

Chapter 1

General introduction and aims

Biology and ecology of bats

After rodents, chiropterans, commonly referred to as bats, contain the largest number of species in a mammal group and are the only mammals capable of true flight (Fenton 1983; Ransome 1990; Merritt 2010). Chiropterans encompass a size range from approximately 1.5 g up to about 1.5 kg, however most species weigh well under 25 g (Simmons and Conway 2003). In fact, Kitti's hog-nosed bat (*Craseonycteris thonglongyai*) at 1.5 g is one of the smallest mammals alive today.

By invading the air, a whole new habitat, new life histories and new diets became available to bats. To add to this diversity a variety of different types of wing morphologies are found within the Chiroptera and these allow different flying capabilities, such as slow but easily manoeuvrable flight or fast flight over long distances (Ransome 1990). These varying flying modes also led to the diversification of ecological niches that chiropterans are able to occupy. Along with their flying abilities most bat species are able to use echolocation to detect prey and obstacles (Fenton 1983; Ransome 1990). Ultrasound may also be used for other needs, such as communication (Fenton 1983). Along with invading the air and therefore many new ecological habitats, bats are also specifically adapted to activity during the night.

Feeding adaptations

The nocturnal behaviour of bats may have evolved because of the presence of diurnal predators that forced bats to forage at night, competition over resources and to avoid daytime heat (Speakman 1995; Jones and Rydell 2003). Therefore, they have different

food sources available to them in comparison to animals that feed largely during the day and as many other animals, especially birds, are diurnal they do not have many competitors for the same food sources. Due to their unique capabilities bats have a wide variety of diets and their food sources range from pollen, nectar, blood, fish, frogs, small mammals and many more (Fenton 1983). However, more than half of all bat species feed on insects and insectivorous species need to consume about 30% or more of their body mass on nights they are active (Jones and Rydell 2003). Insectivorous bats employ a variety of foraging strategies and consume a variety of prey species (Simmons and Conway 2003). These foraging strategies, differences in wing morphologies and echolocation frequencies have largely co-evolved together with their prey. For example, some bat species specialise on specific moths that can hear the calls made by other bats, but not by individuals of these specialised species (Pavey and Burwell 1998). For bats from all types of dietary categories food sources can vary nightly and seasonally and therefore bats have different mechanisms to cope with food shortages. For example, some bat species will migrate to a different location to avoid food shortages whereas others use mechanisms to decrease energy consumption (Fenton 1983).

Reproduction

As in many small mammals, birth and lactation in bats generally occurs during early spring to take advantage of favourable weather and feeding conditions. This is most likely because in bats lactation is energetically more expensive than pregnancy (Neuweiler 2000). While the timing of birth and lactation is similar in most species of bats pregnancy differs, such that the time when development of the embryo commences after copulation varies. Many bat species will mate during autumn before winter, however, gestation length is generally much shorter than the winter period and therefore bats need to compensate for

this to ensure that their young are born in spring. One common approach to ensure this is that sperm are stored until spring when the egg is then fertilised and gestation begins (Racey 1982; Fenton 1983; Neuweiler 2000). Another approach is that fertilisation occurs immediately after mating, but the embryo does not implant and begin to develop until spring (Wimsatt 1960; Racey 1982; Fenton 1983; Neuweiler 2000). Additionally, a developing embryo can be halted if there is inclement weather and development can resume once conditions improve. Therefore, climate has a significant influence on the development of the embryo in bats, such that when feeding and weather are both favourable development will be faster and if conditions are unfavourable development can be paused (Ransome 1990).

Life history

Many small mammals live only for short periods, usually about a year or two. In contrast, despite their small size bats are extremely long-lived. For example, little brown bats (*Myotis lucifugus*) are known to have lived for at least 30 years (Tuttle and Stevenson 1982; Fenton 1983; Barclay and Harder 2003). The ability to fly and also their nocturnal lifestyle contribute to the ability of bats to avoid many predators (Barclay and Harder 2003), with a few exceptions such as the possibility of being prey to owls while they are foraging. It has been shown in other animals that foraging generally increases the risk of an individual being preyed upon (Abrahams and Dill 1989; Brigham et al. 2000).

Therefore, if bats are well concealed while torpid they will be protected from potential predators in comparison to while they are foraging (Wilkinson and South 2002; Sendor and Simon 2003). Additionally, because many bat species spend a large portion of their life torpid, this may also contribute to longevity due to many degrading processes being slowed during torpor, such as oxidative damage (Wilkinson and South 2002; Barclay and

Harder 2003). There are many other factors that may also contribute to longevity in bats, such as features of the mitochondrial genome that possibly prevent oxidative damage to mitochondrial DNA (Munshi-South and Wilkinson 2010). Further, it has been shown that out of all the recent mammalian extinctions only a minute percentage of these species were able to undergo torpor, which further lends support to the theory that torpor may enhance long-term survival and increase longevity (Geiser and Turbill 2009). Regardless, there are still many threats to the survival of bat species, such as man-made toxins and disease. However, one of the largest contributors to the decline of bat populations is the destruction of roosting sites, such as clearing large areas of habitats that remove roosting trees or blocking off caves due to mining practices (Fenton 1983; Pavey 1998; Racey and Entwistle 2003).

