

Chapter 2

Afrotropical Heterothermy: A Continuum of Possibilities

Kathrin H. Dausmann, Julia Nowack, Susanne Kobbe
and Nomakwezi Mzilikazi

Abstract The three closely related primate species *Cheirogaleus medius*, *Microcebus griseorufus*, and *Galago moholi* employ a spectrum of thermoregulatory responses to environmental bottlenecks. *C. medius* is an obligate hibernator, *M. griseorufus* shows extreme flexibility in patterns of heterothermy, ranging from daily torpor to prolonged torpor and hibernation, whereas *G. moholi* becomes heterothermic under extremely adverse conditions only. To gain further insights into the proximate and ultimate factors that favour and constrain torpor use in small primates, we compared the characteristics of *M. griseorufus*, *C. medius* and *G. moholi* as well as the prevailing ambient conditions where each of the species are found. Our analyses did not reveal any fundamental differences in the physiological parameters of heterothermy between the three species that would indicate different underlying physiological mechanisms. Instead we propose that the different modes of reproduction, connected to climatic differences, are the key ultimate causes of the differences in thermoregulatory strategies between the three species. We suggest that the common ancestor of the strepsirrhine primates was a heterothermic endotherm and that the ability to express daily torpor/hibernation is closely linked to ecological and evolutionary forces that favour and prioritise activities such as reproduction.

K. H. Dausmann (✉) · J. Nowack · S. Kobbe
Department of Animal Ecology and Conservation, Biocentre Grindel,
University of Hamburg, Martin-Luther-King-Platz 3,
20146 Hamburg, Germany
e-mail: kathrin.dausmann@uni-hamburg.de

N. Mzilikazi
Centre for African Conservation Ecology, Department of Zoology,
Nelson Mandela Metropolitan University, PO Box 77000,
Port Elizabeth 6031, South Africa

2.1 The Expression of Daily Torpor and Hibernation

The presence of heterothermy in unrelated mammalian groups has intrigued biologists, who have proposed two scenarios for the evolution of heterothermy: (1) the common ancestor of mammals was a heterothermic endotherm and subsequently many lineages lost the ability or propensity to express daily torpor/hibernation, or (2) heterothermy may have evolved repeatedly during the evolution of these lineages and are the result of convergent evolution. These opposing hypotheses are still under contention. For example, monotremes, the so-called primitive mammals, show evidence of ‘proto-endothermy’—i.e., heterothermy is present and endothermy is facultative (e.g., Nicol and Andersen 1996), a pattern also observed in tenrecs (Lovegrove and Génin 2008; Wein 2010). This could be evidence that heterothermy is a plesiomorphic trait. More support for this theory comes from a model proposing that heterothermy was the ancestral condition from which homeothermy derived (Lovegrove 2011) and a maximum likelihood approach reconstructing the probability of heterothermy of late Mesozoic mammals, indicating a single origin of heterothermy in mammals (Lovegrove 2012). Furthermore, expression of heterothermy is flexible: within a single species, some individuals can display daily torpor, whereas others display hibernation (Kobbe et al. 2011). Studies on the ontogeny of torpor support the idea that heterothermy evolved more than once; Geiser (2008) suggested that heterothermy may be a derived trait in placental mammals because in some organisms, such as shrews and hamsters, poikilothermy (i.e., lack of effective endogenous temperature regulation) at birth is followed first by a homeothermic phase and the ability to employ torpor develops later. This ontogenetic sequence may signal the order of evolutionary change provided that ‘ontogeny recapitulates phylogeny’. This argument, in fact, does not deny the possibility that heterothermy in endotherms has indeed evolved multiple times in several lineages (i.e., highly polyphyletic). Dietary habits and body mass correlate with the expression of torpor/hibernation in mammals (e.g., Geiser 1988). Although these factors cannot be viewed independently from phylogeny, these variables may provide a better explanation for the presence of heterothermy. Within the primates, most of what is known about heterothermic responses has been gained from studies on virtually a single family of Malagasy lemurs, the Cheirogaleidae (e.g., Dausmann et al. 2004; Kobbe and Dausmann 2009; Ortmann et al. 1997; Schmid et al. 2000) whose closest relatives (apart from Lorises) are the galagos from mainland Africa, to which they are comparable in terms of body size and life histories.

