

## **Heterothermy in Afrotropical mammals and birds: a review**

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## Abstract

Recent years have seen a rapid increase in the number of Afrotropical endotherms known to avoid mismatches between energy supply and demand by using daily torpor and/or hibernation. Among mammals, heterothermy has been reported in 40 species in six orders, namely Macroscelidea, Afrosoricida, Rodentia, Eulipotyphla, Primates and Chiroptera. These species span a range in body mass of 7 – 770 g, with minimum heterothermic body temperatures ranging from 1 - 27°C and bout length varying from 1 hour to 70 days. Daily torpor is the most common form of heterothermy, with true hibernation being observed in only seven species, *Graphiurus murinus*, *G. ocularis*, *Atelerix frontalis*, *Cheirogaleus medius*, *C. major*, *Microcebus murinus* and *M. griseorufus*. The traditional distinction between daily torpor and heterothermy is blurred in some species, with free-ranging individuals exhibiting bouts of > 24 hrs and body temperatures < 16°C, but none of the classical behaviours associated with hibernation. Several species bask in the sun during rewarming. Among birds, heterothermy has been reported in 16 species in seven orders, and is more pronounced in phylogenetically older taxa. Both in mammals and birds, patterns of heterothermy can vary dramatically among species occurring at a particular site, and even among individuals of a single species. For instance, patterns of heterothermy among cheirogalid primates in western Madagascar vary from daily torpor to uninterrupted hibernation for up to seven months. Other examples of variation among closely-related species involve small owls, elephant shrews and vespertilionid bats. There may also be variation in terms of the ecological correlates of torpor within a species, as is the case in the Freckled Nightjar *Caprimulgus tristigma*.

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## **Introduction**

Heterothermic responses, consisting of facultative, reversible decreases in metabolic rate and body temperature in response to environmental cues such as low temperatures and reduced availability of energy, are widespread among endotherms. By decreasing their body temperature ( $T_b$ ) below normothermic values and temporarily defending much lower setpoints, endotherms can reduce their requirements for energy and water to small fractions of what they would otherwise be. In temperate and boreal latitudes, heterothermic responses are most pronounced during long, severe winters, when low environmental temperatures are usually combined with reduced availability of food (Lyman et al. 1982; Geiser and Ruf 1995). However, heterothermic responses are also widespread among endotherms inhabiting tropical and sub-tropical latitudes, particularly in arid environments and in species whose food resources show large spatial and temporal variation (Geiser and Ruf 1995; Lovegrove 2000; McKechnie and Lovegrove 2002).

In addition to being of profound ecological significance, patterns of heterothermy provide insights into the evolution of endothermy. Malan (1996) and others have raised the possibility that patterns of metabolic rate and  $T_b$  seen in extant heterotherms may echo a pattern of thermoregulation intermediate between ancestral ectothermy and endothermic homeothermy. More recently, Lovegrove (in press) proposed the Plesiomorphic-Apomorphic Endothermy (PAE) model, with the central tenet being that rigid endothermic homeothermy represents an apomorphic state derived from a plesiomorphic state of heterothermic thermoregulation, akin to that observed in several phylogenetically ancient mammalian lineages.

Recent decades have seen a rapid increase in the number and phylogenetic diversity of endotherms known to use heterothermy. At the same time, researchers have gained remarkable insights into the ways in which free-ranging endotherms in natural environments

use heterothermy, thanks in large part to advances in telemetry and data-logging. A proliferation of laboratory-based and field-based studies has revealed that heterothermy is a key component of thermoregulation in all three extant mammalian infraclasses (Lyman et al. 1982; Geiser 1994; Nicol et al. 2008), as well as in birds ranging in size from < 3 g in hummingbirds to 6.5 kg in vultures (Carpenter 1974; Bahat et al. 1998). Researchers have also made significant progress in examining interspecific and intraspecific variation in patterns of heterothermy (e.g., Schmid 2001; Dausmann et al. 2005; Dausmann 2008; Schmid and Ganzhorn 2009) and testing hypotheses regarding ecological determinants of heterothermy via experimental manipulations of the food availability experienced by free-ranging populations (Woods and Brigham 2004; Munro et al. 2005).

The Afrotropical zoogeographical zone consists of Sub-Saharan Africa plus surrounding islands, of which Madagascar is by far the largest and most significant in terms of diversity of endotherms. This region is noteworthy for a number of taxa, including the morphologically and ecologically diverse mammalian superorder Afrotheria, thought to be basal in the eutherian phylogeny (Springer et al. 1997; Robinson and Seiffert 2004). Other endemic groups include the Myzopodidae (a family of bats endemic to Madagascar), two avian orders in Africa (Coliiformes and Musophagiformes) and several avian families in Madagascar (e.g., Mesitornithidae, Brachypteraciidae and Leptosomatidae). The Afrotropical zone is also characterized by a diverse range of climates and habitats, ranging from the hyperarid Namib Desert to the vast lowland rainforests of the Congo Basin. Like the Australasian and Indomalayan zones, large parts of the Afrotropics experience periodic negative anomalies in rainfall associated with the El Niño Southern Oscillation (Stone et al. 1996). The presence of phylogenetically ancient eutherian taxa such as the Afrotheria, together with diverse climates, habitats and strong gradients in climatic variables such as rainfall, collectively make the Afrotropics a region of considerable importance to

physiologists interested in the ecology and evolution of heterothermy in endotherms. In this paper, we review heterothermy in Afrotropical mammals and birds.

## **Data**

We surveyed the literature for studies investigating heterothermy in mammals or birds from the Afrotropics (Table 1). We included studies irrespective of the methods used to measure body temperature, and irrespective of whether animals were free-ranging or captive. This approach introduces two key sources of variation. First, skin temperature ( $T_{\text{skin}}$ ) usually differs from core body temperature ( $T_{\text{b}}$ ). In birds,  $T_{\text{b}}-T_{\text{skin}}$  gradients are typically  $< 4\text{ }^{\circ}\text{C}$  in species  $< 100\text{ g}$  (Brigham et al. 2000; McKechnie et al. 2007; Smit and McKechnie 2008), although they may be greater in larger species (Körtner et al. 2001). Similarly,  $T_{\text{b}}-T_{\text{skin}}$  gradients in Big Brown Bats (*Eptesicus fuscus*) were  $< 5\text{ }^{\circ}\text{C}$  (Willis and Brigham 2003), and  $T_{\text{skin}}$  measured with collars closely tracked core  $T_{\text{b}}$  in Fat-tailed Dwarf Lemurs (*Cheirogaleus medius*; Dausmann 2005). However,  $T_{\text{b}}-T_{\text{skin}}$  gradients are also dependent on air temperature ( $T_{\text{a}}$ ) (e.g., McKechnie et al. 2007; Smit and McKechnie 2010), and thus  $T_{\text{skin}}$  values may not be directly comparable among species, among individuals, or even within individuals. In this review, we combine  $T_{\text{b}}$  and  $T_{\text{skin}}$  data for analyses, but note that this introduces a degree of error. The second issue concerns the observation that heterothermy is generally more frequent and pronounced in free-ranging populations than in captive individuals (Geiser et al. 2000). In particular, minimum  $T_{\text{b}}$  or  $T_{\text{skin}}$  values from captive animals are likely to underestimate the corresponding values for free-ranging individuals in natural habitats (Geiser et al. 2000).