Bat populations in the north-eastern part of the US have been rapidly declining since late 2006 due to a disease caused by a fungus known as white-nose syndrome (Blehert et al. 2008; Boyles and Willis 2010; Reichard and Kunz 2009). This fungus has been shown to be phylogenetically related to *Geomyces* spp. (Blehert et al. 2008). While much research has been undertaken since knowledge of this fungus was made known it is still poorly understood and it is uncertain as to why bat populations are declining so rapidly. One theory is that the fungus is forcing bats to arouse too often during the winter hibernating period and therefore the lack of energetic resources is causing death due to starvation (Boyles and Willis 2010). It is known that the fungus is limited to hibernating species as it cannot survive at ambient temperatures (T_a) above 20°C (Blehert et al. 2008) and hibernating bats do appear to have higher survival rates at T_a s above 20°C (Boyles and Willis 2010). This knowledge and other research being undertaken may help to slow the decline of bat populations due to this disease.

Phylogeny

Chiropterans have long been placed into two suborders, the Megachiroptera and Microchiroptera, with one of the main distinctions being the lack of echolocation in the Megachiroptera. However, recent molecular data have suggested that these groupings may be incorrect and the authors of this work have proposed two new suborders, the Yinpterochiroptera and Yangochiroptera, where the rhinolophoid microbats and megabats make up the Yinpterochiroptera, and the Yangochiroptera contain the remaining species (Teeling et al. 2005; Teeling 2009). My study species, the Australian northern long-eared bat (*Nyctophilus bifax*), belongs to the family Vespertilionidae within the Yangochiroptera (Teeling et al. 2005). However, throughout my thesis I have used the traditional nomenclature and refer to pteropodids as Megachiroptera (megabats) and most insectivorous bats as Microchiroptera (microbats) and the species I focus on belong to the latter.

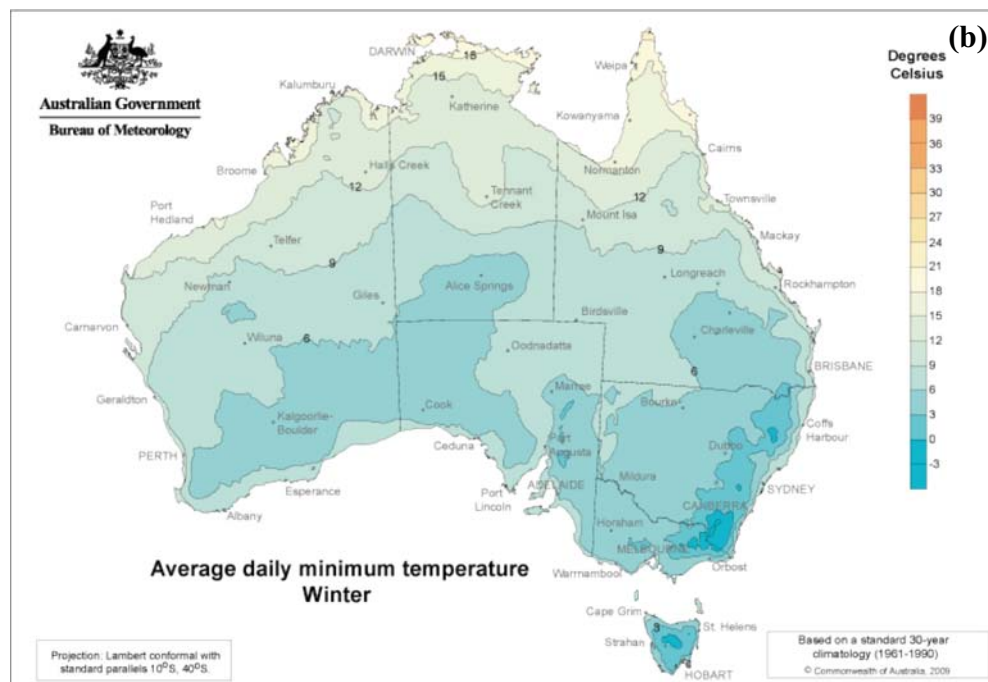
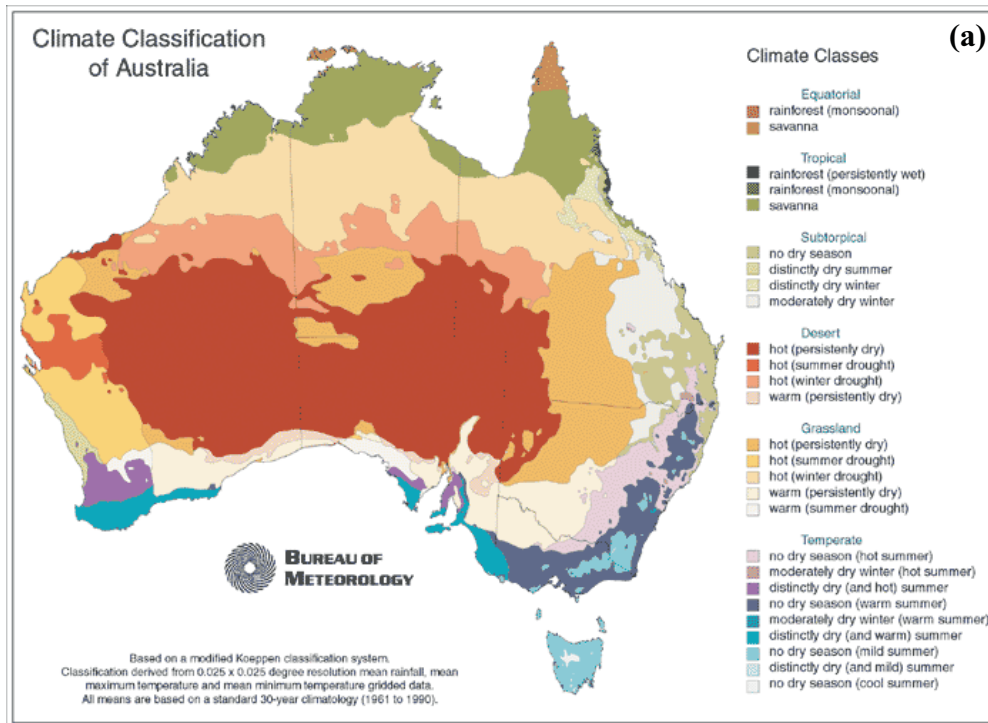
Australia's climate