2.2 So Near Yet So Far

All habitats of the cheirogaleids in Madagascar, as well as of galagos in South Africa (Limpopo and Mpumalanga provinces), are characterised by seasonality and environmental unpredictability. Unpredictability results in periods of resource scarcity during the austral winter that are highly variable within and from year to year. Additionally, Madagascar forests have comparatively lower fruit production than

other tropical forests (Wright 1999). These circumstances pose great energetic constraints, especially to animals relying on highly seasonal high-energy food sources, e.g., small-bodied species with relatively high metabolic rates (MR). Given the relative geographical proximity of Madagascar and South Africa, as well the similarities relating to environmental unpredictability, it seems reasonable to expect comparable adaptations, such as the use of heterothermy, to similar environmental challenges. Admittedly, the geological history and biogeography of Madagascar, especially the long separation from the African mainland (~ 120 mya) may have led to a unique evolution of its mammals, creating an excellent natural experiment.

Currently, within the cheirogaleids heterothermy has been found in mouse lemurs (*Microcebus*), giant mouse lemurs (*Mirza*) and dwarf lemurs (*Cheirogaleus*) (Dausmann 2008; McKechnie and Mzilikazi 2011). A recent study has found torpor in a mainland primate, the African Lesser Bushbaby, *Galago moholi* (Nowack et al. 2010). Among these three closely related genera a spectrum of thermoregulatory responses is evident. *Cheirogaleus medius* is an obligate hibernator (Dausmann et al. 2004). *Microcebus griseorufus* shows extreme flexibility in patterns of heterothermy (Kobbe et al. 2011), whereas *G. moholi* utilises heterothermy under extreme conditions only (Nowack et al. 2010). Together these species provide an excellent opportunity for interrogating the proximate influences on the energy expenditure of small primates. It also raises the question of what the ultimate factors contributing to the reluctant use of torpor by *G. moholi* are. To gain further insights into the proximate and ultimate factors that favour and constrain torpor use in small primates, we compared the characteristics of *M. griseorufus*, *C. medius* and *G. moholi* as well as the prevailing ambient conditions where each of the species are found. The ultimate aim of this summary is to highlight similarities and the differences that have possibly led to the evolution of different thermoregulatory strategies in primates.

Throughout this summary, data were obtained from the literature and from three studies carried out by us over a time span between 3 and 6 years each. *C. medius* was studied in the forest of Kirindy C.F.P./Madagascar, *M. griseorufus* within Tsimanampetsotsa National Park/Madagascar and *G. moholi* in the Nylsvley Nature Reserve/South Africa. In the course of these studies demographic data were obtained by capture–recapture and individual marking. Behavioural data and data on food intake were recorded during nightly tracking of radio-collared individuals. Physiological measurements were performed using temperature-sensitive radio collars and loggers (skin temperature [T_{skin}], as a proxy of body temperature [T_b]), and portable gas analysers (measurement of MR as rate of oxygen consumption). For more detail see Dausmann et al. (2009), Kobbe et al. (2011), and Nowack et al. (2010).

2.3 Habitat and Life Histories

2.3.1 Taxonomy and General Species Description

All three species [*Galago* (Galagidae), *Microcebus* (Cheirogaleidae) and *Cheirogaleus* (Cheirogaleidae)] are strepsirrhine primates and very similar in their

morphological appearance, but belong to two different taxa: the lemuriformes, endemic to Madagascar, and the loriformes, found in Africa and Asia.

M. griseorufus is the smallest of the three species and it occurs in Southern Madagascar (Table 2.1). *G. moholi* occurs in Southern Africa and is slightly heavier than *C. medius* (Western Madagascar). All three species are nocturnal; *M. griseorufus* and *G. moholi* are vertical clingers and leapers, while *C. medius* is an arboreal quadruped.