## **Phylogeny**

Heterothermy is widespread in Afrotropical mammals, with the region being second only to Australasia in terms of the number of mammalian species known to use daily torpor

(Lovegrove 2000). However, with the exception of a single study on *Gerbillus pusillus* from northern Kenya (Buffenstein 1985), the literature on mammalian heterothermy consists entirely of studies on taxa from southern Africa and Madagascar. Excluding bats, 34 species of Afrotropical mammals, representing five orders, have been shown to be heterothermic (Table 1). By far the greatest number of known mammalian heterotherms are within the endemic superorder Afrotheria, with representatives from the Macroscelidea, Chrysochloridae and Tenrecidae (Table 1).

Heterothermy is also common in the Malagasy cheirogaleid primates (Table 1). The Southern Lesser Galago (*Galago moholi*) is the only African mainland primate currently known to use torpor (Nowack et al. 2010). Within the rodents, three families have members that utilize heterothermy, namely Myoxidae, Muridae and Bathyergidae (Table 1). Daily torpor and hibernation also occur in the Eulipotyphla, specifically the Southern African Hedgehog (*Atelerix frontalis*; Hallam and Mzilikazi 2011) and the Greater Red Musk Shrew, (*Crocidura flavescens*; Baxter 1996).

Heterothermy has been investigated in only six species of bats representing three families, with deep torpor and/or hibernation ( $T_b < 15\text{ }^\circ\text{C}$ ) reported in two molossids and one vespertilionid. Only one nycterid, *Nycteris thebaica*, has been investigated to date, and was found to exhibit very limited heterothermy (minimum  $T_{\text{skin}} = 28\text{ }^\circ\text{C}$ ), despite roost temperatures as low as  $14\text{ }^\circ\text{C}$  (D. Cory Toussaint, A.E. McKechnie and R.M. Brigham, unpublished data). Overall, the occurrence of heterothermy in Afrotropical bats remains poorly explored.

Heterothermy has been reported in Afrotropical birds representing five orders, including the Afrotropical endemic Coliiformes (mousebirds). The phylogenetic distribution of avian heterothermy has typically been evaluated using higher-order relationships based on Sibley's and Ahlquist's (1990) DNA-DNA hybridization phylogeny (Geiser 1998;

McKechnie and Lovegrove 2002). However, a radically different avian phylogeny based on the phylogenomic approach was recently proposed (Hackett et al. 2008). In terms of avian heterothermy, the phylogeny of Hackett et al. (2008) is noteworthy in that three highly heterothermic groups, namely caprimulgids (Caprimulgidae, Eurostopodidae, Podargidae, Aegothelidae), hummingbirds (Trochilidae) and swifts (Apodidae), now cluster together within a single clade (Figure 1). This new arrangement resolves the puzzling observation that owls and caprimulgids, which Sibley and Ahlquist placed in a single order, are highly divergent in the extent to which they use heterothermy (Smit and McKechnie 2010). However, the owls' closest relatives in the Hackett et al. (2008) phylogeny are now the mousebirds, a placement that raises much the same question.

Previous analyses based on the Sibley and Ahlquist (1990) phylogeny supported the idea that avian heterothermy is a plesiomorphic trait (McKechnie and Lovegrove 2002), although the large body masses of the most ancient avian groups (e.g., ratites) made this conclusion difficult to verify (Geiser 1998). Rearranging ordinal relationships as per the Hackett et al. (2008) phylogeny strengthens the trend towards heterothermy being more pronounced in older clades, (most notably the caprimulgid/hummingbird/swift group) and less pronounced in more recently-diverged taxa (e.g., Falconidae, Passeriformes) (Figure 1).

Sunbirds (Passeriformes, Nectarinidae) appear to make much more limited use of heterothermy than do hummingbirds, despite considerable convergence in other physiological traits related to the processing of large quantities of dilute nectar (Martinez del Rio et al. 2001). The most thorough study of torpor in sunbirds to date found that Malachite Sunbirds (*Nectarinia famosa*) reduce  $T_b$  to 26.8 °C at  $T_a = 5$  °C (Downs and Brown 2002). However, patterns of metabolic rate and  $T_b$  in this species were inconsistent with typical torpor, in which  $T_b$  tracks  $T_a$  and metabolic rate decreases with  $T_a$  above some threshold, below which thermogenic defence of a  $T_b$  setpoint occurs. Instead, patterns of heterothermy in *N. famosa*

are more similar to those observed in other passerines, suggesting that sunbird “torpor” may in fact be a pronounced form of the shallow heterothermy more typical of this order (McKechnie and Lovegrove 2003).

### **Body mass**

Heterothermy has been investigated in Afrotropical mammals ranging in body mass ( $M_b$ ) from < 10 g to > 500 g (Figure 2). The smallest species in which heterothermy has been investigated include the Large-eared Tenrec (*Geogale aurita*; 6.7 g) as well as the smallest known primate, (*Microcebus myoxinus/berthae*; 30g). At the upper end of the  $M_b$  range, the Southern African Hedgehog is currently the largest known heterotherm. This species exhibits a summer  $M_b$  of ca. 350g and reaches a prehibernation  $M_b$  of ca. 770g. It also displays the lowest  $T_b$  (1.0°C) yet measured in Afrotropical mammals.

Afrotropical bat species in which heterothermy has been investigated vary in  $M_b$  from 10 g to approximately 30 g (Table 1), which represents a relatively small subset of the species that occur in the region. For instance, in the southern African subregion alone the range of  $M_b$  for bats is approximately 4 – 280 g (Skinner and Chimimba 2005). Although a recent study of *Nyctimene robinsoni*, a 50-g Australasian fruit bat, revealed no instances of  $T_b$  below 30 °C in free-ranging individuals (Riek et al. 2010), it is nevertheless possible that some of the larger Afrotropical frugivorous species use heterothermy.

Among Afrotropical birds, heterothermy has been reported in species ranging in mass from 7 g in the Lesser Double-collared Sunbird (*Cinnyris chalybea*; B. Leon and J.R.B. Lighton, unpublished data) to the 150-g African Collared Dove (*Streptopelia roseogrisea*; Walker et al. 1983) (Figure 2).  $T_{skin}$  values of 12.8 °C and 10.5 °C in Freckled Nightjars [*Caprimulgus tristigma granosus* (81 g) and *C. t. lentiginous* (73 g)] respectively represent



the first evidence of  $T_b < 15\text{ }^\circ\text{C}$  in avian species larger than 70 g (reviewed by McKechnie and Lovegrove 2002).

