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SHORT COMMUNICATION

Hibernation and daily torpor minimize mammalian extinctions

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Abstract Small mammals appear to be less vulnerable to extinction than large species, but the underlying reasons are poorly understood. Here, we provide evidence that almost all (93.5%) of 61 recently extinct mammal species were homeothermic, maintaining a constant high body temperature and thus energy expenditure, which demands a high intake of food, long foraging times, and thus exposure to predators. In contrast, only 6.5% of extinct mammals were likely heterothermic and employed multi-day torpor (hibernation) or daily torpor, even though torpor is widespread within more than half of all mammalian orders. Torpor is characterized by substantial reductions of body temperature and energy expenditure and enhances survival during adverse conditions by minimizing food and water requirements, and consequently reduces foraging requirements and exposure to predators. Moreover, because life span is generally longer in heterothermic mammals than in related homeotherms, heterotherms can employ a 'sit-and-wait' strategy to withstand adverse periods and then repopulate when circumstances improve. Thus, torpor is a crucial but hitherto unappreciated attribute of small mammals for avoiding extinction. Many opportunistic heterothermic species, because of their plastic energetic requirements, may also stand a better chance of future survival than homeothermic species in the face of greater climatic extremes and changes in environmental conditions caused by global warming.

Keywords Energy expenditure · Foraging requirements · Survival rates · Global warming · Unpredictable climate

Dedicated to the memory of Donald W. Thomas

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Introduction

Extinction of mammals over the last 500 years is generally attributed to a variety of anthropogenic influences (Flannery and Schouten 2001; Ceballos and Ehrlich 2002; Cardillo et al. 2006; Johnson 2006). Small species, which comprise the vast majority of mammals, are more resistant to extinction than medium-sized and large species, but there is no satisfactory explanation as to why this is so, and why not all small species are equally resistant (Cardillo 2003). Nevertheless, extinctions are clustered within certain taxa that have been most strongly affected by habitat loss or introduced species (Russell et al. 1998). Extinct species generally had relatively small litters and large home ranges, suggesting that low recruitment, exposure to predators, or resource limitations and high energy requirements are important factors contributing to the risk of extinction (Cardillo 2003).

Hibernation (prolonged multi-day torpor) and daily torpor also are clustered within certain taxa and occur predominantly in small species (Geiser 1998; Cooper and Geiser 2008). Torpor is the most effective energy-conserving strategy available to mammals and substantially reduces resource requirements (Geiser and Ruf 1995; Boyer and Barnes 1999; Carey et al. 2003; Geiser 2004). During torpor, body temperature usually falls by ~10 to 35°C and metabolic rate can be as low as 1–10% of that during activity (Geiser and Ruf 1995). Therefore, torpor can permit survival without or on limited food for prolonged periods, often for weeks or months and in the most extreme cases up to an entire year (Geiser 2007; Bieber and Ruf 2009; Körtner and Geiser 2009), and has the potential for mitigating adverse environmental events.

Although it is still widely believed that torpor is restricted to a few cold-climate mammals, it is widespread in all climate zones including the tropics (Geiser 2004; Dausmann 2008; Schmid and Ganzhorn 2009; Stawski et al. 2009). Torpor is employed by members from more than half of all mammalian orders (Monotremata, several marsupial orders, Xenarthra, Pholidota, Rodentia, Macroscelidea, Insectivora, Primates, Chiroptera, Carnivora). These orders contain almost 90% of all mammalian species (Geiser and Ruf 1995; Geiser 1998, 2004), but of course not all species of these orders are heterothermic. Recently, it was estimated that approximately 43% of all Australian terrestrial mammals, for example, employ torpor for energy conservation (Geiser and Körtner 2009). Importantly, the reduced energy requirements during torpor can minimize foraging requirements (Ruf and Heldmaier 2000; Körtner and Geiser 2009) and consequently exposure to predators, which in turn contributes to the increased life span of heterothermic in comparison to homeothermic species (Wilkinson and South 2002; Nicol and Andersen 2006; Bieber and Ruf 2009). As the use of torpor so profoundly affects energy expenditure, foraging requirements, and life span of mammals, we tested the hypothesis that torpor is a crucial attribute that is minimizing extinctions of small mammals.

