

General introduction

Deserts

Arid and semi-arid habitats cover almost one third of the world's land area and represent one of the most demanding ecosystems for living organisms. The formation of arid landforms and diversification of arid flora and fauna occurred about 2.6-5 million of years ago during late Pliocene and Pleistocene. However, throughout the geological evolution, desert areas experienced a variety of changes in extent and intensity of aridity, especially during the Quaternary (about 2 million of years ago), reflecting high biotic diversity that once was represented in these areas (Johnson 2006).

Present deserts are distributed across all continents with 88% occurring in the Old World (Africa, Asia and Europe) and 12% in the New World (North America, South America and Australia) (Degen 1997). In the southern hemisphere major desert regions comprise about 500 million km² and are more diverse than the deserts of the northern hemisphere. These for example, include hyperarid areas such as the Namib (South Africa) and the Atacama (Chile), the semi-arid sandy savannahs of the Kalahari, the continental dunefields of Australia and the high elevation dry Puna grasslands (Argentina) (Trewin 2006a). Australia's arid (3.5 million km²) and semi-arid (1.79 million km²) regions comprise about 5.3 million km² or 69% of the continent, and together they form the largest desert region in the southern hemisphere (Plate 1a) (Taylor 2002).

Deserts have been characterised in a variety of ways based on different climatic factors such as total annual rainfall, solar radiation, rates of evaporation and maximum T_as (Degen 1997). Perhaps, the simplest ways to define deserts is based solely on total annual precipitation (Degen 1997; Trewin 2006a) following one of the earliest attempts made by the German scientist Dr Wladimir Köppen (Köppen 1900), that was later adapted by many other authors. He defined deserts as areas that on average receive less than 245 mm of rainfall per annum, whereas steppes receive 254 to 508 mm. These two categories were later designated as arid and semi-arid habitats and both comprise approximately 14% of the world's continental area each (Degen 1997; Kottek et al. 2006). In Australia, the modified Köppen classification system, which takes into account the mean maximum and minimum temperatures, is still commonly used to define different climatic zones (Plate 1a).

Another more complex and perhaps, more precise way to define aridity, that is also used in Australia, is based on a moisture index which is calculated from weekly precipitation and

evaporation values in conjunction with soil type and soil water availability, with arid areas having an index of ≤ 0.2 (Smyth and James 2004) (Plate 1b). However, in Australia boundaries between “dry” and “wet” areas are somewhat blurred due to absence of large dividing geological barriers such as mountain ranges and therefore, the sharp borders usually shown on maps are arbitrary to a degree (Trewin 2006a).

Australia's desert climate

Desert habitats cover more than a half of the Australian landmass and occupy most of western and central parts of the continent. However none of the Australian deserts are considered to be extreme (i.e. their annual rainfall > 70 mm) and one of the driest areas (the Lake Eyre basin, South Australia) receives approximately 127 mm of the total annual rainfall. In comparison, the Sahara for example, which is one of the most arid deserts, receives only 25.4 mm of rainfall annually (Degen 1997; Trewin 2006a).

Generally, climate of Australian deserts is characterised by erratic and unpredictable rainfall and pronounced daily and seasonal fluctuations in ambient temperature (T_a). Thunderstorms are common, however, they are often “dry” with all rain evaporating before reaching the ground (Trewin 2006a). Rainfall differs not only between seasons, but also from year to year and from decade to decade causing episodes of prolonged droughts and periods of above-normal rainfall. Due to the flat inland terrain, rainfall in arid Australia is mainly caused by a southward extension of monsoonal troughs often in a form of tropical cyclones that move deep inland and northwest cloudbands that bring moisture from the Indian Ocean (Trewin 2006a). These rainfall events are significantly affected by fluctuations in the El Niño Southern Oscillation (ENSO) with La Niña conditions causing higher than average rainfall across all Australia. For example, a La Niña event during the summer 2010-2011 led to wide spread flooding across Australia including several arid regions. As such, in December 2010 my research site, near the small town of Tibooburra (New South Wales, NSW), received 150-300% of its normal December rainfall (National Climate Centre 2011).

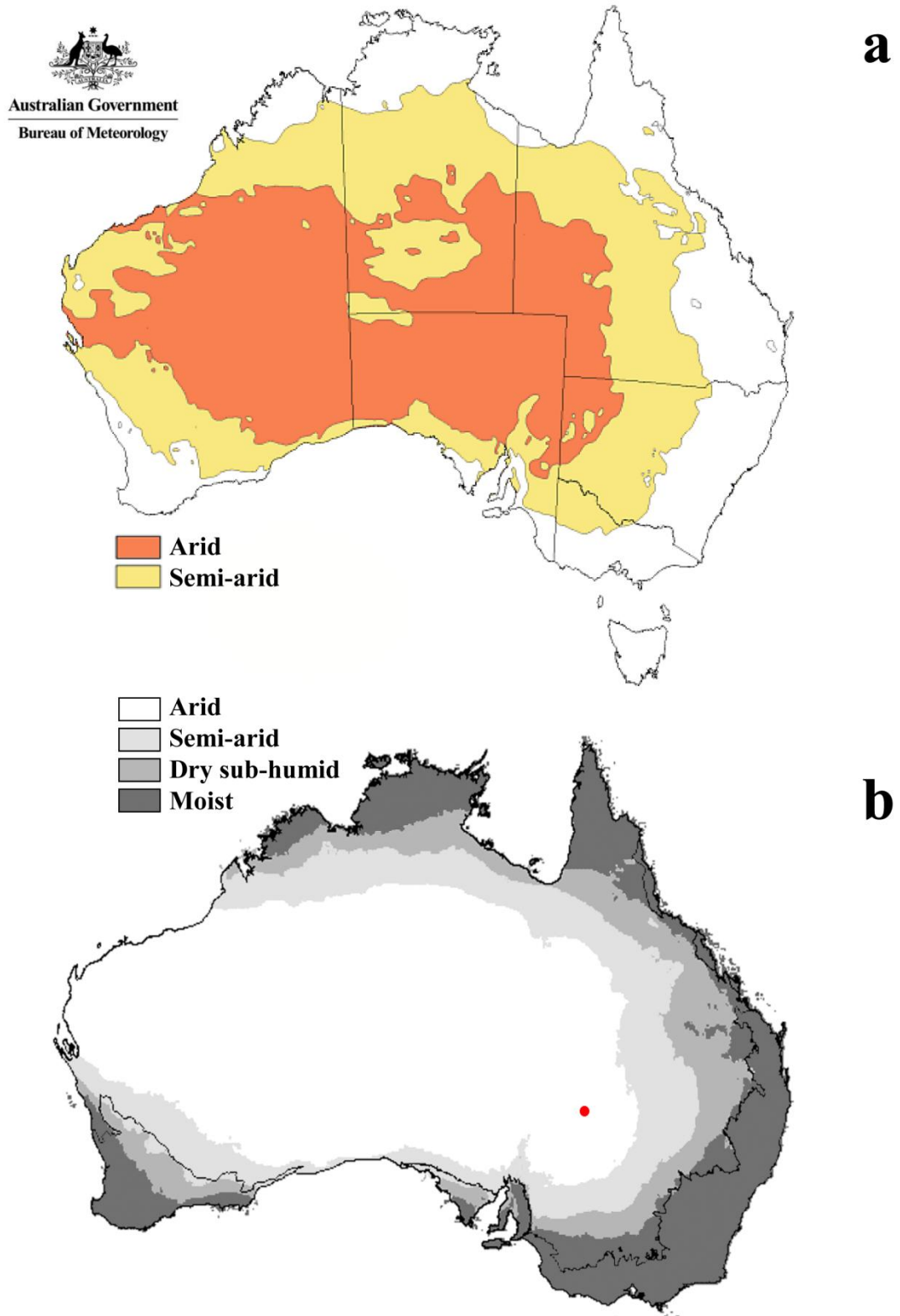


Plate 1. Map of Australia's arid and semi-arid habitats based on the modified Köppen classification system (a) (Bureau of Meteorology, Australia) and a moisture index (b) (Smyth and James 2004). The red dot on the bottom map shows the approximate location of the research site.

Australia's deserts are relatively hot with mean maximum T_a during January exceeding 35°C in most arid and semi-arid areas and in some north-western parts mean maximum T_a can reach 40°C (Pilbara region, Western Australia, WA). Temperature extremes during summer can exceed 48°C and sometimes 50°C (Trewin 2006a). The highest T_a of 48.1°C at my research site was recorded in January 2013. While prolonged hot spells are not uncommon in Australia's deserts, a heatwave recorded in December 2012-January 2013 lasted over three weeks and it was the longest period of extreme heat recorded in Australia since 1972-73 (Bureau of Meteorology 2013). As in many other deserts, daily T_a fluctuations are pronounced in Australia's arid zone and often vary from 15 to 20°C between day and night (Trewin 2006a). Overnight T_a is usually considerably lower than daytime T_a and averages in January range from 17 to 25°C. This T_a can, however, be as high as 35.5°C during hot spells or significantly lower with the passing of a lower pressure system (Trewin 2006a). For example, T_a fell to 12.7°C at the study site in December 2010.

Most Australian deserts are also subjected to a pronounced seasonal temperature cycle. As such, mean daytime T_a during winter is lower and varies from about 15 to 26°C with mean minimum July T_a ranging from 3 to 10°C (Trewin 2006a). Overnight frost is not uncommon and was observed on a few occasions during my winter field work.

The air in Australia's deserts is usually dry with an exception along Pilbara coast (Western Australia), where a sea breeze can bring layers of humid air from the ocean (Trewin 2006a). Annual average relative humidity at 3pm falls below 30% to sometimes below 10% (Trewin 2006a; Bureau of Meteorology, Australia), which, together with strong winds (Tibooburra, NSW, annual wind speed at 3pm = 10-20 km/h; Bureau of Meteorology, Australia), considerably increases evaporation. As such the little rain that falls mostly evaporates with very little runoff (Trewin 2006a). Nevertheless, Australia's deserts include numerous ephemeral salt lakes with the biggest playa Lake Eyre (9500 km²). These are often dry and fill up only after major rain events. A number of inland-flowing rivers such as the Paroo, Bulloo, Diamantina and Cooper Creek drain into the Lake Eyre or evaporate without reaching their destination. Some of the rivers of the Murray-Darling Basin also flow through arid and semi-arid regions of south-eastern Australia. There is also a network of small wells, rock holes, soaks and some artificial dams that provide water for people and wildlife (Trewin 2006a; Trewin 2006b).