### **Thermoregulation during heterothermy**

Among endotherms in general,  $T_b$  during heterothermy varies from just below normothermic values to  $-2.9\text{ }^\circ\text{C}$  in a hibernating Arctic Ground Squirrel (*Spermophilus parryii*; Barnes 1989). Afrotropical endotherms cover most of this range (Table 1), with  $T_b$  ranging from the mid-30's during shallow avian heterothermy (e.g., Red-headed Finch *Amadina erythrocephala*) to  $1.0\text{ }^\circ\text{C}$  in the Southern African Hedgehog (Table 1, Figure 3). Avian minimum  $T_b$ s tend to be higher than those of mammals (Figure 3). Among mammals, it is noteworthy that very low  $T_b$ s similar to those associated with hibernators from temperate latitudes have been reported in a number of Afrotropical species. The shallow reductions in  $T_b$  that occur in many birds are much less common in mammals (Figure 3); at the upper end of the mammalian minimum  $T_b$  spectrum, *Neamblysomnus julianae* lowered its  $T_b$  to a minimum of just  $27^\circ\text{C}$  at an unspecified  $T_a$  in the summertime (Jackson et al. 2009). It is, however, likely that this species attains much lower  $T_b$ s during winter.

Patterns of thermoregulation during heterothermy vary widely across species, and in some cases blur the traditional distinction between daily torpor and hibernation. The latter distinction has largely been based on the duration of torpor, for which bouts lasting  $< 24$  hrs are considered daily torpor and those lasting  $> 24$  hrs, hibernation (Geiser and Ruf 1995). In laboratory settings, these responses tend to be clearly defined, with no species thus far exceeding a duration of 24 hrs for a single bout. Although a number of recent field studies have documented patterns of thermoregulation that clearly match classic hibernation, some spectacular examples of this distinction being blurred are provided by smaller members of the Afrotheria (Lovegrove et al. 2001; Mzilikazi et al. 2002; Mzilikazi and Lovegrove 2004;

Lovegrove and Génin 2008; Scantlebury et al. 2008). In the laboratory, elephant shrews show low  $T_b$ s that are consistent with hibernation, even though the durations of bouts do not exceed 24 hr (Lovegrove et al. 1999; Lovegrove et al. 2001). In the field, however, similarly low  $T_b$ s have been documented, but lengths of bouts occasionally exceed 24 hr and may be as long as 39 hr (Mzilikazi and Lovegrove 2004). Some Malagasy species exhibit patterns of thermoregulation that are even more difficult to classify as daily torpor or hibernation. For instance, Lesser Hedgehog Tenrecs (*Echinops telfairi*) clearly possess the ability to heat endogenously, but free-ranging individuals appeared not to adhere to typical endothermic homeothermy; instead, they were heterothermic for most of the time (bout duration of up to 4 days), interspersed with only brief periods of normothermy (Lovegrove and Génin 2008).

In the classic temperate-zone model of hibernation, heterothermy is interspersed with seemingly obligatory arousal periods during which animals return to normothermic  $T_b$ s for brief periods. However, hibernation in Malagasy mouse and dwarf lemurs challenges both the concept of hibernation being associated with low body temperatures and the obligatory nature of arousals during hibernation (Dausmann et al. 2005; Kobbe et al. 2011). The characteristics of the tree cavities in which the dwarf lemurs hibernate profoundly influence the pattern of hibernation, with well-insulated cavities in trees being associated with approximately constant body temperatures, interspersed with periods of normothermy (Dausmann et al. 2005). Body temperatures of lemurs in poorly insulated tree holes, on the other hand, fluctuated with environmental temperature cycles and as long as a  $T_b$  of 30°C was reached, arousals were unnecessary (Dausmann et al. 2005). The  $T_b$ s of hibernating *M. griseorufus* and *C. medius* passively reached 33.5 and 35.9°C, respectively, while the animals hibernated without arousal for up to 45 and 70 days respectively (Dausmann et al. 2005; Kobbe et al. 2011). These results strongly suggest that the attainment of a high  $T_b$  is a key

determinant of periodic arousals, and moreover that hibernation is not necessarily coupled with low  $T_b$ .

In other instances, species switch between different patterns of heterothermy over short time scales. Male Egyptian Free-tailed Bats (*Tadarida aegyptiaca*) roosting on buildings in Pretoria exhibited daily torpor during mild, sunny winter weather, rewarming to normothermy every evening (Cory Toussaint et al. 2010). However, the arrival of a cold front coincided with a switch to hibernation, with at least two individuals maintaining  $T_b < 20$  °C for 3-4 consecutive days (Cory Toussaint et al. 2010). Similarly, free-ranging Rock Elephant Shrews (*Elephantulus myurus*) routinely entered daily torpor during winter but could readily extend torpor to ca. 39 hr in spring when late cold fronts penetrate the interior of southern Africa (Mzilikazi and Lovegrove 2004).

Heterothermic thermoregulation in mousebirds (Coliiformes) differs from typical heterothermy characterized by an entry phase (rapid reduction in metabolic rate and  $T_b$  below normothermic levels), a maintenance phase (approximately constant  $T_b$ ) and an arousal phase (increase in metabolic rate and  $T_b$  back to normothermic levels) (Lyman et al. 1982). Instead, there is a small initial decrease in  $T_b$ , whereafter it gradually and approximately linearly declines over the entire rest-phase (McKechnie and Lovegrove 2001; McKechnie and Lovegrove 2001). Crucially, however, these patterns of cooling during rest-phase were only evident in single mousebirds not huddling with conspecifics; huddling individuals exhibited approximately constant rest-phase  $T_b$  under artificial as well as natural conditions (McKechnie and Lovegrove 2001; McKechnie et al. 2004; McKechnie et al. 2006). The mousebirds represent an intriguing case study of the interaction between physiological (i.e., heterothermy) and behavioural (i.e., huddling) mechanisms of energy conservation.

In some Afrotropical birds, heterothermic bouts appear to consist of decreases in  $T_b$ , followed immediately by rewarming, without the typical maintenance phase during which a

$T_b$  setpoint is maintained. Such “V”-shaped bouts have been found in a small species of owl, the African Scops-owl (Smit and McKechnie 2010), as well as in free-ranging White-backed Mousebirds (McKechnie et al. 2004).

