

## 12 Djungarian Hamsters – Small Graminivores with Daily Torpor

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### 12.1 Djungarian Hamsters: Through Cold Winters on Hairy Feet

The species of interest in this chapter, the Djungarian dwarf hamster (*Phodopus sungorus*), is sometimes also called the hairy-footed hamster. This name, which refers to fur covering even the soles of the feet in this species, indicates an adaptation to extremely harsh climatic conditions in its natural habitat, the subarid steppes of continental Asia. Among these steppes, the Djungarian (or [D]sungarian, as in 'sungorus') basin in northern China represents the southernmost area of its distribution. These Djungarian plains, as well as the other regions inhabited by *P. sungorus*, such as grasslands and vermouth-steppes in northern Kazakhstan, southern Siberia, the Altai, and Mongolia, are characterised by pronounced seasonal climatic changes. While in summer ambient temperature ( $T_a$ ), e.g. in the Siberian steppe, often rises above  $+30\text{ }^{\circ}\text{C}$ , it regularly drops below  $-30\text{ }^{\circ}\text{C}$  during winter (Köppen and Geiger 1939). In Mongolia, mean monthly surface temperatures in January are as low as  $-25\text{ }^{\circ}\text{C}$ , while the snow cover is thin or absent (Weiner 1987a). Given these environmental conditions, one might expect that Djungarian hamsters, like many other small mammals of the temperate zone, restrict surface activity to the summer months and survive winters via permanent retreat and hibernation in thermally buffered burrows. Surprisingly though, Djungarian hamsters are known to be active, predominantly at night, throughout the year and forage at the surface even in winter at air temperatures of down to  $-40\text{ }^{\circ}\text{C}$  (Flint 1966).

A seasonal strategy that is based on continued foraging activity in this harsh environment has severe obstacles, in particular for a 'dwarf' hamster, weighing only 20 to 40 g. In a mammal of this size, locomotor activity in the cold at high body temperature ( $T_b$ ) leads to tremendous rates of heat loss and energy expenditure, due to its adverse surface-to-volume ratio. Even for a hairy-footed and generally well-insulated hamster, further improvement in insulation by lengthening of the fur is limited by its small size. Thus, maximum energy expenditure in the cold is required at a time of the year when food availability is lowest. Seeds of grass and shrubs (e.g. *Stipa capillata*, *Potentilla*, *Nitraria*) represent the sole food source during winter, while the

moves more than approximately 1 cm (for details see Ruf et al. 1991). Body temperature was measured at 6-min intervals via temperature-sensitive transmitters (Minimitter Model XM, accuracy  $\pm 0.1^\circ\text{C}$ ) that were implanted in the visceral cavity (see Ruf et al. 1991). Metabolic rates were determined in an open-flow, automated 6-channel respirometric system with an accuracy of 0.001 vol%  $\text{O}_2$  and  $\text{CO}_2$  (see Ruf and Heldmaier 1992).

Locomotor activity is presented as number of impulses generated in 6-min bins. Total daily activity duration was estimated from the sum of all 6-min intervals with at least one event occurring. Differences in the variance of mean activity duration and number of events among hamsters exposed to different environmental conditions were tested with Levene's test. Since variances differed significantly (see Table 12.1), the Kruskal-Wallis ANOVA was used to test for differences in activity measures between groups. Groups under identical photoperiods but at different  $T_a$ s were further compared by the use of the Mann-Whitney U-test. Unless stated otherwise, results are given as means  $\pm$  one SD.

An animal was considered to enter daily torpor once  $T_b$  decreased below  $32^\circ\text{C}$ . Accordingly, torpor duration was calculated from the time spent at  $T_b$ s below  $32^\circ\text{C}$ . Resting metabolic rates (RMRs) represent the median of the three lowest successively recorded MRs in inactive hamsters. The average metabolic rate, including both active and inactive periods over a day or certain parts of a day, is called ADMR and AMR, respectively.

