

Changes in rhythmicity of mammals to cope with low food intake and high energy expenditure

Bachelor thesis

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Chapter 1: Introduction

The struggle for life takes many forms, but almost every aspect involves energy. Without this energy, life would not exist. Free-living animals face different energy demands in different seasons, because of seasonal differences in ambient temperature, reproduction, food availability and other factors. If they do not or cannot increase their energy intake, they will start to lose weight and/or experience other deleterious effects like decreased fertility, increased mortality and other fitness loss. Therefore many animals have evolved means of lowering the energy expenditure to better match the energy intake. By doing so they can reach a different energy balance and can limit their weight loss and the other harmful effects. The means of reducing the energy expenditure can be divided into four categories; structural adaptations (i.e. a thicker pelage), physiological adaptations (i.e. digestive efficiency), behavioral adaptations and adaptations in rhythmicity.

In this paper the focus lies entirely on the adaptations in rhythmicity to reduce energy expenditure. Adaptations in rhythmicity include hibernation, daily torpor and time of activity. The animal can change its regular activity rhythm according to the new circumstances and can thereby reduce energy expenditure. The precise options an animal has to use changes in their circadian or annual activity rhythm to reduce energy expenditure are not always clear. This review article is intended to provide an overview to the precise methods animals employ to use changes in their circadian or annual activity rhythm to reduce energy expenditure when food availability is low. The methods that are used are described and its costs and benefits illustrated by some exemplar species.

Chapter 2: Daily torpor

2.1 Introduction

The maintenance of a high body temperature is a considerable cost for small endothermic animals. Small animals have a relatively large surface to volume ratio resulting in high heat loss during cold exposure, high mass-specific BMR in thermo-neutrality, high mass-specific energy expenditure during locomotion and a relatively small capacity for fat storage (Geiser *et al.* 2006). So especially in periods where ambient temperatures are low small animals face higher energetic costs. Thermoregulatory costs account for 40 to 60 % of total daily energy expenditure for small endotherms (Bozinovic *et al.* 2004). To reduce this energy loss, animals have evolved many different adaptations, for example daily torpor. Daily torpor is defined as a controlled reduction in body temperature and MR for less than 24 hours (Geiser, 2004), accompanied by inactivity and absence of locomotion. Most animals go into torpor in the coldest parts of the night, approximately from 03.00 a.m. to sunset. When not in torpor the energy requirements for thermoregulation would be highest in this period because of the large difference between body and ambient temperatures. So daily torpor is a way to combine metabolic down regulation with a change in circadian activity rhythm to reduce energy expenditure for thermoregulation at times when these energy requirements would be the highest.

Daily torpor is a widespread phenomenon. It is found in at least eleven mammalian orders including marsupials (Heldmaier and Elvert, 2004) and in six avian families (McKechnie and Lovegrove, 2002).

2.2 Advantages

Substantial energy savings

The energy that is saved during daily torpor is substantial. During torpor most mammals have a metabolic rate (MR) of 10 to 20% of their normothermic MR. The energy that is saved by employing daily torpor is between 80% and 90% of the energy that is used by normothermic thermoregulation at the same ambient temperatures (Song *et al.* 1995; Geiser, 2004).

Modularity

Whether or not an animal will show torpor is for most species dependent on the energy demand, body weight, and energy intake, and can be varied on a daily basis (Körtner and Geiser, 2000). Generally an animal will show torpor at a specific time of day in a specific season. The duration of torpor can be varied according to food availability and environmental conditions (Christian and Geiser, 2007). This gives the animal the opportunity to fit the number and duration of torpor bouts nicely with its individual energy balance.

2.3 Disadvantages

Harmful physiological effects

Many animal species limit the time they spent in torpor whenever it is energetically possible (Humphries *et al.*, 2003). Sugar gliders for example will show more torpor when ambient temperature is low and rainfall is high, but will skip torpor sessions when food is plenty or the environmental conditions are accommodating (Christian and Geiser, 2007). This avoidance of torpor suggests that there are costs associated with it. There is an indication that torpor reduces immunological abilities, postpones maintenance and repair processes, increases vulnerability to predation (Radzicki *et al.*, 1999) and could impair memory formation and/or

memory maintenance (Millesi *et al.* 2001). It has also been shown that nutrient absorption in the digestive tract is slowed at low body temperatures (Carey, 1989). Daily torpor could also be responsible for accumulation of sleep debt (Daan *et al.*, 1991), reduced synaptic efficacy (Strijkstra *et al.*, 2003) and in reproductive females it can result in slowed growth of young (Racey, 1982). Therefore it is thought that increased torpor usage is associated with decreased fitness (Grinevitch *et al.*, 1995).

Harmful ecological effects

Because torpid individuals are inactive and show a decreased and slowed response to stimuli, it cannot avoid predation when detected by a predator. Therefore daily torpor can increase the risk of predation (Radzicki *et al.*, 1999).