The results of hot climate and unfertile soils place high energetic constraints on arid zone animals. Nevertheless, the diversity of Australia's small desert mammals, such as marsupials, bats and rodents, is surprisingly high with ~28.6% (n = 22) of the insectivorous bat species of five families (Churchill 2008), ~50% (n = 28) of all Australian dasyurid marsupials and ~44% (n = 23)

of the native rodents living within the arid or semi-arid zone (Van Dyck and Strahan 2008). It has been shown that their ability to adapt to the constraints of the arid climate via a variety of behavioural and physiological means may be a reason for their success (Bradley and Yousef 1972; Schmidt-Nielsen 1979; Geiser 2004a).

Problems of being a small mammal

Body dimensions and mass are important variables influencing heat exchange between an animal and its environment as well as energy and water turnover (Calder 1996). The surface area of a small animal is affected by its volume and shape, and the surface to volume ratio increases as size and mass decreases (Schmidt-Nielsen 1979; Schmidt-Nielsen 1997). A common misconception is that small organisms lose more heat and water than large organisms (Lovegrove 1993). Indeed, under similar thermal conditions and similar fur insulation, the rate of loss or gain will be the same between small and large organisms. However, because small animals have proportionally larger surface areas than large animals their loss or gain will be larger relative to their volume (Lovegrove 1993).

Body mass and metabolic rate

Metabolic rate (MR), the energy expended per unit of time to support life processes, is often measured as the rate of oxygen consumption and varies with body mass (BM). The basal metabolic rate (BMR) is the minimum MR in normothermic, resting, post-absorptive, adult and non-reproductive animals within a species-specific range of T_a called the thermo-neutral zone or TNZ. BMR is either expressed as the whole-animal BMR (i.e. $\text{ml O}_2 \text{ h}^{-1}$) or mass-specific BMR (i.e. MR per unit of BM; $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$). It is often used for inter or intraspecific comparisons of MR. Mass-specific BMR increases exponentially as BM of an animal decreases, which means that small animals require more energy and also water per unit of mass than large animals (Withers 1992; Calder 1996; Geiser 2004b; Hill et al. 2008). This relationship has important ecophysiological implications as the relationship between MR and BM pervades almost all physiological functions of an organism. As such small species have also higher heart and breathing rates than large animals, while the relative size of the heart and lungs is independent of body size (Calder 1996; Hill et al. 2008).

Body size and heat exchange

Animals exchange heat with their environment by conduction, convection, radiation and evaporation. All these are surface processes, and therefore the heat exchange of an animal is directly related to its internal (respiratory tract) and external surface area (Schmidt-Nielsen 1997). An object in a surrounding that is warmer than itself, gains heat proportionally to its surface, but in living animal, especially in endothermic mammals and birds with high MR, the total heat load, in addition to the heat gained from the environment, includes metabolic heat. Because MR and, consequently metabolic heat production, increase rapidly with a decrease in body size (Geiser 2004b), a small animal with its larger surface area will have a significantly larger total heat loads than a larger animal. Hence, total evaporative water loss (EWL) needed to maintain a constant body temperature (T_b) also increases with a decrease in body size (Schmidt-Nielsen 1979; Withers 1992; Calder 1996). Because capabilities to store body water and thermal energy are limited, small desert animals are in a far less favourable position for maintaining stable T_b than large animals and therefore, must employ different behavioural and physiological strategies to evade or deal with desert heat.

In a cold environment, however, the problem of rapid heat loss arises due to a large surface area to volume ratio of small mammals, resulting in a large proportion of the body heat being lost to the environment (Schmidt-Nielsen 1997). Thus, to maintain a stable T_b in the cold, small animals have to considerably increase heat production (Schmidt-Nielsen 1997; Geiser 2001), which can be too expensive especially for insectivorous mammals, such as bats, since their primary food source becomes scarce or unavailable at low T_a (Taylor and O'Neill 1988; Turbill et al. 2003a; Turbill 2008; Chapter 1 and 2). Therefore, to overcome unfavourable energetic conditions many small mammals to a large extent abandon thermoregulation at low T_a and reduce their MR and T_b , i.e. enter a state of torpor or hibernation (see below) (Geiser 2001).

Body size and thermal conductance

The thermal conductance (C) is a measure of capacity for the heat flow from an animal to the surroundings and is often measured as the apparent C ($\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$; Schmidt-Nielsen 1997). C is the inverse of insulation and generally changes with size of an animal, but similar-sized animals from different habitats can have different levels of insulation as an adaptation to their environment (Scholander et al. 1950; Degen 1997). Large and medium-sized animals from cold environments have a thick fur and as a result low C that reduces heat loss compared to species from warmer climates (Scholander et al. 1950; Schmidt-Nielsen 1997). Similarly, impressively thick dorsal pelage and plumage of some mammals and birds, such as camels and emus that are

native to hot environments, can be seen as an adaptation to their hot environment as it would function as a thermal shield and reduce heat flux from the environment into the body, but permit heat dissipation from ventral areas (Morrison 1966; Hill et al. 2008).

Small mammals, such as most rodents, shrews and bats, cannot carry a thick pelage as it would impair their ability to move. Therefore, small mammals generally have short fur, which, in addition to the large surface area to volume ratio, results in an even higher C (Bradley and Deavers 1980; Hill et al. 2008). These animals, in order to minimise heat gain/loss either seek favourable microenvironments (i.e. burrows, caves) and/or employ torpor/hibernation (see below) to avoid thermoregulatory problems (Schmidt-Nielsen 1997).

Body size and diet

Because the high food demands of small mammals require a high digestive throughput (Calder 1996), these animals generally need easily digestible food with a high energy content. Therefore, it is not surprising that insects, meat and seeds are the most common food source for small mammals such as shrews, dasyurid marsupials, bats and rodents. Amongst mammals, granivory appears to be exclusive to rodents, particularly small species (Degen 1997). Their diet can undergo seasonal changes and may also include invertebrates, fibrous plant material and fungi (Murray and Dickman 1994; Degen 1997). Such species are less restricted in their dietary requirements and therefore, appear to be energetically in a better position than for example, exclusively insectivorous endotherms, especially during cold periods when availability of invertebrates declines.

Interestingly, insectivorous mammals are more abundant in Australia's deserts than for example in the deserts of North America (Morton 1979). It has been proposed that the relatively mild winters in Australia's deserts provide enough insects for animals to overcome a cool period of the year and thus, support a higher diversity of insectivorous mammals than the much colder winters of North America's deserts (Morton 1979). Nevertheless, even in Australia's deserts during winter, abundance of insects can be reduced substantially from that in summer (Chapter 1). Therefore, arid zone species need to employ a variety of physiological mechanisms to conserve energy as for example, daily torpor and hibernation.

Adaptations to the life in deserts

Sweating, panting, and other means of evaporative cooling that are often observed in mammals and birds are effective mechanisms of heat dissipation. However, evaporative cooling comes at a high price as it requires water potentially causing dehydration and death. Therefore, other physiological and behavioural mechanisms to cope with high environmental or metabolic heat loads such as burrowing, nocturnality, shuttling, change in C and the ability to up and down regulate T_b are usually employed before evaporative cooling commences. Thus, it appears that dissipation of heat by active evaporative cooling is actually often the last resort for desert animals when other defences become inefficient (Hill et al. 2008).

Behavioural adaptations

Burrowing and nocturnal life

One of the reasons that many small to medium-sized arid mammals evolved fossorial and nocturnal behaviour could be to escape the temperature extremes of deserts (Bartholomew 1982; Lovegrove 1993; Degen 1997; Körtner et al. 2008; Körtner et al. 2010). Although burrowing and nocturnal life are also common in other climates, a cool microenvironment of underground shelters and a coolness of the night are critical for survival of desert mammals (Bartholomew 1982).

Thermal properties of burrows depend on soil characteristics, structure, ground cover and depth. For example, during the daytime in winter in a central-Australian desert, soil temperature at the depth of 27 cm can be 24°C cooler than surface temperature and thus, provide substantial buffer from temperature extremes above the ground (Körtner et al. 2008). In addition, burrows can also serve as food storage or be a refuge from predators (Degen 1997). A few authors have reported high relative humidity in burrows of different animals, which could help to reduce EWL in arid environments (Schmidt-Nielsen 1979; Kinlaw 1999; Körtner et al. 2008). However, other authors argued that this might not always be the case (Walsberg 2000). Desert soils are usually a mixture of gravel, sand and clay with little organic material. The relative porosity of sandy soils can allow water vapour to diffuse from burrows, whereas clay soils tend to reduce relative humidity inside of occupied burrows due to their hygroscopic nature. Thus, humidity inside burrows may not always be as favourable as it has been previously thought (Walsberg 2000).

Shuttling and belly-basking

Exposure to high daytime desert temperatures can be minimised by shuttling between cooling and foraging sites. Shuttling behaviour has been reported in several desert-adapted mammals (Lovegrove 1993; Hainsworth 1995; Degen 1997). For example, during the day antelope ground squirrels, *Ammospermophilus leucurus*, shuttle between cool burrows and foraging sites that allows this species to forage in the hot desert and still keep their T_b “cool” (Hainsworth 1995). Another way to offload body heat during the arid day is belly-basking. In the heat of the day, suricates, *Suricata suricatta*, from South Africa as well as some Australian kangaroos, often find shaded areas where they scrape away the hot, top soil layers and lie down on the cooler ground to offload excess heat (Dawson 1983; Lovegrove 1993). However, if T_a exceeds 45°C, red kangaroos, *Macropus rufus*, for example, do not lie down but stand with the tail pulled between the legs to reduce the surface area thus, minimising the radiant heat loads from the ground and sun (Dawson 1983).