Methods

The identity, species name, and taxonomic affiliation of the 61 confirmed extinct mammal species since 1500 AD was obtained from the American Museum for Natural History, Committee on Recently Extinct Organisms (http://creo.amnh.org/). The species were categorized as likely to have been homeothermic or heterothermic (Table 1) by comparison with similar-sized, closely related extant taxa for which thermoregulatory patterns are known (Geiser and Ruf 1995; Geiser 1998; Boyer and Barnes 1999; Nowak 1999; Carey et al. 2003; Geiser 2004; Cooper and Geiser 2008; Turbill et al. 2003; Dausmann 2008; French 2008; Geiser and Körtner 2009). To determine whether extinction of heterothermic and homeothermic mammals over the last 500 years differs significantly, we employed two approaches: (1) a chi-square test was used assuming that 40% and 20% of the approximately 4,800 total species of mammals are heterothermic. The former percentage was selected because it approximates the most reliable estimate of heterothermy of 43% in Australian terrestrial mammal species that is currently available for an entire continent (Geiser and Körtner 2009); 20% heterothermy was tested to introduce a wide safety margin. To avoid the requirement for estimating numbers of homeothermic or heterothermic mammal species, we also tested (2) whether extinctions have occurred randomly among all known extinct homeothermic and heterothermic families by chi square. The family taxonomy from Nowak (1999) was used in this test. The 51 heterothermic families were selected because they are known to be or most likely are entirely heterothermic or contain some heterothermic species. For the selected 99 homeothermic families, 95 are considered to be exclusively homeothermic. However, four families that include extinct species and contain both known homeothermic and heterothermic species (Pteropodidae, e.g., *Pteropus* spp. homeothermic, *Nyctimene* spp. heterothermic; Muridae, e.g., *Rattus* spp. homeothermic, *Peromyscus* spp. heterothermic; Canidae, e.g., *Dusycion* sp. homeothermic, *Nyctereutes* sp. heterothermic; Mustelidae, e.g., *Mustela* spp. homeothermic, *Mephitis* sp. heterothermic) were counted twice (i.e., in both homeothermic and heterothermic families).

Results

Of the 61 extinct mammals (Table 1), 57 species were homeothermic and only four likely were heterothermic (Fig. 1). Significantly more extinct mammals were homeothermic than heterothermic (chi square >6.85, $df=1$, $p<0.01$) assuming that heterothermy is expressed in either 20% or 40% of all mammals. Only four of the 51 mammalian families that contain heterothermic species include extinct species, whereas 22 of the 99 families containing homeothermic species include extinct species (chi square=4.86, $df=1$, $p=0.028$).

Extinct mammals occur in three marsupial and eight placental orders (Table 1). Within these orders, bandicoots (Peramelemorphia), rabbit relatives (Lagomorpha), even-toed ungulates (Artiodactyla), and sea cows (Sirenia) are considered to be entirely homeothermic. For most orders that do contain some heterothermic species, such as the carnivorous marsupials (Dasyuromorphia), possum and kangaroo relatives (Diprotodontia), insectivores (Insectivora), primates (Primates), and carnivores (Carnivora), all extinct species belong to genera or families that are not known to contain any extant heterothermic species, or are substantially larger than extant heterothermic species (Geiser and Ruf 1995; Geiser 1998; Boyer and Barnes 1999; Carey et al. 2003; Dausmann 2008; French 2008). Only the rodents (Rodentia) and bats (Chiroptera) contain extinct species that likely were heterothermic.

The most diverse order, also suffering the most extinctions ($n=26$), are the rodents (Table 1). Many ($n=7$) of the