2.3.2 Similar Habitats, Similar Diets

The habitats of all three species are distributed at comparable latitudes (around the Tropic of Capricorn) and share general habitat characteristics (Table 2.1). All three habitats are characterised by a marked dry season during the austral winter. The habitat of *M. griseorufus* is the most unpredictable of the three areas with an annual average rainfall of less than 500 mm (November–March) and years with almost no rainfall (Ratovonamana et al. submitted). The habitats of *C. medius* and *G. moholi* are less arid (Fig. 2.1); however, annual rainfall also varies highly in amount (from 300/400 mm to over 1,000 mm per year) and timing. Annual average rainfall is 700 mm in the habitat of *G. moholi* [Limpopo parks data (Nylsvley)]. The dry period is often only restricted to 3 or 4 months during mid-winter (Scholes and Walker 1993). Annual rainfall is higher (about 800 mm) for the habitat of *C. medius* (Fietz and Dausmann 2006), but the dry period is extended to 6 or 7 months per year (April–October).

Although the pattern of annual precipitation is most comparable for the habitats of *G. moholi* and *C. medius*, the biomes of *G. moholi* and *M. griseorufus* are more similar. While *C. medius* occurs in tropical dry forests regions, *G. moholi* and *M. griseorufus* inhabit savannah areas with thorny bushes and trees. Ambient temperature (T_a) also varies between the three habitats (Fig. 2.1) and the lowest temperatures are found in the habitat of *G. moholi*. During the hot-wet season T_a is fairly high during the day and seldom decreases below 15°C during the night, whereas night temperature during winter can reach −5°C (Nowack et al. 2010). Temperatures in South and Western Madagascar are about 10°C warmer during summer nights, but never decrease below 5°C during winter nights (Fietz and Dausmann 2006). Daily amplitudes between day and night are high in all three habitat types (*G. moholi* and *C. medius*: 2–35°C, *M. griseorufus*: 6–35°C).

The pronounced seasonality of all three habitats is not only reflected in a decrease in T_a and precipitation, but also in a decline in food and water availability during the dry season. The diet of *G. moholi* and *M. griseorufus* consists mainly of gum and small arthropods. *M. griseorufus* extends its food repertoire to fruits and nectar. Both species increase gum feeding during the winter months: insect and fruit abundances decrease noticeably in winter, whereas gum is available throughout the year (Bearder and Martin 1980; Génin 2008; Nowack et al. submitted). The diet of *C. medius* does not contain any gum, but consists of fruits, flowers, nectar, and a varying proportion of insects. *C. medius* feeds on sugary fruits before hibernation to build a sufficient fat reservoir to fuel energy demands during hibernation (Fietz and Dausmann 2006).

Table 2.1 Life history parameters for *G. moholi*, *M. griseorufus* and *C. medius*

	<i>G. moholi</i>		<i>M. griseorufus</i>	<i>C. medius</i>
Distribution	Southern Africa		South-western Madagascar	Western Madagascar
Habitat	Thornveld savannah		Spiny forest	Deciduous dry forest
Weight	~ 180 g		~ 50 g ^a	~ 150 g ^b
Sexual dimorphism in weight	Males heavier		Females heavier (before winter)	None ^b
Seasonal fattening	No		+ (Hibernation: 49–73 g, prolonged torpor: 47–53 g, daily torpor: 43–48 g, short torpor: 44–46 g)	++ (130–250 g) ^b
Body length	19 cm		15.5 cm ^c	20 cm
Diet	Gum, small arthropods ^{d,e}		Fruits, nectar, insects, small vertebrates, gum ^e	Insects, fruits, flowers, nectar ^b
Seasonal change in diet	Increases gum feeding during winter ^e		Increases gum feeding in winter by 33% of total foraging activity ^f	Eat sugary fruits before hibernation, no food during winter ^b
Gestation time	123 days ^g		52–60 days ^f	60–65 days ^b
Litter size	Mostly twins ^g		1–3, mostly twins ^f	Mostly twins ^b
Birth periods	January/February and September–November ^g		December and February/March ^f	December–February (every second year) ^h
Predation	Mongoose, genets, birds of prey (owls, eagles), snakes ⁱ		Birds of prey (mainly owls), snakes, civets	Birds of prey (owls, hawks), snakes, civets ^b
Estimated average field life span	3–5 years		3–5 years	5–7 years (up to over 12)

^a Kobbe et al. (2011)

^b Fietz and Dausmann (2006)

^c Rakotondranary et al. (2011)

^d Bearder and Martin (1980)