Habitats and climates vary, from the food sources they contain to annual weather patterns, which place different physiological demands on animals. Australia is largely arid (Plate 1a), which means that it has low primary productivity, low food supplies and large daily changes in T_a . All of these factors combine to place energetic constraints on animals, which many overcome via the use of varying energy conservation strategies (Morton 1978). However, Australia also has vast temperate and tropical regions (Plate 1a), which have different climatic regimes compared to arid regions. While average daily minimum T_a during winter in temperate regions reaches well below 0°C , subtropical and tropical regions are much milder but also reach rather low minima that usually remain above 0°C

(Plate 1b). These variations in weather patterns put different pressures on animals living in dissimilar climatic zones.

Climatic differences result in diverse food and water resources, which also vary seasonally with food generally being in short supply during part of the year. Periods of food shortages can vary depending on the type of food the animal consumes and also how the seasons vary in different climatic regions. While winter is most commonly attributed to food shortages, such as decreased insect activity (Taylor 1963), there are many plants on the Australian east coast that produce more nectar during winter in comparison to summer (Ford 2006). This suggests that animals need to compensate for low food availability during some part of the year and they may also need to deal with sudden decreases in food abundance due to unpredictable adverse conditions such as severe storms. Moreover, T_a often has an effect on food availability, for example, insect activity declines with decreasing T_a suggesting that insect abundance can vary on a daily basis (Richards 1989; Turbill 2008). Therefore it is important for animals to adjust their activity and energy use to suit their energy supply and how readily they can refuel (Christie and Simpson 2006).

Plate 1: Maps of the continent of Australia showing (a) climate classification regions and (b) average daily minimum T_a during winter over 30 years (Australian Bureau of Meteorology; <http://bom.gov.au>).



Shelter

Mammals spend a large portion of their life resting and conserving energy within shelters. Many kinds of shelters are used by animals, ranging from underground burrows of ground dwelling animals to roosts under the leaves of trees used by bats (Brigham et al. 1997; Bieber and Ruf 2009). Selection of a suitable shelter will decrease the amount of energy used while the animal is resting and also help with predator avoidance (Bronner et al. 1999; Willis and Brigham 2005). Additionally, the extent of insulation provided by a tree roost can influence hibernation patterns. For example, tropical primates in more insulated roosts exhibit a more stable body temperature (T_b) in comparison to roosts with less insulation, where T_b fluctuates widely on a daily basis resulting in entirely different patterns of hibernation (Dausmann et al. 2005). These differences influence the amount of energy consumed by these animals on a daily basis, but the overall energy saved during the hibernation period was found to be similar between the two different hibernation patterns (Dausmann et al. 2009).

Roost choice is important to bats, particularly while they are hibernating as many species are unable to maintain enough energy stores for long periods at very low T_a s (Henshaw 1970; Ransome 1990; Arlettaz et al. 2000). Also, it would not be beneficial if the roosts become too hot as they could become hyperthermic (Lourenço and Palmeirim 2004; Lumsden and Bennett 2006). Therefore, each species has their own set of requirements when it comes to climate and roost temperatures (Brack 2007). Further, it appears that roost selection is also important during pregnancy and lactation as these stages of reproduction require increased amounts of energy and therefore appropriate roost choice will enable maximal energy savings and also increase the likelihood of offspring survival (Kerth et al. 2001; Chruszcz and Barclay 2002). Roost choice may also vary among individuals of the same species and can impact their individual energy expenditures, such

that bats roosting in more exposed areas will need to expend more energy being vigilant for predators (Lausen and Barclay 2003). Only a few types of roosts have been described above, but it is known that bats make use of a wide variety of roosts including caves, buildings, trees, foliage and many other types of shelter and some roost solitarily while others roost together in large numbers (Fenton 1983). Therefore, due to the wide variety of roosting options available to especially small bats, they may be able to make decisions on where to roost based on their current energetic requirements, reproductive status and presence of predators.