Physiological adaptations

Insulation and thermal conductance

Insulation of different animals varies depending on climate, activity patterns, ecological distribution, habitat and thermal conditions (Bradley and Yousef 1972; Schmidt-Nielsen 1997). Hence the relationship between habitat and C is equivocal (Degen 1997). Generally, animals from arid areas tend to have higher C than species from mesic environments as high C will help with heat dissipation when T_b is above T_a . Also, C tends to be higher for diurnal arid zone mammals than nocturnal species due to the exposure of diurnal mammals to higher T_a (Lovegrove 1993; Degen 1997). Nocturnal desert animals are usually exposed to the lower T_a , often falling below 0°C in winter and thus, good insulation (i.e. low C) is desirable (Lovegrove 1993). Nevertheless, C of desert animals also varies depending on sun exposure. Animals that are often exposed to radiant heat tend to have low C to reduce the heat gain from the environment and this is typically achieved by an increase in fur thickness on sun exposed body parts (Bradley and Yousef 1972; Hill et al. 2008). On the other hand, small mammals that dwell in burrows tend to have higher C, as they are not exposed to the radiation source and high C would facilitate heat loss inside the burrows (McNab 1970; Bradley and Yousef 1972; Degen 1997).

In general, bats have C that is higher than predicted by their BM which can be related to their tropical origin (Griffin 1958), large surface area of wing membranes or a need for effective heat dissipation during flight (Speakman and Thomas 2003). Nevertheless, bats are known for

their ability to employ torpor and hibernate, and high C facilitates rapid heat loss and allows them to attain low T_b quickly during hibernation and torpor (Speakman and Thomas 2003). While high C is less favourable during active arousals, during passive rewarming from torpor it could facilitate an increase in T_b via passive heating and therefore, reduce energetic costs associated with arousals (Geiser et al. 2004).

Basal metabolic rate

Many studies suggest that desert-adapted species on average have lower BMR than their mesic counterparts, presumably due to the low primary productivity of arid regions (McNab and Morrison 1963; Bradley and Yousef 1972; Schmidt-Nielsen 1972; Withers et al. 1979; Degen 1997; Lovegrove 2003; Tieleman et al. 2003; Withers et al. 2006). In fact BMR of desert mammals on average is 40% lower than that of mesic mammals and a similar trend is observed for desert birds (Lovegrove 1993). There are several benefits from having low BMR in the desert environment. Firstly, low BMR reduces the overall energy requirements, which means less food is needed. Secondly, low BMR decreases total endogenous heat production and therefore, reduces the total heat load and may as well delay the onset of hyperthermia in animals exposed to high T_a . Thirdly, because animals with low BMR generally have low T_b and respiratory rates, they consequently have low EWL rates as less water needs to be evaporated to dissipate body heat (given that $T_b > T_a$) and less water is lost during breathing (Bradley and Yousef 1972; Lovegrove 1993; Degen 1997).

Water balance

Life is water-dependent as water is involved in many vital body functions including transport of metabolites and excretion of waste materials (Degen 1997; Hill et al. 2008). Desert animals need to retain water to maintain constant osmolarity of blood and other body fluids, and most mammals can only tolerate water losses of up to ~10% of their body weight before death occurs (Calder 1996; Schmidt-Nielsen 1997).

There are two main ways animals obtain water: preformed water, which is free water that comes with food and drinking water, and metabolic water, which is obtained during the metabolic breakdown of food molecules. Many desert mammals, in particular granivorous rodents, can gain all water they need from food they consume (Degen 1997). These animals have evolved efficient water-conserving mechanisms such as high urine concentrations, “dry” faeces and low EWL that allow them to survive on only dry seeds, their primary food source (Degen 1997). In contrast, water content for diets of insectivorous mammals, such as bats, is significantly higher. However,

so is water loss via excretion due to their protein rich diet which makes them dependent on drinking water (Degen 1997; Webb et al. 1993). This particularly becomes problematic for small tree-roosting desert bats exposed to hot summer conditions during the day, as they usually do not have access to drinking water nor food for more than 10 h in their roosts and have to rely entirely on the body fluids for evaporative heat dissipation. Therefore, to avoid dehydration, these animals need to conserve water before they have an opportunity to restore water balance.

The main revenues of water loss for animals are via cutaneous and respiratory evaporation, urine, faeces, and saliva spreading. Many small arid-adapted species have an ability to minimise water losses through all of these avenues. For example, EWL (cutaneous and respiratory), which may accounts for up to 70% of total water loss (MacMillen 1990), is substantially reduced in arid species compared to mesic species (Bradley and Yousef 1972; Schmidt-Nielsen 1972; MacMillen and Hinds 1983; Degen 1997; Lovegrove 2003; Tieleman et al. 2003; Withers et al. 2006). This, to a large extent, is achieved via a low normothermic MR and also the ability to reduce MR and T_b , i.e. to enter a state of torpor.

Generally, a reduction in respiratory water loss in mammals is achieved via a nasal counter-current heat and water exchange mechanism. This allows water to be recovered from exhaled air when it is cooled by passing over the nasal surfaces resulting in water vapour condensation, which is then recovered during inspiration (Withers 1992; Degen 1997; Schmidt-Nielsen 1997). However, the described mechanism is not unique to the arid endotherms as reduced expired air temperatures have been observed in both desert and non-desert mammals (Schmidt-Nielsen and Jackson 1964; Withers et al. 1979; Degen 1997).

A number of mammals when exposed to heat neither sweat nor pant, but instead spread saliva over vascularized body parts to increase heat loss via evaporation. Saliva spreading has been observed, for example, in rodents (Hainsworth and Stricker 1971; Yanase et al. 1991), several marsupial species (Needham et al. 1974; Hunsaker 1977; Dawson 1983) and bats (Licht and Leitner 1967; Laburn and Mitchell 1975; Welbergen et al. 2008). Water loss via salivation increases with increasing T_a above the TNZ and can account for up to 65% of total EWL at T_a 44°C in some rats (Degen 1997). However, no comparable information is available for bats.

Some arid-adapted species are known for their ability to reduce the amount of water loss in faeces and the lowest faecal water content has been reported for some heteromyid rodents. For example, when water stressed, the Great Basin pocket mouse, *Perognathus parvus*, can reduce water content of its faeces from 40 to 36% (Withers 1982). However, faecal water content to some extent also depends on availability of preformed water in consumed food (Degen 1997) and therefore, high water content can be expected in faeces of insectivorous mammals. In fact, faecal

water content measured for the mesic long-eared, *Plecotus auritus*, and Daubenton's, *Myotis daubentoni*, bats was actually 12% higher than water content in consumed food, suggesting high reliance of these bat species on drinking water (Webb et al. 1993).

The ability of the kidney to produce high urine concentration is also an important factor for conserving water especially in desert environments. In mammals, the concentrating ability of kidneys largely depends on the lengths of loops of Henle located in the medulla of the kidney (Withers 1992). This structure allows mammals to produce urine that is osmotically more concentrated than the blood plasma (hyperosmotic urine) and is an important adaptation for life on land. There is a correlation between the length of loops of Henle and habitat. It has been found that mammals inhabiting fresh water environment have only short loops of Henle, and the renal papilla, which consists mostly of long loops of Henle, is poorly developed. In contrast, in mammals from mesic habitats the renal papilla is more prominent and this structure is most developed in arid adapted mammalian species (Bradley and Yousef 1972; Withers 1992; Brooker and Withers 1994; Degen 1997; Hill et al. 2008).

The concentrating abilities of the kidney also depend on diet. Insectivorous species obtain more preformed water from their food, but in turn need to excrete more nitrogenous waste because of their high protein diet compared, for example, to granivores. Therefore, although they generally do not produce urine concentrations as high as observed in granivorous desert rodents, desert insectivores still tend to produce higher concentrated urine than species from mesic habitats (Degen 1997). For example, Mexican freetail bats, *Tadarida brasiliensis*, which are common in desert habitats, produce significantly higher urine concentrations than mesic big brown bats, *Eptesicus fuscus*, which are occasionally found in deserts (Carpenter 1969). Nevertheless, these results show that even bats endemic to deserts are not entirely independent of free water and presumably, their ability to fly to water sources (Carpenter 1969) and perhaps, the ability to employ torpor (Geiser 2004a) appear essential.

Torpor

Characteristics and importance

Torpor is characterised by controlled reductions in T_b , MR and water loss and is the most effective mechanism for energy and water conservation available to endotherms (Hock 1951; Geiser 2013). Two torpor patterns are common in endotherms: daily torpor and prolonged, multiday torpor (i.e. hibernation) (Geiser and Ruf 1995; Körtner and Geiser 2000). The main difference between these two torpor patterns is the duration of torpor bouts. Daily torpor is

characterised by short torpor bouts and usually lasts for several hours on a daily basis (Geiser and Ruf 1995; Körtner and Geiser 2000). Animals that employ this type of torpor are often called daily heterotherms. Multiday torpor bouts can last from a few days to several weeks and endotherms that are capable of such long periods of torpor are called hibernators (Geiser and Ruf 1995; Körtner and Geiser 2000). Other physiological variables such as T_b and MR during torpor are usually lower in hibernators than in daily heterotherms, but there is some overlap (Geiser and Ruf 1995).

Interestingly, it appears that low T_b s are not a prerequisite for hibernation. Dausmann et al. (2005) found that the tropical fat-tailed dwarf lemur, *Cheirogaleus medius*, in its natural hibernation site, was able to maintain uninterrupted torpor bouts for > 24 days even though T_b and T_a were often above 30°C. Such “warm” hibernation still allowed this species to achieve energy savings of up to 70% compared to the active season (Dausmann et al. 2009).