### 12.3 Model Calculations

To investigate the interrelation between energy gain and energy expenditure during rest and foraging, and their consequences for daily activity duration, we employed several model calculations. The basic assumptions underlying these calculations are virtually identical to the general model outlined by Weiner (Chap. 3), only that in the present chapter we largely focus on the impact of daily torpor on total energy expenditure and its consequences for foraging. Calculations are based on measurements of MRs in hamsters at various behavioural states and environmental conditions that were determined previously or are presented below. Resting MRs of hamsters without nesting material at different  $T_a$ s were calculated from the equation

$$\text{RMR} [\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}] = 5.27 - 0.14 \cdot T_a. \quad (\text{Heldmaier et al. 1982})$$

Metabolic rates of hamsters provided with bedding material at different  $T_a$ s in both the normothermic state (i.e.,  $T_b > 35^\circ\text{C}$ ) and during daily torpor were calculated from

$$\text{MR} [\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}] = 0.01 + 0.108 \cdot (T_b - T_a). \quad (\text{Ruf and Heldmaier 1992})$$

Model calculations are based on the assumption that  $T_b$  during daily torpor is lowered to  $15^\circ\text{C}$  (typical range:  $13\text{--}22^\circ\text{C}$ ; Ruf et al. 1993). Total MRs were calculated assuming an average body weight of winter-adapted hamsters of 25 g (Heldmaier and Steinlechner 1981a).

### 12.4 Adjustment of Locomotor Activity Patterns to Environmental Changes

Djungarian hamsters are principally nocturnal animals, as illustrated in Fig. 12.1. In hamsters at moderate ( $> 18^\circ\text{C}$ ) temperatures with free access to food, 80 to 90% of locomotion occurs during the night. This daily pattern of activity is based on a circadian rhythm with an average period length just below 24 h (Puchalski and Lynch 1988), that is entrained by the LD cycle. Thus, the daily time course of locomotion is altered by seasonal changes of photoperiod (Fig. 12.1). Total amount and net duration of activity stays, however, fairly stable throughout the year (Table 12.1).

In *P. sungorus*, locomotion occurs in 'bursts' that last from several minutes to about 2 h and alternate with episodes of rest and sleep (Heldmaier et al. 1989; Deboer et al. 1994; see also Fig. 12.1). Similar ultradian rhythms of locomotion and rest also characterise patterns of the emergence from, and retreat into artificial burrows (Heldmaier, unpubl. data). Hence, these patterns most likely correspond to a periodically occurring surface activity in free-living hamsters. Also, laboratory measurements that always show a certain

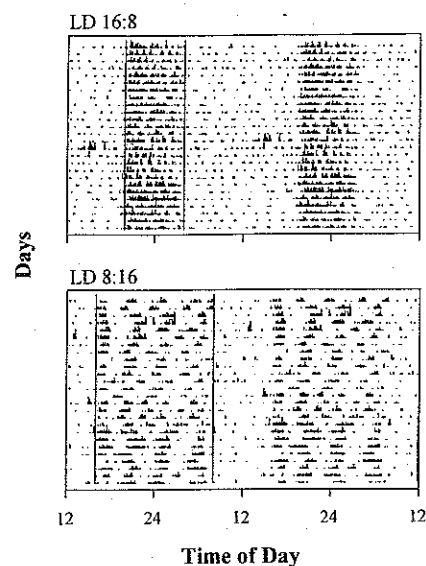


Fig. 12.1. Double plots of locomotor activity in a Djungarian hamster exposed to long photoperiods (LD 16:8, upper panel) and short photoperiods (LD 8:16, lower panel). Locomotion was recorded continuously by the use of infrared movement-detectors. The graphs show the sum of events (movements) within 6-min intervals over 26 days each. Vertical lines in the left half of each graph indicate beginning and end of the dark period

percentage of activity occurring during the daylight hours (Fig. 12.1) seem to reflect natural behaviour. For example, Nekipelov (1960; cited after Flint 1966) found in field studies that surface activity during the day is not unusual in free-living hamsters.

Previous studies demonstrated that in *P. sungorus*, the daily and ultradian time course of general locomotion largely reflects feeding activity (Ruf and Heldmaier 1993). The only obvious disproportion between feeding and general motor activity can be found in summer-adapted hamsters under long photoperiods when food uptake, but not general locomotion, is most intense in the last part of the night. This observation may indicate that, as in other small mammals during summer, locomotion related to sexual activity (namely in males) occurs predominantly in the early part of the night, while foraging and food uptake is delayed (Daan and Aschoff 1982). In winter, when hamsters are sexually completely inactive, aggression and territorial behaviour appear to be largely absent (Müller 1982), and foraging is probably the sole purpose of locomotion.