Energetic requirements

Many of the specialisations that are unique in bats, such as flight and echolocation, are energetically expensive (Neuweiler 2000). Therefore, obtaining enough energy or conserving energy is of vital importance to bats. Animals derive energy by a series of chemical processes that convert food into other forms of chemical energy and heat and all of these processes are termed metabolism (metabolic rate, MR) of the animal (Bartholomew 1982a). All of the various functions that occur within an animal require energy and the energy used to power the most basic life functions is termed basal metabolic rate (BMR). BMR is reached when the amount of energy that is needed to maintain a constant T_b is at a minimum maintenance level and no other physiological thermoregulatory processes are occurring, i.e. the animal is at rest (Bartholomew 1982a; Randall et al. 2002). Specifically, BMR is defined as the state when the animal is adult, resting, post-absorptive and non-reproductive.

Most bats are small and weigh under 25 g and it is well established that as an animal becomes larger the amount of metabolic energy used by 1g of tissue for maintenance processes decreases (Bartholomew 1982a). Therefore, small animals are

consuming more energy proportionally in comparison to larger animals and most bats will have to compensate for this. This effect of body mass on energy consumption, and more specifically on BMR, differs among taxonomic groups and can be influenced by other factors such as diet (Hayssen and Lacy 1985; Willis et al. 2005).

Endothermy

Endothermic animals are able to produce large amounts of their own heat via oxidative metabolism (Bartholomew 1982b). Endothermy has led to many advantages such as increased speed in movement, fast development and distribution to high latitudes and altitudes (Bartholomew 1982b). The energetic requirements of endotherms are high. However, when a homeothermic endotherm is in the range of $T_{a,s}$ defined as the thermoneutral zone (TNZ) they do not have to use extra energy to maintain a high and stable T_b and therefore oxygen consumption is at its lowest (Bartholomew 1982b; Randall et al. 2002; Merritt 2010). Above and below the TNZ oxygen consumption increases and therefore it is beneficial for endotherms, if possible, to remain in environments in which they are exposed only to $T_{a,s}$ in their TNZ. However, this TNZ varies among species and more specifically there is a difference in the TNZ between large and small endotherms. Due to their large surface area to volume ratio small endotherms lose proportionately more heat to the environment in comparison to large animals. Therefore, the range of $T_{a,s}$ encompassed by the TNZ of small endotherms is much narrower in comparison to that of large endotherms. As a result small endotherms will on average use significantly more energy proportionately in comparison to larger endotherms.

While maintaining a high and stable T_b has advantages it is well established that endothermy is energetically expensive (McNab 1982), particularly in homeothermic animals that always maintain a relatively constant high T_b (Bartholomew 1982b).

However, in homeothermic endotherms it can be lethal to let T_b fall and therefore for many endotherms it is important for them to obtain enough energy to maintain a high and stable T_b . For example, many physiological functions can cease or slow down, such as heart rate, if the animal is not normothermic and T_b decreases below the TNZ. Therefore, many species have mechanisms to produce additional heat when T_a decreases below the TNZ. One common mechanism used by homeothermic endotherms is shivering thermogenesis, which increases heat production at low T_a by movement of antagonistic muscles to produce heat (Bartholomew 1982b; Hohtola 2004). Another method of heat production at low T_a is nonshivering thermogenesis, which increases heat production by increasing fat metabolism usually in brown fat that contains large amounts of specialised mitochondria that can produce heat directly by bypassing ATP production (Bartholomew 1982b; Cannon and Nedergaard 2004).

Whereas decreases in T_b and MR will have detrimental effects to many homeothermic species, there are some species that use such decreases in metabolic processes to conserve energy when energy is in short supply, difficult to access or for other reasons. Therefore, a method of conserving energy when T_a decreases below the TNZ is for endotherms to abandon a high T_b and allow their T_b to decrease. Animals that undertake this method of energy conservation are termed heterothermic endotherms.

Heterothermy

When faced with energetic challenges animals employ different mechanisms to overcome or avoid these periods, such as the mechanisms described in the previous section or migrating to a different location for warmer T_a s or switching to a different food supply (Davis 1970). One such mechanism is used by heterothermic endotherms. These endothermic animals are capable of regulating T_b , but are also able to thermo-conform to

allow their T_b to approximate that of T_a (Bartholomew 1982b; Ransome 1990). There are different methods of heterothermic endothermy and one of these is termed regional heterothermy. Endotherms that undergo regional heterothermy maintain a high and stable T_b in most of their body, but allow extremities such as feet and tails to decrease to near T_a (Bartholomew 1982b). This is beneficial as extremities such as wings often lose large amounts of heat to the environment and therefore overall heat loss will significantly decrease by allowing the temperature of such body parts to approach T_a . Regional heterothermy is especially common in large ungulates (Arnold et al. 2004). In addition a few large animals are able to save energy by lowering their whole T_b by just a few degrees when T_a decreases (Schmidt-Nielsen 1979; Nieminen et al. 2005). However, as discussed previously small animals need to deal with much larger proportions of heat loss and energy use and such small decreases in T_b or regional heterothermy will not suffice. Therefore, small heterothermic endotherms often use a method of energy conservation known as torpor.