Torpor is a crucial adaptation for adverse environmental conditions that enhances survival in many species of mammals and some birds. It also appears to reduce the exposure to predators and consequently improves long-term survival (Wang 1989; Geiser and Ruf 1995; Schmid and Speakman 2000; Cryan and Wolf 2003; Geiser 2004b; Geiser and Turbill 2009; Stawski et al. 2009; Körtner and Geiser 2009; Stawski and Geiser 2010; Turbill et al. 2011; Kronfeld-Schor and Dayan 2013). Torpor is widely used especially by small mammals such as microbats, because their large surface area to volume ratio results in considerable energy turnover and water loss and requires large amounts of energy to maintain a constant high T_b , (Wang 1989; Chruszcz and Barclay 2002; Geiser 2004a; Geiser 2006; Geiser and Pavey 2007; Stawski et al. 2009; Geiser and Stawski 2011).

During the reproductive period, although torpor may slow embryonic and neonatal development (Racey 1973; Speakman 2008), a growing number of studies suggest that torpor is an important physiological strategy for energy conservation in reproductive small mammals. Torpor during reproduction has been observed in dasyurid marsupials (Geiser et al. 2005; Körtner et al. 2008), tenrecs (Stephenson and Racey 1993) and bats (Racey 1973; Racey et al. 1987; Audet and Fenton 1988; Grinevitch et al. 1995; Geiser 1996; Geiser et al. 2001; Turbill and Geiser 2006; Willis et al. 2006; Stawski 2010; Dzal and Brigham 2013; Johnson and Lacki 2013; Klug and Barclay 2013; Stawski et al. 2013). These studies suggest that in bats torpor during reproduction is used to permit development of offspring (albeit at a lower rate) despite limited food and water resources.

Torpor in deserts

Hibernation and torpor were traditionally considered as important adaptations to overcome adverse weather and food shortages in temperate to arctic climates (Lyman et al. 1982). However, recent studies showed that torpor is also widely used by animals inhabiting tropical, sub-tropical (Cossins and Barnes 1996; Bonaccorso and McNab 1997; Bartels et al. 1998; Turbill et al. 2003b; Dausmann et al. 2005; Vivier and van der Merwe 2007; Stawski and Geiser 2010; Geiser et al. 2011) and arid habitats (Geiser 2004a; Warnecke et al. 2008; Körtner and Geiser 2009; Körtner et al. 2010; Warnecke et al. 2010; Levy et al. 2011; Grimpo et al. 2013) and these findings include some arid and semi-arid zone bats (Rambaldini and Brigham 2008; Daniel et al. 2010; Bondarenko et al. 2013). Nevertheless, in comparison to temperate-zone mammals, knowledge about thermal biology and energetics of arid zone mammals is still limited and this is especially true for bats.

Torpor is likely to have a crucial function in desert habitats as T_a can be very low. Thus, a reduction in T_b and MR during torpor may help to overcome cold conditions when foraging opportunities are limited and lead to substantial energy and water conservation for animals inhabiting arid habitats (Bradley and Yousef 1972; Degen 1997; Körtner et al. 2008). Even at high T_a energy savings of torpor are substantial (Song et al. 1997; Geiser and Brigham 2000). In addition, an overall cooler body during torpor reduces rates of EWL (Bradley and Yousef 1972; Geiser 2010) and thus saving water, which could later be used for evaporative cooling during the hottest part of the day. For example, two laboratory studies on arid-adapted daily heterotherms, the stripe-faced dunnart, *Sminthopsis macroura*, and the little red kaluta, *Dasykaluta rosamondae*, showed that during torpor EWL is reduced to ~25% of normothermic values (Cooper et al. 2005; Withers and Cooper 2009). Furthermore, in two bat species that have wide distribution including deserts, EWL during torpor can be reduced by up to 90% of normothermic values (Hosken and Withers 1997; Hosken and Withers 1999).

With a few exceptions, most of the data on the thermal biology of Australian desert mammals are available for the infraclass Marsupialia, specifically small dasyurid marsupials. These species are known to employ daily torpor during winter (Geiser and Pavey 2007; Körtner and Geiser 2009; Körtner et al. 2010) and also during the reproductive period (Geiser et al. 2005; Körtner et al. 2008). Further, to minimise reliance on endothermic heat production, some species were observed basking in the sun during rewarming from torpor (i.e. passively rewarming). Such passive rewarming, together with extensive use of torpor, helps to reduce daily energy expenditure by ~50% (Geiser et al. 2004; Geiser and Pavey 2007; Warnecke et al. 2008). These

data suggest that a combination of torpor and passive rewarming is an important physiological trait of these species.

Despite the fact that insectivorous bats are common in Australian deserts, to date no studies on thermal biology and energetics of these bats have been conducted. Torpor, however, has been observed in some Australian bats with wide distribution ranges that includes the arid zone, for example, lesser long-eared bats, *Nyctophilus geoffroyi*, south-eastern long-eared bats, *Nyctophilus timoriensis*, Gould's wattled bats, *Chalinolobus gouldii*, and inland broad-nosed bats, *Scotorepens balstoni*. When studied in the mesic parts of their distribution range, these species showed low T_b and MR during torpor and the measured values were similar to those observed in other hibernators (Geiser and Ruf 1995; Hosken and Withers 1997, 1999; Geiser and Brigham 2000). Moreover, while most arid zone bats roost in trees, there is no detailed information on how Australian bats deal with extreme heat, except for some evidence that suggests substantial increases in T_b , MR, C and EWL of some bat species when exposed to T_a 40°C (Bartholomew et al. 1964; Baudinette et al. 2000). However other bats, such as flying foxes, perish when exposed to extreme heat (Welbergen et al. 2008), illustrating the high risk of hyperthermia when using exposed roosts.

Study site

All field work and laboratory experiments were conducted at Sturt National Park, New South Wales (NSW), Australia near historic Mt Wood Homestead (29°28'S, 142°14'E) located ~22 km east from Tibooburra NSW. Sturt National Park is situated ~183 m above sea level and has an arid climate with 230.3 mm of annual rainfall (mean over 127 years; Tibooburra Post Office NSW, Bureau of Meteorology, Australia). The area includes sparse, open woodlands growing along ephemeral creek lines, grasslands and open gibber and clay pans. During my research, drinking water was always available from two dams that capture flood water from a creek. More detailed description of the field site is given in individual chapters.

Study species

My thesis examines torpor, thermal biology, energetics, activity patterns and roost selection of small desert bats (BM, ~6-10g). The species investigated were the inland freetail bat, *Mormopterus* species 3 (Adams et al. 1988; family Molossidae), the little broad-nosed bat, *Scotorepens greyii* (family Vespertilionidae), and the inland broad-nosed bat, *Scotorepens*

balstoni (family Vespertilionidae). These three bat species were chosen based on the trapping success at the study site and for the purpose of ecophysiological comparison among bats from different families.

Inland freetail bat (*Mormopterus* species 3)

The inland freetail bat (*Mormopterus* species 3) is a species that was previously referred to as *Mormopterus planiceps* by Ride (1970). Later, based on genetic analyses, it was split into two species: *Mormopterus* species 3 and *Mormopterus* species 4 (Adams et al. 1988). These two species were later also distinguished by penis morphology with *Mormopterus* species 3 as a short penis form (5 mm) and *Mormopterus* species 4 as a long penis form (9 mm) (Churchill 2008). The females of these species, however, are still not distinguishable in the field. Moreover, *Mormopterus* species 4 is under consideration to be further split into two subspecies, the south-eastern freetail bat and the south-western freetail bat (Churchill 2008; Van Dyck and Strahan 2008). The distribution of both species overlaps along the semi-arid climatic zone with *Mormopterus* species 3 associated with arid and *Mormopterus* species 4 with mesic and partially semi-arid habitats. Over three years of my field work no male of the long penis form *Mormopterus* was captured at the research site and therefore, all captured *Mormopterus* bats were classified as *Mormopterus* species 3 (short penis form), and throughout my thesis I refer to this species as *Mormopterus*. At the time of the thesis revision, based on a molecular and morphological investigation, a species name was assigned for *Mormopterus* species 3 as *Mormopterus petersi* (Leche, 1884) (Reardon et al. 2014). However, for the purpose of this thesis I used *Mormopterus* species 3.

Mormopterus is a small (mean BM 9.1 g), tree-roosting, insectivorous molossid (Plate 2). It is endemic to Australia and restricted to arid and semi-arid areas south of the Tropic of Capricorn (Churchill 2008). Due to the prevailing taxonomic uncertainty, only fragmentary information on biology and ecology of this species is available. These data show that *Mormopterus* often roosts in tree hollows, cracks and fissures in trees, usually in small colonies of less than 10, but sometimes with other bats such as *S. balstoni*. It also has been observed roosting in man-made structures between roof beams, under corrugated iron roofs and in water pipes (Tidemann and Flavel 1987, data for *M. planiceps*; Churchill 2008). *Mormopterus* usually has several roosts within its home range and periodically moves between them (Churchill 2008). Preferable habitats are open woodland or shrubland in arid areas associated with areas of taller vegetation along river red gum lined water courses. *Mormopterus* is a fast but not very manoeuvrable flier (Bullen and McKenzie

2001, data for *M. planiceps*; Churchill 2008). It tends to forage in open unobstructed areas usually above the tree canopy and sometimes can land on tree trunks and the ground in pursuit of its prey (Churchill 2008).

Females give birth to a single young in November-December and volant individuals have been captured in mid-December (Churchill 2008). Generally, temperate species of Australian molossids undergo a single annual reproductive cycle with insemination occurring in early spring (August-October) and young are born in yearly summer (December-January) (Allison 1989). There are no studies on the thermal physiology of *Mormopterus* or other Australian molossids.



Plate 2. The juvenile inland freetail bat (*Mormopterus* species 3). The inserted map shows a distribution of the species (dark grey) (Churchill 2008).