This conclusion is supported by both field and laboratory studies. As mentioned before, direct observations and analyses of stomach contents have shown that the natural diet of hamsters is basically comprised of seeds from grass and other plants (Flint 1966). Hence, under natural conditions in the Siberian steppe, food comes in small 'bits' with relatively low energy content. Consequently, food uptake will require extensive foraging activity if daily energy demands are to be met. Further, laboratory recordings have shown that locomotion in hamsters can be strongly affected by changes in either metabolic costs of foraging or food availability in the environment. For instance, acclimatisation to low  $T_a$ s in summer-adapted hamsters leads to an overall decrease of activity (Table 12.1), suggesting that locomotion is minimised if metabolic costs for foraging increase. As discussed in more detail elsewhere, cold  $T_a$ s also affect the temporal distribution of activity bursts (Heldmaier et al. 1989). Cold temperatures particularly increase the percentage of activity occurring during daylight from approximately 20 to 30% in cold acclimatised animals, and to more than 50% in suddenly cold exposed hamsters (cf. Weiner in Chap. 3).

These effects of  $T_a$  on locomotion clearly indicate that metabolic costs for heat production can significantly alter activity patterns. One might be tempted to conclude that foraging activity is *always* minimised under conditions of high cold load outside the burrow. However, as shown in Table 12.1, short-day adapted hamsters during winter – on the average – show no significant change of motor activity in response to cold when food is unlimited. Instead, locomotion patterns under short photoperiods at both warm and cold  $T_a$ s are characterised by a large variability among individuals, concerning both the duration and total amount of activity (Table 12.1). As discussed in detail below, the key to understanding this variability and the differential effects of low  $T_a$ s in summer and winter is the occurrence of daily torpor.

Table 12.1. Duration of locomotor activity (h) and number of events (movements) recorded per day in Djungarian hamsters exposed to long (LD 16:8) and short photoperiods (LD 8:16) at warm and cold temperatures ( $n = 8-16$  per group). Cold exposure leads to a reduction of mean activity duration ( $p < 0.003$ ) and intensity ( $p < 0.05$ ) in hamsters under a long photoperiod, but not under a short photoperiod (ns). In long days, cold temperatures also tended to lower the variance among individuals (duration:  $p = 0.10$ ; events:  $p < 0.01$ ), while in hamsters under short days the variability between individuals was unaffected by  $T_a$  ( $p > 0.30$ ; see SD and range)

		LD 16:8		LD 8:16	
		23 °C	5 °C	23 °C	5 °C
Duration	Mean	6.2	4.8	5.3	4.9
	SD	0.94	0.47	1.26	1.06
	Range	3.3	1.4	3.7	4.1
		(4.4–7.7)	(4.4–5.8)	(3.2–6.9)	(2.8–6.9)
Events	Mean	410	244	529	582
	SD	199	51	342	400
	Range	633	180	838	1244
		(191–824)	(158–338)	(70–908)	(182–1426)

Torpor as an energy saving mechanism is absent in long-day adapted hamsters and therefore provides no 'escape' mechanism for energetic challenges in summer. This blockade of voluntary hypothermia in long photoperiods is probably due to an incompatibility of low  $T_b$ s with maintaining sexual activity and functional gonads (Barnes et al. 1986). Not surprisingly then, Djungarian hamsters defend high  $T_b$ s in summer even under conditions of severe shortage of food (Steinlechner et al. 1986). Erratic bouts of hypothermia may eventually occur in summer after prolonged food restriction, but only following a severe decrease in body weight. Before that, a shortage of food (similar to low  $T_a$ s) causes significant extensions of locomotor activity into the daylight. This change of daily rhythms may even lead to a complete inversion of the day/night cycle, with activity and elevated  $T_b$ s occurring predominantly during the day (Steinlechner et al. 1986; Ruf and Heldmaier 1987; K. Gwinner and G. Heldmaier, unpubl.).