2.4 Studies of daily torpor in two species

Here we present two representative studies that illustrate the dynamics of daily torpor and the energy saved by employing it in two species of marsupials.

Sugar glider (Petaurus breviceps)

Christian and Geiser (2007) have measured the torpor pattern of sugar gliders in the field. Sugar gliders (*Petaurus breviceps*) are small (ca. 130 g.) nocturnal marsupials. This species lives an arboreal lifestyle in the open forests of Australia. The diet is mostly composed of arthropods and animal and plant exudates. In winter sap production of eucalyptus trees and arthropod abundance declines while cold and wet weather dominates. These factors make foraging in winter energetically expensive. To reduce the amount of weight loss in winter, sugar gliders can reduce their activity, reduce normothermic body temperature or use daily torpor (Christian and Geiser, 2007).

The measurements of torpor in wild sugar gliders in open eucalypt/acacia woodland in Australia show that sugar gliders use torpor in the colder parts of the night, especially when it also rains. Minimal body temperature fell as low as 14.1 °C (normothermic temperature: 36 °C) and averaged $24.0 \pm 1.3^{\circ}\text{C}$ ($n = 9$; $N = 34$)* with bouts lasting (393.4 ± 35.8 min; $n = 9$; $N = 34$) in ambient temperatures between 8 and 15 °C (Christian and Geiser, 2007). In torpor bouts (defined as body temperature lower than 24.0 °C) energy loss is minimized because MR can be reduced to ~20% of the normothermic values in sugar gliders (Fleming 1980; Christian and Geiser, 2007).

Fat-tailed dunnart (Sminthopsis crasicaudata)

Another study by Holloway and Geiser (1995) describes the energy expenditure of *Sminthopsis crasicaudata* in the laboratory. *Sminthopsis crasicaudata* or fat-tailed dunnart is a small (16 g.) nocturnal dasyurid marsupial. It is found in the mesic to arid regions of central and southern Australia and displays daily torpor both in the wild and in the laboratory. Its diet mostly consists of small arthropods.

Metabolic rates were measured as the rate of oxygen consumption ($\dot{V}\text{O}_2$). The animals were individually housed in a respiratory vessel without food or water during the measurements and $\dot{V}\text{O}_2$ was continually monitored. Holloway and Geiser (1995) found normothermic body temperature displayed a large variation ranging from 30.1 °C to 37.8 °C with a mean value of 33.8 °C. When in torpor, the body temperature ranged from 14.3 °C at ambient temperatures of 10 °C to 29.6 °C at ambient temperatures of 18 °C.

The oxygen consumption at different temperatures and different activity are presented in figure 1. RMR during the daylight hours where 3.82 ± 0.09 ml g/hr at 18 °C and 5.00 ± 0.04

* n = number of observed torpid animals, N = number of occasions torpor was observed

ml g/hr at 12 °C. After the onset of darkness MR increased to maxima of 6.49 ± 0.21 ml g/hr at ambient temperatures of 18 °C and 7.74 ± 0.19 ml g/hr at ambient temperatures of 12 °C because of nocturnal activity. These rates were generally maintained until the animal entered torpor between 03.00 and 05.00 in the morning. When no torpor occurred the MR stayed up until morning, where it went back to RMR. Torpor bouts were marked by a steady decline in MR to 0.72 ± 0.11 ml g/hr at ambient temperatures of 18 °C and 0.41 ± 0.10 ml g/hr at ambient temperatures of 12 °C. This represents a decrease from the resting values of 81.2% at 12 °C and 91.8% at 18 °C. Upon arousing from torpor MR was drastically increased to 7.76 ± 0.43 ml g/hr at 18 °C and 8.51 ± 0.29 ml g/hr at 12 °C before returning to resting levels. The duration of these arousals ranged from 0.81 ± 0.09 hr at 18 °C to 0.67 ± 0.06 hr at 12 °C. Figure 1 provides an overview of the oxygen consumption at 12 °C and 18 °C.

When the costs of arousal, activity and torpor are added and compared to energy expenditure at days without torpor, energy saving is approximately 30 – 50% for a torpor bout of 10 hr. The mean torpor duration of 5 hr results in a 16% reduction of average daily metabolic rate at 12 °C and a 12% reduction at 18 °C. When comparing $\dot{V}O_2$ from onset of a 5 hr torpor bout until arousal with the RMR at the same interval, savings amount up to 43%.