Torpor

One of the most effective energy conservation strategies available to endotherms is torpor. Torpor in mammals is generally described by a controlled reduction in T_b , MR and water loss (Hock 1951; Barclay et al. 2001; Heller and Ruby 2004). A heterothermic endotherm can be either torpid when T_b is low, or normothermic when the individual has a high and stable T_b as in homeothermic endotherms. The inclination to enter torpor is usually increased by low T_a or a decrease in food availability and body size (Wang 1989). However, this is not always the case as some individuals of a species/population will enter torpor even if there is surplus food available (Turbill et al. 2003; Christian and Geiser 2007; Bieber and Ruf 2009). There are several reasons why an animal may use torpor

while it is not energetically constrained, for example torpor may be used to manage energy and/or water requirements as part of a normal daily routine, to conserve energy for leaner times, or individuals may use torpor possibly to avoid predators (Carpenter and Hixon 1988; Bieber and Ruf 2009).

While torpor use provides an effective avenue for energy conservation, the low T_b and MR during torpor may be detrimental for important processes. For example, it can suppress the immune system and cause neural damage (Prendergast et al. 2002; Arendt et al. 2003). This suggests that the costs and benefits from torpor should be balanced depending on energy availability and requirements (Humphries et al. 2003). This cost-benefit approach to torpor use has been observed in many heterothermic species, such that when food is available and weather conditions are favourable they remain normothermic, whereas if both food supplies are low and weather conditions are unfavourable they will enter torpor (Körtner and Geiser 2000a; Christian and Geiser 2007; Landry-Cuerrier et al. 2008). However, as mentioned previously this is not a generic pattern and regardless of whether or not there are negative costs of using torpor, it clearly seems to be an important survival mechanism for many heterothermic endotherms.

Daily versus prolonged torpor

Two main types of torpor have been described: daily torpor and prolonged, multiday torpor. Daily torpor is characterised by torpor bouts that last for a few hours and animals that employ this form of torpor generally feed on a daily basis, cannot use multiday torpor bouts and are referred to as daily heterotherms (Geiser and Ruf 1995; Körtner and Geiser 2000b). In contrast, prolonged bouts of torpor last for several days or even weeks and when these prolonged bouts occur during winter it is termed hibernation and the species hibernators (Geiser and Ruf 1995; Körtner and Geiser 2000b).

Although many variables of daily torpor and hibernation show clear bimodal distributions they are best distinguished by comparing maximum torpor bout duration as many of the other variables, such as minimum T_b , show some overlap between the two types of torpor (Geiser and Ruf 1995). However, during bouts of prolonged torpor hibernators generally show much lower T_b s and MRs in comparison to daily heterotherms. Further, many hibernators exhibit torpor bouts lasting for less than 24 hours, most often during summer (Wimsatt 1969). However, these short bouts of torpor expressed by hibernators appear to be physiologically similar to prolonged bouts of torpor, with the exception of bout duration (Hock 1951). In contrast, torpor bouts shown by daily heterotherms appear to differ physiologically from those bouts shown by hibernators (Geiser 2004a).

Environmental effects on torpor use

Photoperiod influences expression of torpor use in environments where day length varies seasonally. For example, an increase in torpor in response to decreasing day length is an appropriate response to the beginning of winter, which usually means a decrease in food supply and often cessation of reproductive activities (Heldmaier and Steinlechner 1981; Körtner and Geiser 2000b; Geiser et al. 2005). However, in environments where day length changes minimally throughout the year, such as tropical regions, relying on photoperiod as a cue to predict a possible food shortage has limited value. Animals that feed primarily on insect or nectar must adopt or learn to deal with a food supply that is often irregular in abundance (Körtner and Geiser 2000b). Consequently, in regions where photoperiod remains similar during the year it may be more beneficial for an animal to enter torpor based on short-term cues, such as changes in barometric pressure that can

influence the abundance of insects available for feeding on a daily basis (Paige 1995; Turbill 2008).

Torpor use is strongly influenced by T_a in many heterothermic endotherms, such that as T_a decreases torpor use and bout durations increase (Twente and Twente 1965; French 1982; Park et al. 2000). While low T_a does have a negative impact on energy expenditure of endothermic animals and promotes the use of torpor, it seems likely that in some environments torpor is mostly influenced by the availability of energy. Therefore, the increase of torpor use due to a decrease in T_a in some circumstances is merely a side effect of a decrease in food abundance (Wojciechowski et al. 2007), as food sources such as insects decrease with decreases in T_a (Richards 1989).

Torpor thresholds

During torpor T_b can be reduced to about 0.5 to 2.0°C of T_a and particularly in small mammals this minute $T_b - T_a$ differential is reached during steady-state torpor (McNab 1982; Turbill and Geiser 2006). However, most or all heterothermic endotherms appear to have a thermoregulatory threshold or T_b set point, at which individuals initiate regulation of T_b and this generally occurs as soon as the T_a drops below this pre-determined species- or population-specific threshold (Heller and Hammel 1972; Brown 1999; Dunbar and Tomasi 2006). Heterothermic endotherms accomplish this by an increase in MR, which produces heat to elevate T_b (Heller and Hamel 1972; Geiser 2006). This thermoregulatory mechanism ensures that potential negative impacts of low T_b on bodily functions and in extreme cases the possibility of their body fluids freezing is limited or avoided (Henshaw 1970; Barnes 1989). This thermoregulatory threshold appears to be set by long-term natural selection in the wild and is dependent on the climatic variables experienced by the

population (Geiser and Ferguson 2001). This suggests that different climates affect at least some variables of the thermal physiology of heterothermic endotherms.