Little broad-nosed bat (*Scotorepens greyii*)

The little broad-nosed bat (*Scotorepens greyii*) is endemic to Australia and the smallest of the studied species (mean BM 6.4 g) (Plate 3). It is a tree-roosting, insectivorous vespertilionid. *S. greyii* is distributed throughout northern Australia excluding the Cape York Peninsula and reaches inland areas to southern New South Wales (NSW; Churchill 2008; Lumsden et al. 2008). Little information is available on biology of this species. *S. greyii* roosts mostly in tree hollows, but has been also found in man-made structures such as fence parts and unused buildings. Colonies are small, up to 20 individuals (Churchill 2008). Its habitat includes dry grasslands, sandy deserts, riparian woodlands, open woodlands near water, *Melaleuca* and monsoon forest, shrublands and river red gum-lined water courses (Young and Ford 2000; Churchill 2008; Van Dyck and Strahan 2008). *S. greyii* is a moderately fast, agile flier and prefers foraging below the tree canopy in the open space along the vegetation edges (Bullen and McKenzie 2001; Churchill 2008). It also can be seen foraging above water, grasslands or other open habitats (Churchill 2008). This species is often captured near water (Young and Ford 2000). Males had enlarged testes from April till November and most of females were pregnant in November (Young and Ford 2000). Twin young are usually born in October-November and by December they are capable of flight (Churchill 2008). Some data suggest that *S. greyii* undergoes seasonal movements (Churchill 2008). Studies on the thermal physiology of *S. greyii* have not been previously conducted.



Plate 3. The little broad-nosed bat (*Scotorepens greyii*). The inserted map shows a distribution of the species (dark grey) (Churchill 2008).

Inland broad-nosed bats (*Scotorepens balstoni*)

The inland broad-nosed bat (*Scotorepens balstoni*) is a small (mean BM 9.3 g), tree-roosting, insectivorous vespertilionid (Plate 4). *S. balstoni* is widespread in arid and semi-arid areas, but less common than *S. greyii* and is endemic to Australia (Churchill 2008; Van Dyck and Strahan 2008). Little is known about this species. *S. balstoni* roosts in tree hollows in colonies that can reach up to 45 individuals and has been also found under roofs, metal caps of power poles and in water pipes and it sometimes shares roosts with other bats (Churchill 2008; Van Dyck and Strahan 2008). *S. balstoni* is often captured over water along river red gum-lined water courses, open woodlands, mallee, shrublands and grasslands (Lumsden and Bennett 1995; Churchill 2008). This species is a fast (but slower than *Mormopterus*) and agile flier (Bullen and McKenzie 2001; Churchill 2008). It forages below the tree canopy, between trees, along forest edges and in the open areas. The pregnancy, birth and lactation occur in October-February (Lumsden and Bennett 1995; Churchill 2008). Mating has been observed in September in the northern part of its range and twins are usual (Churchill 2008). Only one laboratory observation of the thermal physiology of *S. balstoni* has been published. It shows that *S. balstoni* (BM 7 g) are able to lower T_b to 3.2°C and their minimum torpor MR is as low as 0.044 ml O₂ g⁻¹ h⁻¹ (Geiser and Brigham 2000).



Plate 4. The inland broad-nosed bat (*Scotorepens balstoni*). The inserted map shows a distribution of the species (dark grey) (Churchill 2008).

Thesis aims

Although the insectivorous bat fauna in Australian deserts is diverse (Churchill 2008), it is not well understood how such small tree-roosting mammals can be successful in these demanding habitats. Studies on thermal physiology of some Australian bats indicate that torpor is common in bats with wide distribution ranges that includes arid zone, but nothing is known about thermal energetics of these bats specifically from arid zone areal and how they adapt their energy expenditure to the seasonal changes of climate and food availability. Therefore, I aimed to obtain detailed information on thermal physiology, torpor patterns, thermoregulatory behaviour, foraging activity and roosting ecology of desert bats under natural conditions in relation to climate and season. Because of high T_a and, consequently, elevated EWL in summer, I examined the hypothesis that desert bats will employ torpor not only during cool weather, but also when T_a is high, presumably to reduce water loss. Further, because of intensive solar radiation and pronounced daily T_a fluctuations, I tested the hypothesis that desert bats will rely heavily on passive rewarming during the arousal process to minimise energy and water expenditure. Additionally, I collected data on the thermal, metabolic and hygric physiology of desert bats under controlled conditions to examine how these physiological variables change at different T_a s.

Aims for chapter 1: Some like it cold: summer torpor by freetail bats in the Australian arid zone

Most of the published data on microbat physiological ecology are restricted to the family Vespertilionidae and other bat families have received little scientific attention. Moreover, no field studies on the thermal physiology of desert bats in the wild have been previously conducted. Therefore, the aim of this study was to provide the first quantitative data on thermal biology and torpor patterns in a desert molossid. I used temperature radiotelemetry to examine torpor use in free-ranging (*Mormopterus* species 3 (Adams et al. 1988), henceforth *Mormopterus*) during summer and tested whether and how torpor is affected by thermal conditions and food availability. In addition, I examined whether the variables of torpor differ from that in bats from mesic areas.

Aims for chapter 2: Seasonality of torpor in a desert molossid

Seasonal comparisons of thermal biology and torpor patterns are scarce, particularly in desert bats. In this chapter, I examined and compared the thermal biology of *Mormopterus* in winter (i), during low T_a and limited food availability, with summer (ii), when temperature and food

conditions were favourable and spring (iii), during the reproductive period, when fat reserves are low, but energy requirements are high.

Aims for chapter 3: Thermal biology and roosting ecology in three species of free-ranging desert bats in summer

To examine whether torpor is also common in desert bat species other than *Mormopterus* during summer, this chapter focuses on the comparison of thermal biology, torpor patterns and roost selection of *Mormopterus* and two vespertilionids the little broad-nosed bat (*Scotorepens greyii*, family Vespertilionidae) and the inland broad-nosed bat (*Scotorepens balstoni*, family Vespertilionidae). Further, I report data on the thermo-physiological response of two *Mormopterus* and one *S. greyii* exposed to extreme heat ($T_a > 40^\circ\text{C}$) in the wild.

*Aims for chapter 4: Thermal, metabolic and hygric physiology of two desert bats: *Mormopterus* species 3 and *Scotorepens greyii**

Because of the high variability of daily and seasonal thermal conditions and low primary productivity of arid habitats, desert animals would not be able to survive without adaptive physiological mechanisms for energy and water conservation. Therefore, the aim of this study was to examine physiological responses of two sympatric species of desert bats from the families Molossidae and Vespertilionidae exposed to a range of controlled temperature conditions in captivity. I obtained detailed information on changes in MR, skin temperature (T_{skin}) and EWL of *Mormopterus* and *S. greyii* during heat as well as cold exposure. Physiological variables were compared between these two bat species as well as with species from mesic habitats.

Thesis structure

The data chapters of this thesis (Chapters 1, 2, 3 and 4) are presented in a journal article format. These chapters are closely related to each other, but each focuses on a specific aspect of thermal biology of desert bats, which allows them to be considered as self-contained publications.

References

- Adams M, Reardon TR, Baverstock PR, Watts CHS (1988) Electrophoretic resolution of species boundaries in Australian Microchiroptera. IV. The Molossidae (Chiroptera). *Australian Journal of Biological Sciences* 41:315-326.
- Allison (1989) 43. Molossidae. In: Walton DW, Richardson BJ (eds) *Fauna of Australia*, vol 1B Mammalia. AGPS, Canberra, pp 1-35.
- Audet D, Fenton MB (1988) Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. *Physiological Zoology* 61:197-204.
- Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). *Journal of Comparative Physiology B* 168:233-239.
- Bartholomew GA (1982) Body temperature and energy metabolism. In: Gordon MS (ed) *Animal physiology*. 4 edn. Macmillan Publishing Co., Inc., New York, pp 333-406.
- Bartholomew GA, Leitner P, John EN (1964) Body temperature, oxygen consumption, and heart rate in three species of Australian flying foxes. *Physiological Zoology* 37:179-198.
- Baudinette RV, Churchill SK, Christian KA, Nelson JE, Hudson PJ (2000) Energy, water balance and the roost microenvironment in three Australian cave-dwelling bats (Microchiroptera). *Journal of Comparative Physiology B* 170:439-446.
- Bonaccorso FJ, McNab BK (1997) Plasticity of energetics in blossom bats (Pteropodidae): impact on distribution. *Journal of Mammalogy* 78:1073-1088.
- Bondarenko A, Körtner G, Geiser F (2013) Some like it cold: summer torpor by freetail bats in the Australian arid zone. *Journal of Comparative Physiology B* 183:1113-1122.
- Bradley SR, Deavers DR (1980) A re-examination of the relationship between thermal conductance and body weight in mammals. *Comparative Biochemistry and Physiology A* 65:465-476.
- Bradley WG, Yousef MK (1972) Small mammals in the desert. In: Yousef MK, Horvath SM, Bullard RW (eds) *Physiological adaptations: desert and mountain*. Academic Press, New York, pp 127-142.
- Brooker B, Withers P (1994) Kidney structure and renal indexes of dasyurid marsupials. *Australian Journal of Zoology* 42:163-176.
- Bullen R, McKenzie NL (2001) Bat airframe design: flight performance, stability and control in relation to foraging ecology. *Australian Journal of Zoology* 49:235-261.