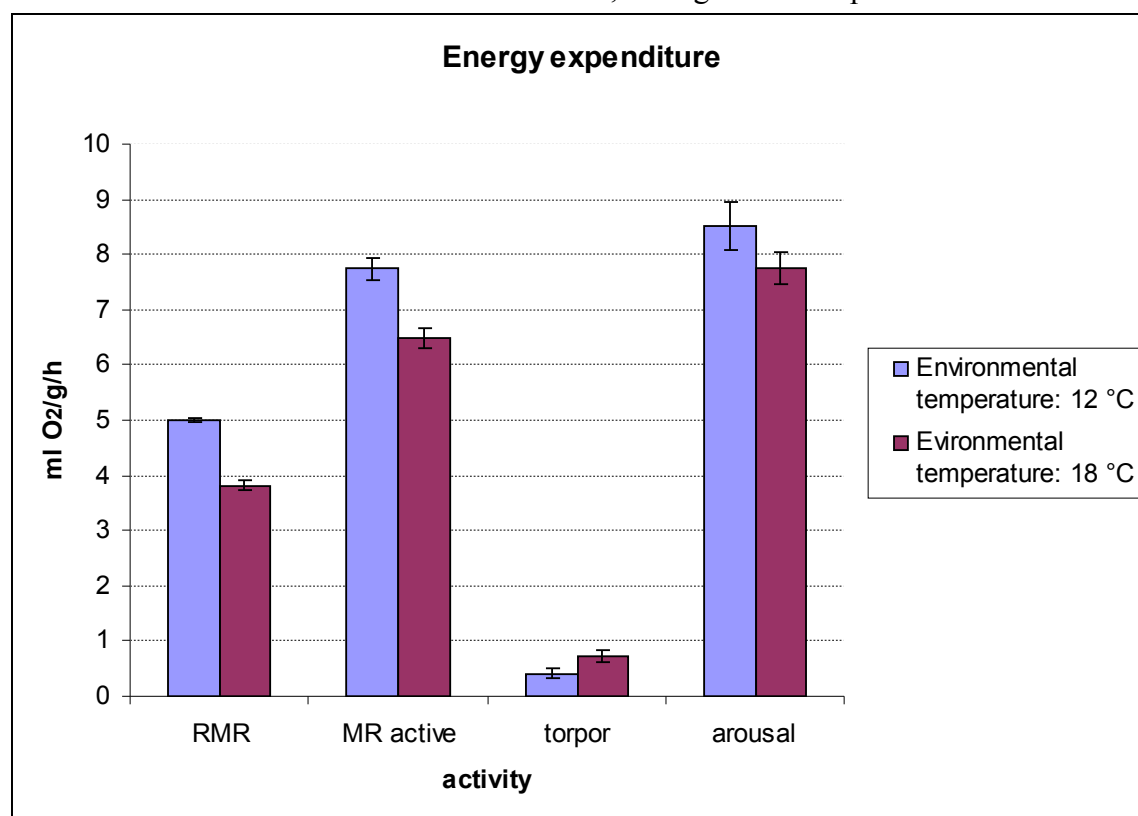


Figure 1. Energy expenditure of *Sminthopsis crasicaudata* during resting, activity, daily torpor and arousal from daily torpor at two different ambient temperatures.

From these two studies, it can be concluded that daily torpor can reduce daily energy expenditure by 12% to 16% in *Sminthopsis crasicaudata* to ~20 % in *Petaurus breviceps*. Other animals that show torpor are expected to have similar energy savings, but this is of course also depended on the duration of torpor bouts.

Chapter 3: Hibernation

3.1 Introduction

Hibernation is defined as a torpor bout that it is maintained for periods longer than 24 hours and it is per definition only present in winter. When a mammal goes into hibernation it will diminish its metabolism and allows its body temperature to drop to a few degrees above ambient temperatures. When the body becomes too cold, the animal will actively generate heat to stay alive (Wilz and Heldmaier, 2000). Hibernation is not one single bout of torpor during winter, but the period of torpor is divided in small bouts of torpor of approximately 2 weeks by periodic arousals. In these arousals the organism actively warms up to normothermic temperature by activation of the major heat-producing mechanisms. It will remain normothermic for a few hours, in which it will predominately sleep (Daan *et al.* 1991). Some species, for example bats, leave their hibernaculum for some time during arousals. Arousals are deemed as essential for hibernation because all hibernating animals show arousals, even though it comes with large energy costs. Most of the energy spent on hibernation is actually spent on the periodic arousals.

3.2 Advantages

Substantial energy savings

Hibernation is the best way of reducing energy expenditure in harsh conditions, for example at ambient temperatures around or below 0 °C.

During hibernation the MR of the animal is greatly reduced. Oxygen consumption and breathing rate will also greatly diminish during hibernation. For example in the marsupial *Dromiciops gliroides* $\dot{V}O_2$ falls to 1% of the euthermic value and respiratory frequency falls from 370 to 2 per minute (Bozinovic *et al.*, 2004). The energy saving is enormous: for example the edible dormouse saves up to 99.6% of its energy when hibernating at 4 °C compared to resting at 4 °C (Wilz and Heldmaier, 2000). Because of this low energy demand most hibernators can survive for several months on fat reserves alone. This is of enormous value for animals living in climates where the environmental conditions or temperature are too harsh to be active in, or in areas where food availability in winter is too low to sustain the organism. Without the energy saving aspects of hibernation, existence in these regions almost does not seem to be possible for those small mammal species.