Table 1 Extinct mammals from 1500 AD

SUBCLASS **Order** *Species* [Family] (Group)	Number of species	Mass range (kg)	Thermoregulatory pattern (justification)
MARSUPIALS			
Dasyuromorphia	1	30	Homeothermic (known heterothermic dasyuromorphs <5 kg)
Thylacinus cynocephalus [Thylacinidae]			
(Tasmanian wolf)			
Peramelemorphia	3	0.2–0.4	Homeothermic (no heterothermy in order)
Perameles eremiana [Peramelidae]			
Chaeropus ecaudatus [Peramelidae]			
Macrotis leucura [Peramelidae]			
(Bandicoots)			
Diprotodontia	6	0.8–15	Homeothermic (no heterothermy in families)
Potorous platyops [Potoroidae]			
Caloprymnus campestris [Potoroidae]			
Lagorchestes asomatus [Macropodidae]			
Lagorchestes leporides [Macropodidae]			
Macropus greyi [Macropodidae]			
Onychogalea lunata [Macropodidae]			
(Kangaroos and relatives)			
PLACENTALS			
Insectivora	5	0.05–1	Homeothermic (related genera homeothermic)
Nesophontes hypomicrus [Nesophontidae]			
Nesophontes paramicrus [Nesophontidae]			
Nesophontes zamicrus [Nesophontidae]			
Nesophontes superstes [Nesophontidae]			
Solenodon marcanoi [Solenodontidae]			
(Nesophonts, Solenodon)			
Chiroptera	8	0.01–1	Mainly Homeothermic (related genera homeothermic) *3 likely heterothermic
Pteropus subniger [Pteropodidae]			
Pteropus tokudae [Pteropodidae]			
Pteropus pilosus [Pteropodidae]			
Pteropus brunneus [Pteropodidae]			
Dobsonia chapmani [Pteropodidae]			
**Nyctimene sanctacrucis* [Pteropodidae]			
**Pharotis imogene* [Vespertilionidae]			
**Mystacina robusta* [Mystacinidae]			
(Mega- and microbats)			
Primates	3	3–75	Homeothermic (no heterothermy in families)
Megaladapis edwardsi [Megaladapidae]			
Palaeopropithecus ingens [Paleopropithecidae]			
Xenothrix mcgregori [Cebidae]			
(Lemur, Monkeys)			
Rodentia	26	0.05–5	Mainly homeothermic (related genera homeothermic) *1 likely heterothermic
Conilurus albipes [Muridae]			
Leporillus apicalis [Muridae]			
Notomys longicaudatus [Muridae]			
Notomys amplus [Muridae]			
Pseudomys gouldii [Muridae]			
Rattus macleari [Muridae]			

Table 1 (continued)

SUBCLASS **Order** *Species* [Family] (Group)	Number of species	Mass range (kg)	Thermoregulatory pattern (justification)
Rattus nativitatis [Muridae]			
Uromys porculus [Muridae]			
Uromys imperator [Muridae]			
Megalomys luciae [Muridae]			
Megalomys desmarestii [Muridae]			
Megaoryzomys curioi [Muridae]			
Nesoryzomys darwini [Muridae]			
Nororhomys vespucii [Muridae]			
Oligoryzomys victus [Muridae]			
Oryzomys nelson [Muridae]			
Oryzomys antillarum [Muridae]			
**Peromyscus pembertoni* [Muridae]			
Brotomys voratus [Echimyidae]			
Geocapromys columbianus [Capromyidae]			
Geocapromys thoracatus [Capromyidae]			
Hexolobodon phenax [Capromyidae]			
Isolobodon montanus [Capromyidae]			
Isolobodon portoricensis [Capromyidae]			
Rhizoplagiodontia lemkei [Capromyidae]			
Plagiodontia ipnaeum [Capromyidae]			
(Mice, Rats, Hutias)			
Lagomorpha	2	0.4–1	Homeothermic (no heterothermy in order)
Prolagus sardus [Ochotonidae]			
Sylvilagus insonus [Leporidae]			
(Pika, Rabbit)			
Carnivora	3	2–100	Homeothermic (related genera homeothermic)
Mustela macrodon [Mustelidae]			
Dusicyon australis [Canidae]			
Monachus tropicalis [Phocidae]			
(Mink, Wolf, Seal)			
Artiodactyla	3	40–800	Homeothermic (no heterothermy in order)
Hippotragus leucophaeus [Bovidae]			
Gazella rufina [Bovidae]			
Hippopotamus lemerlei [Hippopotamidae]			
(Antelope, Gazelle, Hippopotamus)			
Sirenia	1	4,000	Homeothermic (no heterothermy in order)
Hydrodamalis gigas [Dugongidae]			
(Sea cow)			

extinct rodents belong to the rat-like hutias (Capromyidae), which are members of the caviomorph rodents that contain largely homeothermic species, and none of the extant related genera in this group are known to be heterothermic (French 2008). Interestingly, sciurids (ground squirrels and marmots) and glirids (dormice), which are diverse families of rodents containing many hibernators (French 2008) and are of similar size to the hutias, are not listed at all among the extinct mammals. On the other hand, mouse relatives (Muridae) are the rodent family suffering most extinctions ($n=18$). Although extinct murids were small, all but one of the extinct murid rodents likely were homeothermic, as heterothermy is not known to occur in the same genus or related extant genera (French 2008). However, one extinct murid, a deer mouse (*Peromyscus pembertoni*), although relatively large for this genus (60 g), was probably heterothermic, as

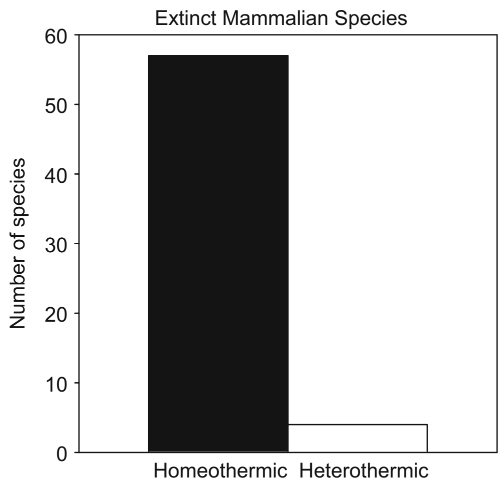

Fig. 1 Homeothermic and heterothermic extinct mammals from 1500 AD

torpor in the genus *Peromyscus* is widespread (Geiser and Ruf 1995; Geiser 2004; French 2008).

