

Review

THE TEMPORAL ORGANIZATION OF DAILY TORPOR AND HIBERNATION: CIRCADIAN AND CIRCANNUAL RHYTHMS

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ABSTRACT

Mammals and birds have evolved the ability to maintain a high and constant body temperature T_b over a wide range of ambient temperatures T_a using endogenous heat production. In many, especially small endotherms, cost for thermoregulatory heat production can exceed available energy; to overcome these energetic bottlenecks, they enter a state of torpor (a regulated reduction of T_b and metabolic rate). Since the occurrence of torpor in many species is a seasonal event and occurs at certain times of the day, we review whether circadian and circannual rhythms, important in the timing of biological events in active animals, also play an important role during torpor when T_b is reduced substantially and may even fall below 0°C. The two distinct patterns of torpor, hibernation (prolonged torpor) and daily torpor, differ substantially in their interaction with the circadian system. Daily torpor appears to be integrated into the normal circadian rhythm of activity and rest, although torpor is not restricted only to the normal rest phase of an animal. In contrast, hibernation can last for several days or even weeks, although torpor never spans the entire hibernation season, but is interrupted by periodic arousals and brief normothermic periods. Clearly, a day is no longer divided in activity and rest, and at first glance the role of the circadian system appears negligible. However, in several hibernators, arousals not only follow a regular pattern consistent with a circadian rhythm, but also are entrainable by external stimuli such as photoperiod and T_a . The extent of the interaction between the circadian and circannual system and hibernation varies among species. Biological rhythms of hibernators for which food availability appears to be predictable seasonally and that hibernate in deep and sealed burrows show little sensitivity to external stimuli during hibernation and hence little entrainability of arousal events. In contrast, opportunistic hibernators, which some-

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times use arousals for foraging and hibernate in open and accessible hibernacula, are susceptible to external zeitgebers. In opportunistic hibernators, the circadian system plays a major role in maintaining synchrony between the normal day-night cycle and occasional foraging. Although the daily routine of activity and rest is abandoned during hibernation, the circadian system appears to remain functional, and there is little evidence it is significantly affected by low T_b . (*Chronobiology International*, 17(2), 103–128, 2000)

ENERGETIC CONSEQUENCES OF ENDOTHERMY AND TORPOR

Endotherms have evolved the ability to produce endogenous heat for maintenance of a high body temperature T_b and thus have achieved a high degree of independence from the restrictions imposed by ambient temperature T_a on ectotherms. While the T_b and metabolism of ectotherms, and hence their mobility, decrease with T_a , endotherms can remain active even when T_a is low. However, this advantage comes at high energetic costs. In contrast to ectotherms, which reduce metabolism with decreasing T_a , homeothermic endotherms must increase their metabolic rate (MR) for thermoregulatory heat production at low T_a to compensate for the increased rate of heat loss. Furthermore, the MR of endotherms exceeds that of ectotherms by a factor of 5–10 even at rest under thermoneutral conditions when metabolism is basal (BMR, maintenance MR without thermoregulation) and T_b is similar. Consequently, under virtually all climatic conditions, the energy turnover of endotherms is much higher than that of ectotherms, and hence it requires a higher rate of food uptake (Bartholomew 1982).

High energetic costs in endotherms are particularly pronounced in small species because the mass-specific BMR increases steeply with decreasing body mass. Moreover, at T_a below the thermoneutral zone, heat loss from the surface of the body increases because the rate of heat loss is determined by the ratio of surface area to body volume, the differential between T_b and T_a , and insulation. Consequently, small endotherms with large surface-to-volume ratios and poor insulation must spend a considerable proportion of their daily energy budget on thermoregulation. To replenish body fuels, some very small mammals and birds consume more food per day than their own body mass (Atchison 1987). Thus, at least in small endotherms, the thermal independence gained by high endogenous heat production is substituted by energetic constraints.

The higher energetic demands imposed by endothermy can be met by higher mobility, longer activity, and better stamina. Activity of endotherms can begin very early in the morning and be extended into late afternoons and, of course, also into the night, when it is too cool for ectotherms. Indeed, most small mammals are nocturnal probably to avoid daytime predators and are better adapted to cold than heat exposure. Nevertheless, in spite of the theoretically higher flexibility in the daily activity pattern, times of activity and foraging in most endotherms are still restricted by the daily light-dark cycle because of various ecological constraints, such as predation pressure or food availability. Surprisingly, even many arctic endotherms continue a daily activity cycle throughout summer, although daily changes in illumination are minute (Swade and Pittendrigh 1967). Only some small burrowing mammals or those with an otherwise extremely cryptic lifestyle have escaped the constraints of the 24h cycle and show a more or less random or polyphasic sequence of activity and resting periods throughout the day (Crowcroft

1954; Godfrey 1955; Aschoff 1962; Erkinaro 1973; Saarela and Hissa 1993). Others, especially those that depend predominantly on visual information during activity or those that rely on darkness to escape detection by predators, often have to abandon foraging for half the day or even longer. Being unable to forage for long periods can be problematic for small endotherms given that their normothermic MR is high even when resting, especially at low T_a . Therefore, many small species use physiological mechanisms to minimize energy expenditure during rest. Since thermoregulation accounts for a large proportion of the energy budget, and a high T_b during rest is not as important as for activity, lowering the T_b periodically can save substantial amounts of energy. Accordingly, small endotherms show larger daily fluctuations in T_b and MR between activity and rest than large endotherms (Aschoff and Pohl 1970; Aschoff 1981; Kenagy and Vleck 1982). This decrease in energy turnover during rest appears to be associated with sleep. Thermoregulation is largely impaired during rapid eye movement (REM) sleep, and the T_b threshold during non-REM (NREM) sleep is lowered (Heller et al. 1978; Berger 1993). Therefore, conservation of energy may be one of many functions of sleep (Heller and Glotzbach 1977; Berger 1993). However, the reduction in T_b during sleep is moderate and, at low T_a , may not suffice to overcome the long time interval between foraging periods.