- Bureau of Meteorology (2013). Extreme heat in January 2013. Special Climate Statement 43.
- Calder WAIII (1996) Size, function, and life history. Dover Publications, Inc., New York.
- Carpenter RE (1969) Structure and function of the kidney and the water balance of desert bats. *Physiological Zoology* 42:288-302.
- Chruszcz BJ, Barclay RMR (2002) Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. *Functional Ecology* 16:18-26.
- Churchill S (2008) Australian bats. 2 edn. Allen & Unwin, Crows Nest.
- Cooper CE, McAllan BM, Geiser F (2005) Effect of torpor on the water economy of an arid-zone marsupial, the stripe-faced dunnart (*Sminthopsis macroura*). *Journal of Comparative Physiology B* 175:323-328.
- Cossins AR, Barnes B (1996) Hibernation - southern discomfort. *Nature* 382:582-583.
- Cryan PM, Wolf BO (2003) Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *Journal of Experimental Biology* 206:3381-3390.
- Daniel S, Korine C, Pinshow B (2010) The use of torpor in reproductive female Hemprich's long-eared bats (*Otonycteris hemprichii*). *Physiological and Biochemical Zoology* 83:142-148.
- Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. *Journal of Comparative Physiology B* 175:147-155.
- Dausmann KH, Glos J, Heldmaier G (2009) Energetics of tropical hibernation. *Journal of Comparative Physiology B* 179:345-357.
- Dawson TJ (1983) Monotremes and Marsupials: the other mammals, vol 150. Studies in Biology. Edward Arnold Limited, London.
- Degen AA (1997) Ecophysiology of small desert mammals. Springer-Verlag, Berlin.
- Dzal YA, Brigham RM (2013) The tradeoff between torpor use and reproduction in little brown bats (*Myotis lucifugus*). *Journal of Comparative Physiology B* 183:279-288.
- French A (1976) Selection of high temperatures for hibernation by the pocket mouse, *Perognathus longimembris*: ecological advantages and energetic consequences. *Ecology* 57:185-191.
- Geiser F (1996) Torpor in reproductive endotherms. In: Geiser F, Hulbert AJ, Nicol SC (eds) *Adaptation to the cold*. 10th International Hibernation Symposium. University of New England Press, Armidale, pp 81-86.
- Geiser F (2001) Hibernation: endotherms. In: eLS. John Wiley & Sons, Ltd, Chichester, pp 1-11.
- Geiser F (2004a) The role of torpor in the life of Australian arid zone mammals. *Australian Mammalogy* 26:125-134.

- Geiser F (2004b) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology* 66:239-274.
- Geiser F (2006) Energetics, thermal biology, and torpor in Australian bats. In: Zubaid A, McCracken GF, Kunz TH (eds) *Functional and evolutionary ecology of bats*. Oxford University Press, New York, pp 5-22.
- Geiser F (2010) Aestivation in mammals and birds. In: Navas CA, Carvalho JE (eds) *Aestivation. Molecular and physiological aspects*. Springer-Verlag, Heidelberg, pp 95-111.
- Geiser F (2013) Hibernation. *Current Biology* 23:R188-R193.
- Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). *Journal of Comparative Physiology B* 170:153-162.
- Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) *Life in the cold. 12th International Hibernation Symposium*. University of Alaska Fairbanks, Alaska, pp 45-56.
- Geiser F, Körtner G, Law BS (2001) Daily torpor in a pregnant common blossom-bat (*Syconycteris australis*: Megachiroptera). *Australian Mammalogy* 23:53-56.
- Geiser F, McAllan BM, Brigham R (2005) Daily torpor in a pregnant dunnart (*Sminthopsis macroura* Dasyuridae: Marsupialia). *Mammalian Biology* 70:117-121.
- Geiser F, Pavey CR (2007) Basking and torpor in a rock-dwelling desert marsupial: survival strategies in a resource-poor environment. *Journal of Comparative Physiology B* 177:885-892.
- Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* 68:935-966.
- Geiser F, Stawski C (2011) Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integrative and Comparative Biology* 51:337-348.
- Geiser F, Stawski C, Bondarenco A, Pavey CR (2011) Torpor and activity in a free-ranging tropical bat: implications for the distribution and conservation of mammals? *Naturwissenschaften* 98:447-452.
- Geiser F, Turbill C (2009) Hibernation and daily torpor minimize mammalian extinctions. *Naturwissenschaften* 96:1235-1240.
- Griffin DR (1958) "Listening in the dark". Yale University Press, New Haven, Connecticut.
- Grimpo K, Legler K, Heldmaier G, Exner C (2013) That's hot: golden spiny mice display torpor even at high ambient temperatures. *Journal of Comparative Physiology B* 183:567-581.

- Grinevitch L, Holroyd SL, Barclay RMR (1995) Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. *Journal of Zoology* 235:301-309.
- Hainsworth FR (1995) Optimal body temperatures with shuttling: desert antelope ground squirrels. *Animal Behaviour* 49:107-116.
- Hainsworth FR, Stricker EM (1971) Relationship between body temperature and salivary secretion by rats in the heat. *Journal de Physiologie* 63:257-259.
- Hill RW, Wyse GA, Anderson M (2008) *Animal physiology*. 2 edn. Sinauer Associates, Sunderland.
- Hock RJ (1951) The metabolic rates and body temperatures of bats. *Biological Bulletin* 101:289-299.
- Hosken DJ, Withers PC (1997) Temperature regulation and metabolism of an Australian bat, *Chalinolobus gouldii* (Chiroptera: Vespertilionidae) when euthermic and torpid. *Journal of Comparative Physiology B* 167:71-80.
- Hosken DJ, Withers PC (1999) Metabolic physiology of euthermic and torpid lesser long-eared bats, *Nyctophilus geoffroyi* (Chiroptera: Vespertilionidae). *Journal of Mammalogy* 80:42-52.
- Hunsaker D (1977) Ecology of New World marsupials. In: Hunsaker D (ed) *The biology of marsupials*. Academic Press, New York, pp 95-156.
- Johnson C (2006) *Australia's mammal extinctions*. Cambridge University Press, New York.
- Johnson JS, Lacki MJ (2013) Summer heterothermy in Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) roosting in tree cavities in bottomland hardwood forests. *Journal of Comparative Physiology B* 183:709-721.
- Kinlaw A (1999) A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* 41:127-145.
- Klug BJ, Barclay RMR (2013) Thermoregulation during reproduction in the solitary, foliage-roosting hoary bat (*Lasiurus cinereus*). *Journal of Mammalogy* 94:477-487.
- Köppen W (1900) Versuch einer klassifikation der klimate, vorzugsweise nach ihren beziehungen zur pflanzenwelt. *Geographische Zeitschrift* 6:593-611, 657-679.
- Körtner G, Geiser F (2000) The temporal organization of daily torpor and hibernation: Circadian and circannual rhythms. *Chronobiology International* 17:103-128.
- Körtner G, Geiser F (2009) The key to winter survival: daily torpor in a small arid-zone marsupial. *Naturwissenschaften* 96:525-530.

- Körtner G, Pavey CR, Geiser F (2008) Thermal biology, torpor, and activity in free-living mulgaras in arid zone Australia during the winter reproductive season. *Physiological and Biochemical Zoology* 81:442-451.
- Körtner G, Rojas AD, Geiser F (2010) Thermal biology, torpor use and activity patterns of a small diurnal marsupial from a tropical desert: sexual differences. *Journal of Comparative Physiology B* 180:869-876.
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259-263.
- Kronfeld-Schor N, Dayan T (2013) Thermal ecology, environments, communities, and global change: energy intake and expenditure in endotherms. *The Annual Review of Ecology, Evolution, and Systematics* 44:461-480.
- Laburn HP, Mitchell D (1975) Evaporative cooling as a thermoregulatory mechanism in the fruit bat, *Rousettus aegyptiacus*. *Physiological Zoology* 48:195-202.
- Levy O, Dayan T, Kronfeld-Schor N (2011) Adaptive thermoregulation in golden spiny mice: the influence of season and food availability on body temperature. *Physiological and Biochemical Zoology* 84:175-184.
- Licht P, Leitner P (1967) Physiological responses to high environmental temperatures in three species of microchiropteran bats. *Comparative Biochemistry and Physiology* 22:371-387.
- Lovegrove B (1993) *The living deserts of South Africa*. Fernwood Press, Vlaeberg.
- Lovegrove BG (2003) The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B* 173:87-112.
- Lumsden L, McKenzie N, Pennay M (2008) *Scotorepens greyii*. IUCN Red List of Threatened Species. www.iucnredlist.org. Accessed 18 December 2013.
- Lumsden LF, Bennett AF (1995) Bats of a semi-arid environment in south-eastern Australia: biogeography, ecology and conservation. *Wildlife Research* 22:217-240.
- Lyman CP, Willis JS, Malan A, Wang LCH (1982) *Hibernation and torpor in mammals and birds*. Academic Press, New York.
- MacMillen RE (1990) Water economy of granivorous birds: a predictive model. *Condor* 92:379-392.
- MacMillen RE, Hinds DS (1983) Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology* 64:152-164.
- McNab BK (1970) Body weight and the energetics of temperature regulation. *Journal of Experimental Biology* 53:329-348.

- McNab BK, Morrison P (1963) Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecological Monographs* 33:63-82.
- Morrison P (1966) Insulative flexibility in the guanaco. *Journal of Mammalogy* 47:18-23.
- Morton SR (1979) Diversity of desert-dwelling mammals: a comparison of Australia and North America. *Journal of Mammalogy* 60:253-264.
- Murray BR, Dickman CR (1994) Granivory and microhabitat use in Australian desert rodents: Are seeds important? *Oecologia* 99:216-225.
- National Climate Centre (2011). An extremely wet December leads to widespread flooding across eastern Australia. *Special Climate Statement* 24.
- Needham AD, Dawson TJ, Hales JRS (1974) Forelimb blood flow and saliva spreading in the thermoregulation of the red kangaroo, *Megaleia rufa*. *Comparative Biochemistry and Physiology A* 49:555-565.
- Racey PA (1973) Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility* 19:175-189.
- Racey PA, Speakman JR, Swift SM (1987) Reproductive adaptations of heterothermic bats at the northern borders of their distribution. *South African Journal of Science* 83:635-638.
- Rambaldini DA, Brigham RM (2008) Torpor use by free-ranging pallid bats (*Antrozous pallidus*) at the northern extent of their range. *Journal of Mammalogy* 89:933-941.
- Reardon TB, McKenzie NL, Cooper SJB, Appleton B, Carthew S, Adams M (2014) A molecular and morphological investigation of species boundaries and phylogenetic relationships in Australian free-tailed bats *Mormopterus* (Chiroptera : Molossidae). *Australian Journal of Zoology* 62:109-136.
- Ride WDL (1970) A guide to the native mammals of Australia. Oxford University Press, Melbourne.
- Schmid J, Speakman JR (2000) Daily energy expenditure of the grey mouse lemur (*Microcebus murinus*): a small primate that uses torpor. *Journal of Comparative Physiology B* 170:633-641.
- Schmidt-Nielsen K (1972) Recent advances in the comparative physiology of desert animals. *Symposia of the Zoological Society of London* 31:371-382.
- Schmidt-Nielsen K (1979) Desert animals: physiological problems of heat and water. Dover Publications, New York.
- Schmidt-Nielsen K (1997) Animal physiology. Cambridge University Press, Cambridge.
- Schmidt-Nielsen K, Jackson DC (1964) Countercurrent heat exchange in the respiratory passages. *Science* 144:567.