### **The role of solar radiation**

The energetic benefits associated with heterothermy are relatively well understood, with the single largest constraint on energy savings being the cost of rewarming to normothermy (Wang 1978; Thomas et al. 1990; Holloway and Geiser 1995). Working on small Malagasy primates, Schmid (1996) published the first of what was to become a series of observations detailing the widespread use of exogenous heat sources by free-ranging animals during arousal from torpor (e.g., Schmid 2000; Geiser et al. 2002; Geiser and Drury 2003). In the Afrotropics, elephant shrews (Mzilikazi et al. 2002), tenrecs (Lovegrove and Génin 2008), and woodland dormice (N. Mzilikazi et al unpublished data), have all been shown to save energy by closely synchronizing their arousal times with the onset of increasing environmental temperatures, as well as by basking. However, there is no evidence that reliance on solar radiation for rewarming compromises the ability to rewarm using endogenous heat sources such as non-shivering thermogenesis (NST) (Mzilikazi and Lovegrove 2006; Jastroch et al. 2007; Scantlebury et al. 2008). In fact, elephant shrews display two distinct patterns of rewarming, the first characterized by slow rewarming rates closely synchronized with ambient temperature and similar to those associated with ectothermic exogenous heating. Their  $T_b$  only dissociates from ambient cycles once  $T_b \approx 25^\circ\text{C}$  has been attained, followed by a second, much faster endogenously-fuelled rewarming rate reminiscent of rewarming in temperate-zone heterotherms (Mzilikazi et al. 2002).

The influence of availability of solar radiation on patterns of heterothermy has received relatively little experimental attention, although Woods and Brigham (2004) found

that artificially shading hibernating Common Poorwills (*Phalaenoptilus nuttallii*) led to substantial differences in rewarming rates and in the frequency of rewarming. Rock Elephant Shrews maintained in outdoor enclosures exhibited more variable bouts of torpor, with overall reductions in depth and duration, as well as slower rewarming rates, when their access to solar radiation was artificially reduced (W. Matten, A.E. McKechnie and N.C. Bennett, unpublished data).

### **Interspecific and intraspecific variation**

The most comprehensive dataset on interspecific variation in heterothermy within a mammalian family in the Afrotropics, and probably globally, emanates from work by Schmid, Ortmann, Dausmann and colleagues at Forêt de Kirindy/CFPF in western Madagascar. At this site, torpor and/or hibernation has been documented in four species, with  $T_b$  minima below 10 °C in at least three, and considerable variation in patterns of heterothermy (reviewed by Dausmann 2008). For instance, Pygmy Mouse Lemurs (*Microcebus myoxinus*) at Forêt de Kirindy/CFPF use only daily torpor, with a mean duration of bouts of 9.6 hr (Schmid et al. 2000). In contrast, Fat-tailed Dwarf Lemurs (*Cheirogaleus medius*) at the same site hibernate continuously for up to 7 months (Dausmann et al. 2004; Dausmann et al. 2005).

In the Kalahari Desert of South Africa, thermoregulation differs substantially between two small (< 100 g) species of owl. Whereas pearl-spotted owlets (*Glaucidium perlatum*) remained normothermic throughout the winter, with  $T_{skin}$  never decreasing below 36.5 °C, African scops-owls (*Otus senegalensis*) at the same study site regularly exhibited shallow torpor, with minimum  $T_{skin} = 29.0$  °C in three individuals (Smit and McKechnie 2010). These authors argued that interspecific variation in thermoregulation reflected activity cycles and diet; pearl-spotted owlets often hunt diurnally and include relatively large vertebrate prey in

their diet, whereas African scops-owls are strictly nocturnal and feed almost exclusively on terrestrial arthropods.

A comparison of winter torpor in two syntopic elephant shrew species similarly revealed considerable interspecific differences. In the arid Namaqualand region of South Africa with winter-rainfall, Western Rock Elephant Shrews (*Elephantulus rupestris*) were highly heterothermic and made extensive use of torpor, but Cape Rock Elephant Shrews (*E. edwardii*) remained predominantly homeothermic and used torpor only occasionally (J.G. Boyles, B. Smit, C.L. Sole and A.E. McKechnie, unpublished data). In contrast, the syntopic vespertilionid bats *Scotophilus dingaani* and *S. mahlanganii* exhibited very similar patterns of heterothermy at a warm, mesic site in eastern South Africa (Jacobs et al. 2007). An individual of *S. mahlanganii* that roosted in tree foliage exhibited patterns of torpor that were virtually identical to those of *S. dingaani* that roosted in buildings, but different from another *S. mahlanganii* that roosted in a tree cavity (Jacobs et al. 2007).

Significant differences in the use of heterothermy have also been observed within a single population between years. Mzilikazi et al. (2006) investigated torpor in free-ranging Southern Lesser Galagos and recorded not a single incidence of heterothermy during the 18-month study period. However, Nowack et al. (2010) re-examined the same population and observed heterothermy in a few individuals during winter 2009. In Southern African Hedgehogs, lighter individuals use daily torpor, whereas heavier individuals utilize hibernation under the same semi-captive conditions (Hallam and Mzilikazi 2011). In free-ranging mouse lemurs (*Microcebus griseorufus* and *M. murinus*), considerable variation in patterns of heterothermy was observed, with some individuals using daily torpor exclusively, while others used hibernation to a larger extent (Schmid and Ganzhorn 2009; Kobbe et al. 2011). Scantlebury et al. (2008) measured  $T_b$  in only two Hottentot Golden Moles (*Amblysomus hottentotus longiceps*), yet observed considerable variation in the use of

hibernation, with virtually no heterothermy in one individual, but multi-day bouts in the other.

Large differences in patterns of heterothermy can also occur among populations within a species. Freckled Nightjars (*Caprimulgus tristigma granosus*) at a mesic site with summer rainfall in eastern South Africa used torpor frequently during winter, but the timing and depth of bouts was not correlated with lunar phase (McKechnie et al. 2007). In contrast, conspecifics (*C. t. lentiginous*) inhabiting an arid region with winter rainfall, torpor was strongly correlated with lunar cycles, with bouts becoming progressively deeper with the waning moon, minimum  $T_b$  occurring at about new moon, and bouts then becoming shallower with the waxing moon (Smit et al. in press). A tight correlation with lunar cycles was also observed on shorter time scales each night; entry into torpor approximately coincided with moonset and rewarming with moonrise (Smit et al. in press). Another example of intraspecific variation in heterothermy concerns Fat-tailed Dwarf Lemurs (*Cheirogaleus medius*): the seven-month hibernation period in a population in a dry forest in western Madagascar contrasts with the four-month hibernation period in a population from rainforest in south-eastern Madagascar (Dausmann 2008; Lahann and Dausmann 2011).