A more pronounced decrease in T_b , often associated with the normal resting time of an animal, occurs in many small mammals and birds and is often referred to as daily torpor. Daily torpor lasts only for several hours, in contrast to hibernation, which is characterized by torpor bouts that last for days, weeks, or even months (MacMillen 1965; Wang 1989; Geiser and Ruf 1995). It has been suggested that daily torpor and sleep are homologous because of similar timing and also by the similarities in EEG patterns (Berger 1993). In mammals, a drop in T_b below 30°C or a reduction in resting MR by more than 25% often are used to qualify daily torpor (Hudson and Scott 1979), whereas during sleep T_b usually is reduced by less than 3°C (Aschoff 1981; Berger and Phillips 1993). In birds, which generally have higher T_b than mammals, the boundary between normal sleep and torpor is less clear-cut; a moderate reduction of T_b of 3°C–5°C intermediate between sleep and torpor is often referred to as *nocturnal hypothermia* for diurnal birds (Reinertsen 1983; Maddocks and Geiser 1997). However, a drop of more than 5°C below resting T_b is usually accepted for defining torpor in birds (Brigham 1992).

In contrast to ectotherms, heterothermic endotherms (i.e., endotherms capable of torpor) are able to arouse actively from torpor by endogenous heat production. Although widely believed necessary, brown adipose tissue (BAT) as a source of nonshivering thermogenesis is not a prerequisite for arousal from torpor (Geiser and Baudinette 1990). Torpor patterns and arousal are very similar in birds, marsupials, monotremes, and placental mammals, although functional BAT has been found only in placentals (Geiser and Ruf 1995; Nicol et al. 1997). The drop in T_b during torpor is also not an indication that thermoregulation during torpor has been abandoned, but is a result of a lowered T_b threshold (Heller and Hammel 1972). Torpid endotherms are able to increase their heat production to prevent T_b from falling below this threshold. The T_b threshold varies widely among species, and on average, the minimum T_b during daily torpor is about 17°C. The MR during daily torpor is about 30% of the BMR for both mammals and birds (Geiser and Ruf 1995). However, the T_a at which torpor occurs is usually well below thermoneutrality, and greater reductions of MR (on the order of 80–90%) are common when the thermoregulatory costs at normothermia are used as point of reference (Holloway and Geiser 1995; Song et al. 1995; Geiser 1998). The decrease in MR during daily torpor

below BMR appears to be explained largely by the temperature effects of the lowered T_b , but some metabolic inhibition, particularly during entrance into torpor, is also possible (Geiser 1988; Geiser and Ruf 1995; Song et al. 1995, 1996; Guppy and Withers 1999). As overall daily energy expenditure is not only affected by the extent of MR reduction, but also by the duration of daily torpor (Hill 1975; Holloway and Geiser 1995; Coburn and Geiser 1998), timing of torpor entry and arousal are of great importance for its effective use.

SEASONALITY OF DAILY TORPOR

In many endotherms living at high latitudes with seasonally predictable climatic conditions, daily torpor is expressed predominantly during the cold season. Animals living in these areas normally reproduce in summer. The period of reproduction is then followed by a period of reproductive quiescence and use of torpor during winter (Bronson 1985; Kenagy 1989). In some species, this annual sequence of reproduction and reproductive quiescence associated with torpor apparently is mediated via the pineal gland and is under photoperiodic control. In the Djungarian hamster (*Phodopus sungorus*), exposure to a short photoperiod leads to testicular regression and the subsequent expression of daily torpor (Heldmaier and Steinlechner 1981). This effect can be simulated with melatonin implants in hamsters held in long photoperiod, whereas pinealectomy prevents any acclimation to short photoperiod and the occurrence of torpor (Vitale et al. 1985; Steinlechner et al. 1986; Ruf et al. 1989). Although responsible for seasonal acclimation, the pineal and its hormone melatonin are not involved directly in the expression of torpor in mammals because torpor persists for several weeks after pinealectomy in hamsters already acclimated to a short photoperiod (Ruby et al. 1989). In birds in which the pineal appears to be one of the pacemakers or even the master pacemaker for circadian rhythms (Ralph et al. 1979; Rusak and Zucker 1979), its influence on torpor is unknown.

Although the effectiveness of photoperiod as the proximate environmental cue for seasonal acclimation in many animals is demonstrated easily by artificially manipulating the photoperiod in the laboratory, a form of endogenous circannual rhythm seems to exist even in short-lived small rodents and birds. The seasonal cycle of some heterothermic endotherms is characterized by a phase of unresponsiveness to a previously effective photoperiod (Reiter 1972; Hoffmann 1973; Zucker and Morin 1977; Bittman 1978; Steinlechner and Heldmaier 1982, 1983). In the Djungarian hamster, for example, which is heterothermic in winter, the spring reversion to the homeothermic summer conditions cannot be prevented by prolonged exposure to short photoperiod, melatonin implants, or castration (Hoffmann 1973, 1978; Steinlechner and Heldmaier 1982, 1983).

However, in contrast to the scenario outlined above for the strong seasonality of daily torpor, the impact of photoperiod on the use of torpor can vary among populations and species. While white-footed mice (*Peromyscus leucopus*) from high latitudes (Connecticut) increase torpor occurrence by 38% at a T_a of 23°C when exposed to short photoperiod, members of the same species from low latitudes (Georgia) do not respond to acclimation to short photoperiod (Heath and Lynch 1983). A similar insensitivity to photoperiod with regard to the expression of daily torpor can be observed in the small marsupial dunnarts *Sminthopsis crassicaudata* from Australia (Holloway and Geiser 1996). It appears, therefore, that daily torpor in many species is not strictly seasonal, and

that it is by no means restricted to cool temperate or subarctic regions. Energetic constraints that demand torpor are just as likely to occur in species that inhabit dry, mesic, and even tropical areas (Hudson 1973; Kulzer and Storf 1980; Bartels et al. 1998; Bonaccorso and McNab 1997; Lovegrove and Raman 1998). Moreover, small endotherms living at high altitudes, at which the climate can be severe even during summer, or those living at low latitudes, at which hot, dry summers and lack of food can be more challenging than winter, may use torpor in summer (Hill 1975; Geiser and Baudinette 1987; Tannenbaum and Pivorun 1989; Holloway and Geiser 1996; Coburn and Geiser 1998; Lovegrove and Raman 1998). Food availability, T_a , and low body energy reserves appear to be the most important stimuli for the expression of daily torpor in the species that use torpor opportunistically. Even in strongly seasonal species such as the Djungarian hamster, these factors normally enhance the response to short photoperiod (Ruf et al. 1993). Likewise, in some opportunistic daily heterotherms in which photoperiod does not govern the expression of torpor, torpor frequency, depth, and length can be modulated by photoperiod to some extent (Lynch et al. 1978; Coburn and Geiser 1998). It is likely that the differences in the seasonality of daily torpor reflect the ecology and habitat of different species. The strong seasonal climatic changes at higher latitudes favor exclusive winter torpor, which represents only the most extreme situation.