- Scholander PF, Walters V, Hock R, Irving L (1950) Body insulation of some arctic and tropical mammals and birds. *Biological Bulletin* 99:225-236.
- Smyth AK, James CD (2004) Characteristics of Australia's rangelands and key design issues for monitoring biodiversity. *Austral Ecology* 29:3-15.
- Song X, Körtner G, Geiser F (1997) Thermal relations of metabolic rate reduction in a hibernating marsupial. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology* 273:R2097-R2104.
- Speakman JR (2008) The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B* 363:375-398.
- Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 430-490.
- Stawski C (2010) Torpor during the reproductive season in a free-ranging subtropical bat, *Nyctophilus bifax*. *Journal of Thermal Biology* 35:245-249.
- Stawski C, Geiser F (2010) Fat and fed: frequent use of summer torpor in a subtropical bat. *Naturwissenschaften* 97:29-35.
- Stawski C, Turbill C, Geiser F (2009) Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *Journal of Comparative Physiology B* 179:433-441.
- Stawski C, Willis CKR, Geiser F (2013) The importance of temporal heterothermy in bats. *Journal of Zoology*:In press.
- Stephenson PJ, Racey PA (1993) Reproductive energetics of the Tenrecidae (Mammalia: Insectivora). II. The shrew-tenrecs, *Microgale* spp. *Physiological Zoology* 66:664-685.
- Taylor J (2002) Population futures in the Australian desert, 2001–2016. Centre for Aboriginal Economic Policy Research, Discussion Paper 231:1-24.
- Taylor RJ, O'Neill MG (1988) Summer activity patterns of insectivorous bats and their prey in Tasmania. *Australian Wildlife Research* 15:533-539.
- Tidemann CR, Flavel SC (1987) Factors affecting choice of diurnal roost site by tree-hole bats (Microchiroptera) in south-eastern Australia. *Australian Wildlife Research* 14:459-473.
- Tieleman BI, Williams JB, Bloomer P (2003) Adaptation of metabolism and evaporative water loss along an aridity gradient. *Proceedings of the Royal Society B* 270:207-214.
- Trewin B (2006a) Climatic aspects of Australia's deserts. In: Trewin D (ed) 2006 Year book Australia, vol 88. Australian Bureau of Statistics, Canberra, pp 1-10.
- Trewin D (2006b) 2006 Year book Australia, vol 88. Australian Bureau of Statistics, Canberra.
- Turbill C (2008) Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. *Journal of Zoology* 276:285-290.

- Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B* 278:3355-3363.
- Turbill C, Geiser F (2006) Thermal physiology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*. *Journal of Comparative Physiology B* 176:165-172.
- Turbill C, Körtner G, Geiser F (2003a) Natural use of heterothermy by a small, tree-roosting bat during summer. *Physiological and Biochemical Zoology* 76:868-876.
- Turbill C, Law BS, Geiser F (2003b) Summer torpor in a free-ranging bat from subtropical Australia. *Journal of Thermal Biology* 28:223-226.
- Van Dyck S, Strahan R (2008) *The mammals of Australia*. 3 edn. New Holland Publishers, Sydney.
- Vivier L, van der Merwe M (2007) The incidence of torpor in winter and summer in the Angolan free-tailed bat, *Mops condylurus* (Microchiroptera: Molossidae), in a subtropical environment, Mpumalanga, South Africa. *African Zoology* 42:50-58.
- Walsberg GE (2000) Small mammals in hot deserts: some generalizations revisited. *BioScience* 50:109-120.
- Wang LCH (1989) Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In: Wang LCH (ed) *Advances in comparative and environmental physiology, animal adaptation to cold*, vol 4. Springer-Verlag, Berlin, pp 361-401.
- Warnecke L, Cooper CE, Geiser F, Withers PC (2010) Environmental physiology of a small marsupial inhabiting arid floodplains. *Comparative Biochemistry and Physiology A* 157:73-78.
- Warnecke L, Turner JM, Geiser F (2008) Torpor and basking in a small arid zone marsupial. *Naturwissenschaften* 95:73-78.
- Webb PI, Speakman JR, Racey PA (1993) Defecation, apparent absorption efficiency, and the importance of water obtained in the food for water balance in captive brown long-eared (*Plecotus auritus*) and Daubenton's (*Myotis daubentoni*) bats. *Journal of Zoology* 230:619-628.
- Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B* 275:419-425.
- Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* 93:80-83.

- Withers PC (1982) Effect of diet and assimilation efficiency on water balance for two desert rodents. *Journal of Arid Environments* 5:375-384.
- Withers PC (1992) *Comparative animal physiology*. Saunders College Publishing, Philadelphia, Pennsylvania.
- Withers PC, Cooper CE (2009) Thermal, metabolic, and hygric physiology of the little red kaluta, *Dasykaluta rosamondae* (Dasyuromorphia: Dasyuridae). *Journal of Mammalogy* 90:752-760.
- Withers PC, Cooper CE, Larcombe AN (2006) Environmental correlates of physiological variables in marsupials. *Physiological and Biochemical Zoology* 79:437-453.
- Withers PC, Lee AK, Martin RW (1979) Metabolism, respiration and evaporative water loss in the Australian hopping-mouse *Notomys alexis* (Rodentia: Muridae). *Australian Journal of Zoology* 27:195-204.
- Yanase M, Kanosue K, Yasuda H, Tanaka H (1991) Salivary secretion and grooming behaviour during heat exposure in freely moving rats. *Journal of Physiology* 432:585-592.
- Young RA, Ford GI (2000) Bat fauna of a semi-arid environment in central western Queensland, Australia. *Wildlife Research* 27:203-215.

Chapter 1

Some like it cold: summer torpor by freetail bats in the Australian arid zone

This chapter has been published:

Bondarenco A, Körtner G, Geiser F (2013) Some like it cold: summer torpor by freetail bats in the Australian arid zone. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* 183:1113-1122.

©Springer-Verlag Berlin Heidelberg 2013. Includes five figures.

Reprint with kind permission of Springer Science+Business Media.

Contribution of co-authors

Gerhard Körtner and Fritz Geiser provided field assistance and project supervision. Fritz Geiser provided field equipment. Drafts of the manuscripts were commented on by both of the co-authors.

Media release

The media release for this chapter, entitled “Torpid secret of arid-zone bat success” by Anna Salleh, was published on the ABC Science Online website and can be accessed via the following link: <http://www.abc.net.au/science/articles/2013/09/30/3856087.htm>.

Chapter 2

Seasonality of torpor in a desert molossid

Abstract

Pronounced daily and seasonal fluctuations in ambient temperature, food availability and unpredictable weather patterns require adaptations in thermoregulatory physiology and behaviour of endotherms inhabiting arid regions. I present temperature-telemetry data on thermal physiology, thermoregulatory behaviour and roost selection for a desert molossid, *Mormopterus* species 3 (~9 g), at Sturt National Park over winter, spring and summer (2010-13). Bats used torpor during all seasons, but torpor patterns were different. In winter *Mormopterus* entered torpor on 100% of all bat-days, 77.3% in spring and 59.5% in summer and the mean torpor bout duration (TBD) was ~28 h in winter and ~6 h in both spring (reproductive female bats) and summer. *Mormopterus* entered multiday torpor bouts lasting up to 7.7 days in winter and 1.6 days in summer, but not in spring. However, under similar thermal conditions TBD was ~40% longer in summer than in winter which, in addition to the lower mean maximum rates of active rewarming observed in summer, could indicate seasonal physiological acclimation. Often, in addition to a long main torpor bout, *Mormopterus* employed one or two short auxiliary bouts, which may represent an important part of the energy saving strategy used by this species. Bats aroused from torpor via passive and partial passive heating on ~70% of all arousals in all seasons. No substantial seasonal changes in roost selection were found and the predominant roost type was a dead tree trunk with multiple cracks and holes. My study provides the first seasonal comparison of thermal biology of an Australian arid zone bat in the wild. It appears that extensive torpor use, passive rewarming and physiological acclimation are important mechanisms for seasonal adjustments of energy and water expenditure in this desert bat.

Chapter 3

Thermal biology and roosting ecology in three species of free-ranging desert bats in summer

A part of this chapter (*Heat exposure*) has been published:

Bondarenco A, Körtner G, Geiser F (2014) Hot bats: extreme thermal tolerance in a desert heat wave. *Naturwissenschaften*. doi: 10.1007/s00114-014-1202-2

©Springer-Verlag Berlin Heidelberg 2014. Includes three figures: Figure 1, 6 and 7.

Reprint with kind permission of Springer Science+Business Media.

Contribution of co-authors

Gerhard Körtner and Fritz Geiser provided project supervision. Fritz Geiser provided field equipment. Drafts of the manuscripts were commented on by both of the co-authors.