Most extinct bats were large homeothermic fruit bats of the family Pteropodidae (Flannery and Schouten 2001; Geiser 2006). However, three extinct bats (*Nyctimene sanctacrucis*, *Pharotis imogene*, *Mystacina robusta*) were small and probably heterothermic, similar to closely related (*Pharotis* is related to *Nyctophilus*) extant relatives (Geiser and Ruf 1995; Sedgeley 2003; Turbill et al. 2003).

Over the last 200 years, Australia is the region with almost half of the mammal extinctions worldwide, which is believed to have been caused by severe habitat degradation and predation linked to the introduction of exotic herbivores (e.g., rabbit, sheep, goat) and carnivores (cat, fox) (Fisher et al. 2003; Johnson 2006; Pavey et al. 2008). Australian extinctions have occurred exclusively in homeothermic species (Geiser and Körtner 2009) and predominantly in the arid zone (Dickman 1996; Johnson 2006). None of the extant macropods, bandicoots and native rodents, which contain most of the extinct species, is known to be heterothermic (Geiser 2004; Tomlinson et al. 2007; Warnecke et al. 2007; unpublished data by the authors). In contrast, the insectivorous/carnivorous dasyurid marsupials, which are most diverse in the Australian the arid zone, and bats have all managed to survive (albeit with some reduction in range, e.g., western quoll) likely because they use torpor extensively in the wild (Körtner and Geiser 2009).

Discussion

Our comparison shows that, in general, small heterothermic mammals seem to have an advantage over those mammals that cannot employ torpor in surviving causes of extinction. This is likely because heterotherms can persist during sudden or prolonged episodes of scarce resources, and, by minimizing foraging, avoid predators or human hunters. Moreover, because life span is generally longer in heterothermic mammals than in related homeotherms (Wilkinson and South 2002; Bieber and Ruf 2009), heterotherms can employ a ‘sit-and-wait’ strategy to withstand adverse periods and then repopulate when circumstances improve. Thus, torpor is likely a crucial but hitherto unappreciated attribute of mammals evading extinction.

With regard to global warming, two scenarios are possible for heterothermic mammals. Those hibernating species in which a well-defined winter dormancy is closely synchronised with historical phenological patterns may suffer because of a mismatch between their behavior and rapidly changing environmental conditions (Inouye et al. 2000). Moreover, a reduction in snow cover, which insulates underground hibernacula against extreme cold, may increase the energetic cost of hibernation and lead to the extinction of some species with limited mountain habitats, such as the mountain pygmy possum (*Burramys parvus*) (Geiser and Broome 1993; Geiser and Körtner 2009). In contrast, many heterothermic mammals such as chipmunks (*Tamias striatus*), some bats, or dasyurid marsupials are more opportunistic in their use of torpor to suit prevailing environmental conditions (Turbill et al. 2003; Frank and Hood 2005; Landry-Cuerrier et al. 2008; Geiser and Körtner 2009; Körtner and Geiser 2009; Stawski et al. 2009). It seems that these heterothermic mammals, especially if they can also shift their distribution range (Humphries et al. 2002), may stand a better chance of surviving future energetic challenges than homeothermic species (Liow et al. 2009). Global warming is predicted to alter local weather patterns and increase the frequency and intensity of severe events, such as droughts, fires, storms, and floods. The history of extinction suggests that those mammals capable of employing torpor to drastically reduce their energy and water requirements during unfavorable conditions will stand a better chance of survival. Indeed, torpor is a particularly common adaptation of species in regions of low productivity and unpredictable but relatively warm climates, such as Australia, Africa, and Madagascar (Lovegrove 2000; Dausmann 2008; Geiser and Körtner 2009). Furthermore, it is clear that cold temperatures are not a prerequisite for energy savings during torpor. Perhaps counter-intuitively, many heterothermic mammal species with their highly plastic energy requirements may be better prepared than homeotherms to overcome the predicted increase in climatic extremes and uncertain changes in local environmental conditions resulting from global warming.

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