Collectively, these studies reveal that a) considerable variation in patterns of thermoregulation can occur within closely related species at a single site, and b) populations within a species can differ substantially in their use of heterothermy. Variation in the use of heterothermy within and between species may be influenced by factors such as availability of food and water, reproductive state, prevailing weather conditions, and innate timing (Heldmaier et al. 1981; Geiser et al. 1986; Kenagy 1986; Song and Geiser 1997; Geiser and Körtner 2000; Mzilikazi and Lovegrove 2002; Lehmer et al. 2006). The accumulation of sufficient body fat prior to the onset of the dry season has also been identified as one crucial factor that determines the pattern of thermoregulation in some species (Kobbe et al. 2011).

## Seasonal variation

Although torpor is traditionally associated with winter, when air temperatures are low and food resources are scarce, several Afrotropical mammals exhibit torpor when summer-acclimated in the laboratory. Indeed, the Afrotropics are second only to the Australasian region in terms of the number of species known to exhibit torpor in summer (Lovegrove 2000). The species that go into torpor in summer under laboratory conditions include *Graphiurus murinus* (Webb and Skinner 1996), *Elephantulus myurus* (Mzilikazi and Lovegrove 2004), *Microcebus murinus* (Aujard et al. 1999), and *Saccostomus campestris* (Lovegrove and Raman 1998). Withers et al. (1980) found torpid *Petromyscus collinus* and *Aethomys namaquensis* in the Namib desert during hot, dry, summer months, but interestingly, not during the remainder of the year. The individuals of both species exhibited  $T_b$ s of about 20°C, were released whilst still torpid and were subsequently recaptured. More recently, summer torpor has also been recorded under free-ranging conditions in *Elephantulus myurus* (Mzilikazi and Lovegrove 2004), *Neamblysomus julianae* (Jackson et al. 2009) and *E. rupestris* (R. Oelkrug, C. Meyer, G. Heldmaier & N. Mzilikazi, unpublished data).

Lovegrove and Raman (1998) suggested that factors that may constrain use of torpor in summer in the Afrotropics include a) relatively warm cycles in  $T_a$  that minimize gradients between  $T_a$  and  $T_b$ , thereby constraining the attainment of low  $T_b$  values during torpor, and b) the coolest part of the daily  $T_a$  cycle coinciding with the period of activity for many nocturnal animals, with periods of relatively low  $T_a$  typically being < 8 hrs. These factors may restrict the evolution of long bouts of torpor in summer as the time available in which to be torpid is typically less than 8 hrs. Nevertheless, even the shortest bouts of torpor in summer should still confer some energetic advantages.



## **Future directions**

### *The evolution of heterothermy*

The evolutionary origins of heterothermy have been the topic of considerable interest in recent decades (Malan 1996; Geiser 1998; Grigg et al. 2004). Most recently, the importance of heterothermy in understanding the evolution of endothermy has been reiterated by the formulation of the Plesiomorphic-Apomorphic Endothermy (PAE) model which posits that rigid homeothermy represents a derived state that evolved from a plesiomorphic, heterothermic mode of thermoregulation (Lovegrove in press).

In the context of the evolutionary origins of heterothermy, a key aspect of the Afrotropical region concerns the presence of the Afrotheria. The significance of this taxon for elucidating the evolutionary history of heterothermy has long been recognized (e.g., Lovegrove et al. 1999; Lovegrove and Génin 2008), and some taxa within this clade, most notably the tenrecs, present opportunities for testing the predictions of the PAE model (Lovegrove in press). Other taxa present in the Afrotropics that are presently un-studied, but which may shed light on the evolution of mammalian heterothermy, include the armadillo (Tubulidentata) and pangolins (Pholidota).

The evolutionary history of heterothermy in birds is more difficult to elucidate, on account of the large body masses of the phylogenetically oldest groups, namely the ratites, Galliformes and Anseriformes (Geiser 1998). Afrotropical taxa that combine relatively small body mass and early divergence in avian evolutionary history (Hackett et al. 2008) include the mesites (Mesitornithidae) endemic to Madagascar and the turacos (Musophagiformes) endemic to Africa.

### *Ecological correlates of heterothermy*

Whereas the roles of variables such as environmental temperature and availability of food as determinants of heterothermy have been relatively well-studied under laboratory conditions (e.g., Canale et al. 2011), far less is known about how these and other variables interact to determine patterns of torpor and/or hibernation in free-ranging populations. Studies that involve experimental manipulation of the amount of food available to wild populations are urgently needed. For many species, artificially increasing availability of food is relatively straightforward; in the case of aerial insectivores like nightjars, for example, the abundance of flying insects can be increased using artificial light to attract insects (Woods and Brigham 2004). Experimentally reducing availability of food is more challenging, and may not be feasible for many species. One alternative is to experimentally increase energy demands, for instance by shaving areas of pelage to increase rates of heat loss, an approach that is currently proving promising in the study of rodents and elephant shrews (J.G. Boyles, B Smit and A.E. McKechnie, unpublished data).

Although measurements of  $T_b$  in free-ranging animals are now quite common, there still remains a paucity of information on the metabolic rates associated with heterothermic states in the wild. It remains possible that animals may be torpid and save energy and water by utilizing metabolic depression (which may not be detected using only measurements of  $T_b$ ) even at higher temperatures. It is perhaps instructive that two small rodents from the Namib desert show torpor in summer in their natural habitats (Withers et al. 1980) but not at other times of the year. The role of torpor at higher temperatures is highly relevant in the face of global climate change.

Conspicuously absent from the literature are studies that investigate the link between depth of heterothermy and ecologically and evolutionarily relevant variables such as ability to respond to external stimuli and to predators. It has been suggested that the limited or complete inability to respond to external stimuli may be one of the factors limiting the use of

heterothermy. Those species, such as elephant shrews, that do not necessarily make use of nests should provide ideal models for such studies. For example, it is interesting that although the Southern Lesser Galago is physiologically capable of entering torpor, the incidence of heterothermy in the wild is extremely low. Tradeoffs between the advantages and the physiological and ecological costs of heterothermy remain to be investigated.

Experimental manipulations of supply and/or demand of energy, combined with investigations of intraspecific variation in heterothermy along environmental gradients of aridity, seasonality of rainfall and other abiotic factors, have tremendous potential to provide insights into the factors controlling the expression of heterothermy. Further partitioning of the expression of intraspecific and interspecific variation in heterothermy into phenotypic plasticity and adaptive variation, however, will require common-garden experiments in which populations are raised under identical conditions, and their heterothermic responses to standardized challenges to their energy balance assessed.