^e Nowack et al. submitted

^f Génin (2008)

^g Pullen et al. (2000)

^h Fietz and Dausmann (2003)

ⁱ Mzilikazi et al. (2006)

Data not cited is unpublished data by the authors

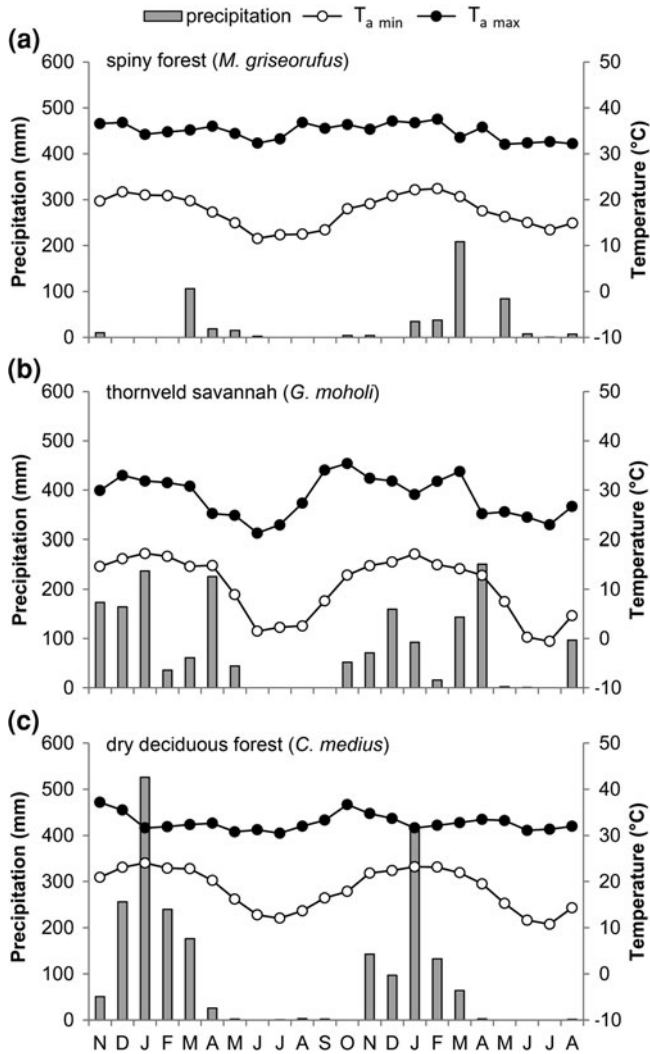


Fig. 2.1 Seasonal variation of ambient temperature (T_a) and precipitation of **a** the spiny forest in South-Western Madagascar 2007–2009 (habitat of *M. griseorufus*), **b** the Thornveld Savannah in South Africa 2009–2011 (habitat of *G. moholi*) and **c** the deciduous dry forest in Western Madagascar 1999–2001 (habitat of *C. medius*) (modified from Fietz and Dausmann 2006)

2.3.3 Social System and Territoriality

G. moholi and *M. griseorufus* have a similar social organisation. They forage solitarily during the night, but females are seldom found nesting solitarily during daytime. They rest in family groups (one or more female and their current offspring, in *G. moholi* sometimes accompanied by the assumptive father) or pairs

(Génin 2008; Nowack et al. submitted). However, in *G. moholi* some (probably subdominant) males are frequently found resting solitarily. In contrast, *C. medius* forms lifelong pair bonds (social monogamy). The pair defends a lifelong territory and usually shares a resting site during daytime; however, they are also solitary foragers and often hibernate separately (Dausmann et al. 2005).

All three species are territorial, but whereas *G. moholi* has been observed to maintain its territorial boundaries throughout the year (Nowack et al. 2010), territoriality of *C. medius* is restricted to the wet season and abandoned during the cold-dry season, when the animals become heterothermic. In *M. griseorufus* we can observe solitary males and females with overlapping home ranges as well as individuals sharing sleeping sites and home ranges (socio-territoriality; Génin 2010).