Torpor use in bats

The high energetic cost of maintaining high T_b at rest is often avoided in small heterothermic bats by lowering their T_b and entering torpor and thus conserving energy. Torpor patterns vary widely among bat species and individually and also vary seasonally throughout the year. Bats inhabiting temperate climates frequently employ prolonged multi-day torpor during winter hibernation and short bouts of torpor lasting less than a day during warmer months (Speakman and Thomas 2003; Geiser 2004b). However, while temporal torpor patterns often appear to vary seasonally, it appears that the physiological variables characteristic of torpor use of some species show little or no seasonal change (Geiser and Brigham 2000). This suggests that the physiology of torpor may be similar regardless of the time of year or the length or depth of torpor bouts. Many bat species do show seasonal pre-hibernation fattening and may accumulate significant fat stores before winter, as it has been found that many species are heaviest at the end of autumn and that their body weight decreases throughout winter (Ellis et al. 1991). However, fattening in bats is often less extreme than in many other hibernators, because of the flying capabilities of bats (Merritt 2010). Nevertheless, it does appear that heterothermy is important to bats to aid in the management of energy use.

Subtropical and tropical climates

Torpor in mammals has been extensively studied in temperate regions (Speakman and Thomas 2003; Geiser 2006), but there are far fewer studies on torpor from subtropical/tropical regions (Turbill et al. 2003; Dausmann et al. 2005; Jacobs et al. 2007; Vivier and van der Merwe 2007). Due to the large increase in the energy required to

maintain a high and stable T_b at T_{as} below $\sim 30^\circ\text{C}$, it would be beneficial for small mammals to use torpor to conserve energy at T_{as} below 30°C . Temperate regions reach very low T_{as} , well below the TNZ, and low T_{as} are generally accompanied by decreases in food availability. However, subtropical/tropical regions have similar challenges that mammals must overcome, such as a decrease in food availability during the typically dry winter and T_a can also decrease well below the TNZ (Turbill et al. 2003; Dausmann et al. 2005). Lack of food and water during winter in subtropical/tropical regions may necessitate torpor use and possibly hibernation if small mammals are to survive. This suggests that energy saving is important in all climatic regions, regardless of the T_a experienced. However, hibernation in the subtropics/tropics may differ from hibernation in temperate regions, as animals in the tropics must deal with a relatively small reduction of T_a during winter and thus limited opportunities to use low T_b for energy conservation (Dausmann et al. 2009).

During the day many bats do not feed or drink and are merely resting in their roost. Therefore, torpor use during the day would be beneficial in all environments to reduce the risk of starvation and dehydration (Genoud et al. 1990). Because daily torpor allows for energy conservation during the day but feeding at night, this pattern of torpor is most likely used by subtropical/tropical species. Turbill et al. (2003) showed that some subtropical bats do use daily torpor regularly. However, prolonged torpor has only been described for primate species inhabiting tropical Madagascar (Dausmann et al. 2005) and has not been found in any bat species that occur in tropical or subtropical environments.

Hibernation in tropical primates

Studies on lemurs from tropical Madagascar revealed surprising results in regard to hibernation. Dausmann et al. (2005) found that low T_b s are not necessary for an animal to

hibernate and that the Malagasy primate, *Cheirogaleus medius*, remained in hibernation for prolonged periods even when T_a and T_b was above 30°C. Several other studies focusing on cheirogaleid primates contributed to this knowledge and established that many species within this group of primates are able to enter hibernation in areas where the lowest mean monthly minimum T_a is 10°C and where T_a s often reach well above 30°C (Schülke and Ostner 2007; Kobbe and Dausmann 2009). Therefore, it seems likely that bats occurring in areas where the lowest mean monthly minimum is 10°C can also express prolonged torpor.

Daily torpor in subtropical and tropical bats

While many studies have examined the use of torpor in microbats from temperate regions, information on torpor use in free-ranging subtropical and tropical bats is scarce. A number of researchers have argued that bats are not able to hibernate when T_a is too high and therefore it is widely assumed that all tropical and subtropical bats are unable to use torpor (Henshaw 1970). Further, McNab (1974) claimed that only small, individual bats are able to hibernate at T_a s above 14°C and that many temperate bats are restricted to temperate regions and unable to occupy tropical regions due to their life cycle and dependency on hibernation. More recent work clearly does not support this view because some species in subtropical/tropical regions do use torpor regularly and species that inhabit both temperate and tropical regions are able to hibernate in temperate regions (Geiser 2006; Turbill and Geiser 2008). This comes as no real surprise as winter in both subtropical and tropical regions usually results in a decrease in the number of insects available and many food plants also become unavailable during certain times of the year (Fenton 1983; Richards 1989).

Megabats primarily occur in tropical and subtropical regions and only a handful of studies have examined thermoregulation in these species. As in temperate regions, food

availability in subtropical and tropical regions also varies seasonally. However, in contrast to most temperate species, subtropical blossom-bats (*Syconycteris australis*) use torpor more extensively in summer than in winter (Coburn and Geiser 1998; Geiser et al. 2005). As the supply of nectar increases during winter in their habitat, the somewhat unusual seasonal expression of torpor use seems again to be explained by food availability (Coburn and Geiser 1998; Geiser et al. 2005). In the laboratory, these subtropical blossom-bats also did not enter torpor at 18°C if food was available, but did so at 25°C if food was withheld which lends further support to the view that torpor use is more dependent on food availability rather than low T_a (Coburn and Geiser 1996). A truly tropical bat, the northern blossom-bat (*Macroglossus minimus*), was only able to enter very shallow daily torpor between T_{as} of 14-25°C and the longest bouts observed were eight hours in duration (Bartels et al. 1998). However, this clearly shows that even in mild, tropical regions bats do use torpor to conserve energy.