As outlined above, torpor and reproduction usually occur at different times of the year. In contrast to daily torpor, which is exhibited during times of low energy availability, reproduction usually can occur only when energy is abundant (Bronson 1985). Therefore, a temporal overlap between reproduction and torpor may appear impossible. In many rodents, torpor and reproduction are indeed exclusive because of energetic and hormonal reasons (Goldman et al. 1986; Kenagy 1989; Geiser 1996). The incompatibility of sex hormones and torpor has been tested by administering sex hormones during the nonreproductive season; especially, testosterone reduced the incidence of daily torpor substantially in hamsters (*Phodopus sungorus*) (Goldman et al. 1986). Even those rodents that exhibit torpor during the summer months seem to reduce their testes before torpor commences (Lovegrove and Raman 1998).

While torpor and reproduction may be mutually exclusive in most rodents (dormice, *Eliomys quercinus*, appear to be an exception; Agid et al. 1978), this is not the case for all mammals. Monotremes, marsupials, some nonrodent placental mammals, and some birds can use torpor even during the reproductive season despite apparent hormonal and energetic incompatibilities. Even pregnant, lactating, or incubating females can enter torpor (see Geiser 1996 for reference); in these cases, torpor is not necessarily a response to severe environmental conditions. Torpor during part of the reproductive season may be used to store energy for later stages of the reproductive cycle, which may represent energetic bottlenecks (Geiser and Masters 1994). Unfortunately, beyond the fact that torpor and reproduction are in principle not exclusive, little is known about the endocrinological effect of sex hormones on torpor in nonrodent species.

TIMING OF DAILY TORPOR

If torpor is an extension of sleep, it should be restricted to the animal's rest phase. Indeed many, but not all, daily heterotherms show this daily organization of torpor. Torpor during the rest phase does not interfere with foraging, but possibly with the process of digestion, sleep, and other metabolic functions (Geiser and Baudinette 1987; Ruf et

al. 1991; Deboer and Tobler 1994). This may be the reason why most daily heterotherms use torpor only occasionally when food is abundant (spontaneous torpor) and the T_a is high. Food restriction and/or low T_a , which demand higher thermoregulatory investments, usually increase torpor frequency considerably (induced torpor). In contrast to spontaneous torpor, induced torpor in many daily heterotherms is not restricted to the rest phase (Geiser and Baudinette 1987, 1988; Holloway and Geiser 1995; Ortmann et al. 1996; Brigham et al. 1998; Körtner and Geiser 1998b, 2000). Especially when food availability is weather dependent, as in insectivorous and nectarivorous animals, foraging can become futile, and torpor during the activity phase may be used to minimize energy loss. Timing of daily torpor, therefore, should be dependent on the animal's ecology and the prevailing environmental conditions. Torpor should be restricted mainly to the rest phase when severe climatic conditions affect energy expenditure predominantly, but food availability remains sufficient. If, however, adverse weather conditions reduce food availability as well, then torpor is likely to commence during the normal activity phase. Although torpor in the latter case will reduce energy expenditure, the daily energy balance becomes negative nonetheless because foraging is curtailed. Since this loss in body energy reserves has to be recouped, animals that enter torpor during their normal activity period should show a lower torpor frequency than those that restrict torpor to the rest phase unless energy expenditure can be sustained for prolonged periods by excessive body fat stores, which are restricted to large species. This tenet is supported by field observations on caprimulgiform birds. Free-ranging nocturnal owl-nightjars (*Aegotheles cristatus*, 50 g), which enter torpor predominantly during their daytime rest phase, can show torpor for several hours almost every morning during winter, but then forage during the following night (Brigham et al. 1998). In contrast, the related sympatric tawny frogmouth (*Podargus strigoides*, 500 g) enters torpor predominantly during the second half of their nightly activity phase, but in this species, torpor occurs less frequently (Brigham et al. 1998; Körtner and Geiser 1998b). However, the natural occurrence of daily torpor has been measured in very few species, and more data are needed to establish whether other species also follow this pattern.

Regardless of whether daily torpor is restricted to the rest phase or whether it commences during the normal activity period, the exact timing of torpor entry is highly variable. As the main function of torpor appears to be energy conservation, the timing of torpor entry should be dependent on food availability and energy use, especially when torpor is entered during the activity phase. Pocket mice (*Perognathus californicus*) compensate for a variable food supply by undergoing variable periods of daily torpor (Tucker 1962). If the food supply is low, torpor commences significantly earlier in the night, and bout length is longer than when food is abundant (Tucker 1962). Similarly, torpor entry in the marsupial Kultarr *Antechinomys laniger* occurs earlier on cold than on warm nights, and time of entry is a direct function of T_a and thus of energy use during the activity phase (Geiser 1986). Tawny frogmouths enter torpor earlier during cold nights, when availability of insects is likely to be low, whereas arousal always occurs shortly before sunrise (Körtner and Geiser 1998b). Similar observations have been made in the rufous hummingbird (*Selasphorus rufus*) (Hiebert 1992), although in this species, torpor is restricted entirely to the rest phase. Timing of torpor entry in rufous hummingbirds as in pocket mice is a function of the amount of food provided on the previous day, whereas timing of arousal remains unchanged (Tucker 1962; Hiebert 1992).