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Table 1. Afrotropical mammals and birds in which heterothermy has been reported. Where available, normothermic body temperature ( $T_{norm}$ ), minimum body temperature ( $T_{min}$ ) and duration of bouts are shown. The column labelled *Method* indicates the method used to measure body temperature: “Implant” = implanted transmitter, data logger or thermocouple, “Subcut.” = subcutaneous, etc. References: 1. Mzilikazi et al. (2002), 2. Lovegrove et al. (1999), 3. Lovegrove et al. (2001), 4. Lovegrove et al. (2001), 5. Oelkrug et al unpublished, 6. Geiser & Mzilikazi in press, 7. Bennett and Spinks (1995), 8. Fielden et al. (1990), 9. Scantlebury et al. (2008), 10. Jackson et al. (2009), 11. Lovegrove and Génin (2008), 12. Stephenson and Racey (1994), 13. Stephenson and Racey (1993), 14. Stephenson and Racey (1993b), 15. Mzilikazi unpublished data, 16. Perrin and Ridgard (1999), 17. Buffenstein (1985), 18. Lovegrove and Raman (1998), 19. Mzilikazi and Lovegrove (2002), 20. Ellison (1995), 21. Withers et al. (1980), 22. Bennett et al. (1993), 23. Streicher (2010), 24. Dausmann et al. (2005), 25. Blanco and Rahalinarivo (2010), 26. Lahann (2007), 27. Schmid (2000), 28. Schmid and Ganzhorn (2009), 29. Schmid et al. (2000), 30. Dausmann et al. (2008), 31. Kobbe et al. (2011), 32. Nowack et al. (2010), 33. Baxter (1996), 34. Hallam and Mzilikazi (2011), 35. Cory Toussaint et al. (2010), 36. Vivier and van der Merwe (2007), 37. Jacobs et al. (2007), 38. Brown (1999), 39. D Cory Toussaint, A.E. McKechnie and R.M. Brigham, unpublished data, 40. McKechnie and Smit (2010), 41. McKechnie and Lovegrove (2001), 42. Prinzinger et al. (1981), 43. McKechnie and Lovegrove (2001), 44. McKechnie et al. (2004), 45. Hoffmann and Prinzinger (1984), 46. Hoffmann and Prinzinger (1984), 47. Schaub et al. (1999), 48. McKechnie et al. (2007), 49. Smit et al. (in press), 50. Smit and McKechnie (2010), 51. Walker et al. (1983), 52. Schleucher (2001), 53. Sapsford (1986), 54. Cheke (1971), 55. B. Leon and J.R.B. Lighton, unpublished data, 56. Downs and Brown (2002), 57. McKechnie and Lovegrove (2003).

Species	$M_b$ (g)	$T_{norm}$ (°C)	$T_{min}$ (°C)	$T_{norm} - T_{min}$ (°C)	<i>Method</i>	Duration of Bout		Field/lab	Reference	
						mean (hr)	range (hr)			
<b>Mammals</b>										
Macroselidea										
Macroselidae										
Eastern Rock Elephant Shrew	<i>Elephantulus myurus</i>	56.6	34.2	7.5	26.7	Implant	8.8	1 - 39	Field	1
Round-eared Elephant Shrew	<i>Macroselides proboscideus</i>	46.0	37.5	9.41	28.1	Implant			Lab	2
North African Elephant Shrew	* <i>Elephantulus rozeti</i>	45.3	37.1	5.1	32.0	Implant	9.45	1 -17.3	Lab	3,4
Western Rock Elephant Shrew	<i>Elephantulus rupestris</i>	53-61		16		Implant			Field	5
Cape Rock Elephant Shrew	<i>Elephantulus edwardii</i>	47.5				Implant	17.3	6.5-44	Lab	6
Afrosoricida										
Chrysochloridae										
Cape Golden Mole	<i>Chrysochloris asiatica</i>	34-60	32.9	25.7	7.2	Rectal			Lab	7
Namib Desert Golden Mole	<i>Eremitalpa granti</i>	26.1	34.7	19.3	15.4	Rectal			Lab	8
Hottentot Golden Mole	<i>Amblysomus hottentotus longiceps</i>	70.5	33.3	8.6	24.7	Implant		Up to 4 days	Field	9
Juliana's Golden Mole	<i>Neamblysomus julianae</i>	35		27		Implant			Field	10
Tenrecidae										

Lesser Hedgehog Tenrec	<i>Echinops telfairi</i>	132		12.51		Implant		Up to 4 days	Field	11
Highland Streaked Tenrec	<i>Hemicentetes nigriceps</i>	101.9			1.5	Rectal				12
Lowland Streaked Tenrec	<i>Hemicentetes semispinosus</i>	133			1.7	Rectal				12
Large-Eared Tenrec	<i>Geogale aurita</i>	6.7	30.8	24.9	5.9	Rectal				13
Dobson's Shrew Tenrec	<i>Microgale dobsoni</i>	44.6	34.8	24.2	10.6	Rectal				14
Talazac's Shrew Tenrec	<i>Microgale talazaci</i>	44	34.2	27.4	6.8	Rectal				14
Rodentia										
Myoxidae										
Woodland Dormouse	<i>Graphiurus murinus</i>	45		1.5		Implant	32.5	2.5 - 7.7 days	Field	15
Spectacled Dormouse	<i>Graphiurus ocularis</i>	67.8		11.0		Implant	176	2-13 days	Lab	16
Muridae										
Least Gerbil	<i>Gerbillus pusillus</i>	12.6	35.2	16.7	18.5	Rectal	20		Lab	17
Pouched Mouse	<i>Saccostomus campestris</i>	86.8	35.2	21	14.2	Implant	5.29	up to 10.8	Lab	18
Pouched Mouse	<i>Saccostomus campestris</i>	59.6	34.3	28	6.43	Implant	2.9	1 - 6.8	Lab	19
Fat Mouse	<i>Steatomys pratensis</i>	15.6	37	13	24	Rectal	19.5		Lab	20
Pygmy Rock Mouse	<i>Petromyscus collinus</i>	19	33.6	18	15.6	Rectal			Field	21
Namaqua Rock Mouse	<i>Aethomys namaquensis</i>	46	34.9	19.8	15.1	Rectal			Field	21
Bathyergidae										
Mashona Mole Rat	<i>Cryptomys hottentotus darlingi</i>	60	33.3	26.8	6.5	Rectal			Lab	22
Damaraland Mole Rat	<i>Fukomys damarensis</i>	88-202	35	28.5	6.5	Implant			Field	23
Primates										
Cheirogalidae										
Fat-tailed Dwarf Lemur	<i>Cheirogaleus medius</i>	130 - 250	36	9.3	26.7	Skin/Implant		Up to 70 days	Field	24
Furry-eared Dwarf Lemur	<i>Cheirogaleus crossleyi</i>	256-314		9.0		Skin	106.4		Field	25
Greater Dwarf Lemur	<i>Cheirogaleus major</i>	414				Observation			Field	26
Grey Mouse Lemur	<i>Microcebus murinus</i>	58.8	36.3	20.9	15.4	Skin	10.3	5 – 17.5	Field	27