Chapter 4

Thermal, metabolic and hygric physiology of two desert bats:

Mormopterus species 3 and *Scotorepens greyii*

Abstract

Little is known about thermal energetics and heat tolerance of desert mammals, particularly bats and to date no such studies have been conducted in Australia. Therefore, I studied torpor use, thermal and hygric physiology of two desert bats, *Mormopterus* species 3 (body mass, BM, 8 g; n = 9; henceforth *Mormopterus*) and *Scotorepens greyii* (BM 6 g; n = 11; henceforth *Scotorepens*) in a field laboratory at Sturt National Park during summer. I used flow-through respirometry to quantify metabolic rates (MR), skin temperatures (T_{skin}), evaporative water loss (EWL) and thermal conductance of normothermic and torpid bats over air temperatures (T_a) from 5 to 42°C. The basal metabolic rate (BMR) of normothermic bats was $1.03 \pm 0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in *Mormopterus* and $1.15 \pm 0.04 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in *Scotorepens*. These BMR were only ~60% of values predicted by an allometric equation for bats and ~10-57% lower than BMR for temperate, subtropical and tropical bats. The standard wet thermal conductance (C_{wet}) of normothermic individuals below the thermo-neutral zone (TNZ) was $0.422 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ in *Mormopterus* and $0.430 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ in *Scotorepens*. All bats entered torpor on average 1.4 h after they were placed in the metabolic chamber at T_a 5-30°C. Torpor significantly reduced MR and EWL and their minimum values were only 2.7% and 10.7% of that of normothermic bats in the TNZ (*Mormopterus*) and 3.5% and 15.4% (*Scotorepens*). The minimum torpor MR (T_a ~30-36°C) was $0.028 \pm 0.007 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in *Mormopterus* and $0.040 \pm 0.015 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in *Scotorepens* and their T_{skin} fell to ~6°C. MR and EWL during torpor increased exponentially with T_a , suggesting that physical temperature effects are important in their regulation. However, the ability of both species to reduce normothermic MR by up to 45% below BMR within the TNZ in addition to the generally high Q_{10} values (> 3), suggest that metabolic inhibition was also involved in lowering MR. During heat exposure ($T_a > 40^\circ\text{C}$) MR of *Mormopterus* and *Scotorepens* was ~130% of BMR reflecting increased evaporative cooling. Both species were able to tolerate T_a s up to 42°C without visible signs of stress. The point of relative water economy was better for *Mormopterus* (12.7°C) than *Scotorepens* (7.0°C), but water balance capabilities of both species exceeded those of tropical

cave-dwelling bats. My study provides new data on thermal energetics and hygric biology of two desert bats. It demonstrates that *Mormopterus* and *Scotorepens* are well adapted to low and high T_a s, and that deep torpor bouts, low BMR, metabolic inhibition and heat tolerance appear to be adaptations of these species to the aridity of their environment.

Conclusions

The main focus of my PhD thesis was on examining the ecological physiology and torpor use of three insectivorous, tree-roosting desert bats, *Mormopterus* species 3, *Scotorepens greyii* and *Scotorepens balstoni*. My work has generated novel data on the thermal physiology, torpor patterns, thermoregulatory behaviour, foraging activity and roosting ecology of these desert bats in the wild in relation to climate and season. In addition, I gathered new information on the thermal, metabolic and hygric physiology of captive *Mormopterus* and *S. greyii* under different thermal conditions. The results of my project contributed to a better understanding of how small insectivorous bats are physiologically adapted to the constraints of their desert environment and helped to unveil reasons of their success in the arid zone.

My study provides the first observation of thermal biology, activity and torpor patterns of an arid zone molossid during summer (Chapter 1). As it was hypothesised, despite high T_a s and abundant food, *Mormopterus* employed torpor regularly in summer and even entered prolonged torpor (> 39 h) during cool summer weather. The data also showed that torpor use and activity were affected by T_a . However, under the same thermal conditions, *Mormopterus* remained torpid almost 2-fold longer compared to bats from mesic environments, which could be an acclimation to prevailing climatic conditions in the desert.

In winter (Chapter 2), *Mormopterus* did not migrate from their desert habitat, but instead employed daily and multiday torpor bouts lasting up to 7 days. My study has provided clear evidence that *Mormopterus*, under winter conditions, behaved like a hibernator. However, when compared to the six months uninterrupted hibernation in caves and burrows typical for many hibernators, *Mormopterus* often foraged after arousals. These data suggest that the combination of short torpor, multiday torpor and regular foraging allows this species to overcome the coldest period of the year. Interestingly, my data indicate that under similar thermal conditions TBD was ~40% longer in summer than in winter and this, in addition to the lower mean maximum rates of active rewarming from torpor in summer, suggests that seasonal changes in torpor patterns of *Mormopterus* can be caused by not only temperature effects, but also physiological acclimation. Because water is often a concern in desert environments, especially for tree roosting bats during summer, it is likely that longer torpor bouts will provide additional water and energy savings for *Mormopterus* during the hottest part of the year.

During the spring reproductive period (Chapter 2), despite the fact that torpor can slow embryonic development, pregnant *Mormopterus* employed torpor often on a daily basis and were

able to enter prolonged torpor (> 12 h), demonstrating its importance for this species even during gestation. Torpor patterns during gestation were similar to those observed in non-reproductive bats in summer, suggesting that the reproductive conditions has little effect on torpor patterns presumably, because energetic benefits of torpor still outweigh possible risks of lengthening gestation.

In addition to energy saving achieved by torpor *per se* in all seasons, *Mormopterus* often rewarmed from torpor via passive heating in summer, winter and spring (40-73% of all arousals) (Chapter 1 and 2), supporting my hypothesis. Such entirely passive rewarming has been observed for the first time in bats. Clearly torpor and passive rewarming are main physiological mechanisms of energy and water conservation that allow *Mormopterus* to cope with challenging conditions of the arid climate throughout the year.

My study has demonstrated that torpor is also common in other desert bats such as *S. greyii* and *S. balstoni* (Chapter 3). All three species spent similar time torpid per day (~7 h), but rewarming patterns differed. *S. greyii* and *S. balstoni* used passive rewarming ~35% less often than *Mormopterus* which presumably, can be explained by interspecific variations in roost selection (Chapter 2 and 3). Although most bats selected a similar roost type, which was a dead, hollow tree trunk with multiple holes and cracks, *Mormopterus* often roosted in open areas high above the ground, whereas *S. greyii* and *S. balstoni* were found roosting in more cluttered habitats and close to the ground. Selecting high isolated roost sites that are exposed to solar radiation and higher wind speeds could facilitate extensive use of passive rewarming in the morning and help to dissipate excess heat by increased convective cooling during the hottest part of the day. These roosting habits may allow *Mormopterus* to better manage its energy and water resources on the daily basis than *S. greyii* and *S. balstoni* (Chapter 3).

However, despite the energetic benefits sun-exposed roosts can provide on most days, they actually can be dangerous for bats in extreme heat. My observations of T_{skin} fluctuations of *Mormopterus* and *S. greyii* during the heat wave in January 2013 have provided the first insight into a thermo-physiological response of desert bats to extreme heat in the wild (Chapter 3). These data demonstrate that slender tree trunks provide significantly less insulation from extreme heat than larger ones and therefore, appropriate roost selection can be a key factor for bats survival under severe heat stress conditions. Both species were able to endure a substantially elevated T_{skin} and T_{b} and these values were above the measured lethal T_{b} for most placental mammals (42-44°C), indicating that these desert bats are well adapted to deal with extreme heat.

Available data on desert-adapted species demonstrate that low BMR is common among small arid mammals. My study showed that BMR of *Mormopterus* and *S. greyii* was ~60% lower

than BMR predicted by an allometric equation for bats and 10-57% lower than BMR in mesic bat species of similar size (Chapter 4). Further, I found that during torpor, both species were able to reduce MR and T_b to the minimum values similar to other hibernating endotherms. In addition, torpor substantially reduced EWL over a temperature range of 5-30°C, demonstrating that torpor is not only efficient mechanism of energy, but also water conservation in these desert bats.

Interestingly, Q_{10} values calculated for normothermic and torpid *Mormopterus* and *S. greyii* were all above those characteristic for temperature effects on MR (Chapter 4). Both bats also employed torpor at the lower end of the TNZ and even were able to reduce their MR to 74% of BMR values at T_a 35°C, suggesting that metabolic inhibition, in addition to temperature effects, plays an important role in down-regulating MR in these desert bats. Further, captive *Mormopterus* and *S. greyii* showed a high heat tolerance and were able to withstand T_{as} up to 42°C (maximum T_a tested) without visible signs of stress, which was achieved via substantial increases in evaporative cooling and adjustments in thermal conductance. The water regulatory efficiency (T_a at MWP = EWL) was better in *Mormopterus* (12.7°C) than in *S. greyii* (7.0°C), but both species had a more favourable water balance than tropical cave-dwelling bats (Chapter 4).

Overall, the results of my study have provided substantial new knowledge about the thermal biology and energetics of free-ranging and captive desert bats. This study demonstrates that torpor and passive rewarming are two main mechanisms for energy and water conservation employed by desert bats in the wild. These, in addition to low BMR, low EWL, metabolic inhibition and high heat tolerance could be key physiological adaptations of bats to the constraints of their arid environment. As thermal physiology governs selection of roosts and habitats, this knowledge will help to understand what habitats are of the primary importance for arid zone bats, provide a stronger scientific basis for sustainable planning and protection and therefore, can be used to promote bat conservation.

Appendices

Appendix 1. List of T_a s cited in the text of Chapter 4 and their actual corresponding values \pm SD measured during each experiment.

T_a (°C) cited in the text	Actual values, T_a (°C) \pm SD	
	<i>Mormopterus</i> species 3	<i>Scotorepens greyii</i>
5 (torpor)	4.8 \pm 0.2	4.9 \pm 0.3
5 (normothermia)	5.4 \pm 0.8	5.5 \pm 0.4
10 (torpor)	9.8 \pm 0.4	9.9 \pm 0.1
15 (torpor)	15.1 \pm 0.1	15.0 \pm 0.1
15 (normothermia)	15.1 \pm 0.1	15.1 \pm 0.1
20 (torpor)	19.6 \pm 0.3	19.9 \pm 0.04
20 (normothermia)	19.8 \pm 0.3	-
25 (torpor)	25.0 \pm 0.1	25.0 \pm 0.04
25 (normothermia)	25.1 \pm 0.1	25.0 \pm 0.1
30 (torpor)	30.1 \pm 0.3	29.7 \pm 0.2
30 (BMR)	30.1 \pm 0.2	30.0 \pm 0.4
35 (BMR)	35.6 \pm 1.2	34.9 \pm 0.2
35 (hypometabolism)	35.1 \pm 0.2	35.0 \pm 0.1
40	40.0 \pm 0.1	40.0 \pm 0.1
41	-	41.0 \pm 0.2
42	41.9 \pm 0.2	42.0 \pm 0.02