Thus, the timing of torpor entry appears to be a function of the depletion of energy reserves. Time of arousal, on the other hand, seems less flexible and appears to be

governed to a large extent by circadian rhythms. However, the timing of arousal differs significantly among species. Surprisingly, most arousals occur well before the onset of the activity phase, although arousals shortly before activity as observed in several species would appear most beneficial from an energetic point of view (Ruf et al. 1989; Coburn and Geiser 1998). However, arousals are also energetically the most expensive part of a torpor bout, and costs could be minimized if torpid animals would synchronize arousal with what would be the warmest part of the day under natural conditions. Especially, species that use shallow burrows or tree hollows as shelter during summer torpor could save much energy via passive rewarming by the increasing T_a (Ortmann et al. 1996; Schmid 1996; Lovegrove et al. 1999). Thus, arousals in the laboratory near midday, as observed in many nocturnal species, could reflect the natural daily T_a cycle. Since daily patterns of T_a in the field can be buffered and delayed considerably in the shelter of a torpid animal (Lovegrove et al. 1991), some of the differences among species in the temporal organization of daily torpor, particularly the timing of arousal, may reflect the insulative properties of shelters or roosts selected for torpor (Schmid 1996; Körtner and Geiser 1998b; Lovegrove et al. 1999). However, although the arguments for a link between a daily T_a cycle and the timing of arousals may appear compelling, no definite conclusion can be drawn without further field studies.

DAILY TORPOR AND THE CIRCADIAN SYSTEM

Since animals that undergo daily torpor still retain a daily cycle of activity and rest, daily torpor is part of the normal circadian organization. Indeed, it appears that a functional circadian system is a prerequisite for the expression of daily torpor since bilateral lesions of the SCN (suprachiasmatic nuclei), the “master clock” for circadian rhythms in mammals (Rusak and Zucker 1979; Rusak 1989; Miller 1993), interfere with the occurrence of spontaneous daily torpor in Djungarian hamsters (Ruby et al. 1989). However, induced torpor after prolonged starvation is possible even after SCN ablation (Ruby and Zucker 1992). Similarly, torpor can be induced in Djungarian hamsters acclimated to a long photoperiod that do not enter torpor spontaneously (Steinlechner et al. 1986). In both instances, the temporal structure of torpor was disrupted, indicating that, under these conditions, torpor represents an artificial state.

A link between the circadian system and daily torpor is emphasized further by the observation that an 8h shift in the photophase results in a corresponding shift in timing of spontaneous torpor in the marsupial dunnart *Sminthopsis macroura* after only 2–3 days (Geiser and Baudinette 1985). Moreover, Djungarian hamsters held under constant darkness or constant dim light show free-running patterns of activity and spontaneous torpor, and torpor remains synchronized with the shifting rest phase of the animal (Ruf et al. 1989). Exposure to constant light can be interpreted as a long photoperiod and prevents spontaneous torpor by Djungarian hamsters (Ruf et al. 1989), but constant illumination is also known to interfere with the expression of other circadian rhythms in nocturnal animals (Daan and Pittendrigh 1976).

Entrainment of the circadian system to the normal day-night cycle is achieved predominantly by photic stimuli. However, in contrast to most homeothermic endotherms (Rusak and Zucker 1979), some daily heterotherms are also sensitive to daily fluctuations in T_a , which can act as a weak zeitgeber in the absence of light stimuli (Erkert and Rothmund 1981; Francis and Coleman 1990). The temperature sensitivity of the circadian

system in daily heterotherms and the fact that during torpor T_b is lowered raise the question as to whether daily torpor provides feedback to the organization of circadian rhythms. Unfortunately, the period τ of free-running circadian rhythms is not fixed, but is influenced by external and internal factors such as T_a , illumination, age, and circannual changes (Mrosovsky et al. 1976; Pittendrigh and Daan 1976a; Lee et al. 1986). Although such changes complicate the issue, Thomas et al. (1993) could establish that, at the same T_a , the τ of Djungarian hamsters, which exhibited torpor, was shorter than τ from individuals that remained normothermic. This observation could mean that either torpor shortens τ , which would suggest overcompensation for possible temperature effects on the circadian system, or that hamsters with a shorter τ are more likely to enter torpor. The authors favored the former interpretation (Thomas et al. 1993), but further experiments on the same species have shown that the circadian system, including τ of individual hamsters that respond to short photoperiod exposure and subsequently enter torpor, indeed differs from that of hamsters that do not respond to change in photoperiod. Nonphotoperiodic hamsters do not change fur color, do not reduce testis and body mass, and resist entering torpor under a short photoperiod (Puchalski and Lynch 1986; Lynch et al. 1993). This result, however, does not preclude any possible feedback mechanism of torpor on the circadian system, although the circadian systems of daily heterotherms apparently are highly temperature compensated.

HIBERNATION

While daily torpor is incorporated into the normal daily activity-rest cycle, hibernation clearly is not. Torpor bouts during hibernation extend over days, weeks, or even months (Harmata 1987), but never span the entire hibernation season. All hibernators that have been studied to date arouse from torpor at regular intervals (Lyman et al. 1982). Hibernators on average are larger (median 85 g) than daily heterotherms (median 19 g), although there is considerable overlap in size between the two groups (Geiser and Ruf 1995). The MR during hibernation is much lower than during daily torpor and is on average only 5.8% of BMR (Geiser and Ruf 1995) and often is less than 1% of the resting MR at low T_a (Song et al. 1997; Geiser 1998). As torpor bouts during hibernation are much longer and MR is lower than those during daily torpor, energy savings accrued from using hibernation are far greater than during daily torpor (Wang 1978; Geiser and Ruf 1995). The drop of MR in hibernators appears to be facilitated by very low T_b , which are usually around 6°C but extremes below 0°C occur (Barnes 1989; Geiser and Ruf 1995). However, temperature effects are often not sufficient to explain entirely the substantial reduction of MR. It appears that metabolic inhibition is used extensively, particularly in small hibernators, during torpor entry and at high T_b (Geiser 1988; Malan 1993; Song et al. 1997; Guppy and Withers 1999). Torpid hibernators show by far the greatest reduction in energy expenditure known in endotherms.