Interestingly, this degree of flexibility in activity patterns that can be modulated by environmental conditions seems to be largely species specific. For instance, similar food restriction-induced extensions of locomotion into the day were also found in house mice, but not in another Cricetid species, the deer mouse (Blank and Desjardins 1985). The fact that a more flexible response is present in Djungarian hamsters suggests that in this species, energetic demands can override the impact of predation risks on daily partitioning of locomotion. Thus, in *P. sungorus*, energy availability and particularly metabolic costs of foraging activity, represent most important variables in the regulation of duration and daily patterns of locomotion. Further understanding of these regulating mechanisms, therefore, requires information on the actual energetic costs of motor activity in this species.

## 12.5 Energy Requirements for Activity – The Impact of Cold Load

Metabolic costs for the transport of mass are directly related to body weight (e.g. Taylor et al. 1970). Since Djungarian hamsters reduce body weight towards winter, energy requirements for locomotion decrease, on the average by 23% (Heldmaier and Steinlechner 1981a). However, as pointed out by several authors, by far the most important factor for metabolic costs of activity is the time an animal spends outside its thermally buffered burrow (Wunder 1978; Bronson 1989). These costs dramatically increase at low  $T_a$ s during winter. Figure 12.2 shows MRs of 12 hamsters exposed to  $T_a$ s between +23 °C and -50 °C with maximum values reflecting intensive locomotion. As indicated by the upper curve through mean maximum values of the 12 individuals at each  $T_a$ , activity-induced metabolism first increases as  $T_a$  is lowered and then declines at  $T_a$ s below -30 °C. At even lower  $T_a$ s (< -30 °C) hamsters begin to encounter an important constraint to activity in the cold, namely their peak MR. In this case of cold acclimatised hamsters in summer, peak MRs varied around 15 ml O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> (but see Heldmaier 1989).

The initial increase in the difference between activity and resting metabolism is probably due to an impairment of thermal insulation in hamsters that move and run, instead of sitting in a curled position (cf. Wunder 1975). However, MRs during intense activity at  $T_a$ s between +23 °C and -30 °C stayed fairly close to a factor of 2 above RMRs ( $1.89 \pm 0.97$ ). This factor is very similar to estimates of metabolic costs of activity derived from continuous long-term recordings of oxygen consumption. In *P. sungorus* living under moderate cold load ( $T_a$  0–15 °C) mean ADMRs are typically 25 to 30% higher than RMRs (Wiesinger 1989; Ruf and Heldmaier 1992). Since mean activity

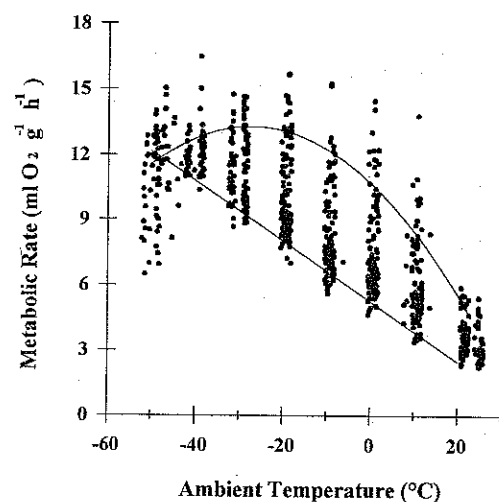


Fig. 12.2. Metabolic rates (MR) of 12 Djungarian hamsters exposed to ambient temperatures between +23 °C and -50 °C. The metabolic rate was measured at 6-min intervals. The linear regression line was fitted to resting MRs in euthermic hamsters. Sharply decreasing MRs at  $T_a$  -50 °C originate from hamsters that became hypothermic. The upper curve was fitted to means of individual maxima at each temperature step

duration ranges around 5 to 6 h per day (Table 12.1) this total elevation means that during activity, average MRs were 2–2.5 times above RMRs.