Reduced risk of predation

When an animal goes into hibernation, most species will stay in their hibernaculums for 4 to 6 months. In this time the animals will not be exposed to their regular predators, for example birds of prey (Bieber and Ruf, 2009). For species where predation is one of the major causes of death, this advantage is huge.

In an evolutionary perspective, the use of hibernation by a species forces its predators to switch diet or migrate, especially if this predator is a specialist. This imposes a problem on the predators, which could result in less overall predation or less predation right after hibernation.

3.3 Disadvantages

Hibernation is shown to impose costs on animals. These costs are both in the harmful physiological effects of hibernating, as well as in the costs of being unable to respond to stimuli.

Harmful physiological effects

It has been determined that animals show poor memory retention after hibernating. When ground squirrels (*Spermophilus citellus*) are trained to complete a task involving spatial memory and an operant condition test, they perform poorly when tested again after hibernation compared to a control group which did not hibernate. This shows that hibernation has a negative effect on memory retention (Millesi *et al.* 2001).

Immunocompetence is also reduced when hibernating, making the animal vulnerable to infections and parasites during and shortly after hibernating (Luis and Hudson, 2006).

It has also been shown that nutrient absorption in the digestive tract is slowed at low body temperatures (Carey, 1989) and in reproductive females hibernation can result in slowed growth of young (Racey, 1982). Daily torpor could also be responsible for accumulation of sleep debt (Daan *et al.*, 1991) and reduced synaptic efficacy (Strijkstra *et al.*, 2003). In males sperm cell production is inhibited during hibernation because of low body temperatures and low MR (Racey, 1982).

It is thought that the periodic arousals are used to restore the maintenance of cells, restore immunological processes to some degree and remove deleterious substances in the brain. Since the harmful physiological effects of hibernation can still be measured, in spite of the fact that all hibernating species show arousals, those harmful effects must be quite large and pervasive.

Decreased vigilance

Hibernating animals have a decreased sensitivity to stimuli and therefore cannot quickly respond to threats. Arousal from hibernation can take several minutes to several hours. This makes them more vulnerable for predation. (Radzicki *et al.*, 1999).

Animals that store food are susceptible to hoard pilferage because of their decreased sensitivity to stimuli and inability to quickly respond to the intruder. When the hoard is being stolen, the hibernator will almost certainly die.

Reliability on hibernaculum

A hibernator is highly reliable on the integrity and suitability of its hibernaculum. When a hibernator is dispelled from its hibernaculum, exposure and the inability to find a suitable new hibernaculum soon enough cause it to almost inevitably die. Unexpected adverse circumstances in the hibernaculum can have the same effect.

3.4 Examples of two species using hibernation

Dromiciops gliroides

Bozinovic *et al.* (2004) have studied the energy saving of hibernation in the microbiotheriid marsupial *Dromiciops gliroides*. *Dromiciops gliroides* is a small (ca. 40 g.) nocturnal marsupial that is found in the northern part of the temperate forest of southern South America. Within the three recognized orders of marsupials in South America (the Paucituberculata, Didelphimorphia and Microbiotheria) it is the only living representative of the otherwise extinct lineage of Microbiotheres. *Dromiciops gliroides* inhabits humid, cool and dense forests where it lives an arboreal lifestyle. Its diet consists of fruits and small arthropods. *Dromiciops gliroides* displays daily torpor as well as hibernation. Here we will focus only on hibernation, defined as torpor bouts lasting > 24 h. Wild *D. gliroides* were captured and kept in captivity. Measurements were taken in a closed respirometry system. Torpor was induced by depriving the animals of food.

Normothermic *D. gliroides* were found to have a RMR of 0.79 ± 0.01 ml O₂/g/h. Body

temperature was between 33.9 °C and 36.4 °C. When in hibernation for 5 – 6 days the $\dot{V}O_2$ fell to 1% of normothermic values, ranging from 0.03 to 0.06 ml O_2 /g/h at ambient temperatures of 12.5 °C. Body temperature was 0.7 °C above ambient temperature, 13.2 ± 0.01 °C. Breathing rate decreased from 370 to 2 per minute.

When hibernating at 17.5 °C, MR was slightly higher than at 12.5 °C with a $\dot{V}O_2$ of 0.08 ml O_2 /g/h. This was maintained for 2 days. Hibernation at 20 °C resulted in a $\dot{V}O_2$ of 0.12 ml O_2 /g/h. This means MR was 3% and 5.7 % of the normothermic value, respectively.

Figure 2 gives an overview of the oxygen consumption at rest or during hibernation at various ambient temperatures.