As MR during torpor in hibernators is extremely low, stored energy would last for very long time periods if they would remain at these low levels throughout the hibernation season. Therefore, it appears counterproductive that hibernators arouse at regular intervals and use energetically wasteful endogenous heat production. Although many attempts have been made, the enigma of periodic arousals has never been resolved. Apparently, all hibernators show these arousals, although hibernation probably has evolved several times independently in several mammalian lineages and birds (Geiser 1998).

Several hypotheses have been put forward. One proposes that accumulation or depletion of certain metabolites (or, in bats, water) during torpor requires periodic normothermic periods for reestablishing homeostatic balance (Pengelley and Fisher 1961; Galster and Morrison 1970; French 1985; Thomas and Geiser 1997). Torpor bout length does vary with T_a and hence T_b (Twente and Twente 1965; French 1985), but although significant, the correlation of torpor bout length and MR during torpor is poor when torpor bouts at T_a below and above the T_b threshold of torpid hibernators are considered (Geiser and Kenagy 1988). If, however, MR is considered together with T_b in multiple regressions, the correlation with torpor bout duration is improved considerably, and it has been proposed that impaired neural sensitivity at low T_b together with MR provide a reasonable explanation for the thermal sensitivity of torpor bouts (Geiser and Kenagy 1988). Unfortunately, the proposed imbalance in metabolites has never been clearly demonstrated (Willis 1982).

A variation of the metabolite hypothesis is based on the observation that some hibernators sleep for much of the intermittent normothermic periods. It has been proposed that an accumulation of a sleep deficit induces arousals (Daan et al. 1991; Trachsel et al. 1991; Barnes et al. 1993). Even if daily torpor and hibernation have originated from sleep, the function of sleep may be impaired at T_b below the normal sleep level of normothermic endotherms (Heller and Glotzbach 1977; Heller et al. 1993). Of course, this applies only if sleep, particularly NREM sleep, is a physiological correlate of a recuperative process (Daan et al. 1984), an assumption that does not enjoy a wealth of direct evidence (Borbély 1990; Berger 1993, 1998). Unfortunately, the function of sleep is just as obscure as arousals from hibernation, and electroencephalograms (EEGs) used to characterize the sleep status are only measurable at relatively high T_b . Nevertheless, slow-wave-activity (SWA; lower frequency spectrum of NREM sleep) intensity correlates with torpor bout length at high T_a (Larkin and Heller 1996; Strijkstra and Daan 1997a). If, however, the whole T_a spectrum below and above the T_b threshold over which hibernation occurs is scrutinized, this correlation vanishes, refuting a direct link between arousals and sleep (Strijkstra and Daan 1997b; Berger 1998). Furthermore, although the patterns of SWA immediately after arousal are similar to those observed after sleep deprivation in normothermic animals, these similarities appear to be superficial, and it now seems unlikely that a sleep debt occurs during torpor (Strijkstra and Daan 1998).

Another attempt to explain periodic arousal is concerned with lengthening of the normal circadian rhythm, again due to the low T_b during torpor (Strumwasser 1959; Willis 1982). We deal with this hypothesis in more detail below in the discussion of circadian rhythms during hibernation.

All of the above proposals assume that arousals are counterproductive and should be avoided whenever possible. French (1985) questioned this approach by arguing that, with the strong selection pressure that should act against arousals, they should occur much less frequently than they do. Because large hibernators, which can carry larger fat reserves, arouse more often than small hibernators, which are energetically more challenged, he proposed that hibernators arouse as often as is energetically possible, and that they favor normothermia over torpor. Nevertheless, the assumed positive aspect of prolonged normothermia during hibernation has yet to be identified, whereas the negative energetic aspects are obvious. Arousals and normothermic periods during hibernation are clearly energetically expensive and account for about 70% of the energy expenditure during the hibernation season in ground squirrels *Spermophilus richardsonii* (Wang 1978).

Although foraging during arousals would seem a likely activity, only a few hibernators forage during interbout normothermic periods, and even if they do forage, energy expenditure (at least in small species) cannot be balanced on a daily basis, in contrast to many species using daily torpor (Brigham 1987). Hibernation generally is a period of negative energy balance despite the low MR, and it requires the accumulation of energy stores during the active season of the year. Consequently, hibernation is embedded into a seasonal or annual, rather than a daily, framework.

SEASONAL CYCLES AND CIRCANNUAL RHYTHMS IN HIBERNATORS

The yearly organization of hibernation is reflected by a strong circannual rhythm of hibernation and activity in many long-lived hibernators. In ground squirrels, marmots, and other hibernators, physiological and morphological variables such as reproduction, activity, food consumption, body mass, and torpor follow a circannual cycle even under constant photoperiod and temperature (Pengelley and Fisher 1957; Kenagy 1980; Mrosovsky 1980; Ward and Armitage 1981). Hibernation patterns also vary seasonally; torpor bouts are longest and deepest during the middle of the hibernation season, whereas bouts at the beginning and end of the hibernation season tend to be short. Although the lengthening in bout duration in autumn follows the normal seasonal decline of T_a in underground hibernacula (Walhovd 1976; Wang 1978; Arnold et al. 1991; Grigg et al. 1992; Körtner and Geiser 1996), the change also persists under constant laboratory conditions, indicating involvement of an endogenous circannual cycle (Pengelley and Fisher 1961; Fisher 1964; French 1985; Geiser, Hiebert, et al. 1990). The seasonal change of torpor bout length shows strong correlations with the minimum T_b and MR at different times of the hibernation season (Geiser, Hiebert, et al. 1990). This suggests that either all variables are under circannual control or that one or some of these variables are controlled by a circannual rhythm and affects the other in turn.

This circannual rhythm is apparently not derived from the circadian rhythm by frequency demultiplication (Saarela and Reiter 1994). When subjected to constant illumination, even τ of the circadian activity cycle follows a circannual rhythm (Mrosovsky et al. 1976; Lee et al. 1986). Furthermore, a circannual rhythm can persist even after ablation of the SCN, whereas the circadian rhythm is abolished (Ruby et al. 1996, 1998). The long-term timing and structure of the circannual cycle, including hibernation, however, is altered after SCN ablation. It appears, therefore, that the brain area responsible for circadian rhythms is also involved in circannual rhythms, but it seems to have only a modulating function on circannual rhythms (Zucker et al. 1983).