Hence, both of the above approaches yield a factor of about two times RMR for metabolic costs of activity, which probably represents a conservative measure, because MRs were measured in dry environments without wind. This magnitude of locomotion-induced increase of MR is well in the range of observations in other small mammals and, according to the model proposed by Wunder (1975), should be expected in a hamster running at an average speed of 3 km/h. To illustrate the impact of these metabolic costs one might, for example, compare the energy expenditure of a hamster in its nest at  $T_a$  0 °C and foraging on the surface at  $T_a$  -20 °C. In the first situation, metabolism consumes about 75 J g<sup>-1</sup> h<sup>-1</sup>, while during locomotion outside the burrow energy requirements are more than four times higher, i.e., 320 J g<sup>-1</sup> h<sup>-1</sup>. Therefore, if environmental temperatures are low, any mechanism suited to reduce the need for foraging should be highly adaptive. Not surprisingly then, as  $T_a$  in the natural environment decreases towards winter, Djungarian hamsters do in fact develop such a mechanism, namely daily torpor.

## 12.6 Locomotion and Daily Torpor: Interactions

Daily torpor in *Phodopus* – although it ultimately represents a response to cold load and shortage of food – is induced by another, proximate signal, the shortening of the photoperiod in fall (Heldmaier and Steinlechner 1981b). This mechanism is, however, responsible for the majority of seasonal adaptations in Djungarian hamsters (for reviews see Hoffmann 1979; Heldmaier 1989). In naturally changing photoperiods, torpor first occurs in October, and then increases in depth, duration, and frequency until midwinter. Spontaneous torpor is almost completely restricted to the day (the photophase), and locomotor activity is resumed each night. An example for the daily alternation between torpor and nocturnal normothermia and activity is illustrated in Fig. 12.3.

Torpor episodes vary considerably, in particular between individuals. Torpor depth may range from 12 to 30 °C, and torpor duration from only 15 min to more than 12 h. Most importantly, hamsters significantly differ in their tendency to exhibit torpor. Certain individuals may be found torpid every day (e.g. Fig. 12.3), while others exhibit torpor only occasionally, at least if food is abundant (Heldmaier and Steinlechner 1981b; Ruf et al. 1991). Similar to other species, Djungarian hamsters immediately increase their frequency of torpor episodes in response to food restriction (Tucker 1966; Hudson 1978; Tannenbaum and Pivovarov 1987; Ruf et al. 1993). Thus, daily torpor, during which MRs are lowered down to 30% of normothermic RMRs, clearly helps to counteract short-term energetic jeopardy.

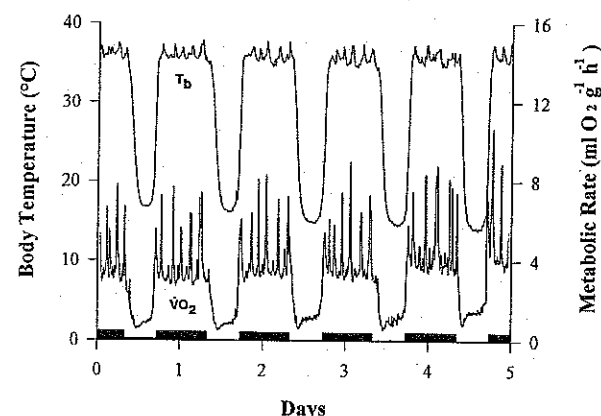


Fig. 12.3. Records of body temperature and metabolic rate in a winter-adapted hamster that displays daily torpor at  $T_a$  5–15 °C. During torpor, body temperature and metabolic rate are significantly lowered for several hours. At night, activity is resumed as indicated by nocturnal peaks in metabolic rate. Black bars on the abscissa indicate hours of darkness

Energy savings via daily torpor linearly increase with its daily duration, and (at  $T_a$ s of 0–15 °C) prolonged torpor episodes with a duration of 9 h lower total energy requirements by 30% (Ruf and Heldmaier 1992). However, this estimate is based on comparisons of days with and without torpor within the same individuals and ignores important associated behavioural differences between hamsters, in particular concerning the intensity of locomotion. If those interactions between torpor and activity are considered, the total benefits of combined thermoregulatory and behavioural adjustments turn out to be much more significant.