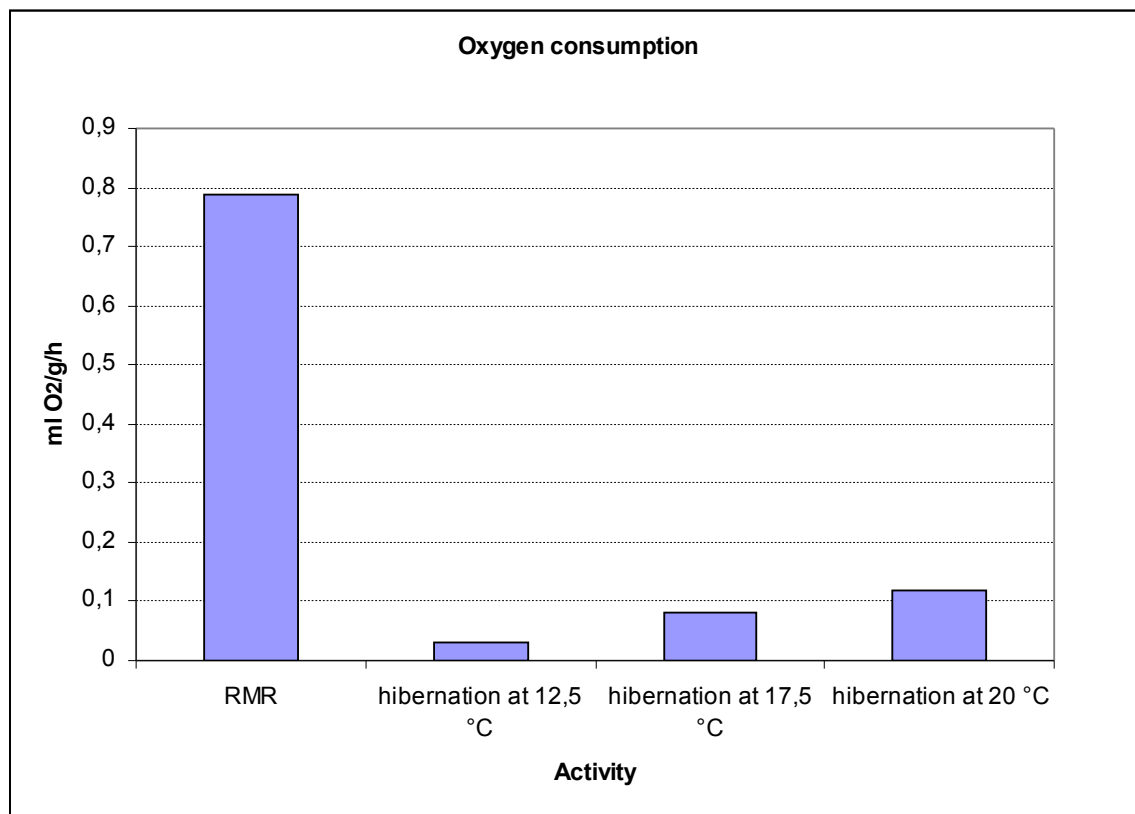


Figure 2. Oxygen consumption by *Dromiciops gliroides* during resting and during hibernation at various ambient temperatures.

Chapter 4: Estivation

Low food availability and high energy expenditure are not exclusively found in cold winter climates, but can also occur in hot, dry climates in summer. Desert ecosystems face a shortage of water in the dry season, which is accompanied by a shortage of food for many animals. Most plants do not grow, seed or fruit in this period, which increases the difficulty an animal has to find food. Avoiding adverse circumstances like high temperatures can also shorten the time available for foraging.

Some dessert mammals have therefore evolved a state similar to hibernation called estivation (aestivation). Unlike hibernation estivation occurs by definition only in summer. It is characterized by a lowered body temperature to approximately match the environment and a reduction in MR. Because estivation only occurs in summer, the body temperature during estivation is much higher than during hibernation. It seems that no qualitative metabolic differences exist between hibernation and estivation, but instead that all differences in body temperature, rate of heat loss, duration of arousals and potential energy saving arise because of differences in ambient temperature (Wilz and Heldmaier, 2000).

4.1 Advantages

Energy saving

Estivation allows mammals to save energy when food availability during drought in arid regions is low. When in estivation, the MR can be greatly reduced, resulting in substantial energy saving. For example in the edible dormouse (*Glis glis*) oxygen consumption is reduced by 85.3 %. This allows the animal to survive though the period of drought on its fat reserves (Wilz and Heldmaier, 2000).

Reduced risk of predation

An additional advantage of the inactivity is the reduced risk of predation. Retreating to underground burrows entirely protects small mammals from most avian predators, i.e. birds of prey such as owls (Radzicki *et al.*, 1999).

4.2 Disadvantages

Harmful physiological effects

Occurrence of estivation is mostly limited to periods with low food availability. This indicates that there are also detrimental effects associate with it. Because of the great similarity with hibernation, it is likely that the same detrimental effects are also associated with estivation. For these effects, see Chapter 3.3.

When comparing the energy saved by estivation with the energy saved by hibernation, the savings are lower during estivation. It is not clear why this is the case, but it probably involved the duration of the dormancy bouts and the arousal characteristics. The energetically expensive arousals take place more often when ambient temperatures are higher ([Park *et al.* 2000](#)). Why the arousals take place more often at higher temperatures is not certain, but some say it could be possible that this reflects the elevated costs of maintaining the metabolic needs of the cells without the protecting and preserving effects of cold temperature.