ZEITGEBER FOR CIRCANNUAL RHYTHMS

Characterizing circannual rhythms and studying the influence of environmental variables such as photoperiod and T_a on them are notoriously difficult because, even in long-lived species, only a few cycles can be observed (Mrosovsky 1990). This also precludes the practice of studying the same individual under different conditions, as commonly employed for studying circadian systems. Age effects may represent further po-

tential problems. Nevertheless, in spite of the above-mentioned limitations, some information on circannual cycles in hibernators is available.

It appears that, in some species, hibernation follows a strong circannual rhythm, whereas in others, it is a function of environmental variables. The circannual rhythm of hibernators such as ground squirrels and marmots shows remarkably little response to photoperiod, which functions as the main zeitgeber for the circadian system and is also responsible for seasonal acclimation in many endotherms (Hock 1955; Pengelley and Fisher 1963; Davis 1967, 1976). Nevertheless, Northern Hemisphere marmots transferred to the Southern Hemisphere do acclimate slowly to the reversed photoperiodic cycle (Davis and Finnie 1975). Moreover, pinealectomy, which interferes with the interpretation of photic stimuli, has long-term effects on the timing of hibernation or may even impair hibernation in ground squirrels (*Spermophilus* spp.) (Phillips and Harlow 1982; Harlow and Walters 1983; Stanton et al. 1986). Because pinealectomy shortly prior to the hibernation season has no immediate effect, but is effective when conducted in summer or in the previous year (Harlow et al. 1980; Harlow and Walters 1983), photoperiodic sensitivity of the circannual cycle appears to be restricted to a narrow time period during summer (Harlow and Walters 1983).

While the effect of photoperiod as a zeitgeber appears to be weak and possibly limited to a short period during summer, T_a can have a strong influence on the circannual cycle length. When kept under constant T_a , the overall length of the circannual cycle is shorter at high than at low T_a (Pengelley and Fisher 1963; Joy and Mrosovsky 1983; Mrosovsky 1986). Moreover, changes in T_a can act directly as a zeitgeber for the circannual rhythm (Mrosovsky 1990). Exposure to cold in spring delays the following phases of the circannual cycle in comparison to individuals continuously held at warm T_a . In fact, cold exposure in spring can arrest the circannual cycle at least for several months. In contrast, cold exposure in autumn accelerates fattening and advances hibernation (Joy and Mrosovsky 1983, 1985). Although these findings seem to suggest a phase-response curve similar to the effects of light pulses on the circadian system, long-term studies that include the following years after the manipulation question these initial findings, at least as far as golden-mantled ground squirrels are concerned. It appears that only spring cold exposure has a lasting effect over the consecutive years, which means that a true phase shift has occurred. Cold exposure in autumn alters the timing of the circannual cycle, but only within the year of exposure (Mrosovsky 1990). Consequently, cold exposure in autumn masks the rhythms without having an effect on the phase of the circannual rhythm. It therefore appears that both photoperiod and T_a are effective as zeitgeber only temporally and act during different time periods. Although the lack of data precludes a generalization of this model, it appears worthwhile to illuminate its ecological significance.

Obviously, T_a plays an important ecological role in the yearly cycle of hibernators as it will affect food availability and energy expenditure. Reproduction must be completed within a limited time frame, particularly for large hibernators, for which an early start of reproduction would be favorable as juvenile development takes a long time and offspring must be big and fat enough if they are to survive the following hibernation season. To maximize juvenile survival, large hibernators, which can survive for a considerable time on body fat even when normothermic, often emerge long before new food becomes available (Arnold et al. 1991; Beard et al. 1992; Michener 1998, Buck and Barnes 1999), a strategy that extends the time available for juvenile growth (Murie and Harris 1982).

Of course, premature termination of the hibernation season can be potentially disastrous under adverse weather conditions (Morton and Sherman 1978). Since the timing of snow melt and weather in spring vary among years, fine tuning of spring emergence according to the climatic conditions is advantageous even in large hibernators. For this purpose, T_a , although well buffered in underground hibernacula, is the most appropriate stimulus and possible zeitgeber that can modulate the timing of emergence within the rather rigid framework of a circannual in ground squirrels (Davis 1977; Michener 1977; Mrosovsky 1980; Murie and Harris 1982). A warm spring advances final emergence, while cold weather has a delaying effect (Michener 1977; Murie and Harris 1982). Hoarding species such as chipmunks (*Eutamias sibiricus*) also show flexibility of spring emergence according to T_a (Kawamichi and Kawamichi 1993). Similar to photoperiod, which appears to have an effect on the circannual cycle during summer, the sensitivity toward T_a changes is most pronounced in late winter/spring (Mrosovsky 1986). Since female ground squirrels and other large hibernators come into estrus only days after emergence, males tend to terminate hibernation and become active several days or weeks before females to activate their testes and to optimize their mating chances (Murie and Harris 1982; Barnes et al. 1986; Kenagy 1989; Michener 1992, 1998). Accordingly, male ground squirrels appear more susceptible to variations in spring T_a than females (Joy and Mrosovsky 1985). Given that these hibernators remain in their underground hibernacula for sometimes more than half the year without receiving any photoperiodic cues, the use of T_a rather than photoperiod as the zeitgeber for a circannual cycle during winter makes sense. As we have seen above, however, the function of photoperiod is not abolished in seasonal hibernators, but both environmental variables appear to act as a zeitgeber, photoperiod during summer and T_a during winter/spring.