At first sight it may seem that there is little relation between torpor and activity, since torpor occurs during the daylight resting phase of hamsters. If anything, one might expect that the loss of about 10 to 20% daylight activity, which is replaced by torpor, might be compensated for by increased locomotion in the subsequent night. However, as illustrated in Fig. 12.4, the opposite is true. This comparison among individuals of long-term (4 weeks) mean daily times spent in torpor and at locomotor activity reveals that the daily activity period significantly decreases as torpor increases. For example, in this group hamsters that constantly remained normothermic were active for about 6.2 h per day, whereas hamsters that spent an average of 6 h per day in torpor (that is, including both days with and without torpor) also reduced their daily activity period by 37% to 3.7 h only. Earlier studies have shown that it is in fact mainly *nocturnal* activity that is reduced in both intensity and duration in hamsters that frequently exhibit torpor (Ruf et al. 1991; Ruf and Heldmaier 1993). Expectedly, as shown in Fig. 12.4 (upper line), torpor also replaces a certain amount of resting periods, but, in view of the above

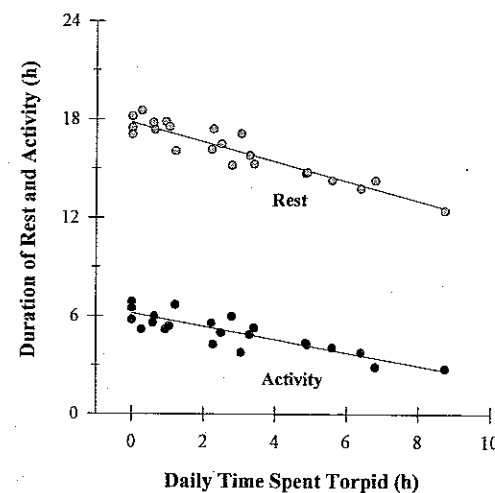


Fig. 12.4. Duration of daily periods of rest (grey dots) and activity (black dots) as a function of the daily time spent torpid. Data points represent means from continuous 3–4-week recordings in 22 hamsters

data on the impact of activity on energy expenditure, the reduction of locomotion periods will be energetically much more significant.

An estimate of the exact magnitude of additional energy savings by a torpor-linked decrease in activity can be obtained from measurements of ADMRs in hamsters with different long-term tendencies for torpor. Since individuals also differ slightly in fur insulation and body weight, and consequently in total thermal conductance (cf. Ruf et al. 1993), comparisons of these energetic effects are best based on calculations of the purely activity-induced increase of metabolism, i.e., the difference between average and resting MRs. Figure 12.5 shows 3-week means of this measure in hamsters with a different proneness for torpor. If locomotor activity was unaffected by the exhibition of torpor, activity-induced metabolism should stay constant and equal among individuals during the normothermic part of the day. However, since torpor is accompanied by a reduction of locomotion, energy expenditure during normothermia (mainly during night) also significantly decreases as the mean time spent hypothermic increases (Fig. 12.5, upper line). From this separate calculation of total daily and nocturnal (activity-induced) metabolism it becomes clear that the magnitude of energy savings via reduced activity is about equal to the immediate effect of torpor via reduction of  $T_b$  and heat loss during the day. In other words, even in hamsters under moderate cold load (at  $T_a$ s above 0 °C) each Joule of energy saved by torpor during daytime saves at least another Joule at night, because it allows for a shortening of foraging activity. This relation will further change in favor of nocturnal, activity-related energy savings when  $T_a$  is lower than in the experiment presented here.

It should be emphasised that Figs. 12.4 and 12.5 are based on long-term comparisons between individuals that showed distinct 'preferences' for either