Reproductive patterns vary markedly between the three species (Table 2.1). *C. medius* usually reproduce only every second year (Fietz and Dausmann 2003) and give birth to twins after a gestation time of 60–65 days, which is only slightly longer than that of the almost three times smaller *M. griseorufus* (52–60 days) (Fietz and Dausmann 2006; Génin 2008). In the first 2 weeks after birth, both parents share babysitting duties; later, the parents guide the young during foraging (Fietz and Dausmann 2003). *M. griseorufus* and *G. moholi* have two reproductive periods per year, also usually giving birth to twins. Due to the relatively short gestation time, both birth periods of *M. griseorufus* occur during the hot-wet season. Parental care rests solely with the females, and young are independent after a few weeks. Within socio-territorial female pairs, alloparental care is a common phenomenon due to overlapping lactation periods (Génin 2008). Gestation time of *G. moholi* is about twice as long (123 days) and females give birth once shortly before the dry and cold winter time and once shortly after winter (Pullen et al. 2000). The young are weaned after few weeks and infants seldom have any contact with adult individuals other than the mother (Bearder 1969).

2.3.4 Predation and Mortality Rates

Various predators are described for each species (Table 2.1). Mortality rates of *C. medius* differ with habitat, but lie between 16 and 30% within the dry deciduous forest (Lahann and Dausmann 2011). Mortality rates are not known for *M. griseorufus* and *G. moholi*, but life spans in the wild are presumably considerably shorter than for *C. medius*.

2.4 Energy-Saving Responses: Three Species—Three Strategies

Heterothermy is utilised in all three species in order to cope with unfavourable conditions [during the southern winter or cold-dry season, respectively (i.e. between April and October)], however, in very different extent and variation (Table 2.2).

2.4.1 Differences in Energy-Saving Strategies

Most strikingly, there are great differences in the percentage of the population that becomes heterothermic. While 100% of *C. medius* and *M. griseorufus* employ heterothermy throughout (*C. medius*) or at some point (*M. griseorufus*) during winter, barely a fourth of the population of *G. moholi* becomes heterothermic at all (Nowack et al. 2010, unpublished data). Thus, between these three species we observe a continuum of different heterothermic responses: while *C. medius* is an obligate hibernator with all individuals hibernating throughout the dry season between mid-April and mid-October (Dausmann et al. 2004), *M. griseorufus* is physiologically more flexible (Kobbe et al. 2011). A part of the population of *M. griseorufus* stays normothermic most of the winter time and shows only spontaneous short torpor bouts whenever it seems necessary. However, most individuals use daily torpor and some individuals additionally enter prolonged torpor bouts for up to several days. The most extensive heterothermic behaviour we observe in this species is long-term hibernation. Similar to *C. medius*, hibernating individuals of *M. griseorufus* remain completely inactive up to 6 months during the dry season. *G. moholi* is also capable of heterothermy, however, in contrast to *M. griseorufus* and *C. medius* individuals exclusively use short torpor bouts on especially adverse conditions and not as a routine behaviour (Nowack et al. 2010). *M. griseorufus* and *C. medius* use tree holes for torpor and hibernation and the same is assumed, but yet needs to be ascertained, for *G. moholi*.

2.4.2 Influence of Body Mass, Sex and Age on Energy-Saving Strategies

In *C. medius* all individuals hibernate throughout the dry season regardless of their age, body mass or sex. Even juveniles display hibernation although they seem to be active longer than adults (Dausmann et al. 2005). Prior to hibernation *C. medius* accumulates large quantities of fat in the tail and on the body in order to survive many months without food intake (Fietz and Dausmann 2006). This seasonal body fattening also occurs in *M. griseorufus*, but in varying extent between individuals. Thermal behaviour utilised by *M. griseorufus* strongly depends on the individual's body condition before winter. Only the heaviest individuals hibernate up to several months. Individuals without sufficient fat stores occasionally use short torpor bouts and animals with intermediate body masses display daily torpor or prolonged torpor (Kobbe and Dausmann, unpublished data). In contrast to another mouse lemur species (*M. murinus*; Schmid 1999), *M. griseorufus* does not show any sex-specific differences in heterothermy (Kobbe et al. 2011). Compared to the cheirogaleids the thermal behaviour of *G. moholi* differs in so far as the exhibition of heterothermy does not seem to depend on body mass primarily but rather on the individuals' age and/or sex. Only subadults and juveniles, and mainly males use torpor during winter (Nowack et al. 2010, unpublished data).