4.3 Examples of a species employing estivation

Here we present one representative studies that illustrate the dynamics of estivation in one mammalian species and the energy saved by employing it.

Edible dormouse (Glis glis)

Wilz and Helmaier (2000) studied the energy saved during estivation by the edible dormouse *Glis glis*. The edible (or fat) dormouse *Glis glis* is a small (90 - 150 gram) nocturnal rodent belonging to the family of Gliridae. It is found in woodlands and shrub zones in central, southern and eastern Europe. Their main diet is fruit and seeds, but also insects and leaf-buds are eaten (Fietz *et al.* 2004).

In this experiment estivation was defined as torpor bouts lasting > 1 day in summer. The average minimum energy expenditure during estivation is 0.031 ml O₂/g/h at ambient temperatures ranging from 15 °C to 20 °C. During normothermia oxygen consumption is in the range of 180 to 230 ml O₂/g/h in this range of ambient temperatures.

To estimate the energy saving per day by employing estivation, a comparison of the Average Daily Metabolic Rate (ADMR) during days in normothermia and days with estivation has been made. The ADMR of normothermic dormouse was estimated at 5.1 L O₂/d. At days in estivation without arousals, ADMR was approximately 0.75 L O₂/d. This is an energy saving of 85.3 %. Because the costs of arousal can have a large influence on the possible energy saved by employing estivation, an estimation has been made of these costs. During arousal for estivation at ambient temperatures of 16 °C, oxygen consumption is approximately 0.9 ml O₂/g/h. Arousal duration at this temperature averages approximately 2 hours. One arousal bouts therefore costs 1.8 ml O₂/g, for a dormouse of 130 g this is approximately 0.234 L O₂.

Estivation bouts lasted between 69 and 109 h. Taking this into account, ADMR during an estivation bout of 72 hours including the cost of arousal can be estimated to be approximately 0.828 L O₂/d. This is an every saving of 83.8 % compared to normothermia. This indicates that arousal costs barely affect the amount of energy saved by employing estivation.

By employing estivation the edible dormouse *Glis glis* realizes a substantial energy saving compared to remaining euthermic.

Chapter 5: Inversion of circadian activity rhythm

5.1 Introduction

Animals have a certain circadian rhythm that is relatively constant over the year on most parameters like timing of activity and bout duration. Some species are day active, others night active, and some are active in periodic bouts all over the day. All species have evolved a temporal pattern of activity that matches its specific ecology. Because of a change in light conditions, temperature and reproduction this circadian rhythm can fluctuate, but on most aspects it does not change much from day to day. But when times get rough and food is in short supply, some species change their normal circadian rhythm to reduce energy expenditure. Night active animals can become active during the day to take advantage of the elevated ambient temperature of the day compared to the night. This inversion of circadian activity rhythm may be beneficial for multiple reasons.

5.2 Advantages

Reduction of heat loss

Inversion of the circadian activity rhythm from night-active to day-active can reduce energy expenditure because activity in higher ambient temperatures greatly reduces the heat loss compared to activity in a colder period. The difference in temperature between day and night can range from a few degrees to 40 degrees Celsius. The larger the difference between ambient temperature and body temperature, the more energy can be saved on thermoregulation.

Reduction of arousal costs

Arousal from daily torpor or hibernation is a costly process. During torpor the body temperature has dropped to 2 – 15 °C above ambient temperature, but needs to be elevated to the normothermic body temperature of 34 – 37 °C. An animals that arouses at a higher ambient temperature, reduces the energy needed for warming to normothermic temperature. A changed in arousal timing from night to day can take advantage of this.

Increased food availability

Insectivorous species depend on the abundance of insects. The activity of the insects in their turn is restricted by ambient temperatures, therefore ambient temperatures are positively correlated with insect abundance (Taylor and O'Neill, 1988). When ambient temperatures reduce insect abundance in the normal activity period of an insectivore, then it can pay off to change the activity interval from night to day.

Decreased intraspecific competition

Individuals that shift from the normal activity phase to a new activity phase can escape from intraspecific competition, for example competition for food. If all animals are active at the same time, dominant individuals can limit the access to food for subordinate individuals. When a different activity period than the other members of the species is chosen, these subordinate individuals are free from their dominant competitors (Körtner and Geiser, 2000). This only applies if some animals in a population experience different energy balances, for example differences in fat reserves or energy demand. Subordinate individuals with low fat reserves are thought to be the most likely to switch.

5.3 Disadvantages

A number of disadvantages are associated with the change in circadian rhythm. These have mostly to do with the maladaptation to the circumstances in the new activity phase.

Suboptimal activity pattern

The regular activity pattern displayed by animals has to have some advantage over other possible activity patterns. This regular rhythm has evolved by selective pressures that could or do still play a role in different seasons. For example, bats that become crepuscular active instead of night active in winter suddenly face new predators, for example day-active birds of prey.