T_a during winter in subtropical and tropical regions often decreases, reducing insect numbers and limiting the amount of food available to insectivorous microbats (Richards 1989). The use of torpor by tropical and subtropical insectivorous microbats has only been examined in a small number of studies. Laboratory studies conducted on two tropical microbats and five subtropical microbats found that all species studied were able to enter short bouts of torpor (Genoud et al. 1990; Genoud 1993). Recent studies undertaken on subtropical microbats from South Africa found that these bats entered daily torpor throughout the year (Jacobs et al. 2007; Vivier and van der Merwe 2007). Importantly, all of the mentioned studies failed to observe prolonged torpor bouts. However, since these studies were able confirm that torpor occurs in subtropical and tropical microbats at T_{as} of 30°C, energy conservation via the use of torpor must be important to their survival.

Therefore, it seems feasible to predict that subtropical and tropical microbats are also able to undergo prolonged torpor during extended periods of adverse conditions.

As in other countries, thermoregulation in Australian microbats has been extensively studied in temperate regions, but relatively few studies have been conducted in tropical or subtropical regions. Even though hibernation occurs in some temperate zone Australian bats (Geiser 2006; Turbill and Geiser 2008), there is no evidence of tropical or subtropical bats using hibernation. One of the few studies undertaken on a subtropical Australian microbat, *Vespadelus pumilus*, showed that four individuals of this species used torpor every day in the morning and afternoon during summer (Turbill et al. 2003). These bats entered torpor even when food was readily available and the weather was mild, supporting the view that use of torpor is important to subtropical Australian microbats.

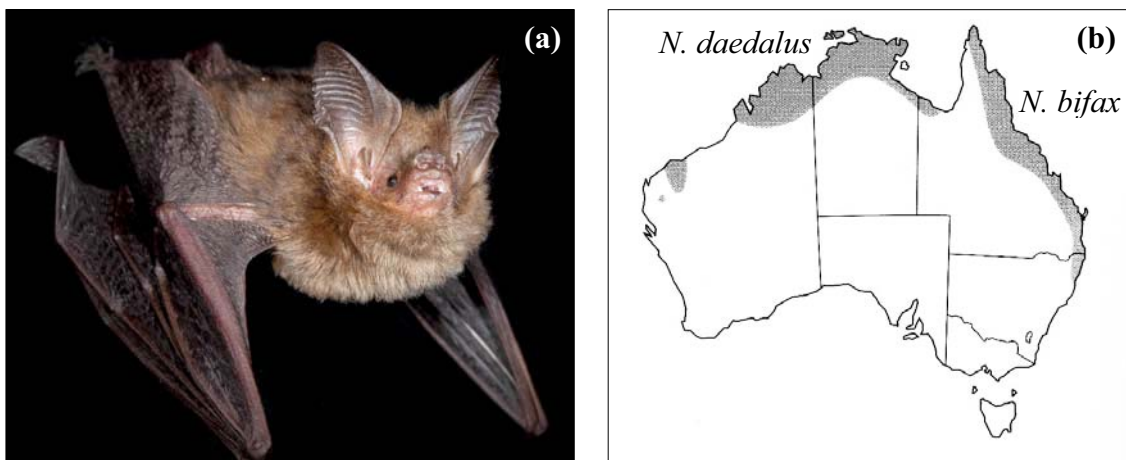
Study species: Northern long-eared bats (*Nyctophilus bifax*)

My thesis focuses on the effect of temperature, season and different distribution ranges and therefore climates on the thermal physiology, activity patterns and torpor of an insectivorous microbat, *N. bifax* (Plate 2a). *N. bifax* are vespertilionid bats restricted entirely to tropical and subtropical regions with an east coast distribution in Australia from the top of Cape York Peninsula in the north to the northern parts of New South Wales in the south (Plate 2b; Churchill 1998). They have an average body mass of 9.3g, with females generally being larger and heavier than males (Friend and Braithwaite 1986; Churchill 1998; Milne et al. 2005). *N. bifax* prefer rainforest habitats, mainly roost in trees and have been found roosting in locations ranging from under bark, in tree hollows and in foliage (Lunney et al. 1995; Churchill 1998). Individuals tend to change roosts frequently, but within a small area and among a few trees (Lunney et al. 1995). They prefer to hunt for insects along forest edges and characteristically feed on moths (Churchill 1998; Menkhorst

and Knight 2001). Females typically give birth to twins in October to November and then lactate from November to December (Churchill 1998). It is known that females move their offspring often during the lactating period and are able to carry both twins at once, which is about 95% of the females body mass (Lunney et al. 1995; Churchill 1998). Only a few studies have been conducted on this species, and these have focused predominantly on their ecology and roosting habits.