Table 2.2 Heterothermic parameters for *G. moholi*, *M. griseorufus* and *C. medius* (N gives number of individuals, n number of days)

Heterothermy	<i>G. moholi</i>		<i>M. griseorufus</i>		<i>C. medius</i>	
	Torpor under especially adverse conditions ^a		Short, daily or prolonged torpor hibernation ^b		Obligate hibernation ^c	
% of heterothermic individuals during winter	26 (N = 8)		100 (N = 16) ^b		100 (N = 66) ^d	
Sex-specific heterothermy?	Mostly males		No ^b		No ^d	
Differences in age of heterothermic animals?	Subadult/juvenile ^a		Unknown, probably yes due to lower body mass in juveniles		Juveniles shortened hibernation period ^e	
Occurrence of heterothermy	April–end of August		April–November ^b		Adults: Mid-April to Mid-October; juveniles might be active until end of May ^e	
Absolute $T_{\text{skin min}}$ during torpor/hibernation (°C)	13.7		Short torpor: 10.5, daily torpor: 7.5, prolonged torpor: 7, hibernation: 6.5 ^b		9.3 ^d	
Mean $T_{\text{skin min}}$ during torpor/hibernation (°C)	21.2 ± 5 (N = 8)		16.42 ± 1.63 (N = 16) ^b		18.2 ± 2.8 (N = 30) ^e	
Mean TMR _{min} (ml O ₂ h ⁻¹ g ⁻¹)	0.3 ± 0.2 (N = 4)		0.13 ± 0.05 (N = 4)		0.14 ± 0.058 (N = 11) ^e	
Mean TMR ($T_{\text{skin}} < 30^{\circ}\text{C}$)	0.6 ± 0.2 (N = 4)		0.28 ± 0.16 (N = 4)		0.29 ± 23.2 (N = 11) ^e	

(continued)

Table 2.2 (continued)

	<i>G. moholi</i>	<i>M. griseonifus</i>	<i>C. medius</i>
Mean duration of torpor bouts/hibernation bout ^g	5.5 ± 3 h (<i>N</i> = 6, <i>n</i> = 6)	Short torpor: 5.6 ± 2.3 h (<i>N</i> = 4, <i>n</i> = 147) ^f Daily torpor: 8.7 ± 1.5 h (<i>N</i> = 5, <i>n</i> = 504) ^f Prolonged torpor: ~43.8 ± 19.9 h (<i>N</i> = 4, <i>n</i> = 6) ^f Hibernation: 12.3 ± 1.3 days (<i>N</i> = 3, <i>n</i> = 17) ^f Torpor: 29–80 (between May and October) Hibernation: 100 ^b ~80	6.7 ± 3.9 days (<i>N</i> = 5, <i>n</i> = 14) ^e
Frequency of torpor during winter (%)	Seldom ^a		Hibernation: 100 ^d
Daily energy savings through heterothermy (<i>T</i> _{skin} < 30°C) (%)	~66		~72 ^c

^a Nowack et al. (2010)
^b Kobbe et al. (2011)
^c Dausmann et al. (2009)
^d Dausmann et al. (2004)
^e Dausmann et al. (2005)
^f Kobbe and Dausmann (2009)
^g Between arousal

Data not cited in unpublished data by the authors

2.4.3 Physiological Characteristics of Heterothermy

2.4.3.1 Hibernation Bout Duration

The duration of torpor bouts are most extensive in those species and individuals that undergo hibernation. The longest hibernation bout (>70 days) without any active heat production was observed in *C. medius* (after that the logger stopped recording; Dausmann et al. 2005). The second longest bouts (45 days) were observed in hibernating individuals of *M. griseorufus* (Kobbe and Dausmann 2009). However, the average hibernation bout length of *M. griseorufus* was 12 days, and was thus twice as long as in *C. medius* with 6 days (Table 2.2). We attribute these differences to variations in insulation capacities of the tree holes used as hibernacula. While *M. griseorufus* uses only comparatively thin-walled poorly insulated tree holes, resulting in fluctuating T_a and T_b , and reducing the need of arousals, *C. medius* additionally uses thick-walled, well-insulated tree holes, necessitating regular arousals, thus decreasing the average value.