When a species changes its activity pattern, it can also encounter new competitors for resources, and therefore have to increase foraging effort.

Nocturnal and diurnal activities are accompanied by physiological, behavioral and anatomical adaptations. For example; the retina is very different between diurnal and nocturnal animals. Therefore, transitions between nocturnal and diurnal lifestyle are relatively rare (Daan, 1981).

Desynchronized conspecifics

If not all members of a social species use the same circadian activity rhythm, the group becomes desynchronized. Species that huddle to reduce thermoregulatory costs, cannot effectively use this tactic anymore. This imposes a larger cost for thermoregulation (Körtner and Geiser, 2000). Species that normally forage in groups can miss the protection from predators by the vigilance of conspecifics when active in desynchrony with group members.

5.4 Studies of changing circadian rhythm in two species

Here we present two representative studies that illustrate the use of changes in circadian rhythms in two species.

Long-eared bat (Nyctophilus spp.)

Turbill and Geiser (2008) studied the activity, body temperature and roosting site choice in the long-eared bat *Nyctophilus geoffroyi* and *N. gouldi* during the hibernation season. These small bats (7.5 – 8.5 g) live in the open forest of the Northern Tablelands of New South Wales, Australia. These tree-roosting bats feed on insects and are nocturnal. In winter they hibernate in tree cavities or under exfoliated tree bark. During the periodic arousals of hibernation the bats leave their roosts, probably to drink water and the males possibly also to search for mating opportunities (Racey, 1982).

Turbill and Geiser report that the bats mostly use roosting sites on the northern side of the tree. This part gets most heated up by the sun because it has the longest sun exposure, also in winter. They proposed that torpid bats use the warming of their roost by the sun as a way to passively warm their bodies by as much as 20 °C. When they are passively warmed, they will more often arouse from torpor and increase their MR to attain normothermic temperature than on colder days.

The choice of a northern roosting place under tree bark combined with the arousals at days with a temperature above average will result in a reduction in energy expenditure. The warmer nights will most likely result in more insects to feed on during the arousal (Taylor and O'Neill, 1988). Feeding during winter will prolong the possible hibernation period and result in less weight loss.

This method combines the energy saving aspects of hibernation with a method to reduce the costs of arousals that accompany hibernation. This qualifies as activity changes in circadian

rhythm to reduce energy expenditure because the bats show a different circadian activity pattern in winter than in summer.

Large mouse-eared bat (Myotis myotis)

A different study on a species of bat, the large mouse-eared bat *Myotis myotis*, also shows changes in circadian rhythm when food is in short supply. *Myotis myotis* is a small (25 g) bat that lives in Eurasia and feeds on arthropods. The activity pattern consists of nocturnal activity in summer, and hibernation in winter. In summer daily torpor occurs during the day and is terminated at dusk (Harmata, 1987).

Wojciechowski *et al* (2007) induced daily torpor in wild-caught bats by exposing them to low temperatures and to the natural light-dark cycle of summer. Some animals were fed every day, while others were fastened for 2 days prior to the measurements. A large difference in activity was found between fed and fastened individuals; fed bats were active for $22.60 \pm 4.71\%$ of the experiment, while fastened individuals were only active for $1.06 \pm 0.51\%$ of the experiment. The food restriction also has a significant influence on the timing of activity [4-way ANOVA: $F(1,68)=15.63$, $P<0.001$]. Fed bats were much more active by night than by day (LSD: $P<0.001$), while fastened ones reduced night time activity to the same level as during the day.

When the animals were exposed to cold temperatures in summer the effect was even more clear. Fastened bats aroused from torpor in the late afternoon, became active for ± 1 h. and returned to torpor for the rest of the time. Fed bats aroused from torpor at dusk.

This change in circadian rhythm is advantageous for two possible reasons. First the lower energy expenditure when arousing from torpor in the warmer part of the afternoon compared to arousing in the cool night. Second, the higher food availability in the afternoon caused by the higher ambient temperatures at day compared to the night. Ambient temperatures are positively correlated with insect abundance (Taylor and O'Neill, 1988). When nights are cold, insect abundance will greatly fall, and food intake for bats will be higher during the day. The ambient temperature can also be used by the bats as a predictor of food availability, and can regulate torpor use (Park *et al.*, 2000).

Chapter 6: Changing annual activity pattern

6.1 Introduction

Animals do not only have a circadian rhythm, but also an annual rhythm that is somewhat constant when comparing different years. This rhythm shows itself in time of reproduction, body mass, amount of activity and usage of torpor, and seems largely covered by the changing seasons, which influence reproduction, food availability, predation, length of day and temperature. However, some animals have very different annual rhythms when comparing one year to another. This change in annual rhythm can be a way to cope with low food availability and high energy expenditure when these factors are variable from year to year.

The changes in the annual activity pattern could be to go into estivation, daily torpor or hibernation or to stay active. Years without estivation can be followed by a year of estivation, or daily torpor in winter can be changed into hibernation by some species. Essentially the animal combines the ability to use daily torpor, hibernation and estivation with a mechanism to choose the correct timing and duration of each method. Here we will take a look at the possibilities, benefits and disadvantages of changing the annual rhythm.