N. bifax are commonly referred to as northern long-eared bats and as eastern long-eared bats (Churchill 1998; Parnaby and Churchill 2008). Throughout my thesis I refer to my study species as the northern long-eared bat. Further, *N. bifax* was previously split into two subspecies. *N. bifax bifax* was distributed along the east coast of Australia and *N. bifax daedalus* in the northern parts of the Northern Territory and Western Australia (Plate 2b). However, a recent study has shown that *N. bifax daedalus* are part of the species group *N. daedalus*, and therefore the east coast population of *N. bifax bifax* is a separate species, *N. bifax* (Parnaby 2009). Therefore, as I studied the east coast population, throughout my thesis I refer to my study species as *N. bifax*.

Plate 2: (a) Picture of *N. bifax* (Gerhard Körtner 2009). (b) Map of Australia showing the distribution of eastern *N. bifax* and northern *N. daedalus* (Churchill 1998).



Aims of the thesis

All of the studies that have been conducted on thermoregulation of tropical and subtropical mammals show that it is possible for a mammal in these regions to use torpor efficiently and to their benefit. Further, temperate bats have been found to remain torpid for prolonged periods at T_{as} that are often experienced by bats from tropical and subtropical regions. Therefore, I aimed to examine the hypothesis that a subtropical/tropical bat species will undertake prolonged bouts of torpor during adverse conditions. I also tested the hypothesis that thermal physiology and torpor use will vary seasonally and also between different populations of the same species in different habitats. As most bat species inhabit tropical regions (Wimsatt 1969; Kalko 1995) such studies would be very beneficial to the understanding of how bats are able to adapt to varying climates.

Aims of chapter 2

Little scientific information has been published about *N. bifax* and as shown in the previous section the information available focuses on general biology, such as reproductive times of year and some data on roosting habits. Therefore, I aimed to provide data on the best methods of capturing *N. bifax* and the subsequent care of this species while in captivity. Further, I also aimed to gather information regarding the influence of weather conditions on the availability of insects throughout the year at a subtropical and tropical site where *N. bifax* reside.

Aims of chapter 3

Information on torpor use by subtropical Australian bats is scant and there is no information on prolonged torpor for any species. My aim therefore was to gather data on torpor from populations of *N. bifax* from a subtropical habitat in the field during colder and

drier times of the year when food availability is restricted. I undertook this research to determine whether or not subtropical bats are able to enter prolonged torpor in the face of adverse conditions.

Aims of chapter 4

It has been hypothesised that species that use torpor will only express torpor if they are in poor body condition and avoid torpor when possible due to the associated costs. While this hypothesis has been supported by a number of species that undergo torpor, other species may use torpor even when they are not energetically constrained. The aim of my study was to re-examine this hypothesis by obtaining data on torpor use by *N. bifax* from a subtropical region during summer in relation to body condition when food is abundant and weather conditions mild, so therefore they should not be energetically constrained.

Aims of chapter 5

Detailed knowledge about seasonal changes in patterns of torpor use throughout the year in a free-ranging microchiropteran species from the same habitat is poor. The few studies that have been undertaken show that torpor patterns are similar between seasons in subtropical species, but that torpor bout duration is often longer during winter in temperate species. Therefore, I aimed to provide new data on torpor use by subtropical *N. bifax* during summer and winter to determine if there are any differences in torpor use due to differences in weather conditions and insect abundance.

Aims of chapter 6

Reproduction in mammals is energetically expensive and pregnancy and lactation in females is particularly expensive. While torpor use provides energetic savings during times of energy shortage there are also costs associated with torpor use, particularly to pregnant

and lactating females. For example, torpor use during pregnancy will delay the birth of the foetus. However, this delay in pregnancy may sometimes be beneficial as lactation is more energetically demanding than pregnancy and therefore birth can be delayed until weather and feeding conditions are optimal for foraging during lactation. I aimed to compare torpor use between male and female subtropical *N. bifax* during spring when females were pregnant to resolve how reproduction affects thermal biology of the species.

Aims of chapter 7

Data on the use of torpor by tropical microbats are scarce and most studies have been undertaken on tropical megabats and these only observed short bouts of torpor. Prolonged bouts of torpor by cheirogalid primates have been found during winter in a tropical habitat. Additionally, winter in tropical habitats is often associated with very dry conditions and also decreases in T_a and food abundance. I proposed to obtain data in the field for *N. bifax* from a tropical habitat to see whether a tropical microbat species is able to undergo torpor at all and if expressed then do they show prolonged bouts of torpor during particularly adverse weather conditions.

Aims of chapter 8

The thermal physiology of a species can vary seasonally and within their range, i.e. northern populations can have a different BMR in comparison to southern populations. Further, it has been suggested that the physiology of torpor differs between temperate and tropical hibernators. I aimed to collect data on the thermoenergetics of *N. bifax* from a subtropical region over various seasons to determine if they are compensating for changes in weather and food abundance annually. I also aimed to collect similar data during winter from the Australian tropics to determine if they show specific adaptations to their tropical

habitat. Additionally, I aimed to compare the results of this study to previous results of the physiology of torpor of temperate hibernators.

Thesis structure

Most of the chapters of this thesis, from chapter 2 though to chapter 8, have been written in the format of journal articles. Some of these chapters (chapters 3, 4, 5 and 6) have already been published in journals and statements at the beginning of each of these chapters confirm this. The remaining result chapters will also be published as journal articles.

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