:165–179.

Kenagy, G. J. (1980). Interrelation of endogenous annual rhythms of reproduction and hibernation in the golden-mantled ground squirrel. *Journal of Comparative Physiology* 135:333–339.

Kenagy, G. J. (1981). Effects of day length, temperature, and endogenous control on annual rhythms of reproduction and hibernation in chipmunks (*Eutamias* ssp.). *Journal of Comparative Physiology A* 141:369–378.

Kenagy, G. J. (1985). Seaonal reproduction patterns in five coexisting California desert rodent species. *Ecological Monographs* 55:371–397.

Kenagy, G. J., and Barnes, B. M. (1988). Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. *Journal of Mammalogy* 69:274–292.

Lyman, C. P., Willis, J. S., Malan, A., and Wang, L. C. H. (1982). *Hibernation and Torpor in Mammals and Birds.* London, Academic Press.

Michener, G. R. (1977). Effect of climatic conditions on the annual activity and hibernation cycle of the Richardson's ground squirrels and Columbian ground squirrels. *Canadian Journal of Zoology* 55:693–703.

Millesi, E., Huber, S., Everts, L. G., and Dittami, J. P. (1999). Reproductive decisions in female European ground squirrels: Factors affecting reproductive output and maternal investment. *Ethology* 105:163–175.

Müller, A. E. (1998). A preliminary report on the social organisation of *Cheirogaleus medius* (Cheirogaleidae; Primates) in north-west Madagascar. *Folia Primatologica* 69:160–166.

Müller, A. E. (1999). Social organization of the fat-tailed dwarf lemur (*Cheirogaleus medius*) in northwestern Madagascar. In Rakotosamimanana, B., Rasamimanana, H., Ganzhorn, J. U., and Goodman, S. M. (eds.), *New Directions in Lemur Studies*. New York, Kluwer Academic/Plenum, pp. 139–157.

Murie, J. O., and Harris, M. A. (1982). Annual variation of spring emergence and breeding in Columbian ground squirrels (*Spermophilus columbianus*). *Journal of Mammalogy* 63.

Pages, E., and Petter-Rousseaux, A. (1980). Annual variations in the circadian activity rhythms of five sympatric species of nocturnal prosimians in captivity. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J.-J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour*. New York, Academic Press, pp. 153–167.

Petter, J. J. (1978). Ecological and physiological adaptations of five sympatric nocturnal lemurs to seasonal variations in food production. In Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology*, Vol. 1. New York, Academic Press, pp. 211–223.

Petter, J. J., Albignac, R., and Rumpler, R. (1977). *Faune de Madagascar: Mammifères Lémuriens*. Paris, OSTOM CNRS.

Petter-Rousseaux, A. (1980). Seasonal activity rhythms, reproduction, and body weight variations in five sympatric nocturnal prosimians, simulated light and climatic conditions. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J.-J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour*. New York, Academic Press, pp. 137–152.

Petter-Rousseaux, A., and Hladik, C. M. (1980). A comparative study of food intake in five nocturnal prosimians in simulated climatic conditions. In Charles-Dominique, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, A., Petter, J.-J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology and Behaviour*. New York, Academic Press, pp. 169–179.

Schmid, J. (1999). Sex-specific differences in activity patterns and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. *Journal of Mammalogy* 80:749–757.

Schmid, J., and Kappeler, P. M. (1994). Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia Primatologica* 63:162–170.

Schmid, J., and Kappeler, P. M. (1998). Fluctuating sexual dimorphism and differential hibernation by sex in a primate, the gray mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology* 43:125–132.

Schmid, J., and Speakman, J. R. (2000). Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): A small primate that uses torpor. *Journal of Comparative Physiology B* 170:633–641.

Schmid, J., Ruf, T., and Heldmaier, G. (2000). Metabolism and temperature regulation during daily torpor in the smallest primate, the pygmy mouse lemur (*Microcebus myoxinus*) in Madagascar. *Journal of Comparative Physiology B* 170:59–68.

Schülke, O., and Kappeler, P. M. (2003). So near and yet so far: Territorial pairs but low cohesion between pair partners in a nocturnal lemur, *Phaner furcifer*. *Animal Behavior* 65:331–343.