6.2 Advantages

Modularity

The animal can determine from year to year what the best strategy would be: go into hibernation, estivation or daily torpor or remain active. The timing, duration and combination of these methods can be varied according to need. Therefore it is highly modular and optimally adapted to the current conditions. In summers where food is abundant estivation is not necessary, and the summer can be used for food gathering or reproduction instead. In relatively mild winters hibernation can be substituted by daily torpor. Every season can be spent with an activity and dormancy rhythm that best fits the circumstances.

6.3 Disadvantages

A number of disadvantages are associated with combining the ability to use daily torpor, hibernation and estivation with a mechanism to choose the correct timing and duration of each method. These include decreased specialization and lack of reliable indicators.

Decreased specialization

The animal has to be able to use and regulate all three methods of energy saving effectively. There is an indication that daily torpor, hibernation and estivation use the same metabolic mechanism (Wilz and Heldmaier, 2000). All differences found in MR, body temperature and cooling rate are probably caused by the different ambient temperatures and the duration of the torpor bout (Wilz and Helmaier, 2000). However, it is likely that daily torpor, hibernation and estivation still require different regulation mechanisms, for example in the timing of arousal.

Lack of reliable indicators

For accurate and effective usage of the three major rhythmic energy saving methods the animal has to have reliable indicators of circumstances to come. For example it has to have an indicator of upcoming food availability and temperature. When a harsh winter season has already begun it may be too late to start accumulating fat reserves for hibernation.

A bad choice could have devastating results for the reproductive success or survival of the

animal. For example hibernating in a time when enough food is available, will greatly reduce the fat reserves of the individual, as well as impose the negative physiological effects of hibernation itself. Estivation and reproducing in summer cannot both be carried out in the same time. Employment of estivation when reproduction was likely to be successful could impose a serious fitness loss.

But reliable indicators of upcoming weather conditions and food availability are most likely very limited. The edible dormouse (*Glis glis*) uses food availability and quality as indicator of the availability of seeds in autumn (Fietz *et al.* 2004).

6.4 Studies on species using a change in annual rhythm

Although many species that use torpor can change their annual rhythm to some extent, limited information is available on species that use this method regularly. Here we describe a representative study on this method of energy saving.

Edible dormouse (Glis glis)

Wilz and Heldmaier (2000) did a study on an animal that is a perfect example of this annual rhythm management: the edible dormouse (*Glis glis*). See chapter 3 for more information about this species.

Edible dormice are closely adapted to the temporally availability of beechnut and acorn in autumn in central and northern Europe. The seeds of beechnut and acorn are distributed in so-called mast seeding years; in these years the seeds are overabundant. These mast years are interrupted by years with poor seeding in which almost no acorn and beechnuts are produced. Late in the summer season females give birth to one single litter, but only in mast seeding years. The pups are nursed during the autumn when plenty of seeds are available. In years without mast seeding, reproduction is skipped for a full year by some or all females of a population of dormice. In years when reproduction is skipped, females and males drastically change their annual activity rhythm compared to reproducing years (Wilz and Helmaier, 2000).

In mast seeding years dormice hibernate from October to May/June in Germany after which they remain active until winter. In poor seeding years they limit their activity from six months to just two weeks per year in the start of spring (May/June). The rest of the year they remain dormant, employing hibernation in winter and estivation in summer and relying on the body fat they accumulated in the activity period (Bieber and Ruf, 2009).

Chapter 7: Discussion and conclusion

Comparing all different methods for coping with low food availability and high energy expenditure, some methods save more energy than others. Hibernation seems to be the most energy-conserving per time unit. This has to do with the duration of reduced MR and possibly also the low ambient temperatures common during hibernation. Estivation is also very energy-conserving and is closely followed by daily torpor. Changes in circadian or annual rhythms are hard to compare with hibernation, estivation and daily torpor because of the difficulty in assessing the energy spent and the alternatives.

Although many methods to reduce energy expenditure in challenging circumstances are described in this thesis, one can never be complete. The aim of this paper is to give an overview of the various methods to save energy using rhythmicity and illustrate this with some model species.

Many species have still to be studied on their methods and the costs and benefits associated with it. Some are known to employ the energy saving methods described here, but are never studied on the energy saved. Other species are not even studied on their ability to use dormancy and the other methods described here. A lot of work has to be done in this field to provide a complete scope on this interesting animal quality. The limitations in the methods of measuring energy expenditure in wild animals or in high ambient temperature also limit the amount of information that can be gathered.

The great diversity of methods to cope with high energy demand and low energy intake is fascinating. Although this thesis only focuses on a small portion of these methods, I hope it illustrates the diverse aspects of the costs and benefits associated with them.

Chapter 8: References

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Picture on front page: Japanese dormouse (*Glirulus japonicus*) in dormancy.