For herbivorous ground squirrels and marmots living at high latitudes, food availability is seasonally predictable. This predictability is probably the underlying reason for the strong seasonal cycle observed for these species (Pengelley and Fisher 1957; Barnes and Ritter 1993). However, the ground squirrel/marmot model does not apply to all hibernators. Many mammalian orders contain hibernators, many of which are not herbivorous and may even be found in the tropics (Hladik et al. 1980; Schmid 1996). Hibernation (or perhaps better, "prolonged torpor" for avoidance of the seasonal connotation) in many species is highly opportunistic, and its use is often similar to that of daily torpor in many insectivorous mammals and birds. For these animals, food availability is only partly determined by season, but is predominantly weather dependent. Pygmy possums (*Cercartetus* spp., 10–30 g) enter prolonged torpor at any time of the year when exposed to low T_a (Geiser 1987). The mountain pygmy possum (*Burramys parvus*, 50 g) appears to be a seasonal hibernator under natural conditions; however, activity and foraging continue, at least through parts of the hibernation season (Broome and Geiser 1995; Körtner and Geiser 1996, 1998a), as it does in other insectivorous hibernators such as bats, hedgehogs, and echidnas (Brigham 1987; Fowler and Racey 1990; Grigg et al. 1992). For ground squirrels using underground hibernacula with sealed entrances, activity after arousal during the hibernation season would be rather difficult. Consequently, hibernators that show some activity during winter often reside in shallow hibernacula situated in hollow logs, in caves, under leaf litter, or, as for mountain pygmy possums, in cracks between rocks. Furthermore, opportunistic hibernators do not necessarily have strong circannual cycles. In mountain pygmy possums the seasonality of reproduction and hibernation soon becomes asynchronous when they are transferred into the laboratory, even when the natural yearly cycle of photoperiod and T_a is maintained (Geiser, Sink, et al.

1990; Körtner and Geiser 1995). In the laboratory, the species may reproduce for most of the year (Thomas 1982; Kerle 1984), and hibernation is abolished entirely in laboratory-bred individuals (Geiser, Sink, et al. 1990). Similar observations have also been made in free-ranging mountain pygmy possums lived near ski resorts and hibernated inside buildings. These individuals terminated hibernation with the beginning of the skiing season in early winter when tourists arrived, heated the lodges, and unintentionally fed the possums (Körtner and Geiser 1998a). The normal seasonality of hibernation observed in the wild is therefore not a direct result of an circannual rhythm, but merely reflects the climatic conditions and food availability. The relatively high independence of mountain pygmy possums from photoperiod and from a strong innate annual cycle allows greater flexibility in a habitat in which seasonal changes in climate and food availability are highly variable. However, prehibernation fattening is a prerequisite for most hibernators, including mountain pygmy possums. The environmental factors that trigger fattening and hibernation entry in mountain pygmy possums before food availability declines are largely unknown. In contrast, spring emergence in the species appears to be linked with periodic activity during the hibernation season, which in turn is controlled by the circadian system, discussed next.

HIBERNATION AND CIRCADIAN RHYTHMS

Although the metabolism in most brain areas is reduced substantially during hibernation, the SCN is a notable exception, and it maintains a high metabolism during torpor (Kilduff et al 1993). Since the SCN is known to regulate the circadian system in mammals, the persistence of circadian rhythms during even deep hibernation appears to be at least possible. However, the performance of the circadian system during hibernation is difficult to assess because most variables normally measured in normothermic animals, such as variations in T_b , locomotor activity, food consumption, and drinking activity, are largely abolished during hibernation. Periodic arousals are perhaps the most reliable indicators, although the relatively few arousals during a hibernation season render only a limited number of cycles for assessment.

Since hibernation patterns of prolonged torpor interspersed by arousals resemble the daily pattern of activity and rest in normothermic animals, albeit on a different time-scale, the argument that hibernation bouts result from an extended circadian cycle caused by the low T_b during torpor appears compelling (Heller et al. 1989). The similarities between torpor and sleep, as discussed, support this hypothesis to a certain extent. Torpor bouts become longer with decreasing T_a (Twente and Twente 1965; French 1985; Geiser and Kenagy 1988), but this relationship holds true only until the T_b threshold for thermoregulation during torpor is reached. Below this point, the animal defends its T_b by increasing its MR, and although T_b remains largely stable, torpor bouts shorten at T_a below the T_b threshold (Pengelley and Kelley 1966; Geiser and Kenagy 1988; Geiser and Broome 1993), suggesting that torpor bout length is not a simple function of T_b and thus is not caused by a temperature-dependent prolongation of the circadian cycle (Heller et al. 1993). Furthermore, the assumption of an impaired temperature compensation of the circadian system is also not substantiated by observation of ectotherms (Hastings and Sweeney 1957; Rusak and Zucker 1979; Bünnig 1986) or daily heterotherms (see above), both of which show competent temperature compensation.

Small circadian fluctuations in T_b or MR observed during torpor in some hibernators (Menaker 1959; Pohl 1961; Grahn et al. 1994) also do not support the hypothesis of the lengthening of the circadian cycle by low T_b . However, results regarding circadian fluctuations during hibernation appear to differ among species, and have been described in only a few. Some bats show circadian fluctuations in MR and T_b either only at the beginning of or intermittently throughout the hibernation season (Menaker 1959; Pohl 1961). More recently, extremely variable circadian T_b fluctuations have been described for golden-mantled ground squirrels (*Spermophilus lateralis*) (Grahn et al. 1994). In all these species, the amplitude of circadian fluctuations is minute, and this might render them undetectable in many hibernators, or they can only be detected when special precautions are taken to eliminate T_a fluctuations during the experiment and when the sensitivity of the equipment is appropriate. Large variations in τ between successive torpor bouts of individual golden-mantled ground squirrels, ranging from 19h–28h (Grahn et al. 1994), further complicate rhythm analysis. If Grahn et al. (1994) had not measured circadian fluctuations in T_b during torpor, it would have been impossible to detect any daily periodicity in arousal patterns for this species. Nevertheless, the few examples that have demonstrated the persistence of circadian rhythms during hibernation suggest that they do persist in some, if not all, hibernators.