2.4.3.2 Torpor Bout Duration

The average duration of daily torpor bouts was longer in *M. griseorufus* than in *G. moholi*. However, in both species torpor bouts can range between 2 and 11 h (Table 2.2). As mentioned above the duration of torpor in *M. griseorufus* is strongly correlated to the body condition of the individual and T_a . *G. moholi* also undergoes torpid states only during the cold and dry season (from April to end of August) when food abundance and T_a are low, but heterothermy appears to be neither physiologically necessary nor possible for all individuals. Food-deprived juvenile and subadult individuals always entered torpor during the cold-dry season, but never during the hot-wet season. The length of torpor bouts seems to depend mainly on T_a (Nowack et al. 2010, unpublished data). *C. medius* only show daily torpor at the beginning of the hibernation season, so-called test drops (Dausmann et al. 2005). Prolonged torpor occurs only in *M. griseorufus* and only on occasions, where T_a decreases below a certain threshold (<9°C, Kobbe et al. 2011). Only individuals that have enough fat reserves to sustain the additional energetic demands before resuming delayed food intake can utilise this option.

2.4.3.3 General Patterns of Body Temperature

All three species show the regular pattern of T_b of small mammals during normothermia: T_b fluctuates around 37°C, with slightly lower values during the day, when the animals are resting (Dausmann et al. 2005; Kobbe et al. 2011; Mzilikazi et al. 2006).

General patterns of T_b in heterothermic individuals are also similar among the three species: T_b passively follows T_a for most of the heterothermic phase, and thus

T_b mainly depends on T_a and the insulation capacities of the resting place. Due to the differences in energy-saving strategies and environmental conditions (i.e. T_a) minimal T_{skin} ($T_{\text{skin min}}$) during heterothermy shows a significant variation among the species. In *M. griseorufus*, $T_{\text{skin min}}$ values seem to be strongly associated with the length of the heterothermic period. Both mean and absolute $T_{\text{skin min}}$ are lowest in hibernating *M. griseorufus* (6°C) and highest in individuals that enter short torpor bouts (absolute $T_{\text{skin min}}$ 10.5°C) (Kobbe and Dausmann 2009; Kobbe et al. 2011). $T_{\text{skin min}}$ of hibernating *C. medius* has been found to decrease down to 9.3°C (Dausmann et al. 2005; Table 2.2). The highest mean and absolute $T_{\text{skin min}}$ during heterothermy occur in *G. moholi*, where T_{skin} rarely decreases below 18°C (Nowack unpublished data). In cases where it did decrease below this value (two juveniles under laboratory conditions), the individuals had substantial difficulties rewarming from torpor.

2.4.3.4 Metabolic Rate

We were able to measure the MR of heterothermic individuals (torpid MR: TMR): of hibernating *C. medius* (Dausmann et al. 2009), torpid (but not hibernating) *M. griseorufus* and torpid *G. moholi*. The energy consumption of hibernating *C. medius* and torpid *M. griseorufus* are comparable (Table 2.2). This is due to the relatively low T_b during torpor bouts that occur in *M. griseorufus*. In contrast, *G. moholi* expends more than twice as much energy as the two cheirogaleid species during heterothermy, as anticipated from the higher minimal T_b during torpor.

In order to compare the potential of energy savings by heterothermy between all three species we compared average TMR to average MR during normothermia. In all three species heterothermic individuals utilise about 70% (between 66 and 80%) less energy per hour than normothermic animals (Table 2.2). Total energy savings depend not only on TMR but decisively also on the duration of the heterothermic period, i.e. on the particular thermal strategy. Thus we find a great variation of total energy savings by heterothermy among species and/or individuals with hibernating *C. medius* and *M. griseorufus* saving most and *M. griseorufus* and *G. moholi* with short torpor bout saving least.

2.5 Résumé

Our analyses did not reveal any fundamental differences in the physiological parameters of heterothermy between the three species that would indicate different basic physiological mechanism. Rather, patterns of T_b and MR during heterothermic phases, as well as length and depth of these, seem to follow general rules in all three species, depending on environmental variables, such as T_a , and individual variables, such as body condition, sex and age.