Grey Mouse Lemur	<i>Microcebus murinus</i>	66-89		11.5		Implant	-	Up to 30 days	Field	28
Pygmy Mouse Lemur	<i>Microcebus myoxinus</i>	31	35.2	6.8	28.4	Implant	9.6	4.6 – 19.2	Field	29
Coquerel's Mouse Lemur	<i>Mirza coquereli</i>								Field	30
Reddish-gray Mouse Lemur	<i>Microcebus griseorufus</i>	47–83	34.6	6.5	28.1	Skin	883.2	Up to 45 days	Field	31
Galagidae										
Southern Lesser Galago	<i>Galago moholi</i>	95-108	35.3	21.8	13.5	Skin			Lab/Field	32
Eulipotyphla										
Soricidae										
Greater Red Musk Shrew	<i>Crocidura flavescens</i>	31.5		19		Skin			Lab	33
Erinaceidae										
Southern African Hedgehog	<i>Atelerix frontalis</i>	394-767		1.0		Implant	16	0.66 – 116	Field	34
Chiroptera										
Molossidae										
Egyptian Free-tailed Bat	<i>Tadarida aegyptiaca</i>	16.9	36	6.2	29.8	Skin		2 – >84	Field	35
Angolan Free-tailed Bat	<i>Mops condylurus</i>	24-34	37.1	13.1	24	Skin			Field	36
Vespertilionidae										
African Yellow Bat	<i>Scotophilus dinganii</i>	28.9		18.5		Skin	15.0	Up to 17		37
(recently described species)	<i>Scotophilus mhlanganii</i>	28		18.2		Skin	17.2			37
Schreiber's Long-fingered Bat	<i>Miniopterus schreibersii</i>	10.2	36.6	6	30.6	Subcut.			Lab	38
Nycteridae										
Egyptian Slit-faced Bat	<i>Nycteris thebaica</i>	11	34	28.4	5.6	Skin				39
<b>Birds</b>										
Piciformes										
Lybiidae										
Acacia Pied Barbet	<i>Lybius leucomelas</i>	35.3	37.7	31.3	6.4	Skin			Field	40
Coliiformes										

Coliidae										
Speckled Mousebird	<i>Colius striatus</i>	51	36	18.2	17.8	Implant		Up to 12	Lab	41
Red-backed Mousebird	<i>Colius castonotus</i>	58	38.5	20	18.5	Implant			Lab	42
White-backed Mousebird	<i>Colius colius</i>	35.1	35	26	9	Implant	2.5		Field/lab	43,44
Red-faced Mousebird	<i>Urocolius indicus</i>	53	38.6			Implant			Lab	45
Blue-naped Mousebird	<i>Urocolius macrourus</i>	49	37.9	22	15.9	Implant			Lab	46,47
Caprimulgiformes										
Caprimulgidae										
Freckled Nightjar (eastern)	<i>Caprimulgus tristigma granosus</i>	81	38.8	12.8	26	Skin		Up to 12	Field	48
Freckled Nightjar (western)	<i>Caprimulgus tristigma lentiginosus</i>	73	39.2	10.5	28.7	Skin	6.4	1.4 – 15	Field	49
Strigiformes										
Strigidae										
African Scops-owl	<i>Otus senegalensis</i>	60.6	36	29	7	Skin		0.5 – 2	Field	50
Columbiformes										
Columbidae										
African Collared Dove	<i>Streptopelia roseogrisea</i>	150	38.5	32	6.5	Implant			Lab	51
Namaqua Dove	<i>Oena capensis</i>	36	38.4	34.4	4	Cloacal			Lab	52
Ciconiiformes										
Falconidae										
Pygmy Falcon	<i>Polihierax semitorquatus</i>	60.5	37.5	31	6.5	Implant			Field	53
Passeriformes										
Nectariniidae										
Eastern Double-collared Sunbird	<i>Nectarinia mediocris</i>	7.3	37.3	24	13.3	Cloacal			Lab	54
Tacazze Sunbird	<i>Nectarinia tacazze</i>	11		27		Cloacal			Lab	54
Lesser Double-collared Sunbird	<i>Nectarinia chalybea</i>	7		23.3		Cloacal			Lab	55
Malachite Sunbird	<i>Nectarinia famosa</i>	16.5	39.5	25.4	14.1	Implant		Up to 10	Lab	56
Passeridae										

Red-headed Finch

*Amadina erythrocephala*

21.5

39.6

34.8

4.8

Cloacal

Lab

57

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\**E. rozeti* is strictly speaking a Palearctic species, since it occurs only in North Africa