If time of arousal from hibernation is not the result of a lengthened circadian cycle, the question arises whether the patterns of hibernation are governed by the circadian system at all. It is possible that arousals do occur at a certain phase angle of the circadian cycle, but are not expressed on a daily basis (Strumwasser et al. 1967). The hibernation season usually begins with a series of short torpor bouts called “test drops” that, in their temporal organization, resemble daily torpor (Strumwasser 1959). Bouts then become successively deeper and longer. During this initial period, hibernation may follow a daily cycle, with arousals occurring at a certain time of day (Strumwasser 1959; Pohl 1961). In species in which torpor bouts remain relatively short, such as the pocket mouse (*Perognathus longimembris*), these patterns remain discernible (Brower and Cade 1971; French 1977b), and torpor remains entrained to a light-dark cycle. To assist the synchronization of foraging with the normal day-night cycle, T_a fluctuations can act together with photoperiod as a zeitgeber as in some daily heterotherms (Lindberg and Hayden 1974; Waldhovd 1976). High T_a also encourage foraging in *Perognathus longimembris* (French 1977a). The persistence of a circadian rhythm, its entrainability to various external zeitgebers, and the overall sensitivity to T_a changes clearly are advantageous in hibernators such as pocket mice, which interrupt the hibernation season with bouts of foraging. Foraging also occurs, as mentioned above, in many insectivorous hibernators. For example, in captive and free-ranging mountain pygmy possum, arousals stay entrained with the day-night cycle throughout the hibernation season, although torpor bouts can exceed 2 weeks (Körtner et al. 1998; Körtner and Geiser 1998a). Mountain pygmy possums hibernate in deep rock crevices and normally emerge from their hibernacula for a short time period after arousal. These bouts of activity outside the hibernacula appear sufficient to reset the circadian clock, which in turn governs the timing of the next arousal (Körtner et al. 1998).

Activity during the hibernation season appears again to be the driving force for a strong expression of a circadian rhythmicity and entrainment. Frequent activity ensures that mountain pygmy possums can emerge and reproduce from the beginning of snow melt when new food becomes available. Since this little marsupial does not have enough body fat stores to survive prolonged normothermic periods without feeding, this opportu-

nistic behavior ensures the earliest possible mating season without taking excessive risks (Körtner and Geiser 1996, 1998a). In several other insectivorous species that have been tested for rhythmicity, such as bats or hedgehogs, arousals also seem to follow a persistent, entrainable circadian rhythm (Pohl 1967; Twente and Twente 1987; Fowler and Racey 1990). These observations are further supported by the finding that, in some bat species (*Myotis spp.*), pineal secretory activity actually increases during the hibernation season (Quay 1976). However, generalizing these patterns would be premature as some evidence suggests that, arousals were not entrained to a particular time of day, although three species of free-ranging bats were usually more active during the night than during the day during the hibernation season (Thomas 1993). Some discrepancies among studies may be due to different experimental designs, but clearly the circadian organization of hibernation varies widely among species, probably reflecting differences in their ecology.

While pygmy possums, hedgehogs and some bats show an opportunistic hibernation strategy with torpor interspersed with foraging, many hibernators, notably high-latitude northern rodents, never leave their hibernacula from autumn until emergence from hibernation in spring. Entrained arousals, as observed in opportunistic hibernators, are not significant for rodent hibernators in deep burrows, and possible zeitgebers, such as light exposure and daily fluctuations of T_a , should be largely nonexistent. Nevertheless, in some of these underground hibernators that show no surface activity, circadian rhythmicity remains detectable and can even be entrained by a light-dark or T_a cycle (Pohl 1967; Strumwasser et al. 1967; Daan 1973; Canguilhem et al. 1994). However, in other species, a deterioration of the circadian system during the hibernation season becomes apparent. In the European hamster (*Cricetus cricetus*), for example, entrainment to a light-dark or T_a cycle is restricted to entries into torpor, whereas arousals appear to occur at random or follow an unentrained circadian cycle (Canguilhem et al. 1994; Wollnik and Schmidt 1995; Waßmer and Wollnik 1997). Therefore, if induction of arousals by disturbance in the laboratory is excluded, the periodicity underlying arousals from and entries into torpor seems to follow independent rhythms, perhaps explained by the dual-oscillator model proposed for circadian rhythms (Pittendrigh and Daan 1976c). In the Turkish hamster (*Mesocricetus brandti*), both entries and arousals are periodic, but are not entrained by an artificial light-dark cycle (Pohl 1987, 1996). The question arises whether these hibernators cannot perceive light stimuli or whether the circadian rhythm τ lengthens to such a degree during hibernation that it is unentrainable by a 24h light-dark cycle because, in nocturnal rodents, τ and the length of the light-dark cycle have to be fairly close to achieve entrainment (Pittendrigh and Daan 1976b). Since light-dark cycles that are longer than 24h also fail to entrain arousals in *Mesocricetus brandti*, the first explanation appears more likely (Pohl 1996). Insensitivity to light in some hibernators is also corroborated by reduced pineal size in ground squirrels (*Spermophilus erythrogenys*) (Ralph et al. 1979) and the apparent lack of any circadian melatonin cycle in marmots and golden hamsters (Florant et al. 1984; Janský et al. 1989). In contrast, hibernating bats and dormice (*Muscardinus avellanarius* and *Glis glis*) are entrainable to a light-dark cycle, and their pineal glands remain active throughout winter (Ralph et al. 1979). However, more species have to be investigated before variations in pineal function and entrainability of periodic arousals can be linked to the different types of hibernacula and hibernation strategies.

In conclusion, a functional circadian system during hibernation and daily torpor appear most pronounced in those species that still forage periodically during winter, such as opportunistic hibernators and daily heterotherms. The timing of arousals from torpor

in these species appears to be governed by the circadian system, which is often entrained by photic stimulation. However, since light may not penetrate into the shelters sought for hibernation, daily T_a fluctuation may become an important zeitgeber for these species. In contrast, hibernators that use deep and secluded underground burrows, show no surface activity, and rely entirely on body fat stores or food caches do have little use for activity synchronized by circadian rhythms. Consequently, in many hibernators, the sensitivity to entraining agents weakens, and τ might vary profoundly over time. The expression of circadian rhythms during hibernation, therefore, makes ecological sense and appears as variable as the different hibernation strategies employed by mammals and birds.

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