In our opinion, the finding that galagos and lemurs employ the same basic physiological mechanisms when using heterothermy suggests that the common

ancestor of these two groups was also heterothermic. Particularly since galagos only use this energy-saving mechanism sporadically it seems unlikely that they also evolved this capability convergently. Rather: they ‘still’ possess the ability, but only resort to it under exceptional circumstances. A plesiomorphic origin of heterothermy in mammals has also been suggested by Lovegrove (2011, 2012).

Environmental variables of the different habitats also did not show any substantial differences, the most important one being marked differences in the degree of unpredictability of rainfall. While the habitat of *C. medius* is highly seasonal, this seasonality, including food and water availability, is very predictable. The climate of the habitat of *M. griseorufus*, though showing the same seasonality, has much less precipitation, which additionally occurs very unpredictably within and between years, and can be totally skipped in some years. The habitat of *G. moholi* is less seasonal, rainfall being distributed more evenly over the year in amount and timing.

The most striking difference between *G. moholi*, *M. griseorufus* and *C. medius* is their differing reproductive strategies. Reproduction is a large component of energy budgets. In evolutionary terms, the ultimate goal of any animal should be the maximisation of its proportion of genes in the next generation. This can either be achieved by producing more offspring in a short period, or by reducing fecundity, but reproducing over a longer period. We propose that the different modes of reproduction, connected to climatic differences, are the key to the ultimate causes of the differences in thermoregulatory strategies between the three species. In the dry forest, rainfall is seasonal, but very predictable. Thus, *C. medius* can prepare for a defined period of scarcity when food is reliably abundant and hibernate during winter, reliably encountering food and water during the summer months, enabling itself and its offspring seasonal fattening before, and replenishment after hibernation. Frequent reproduction is not an option for *C. medius*, possibly because of the extensive and time-intensive parental care of both parents that is needed for the successful upbringing of offspring (Fietz and Dausmann 2003). Hibernating animals generally have a higher annual survival (Turbill et al. 2011) and *C. medius* may therefore use this energy-saving strategy during the lean dry season that cannot be used for reproduction anyway, to compensate less frequent reproduction events by a longer life. Other cheirogaleids in the dry forest are either smaller, and thus may not be able to store sufficient amounts of fat to make 7 months long hibernation an option (Dausmann 2008); or they are able to exploit a more exclusive or less seasonal spectrum of food: *Mirza coquereli* includes animal prey in its diet, and *Phaner furcifer* mainly feeds on tree exudates, both of which are available throughout the year.

G. moholi, on the other hand, lives in a less seasonal habitat and can successfully raise young throughout the year and thus reproduce more often, an option not available to *C. medius*. They, therefore, largely forgo the advantages of heterothermy in favour of reproduction possibilities, except in rare events. We assume that the physiological potential of entering energy-saving heterothermic states is only tapped by individuals that are unable to participate in reproduction at that point, e.g. young males without a territory. Females can already become pregnant at the age of 6 months, and due to their long gestation period, they are either

pregnant or lactating most of the year. Since both activities are seriously impaired by heterothermy (e.g., Farmer 2000; Wilde et al. 1999), this would explain why females are rarely encountered torpid. Adult males, on the other hand, presumably cannot afford to spend time in a ‘suspended’ state at any time of the year, neglecting territory defence (Nowack et al. 2010) and possibly mate guarding.

M. griseorufus inhabits the most unpredictable habitat and is the most flexible of the three species. Hibernation seems to be the preferred strategy for these animals, but can only be adopted by individuals whose body condition (fat stores) is sufficient to fuel long-term hibernation over several months with uncertain conditions when resuming activity. When hibernation is not possible, *M. griseorufus* can employ daily torpor or prolonged torpor, ‘deciding’ on a day-to-day basis, depending on their own current body condition and current ambient conditions. With this very flexible opportunistic strategy, they can brave the unpredictability of their habitat and are best equipped to adjust quickly to changing conditions.

In conclusion, the thermoregulatory physiology of *C. medius*, *M. griseorufus* and *G. moholi* is tightly adapted to the environmental conditions of the habitats, where the species evolved, in combination with reproductive possibilities, highlighting how flexibly physiological traits can be expressed.

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