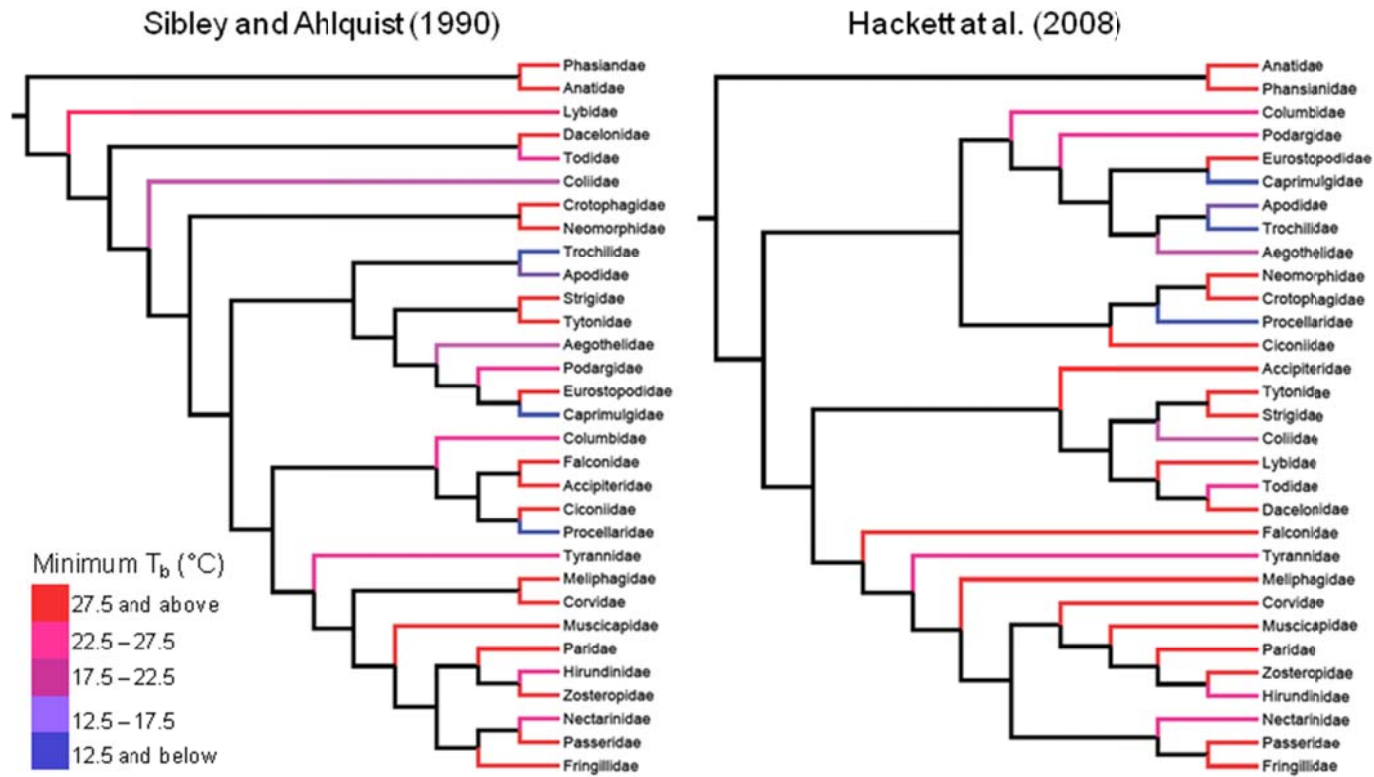


Figure 1. Avian minimum body temperatures during heterothermy mapped onto the phylogenies of Sibley and Ahlquist (1990) and Hackett et al. (2008). Ordinal relationships differ considerably between these phylogenies, and the Hackett et al. (2008) tree supports the view that heterothermy tends to be more pronounced in phylogenetically ancient taxa.

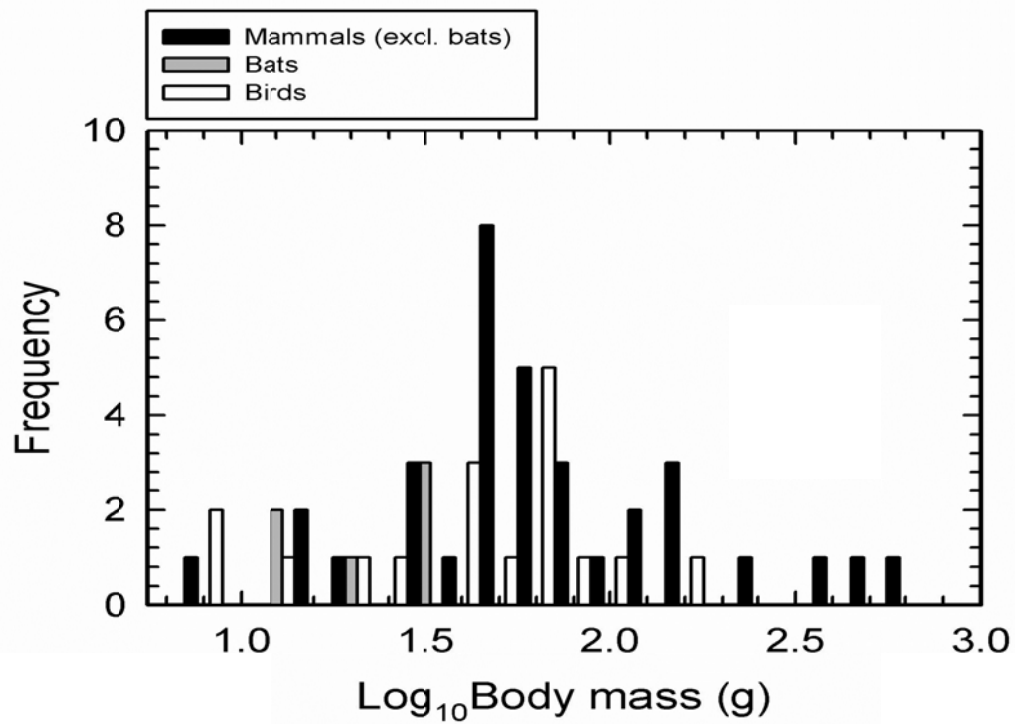


Figure 2. Body masses of Afrotropical endotherms in which heterothermy has been reported. In the case of species for which a range in body mass is reported in Table 1, the mid-point of the range is plotted here.

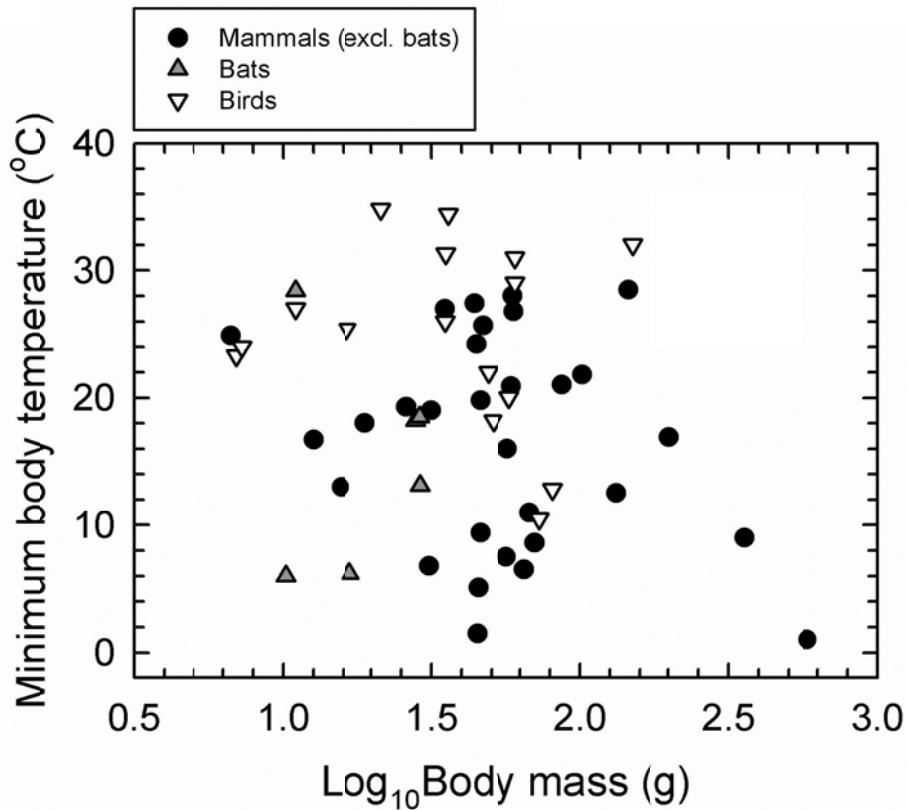


Figure 3. Relationship between body mass and minimum body temperature observed during heterothermy for Afrotropical endotherms. In the case of species for which a range in body mass is reported in Table 1, the mid-point of the range is plotted here.