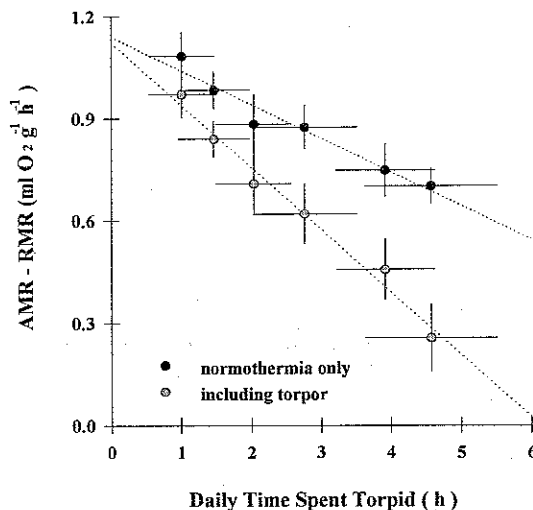


Fig. 12.5. Activity-induced metabolic rate (AMR-RMR) as a function of the daily time spent torpid (means of 6 hamsters recorded over 20 days). Energy expenditure was calculated separately for the entire day (including torpor, grey dots) and for the daily period spent at normothermic body temperatures ( $> 35^{\circ}\text{C}$ , black dots), i.e., mainly night-time hours

high levels of activity and low torpor frequency or vice versa. These differences also explain the tremendous variability of locomotion under short days pointed out above (see Table 12.1). These individual characteristics lead to long-term energy requirements and rates of food uptake that can differ by more than 70% between highly active, normothermic, and fairly inactive, torpor-prone hamsters (Ruf et al. 1991). Hence, at least under conditions of unlimited food supply and temperatures above freezing, Djungarian hamsters employ highly variable individual energetic strategies to cope with identical environmental conditions. As discussed below, this large range of possible 'solutions' for the problem of maintaining stable energy budgets may, however, shrink under natural conditions in the Djungarian or Siberian winter.

## 12.7 Budgeting of Time and Energy Under Natural Conditions

The above information on energetic impacts, relations, and feedback interactions of locomotion, food uptake, rest, and torpor, may be integrated in some model calculations that also attempt to include the principal environmental conditions experienced by hamsters in the wild. Prior to a discussion of these calculations, several important constraints and limitations to budgeting of time and energy have to be pointed out.

First, since peak MR in *Phodopus* never exceeds about  $18 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (Heldmaier et al. 1989), extensive locomotion becomes virtually impossible at very low ambient temperatures (at  $-50^{\circ}\text{C}$  or below). Second, an increase of

activity duration is limited because hamsters normally spent more than 12 h per day asleep (Deboer et al. 1994). Any significant reduction of this period will be prevented by the mechanisms responsible for homeostatic sleep-regulation (Borbély 1982; Daan et al. 1984; Deboer and Tobler 1994). Third, either the size and capacity of the digestive tract or other constraints in energy turnover (see Hammond and Diamond 1997) limit maximum daily energy assimilation, in the case of winter-adapted hamsters to approximately  $80 \text{ kJ}$  per animal per day (calculated from Weiner 1987b). If energy balance, namely stable fat stores and body weights, are to be maintained energy expenditure must not exceed this limit (cf. Weiner in Chap. 3).

Based on these constraints and measurements of MRs during activity, rest, and torpor, the required minimum duration of foraging activity and corresponding daily energy expenditure can be estimated (Fig. 12.6). These calculations were carried out for two environmental temperatures outside the burrow,  $0^{\circ}\text{C}$  and  $-30^{\circ}\text{C}$ , while a constant  $T_a$  of  $0^{\circ}\text{C}$  inside the burrow was assumed. The other important environmental variable, accessibility of food or, more precisely, energy gain per hour of foraging, was varied continuously between  $0$  and  $30 \text{ kJ h}^{-1}$ . Energy gains around  $30 \text{ kJ h}^{-1}$  seem to be typical for a terrestrial seed eater with a body weight of  $25 \text{ g}$  (Weiner, Chap. 3). Thus, the range of foraging rates investigated here reflects very low up to average food abundance, as can be expected to occur in winter environments. The assumptions underlying these calculations may of course not accurately represent conditions and metabolic costs for free-living hamsters. This, however, will not affect the principal relations between variables and conclusions discussed here.

In general, the upper panel of Fig. 12.6 illustrates that the daily minimum time period required for foraging increases exponentially as energy availability decreases. This is because each minute spent outside the burrow not only increases total energy intake, but also has additional metabolic costs that require further foraging. Secondly, it becomes clear that temperatures outside the nest dramatically affect the range of possible energy gains under which hamsters can still keep daily MRs below maximum energy assimilation, and thus maintain stable energy budgets (Fig. 12.6, lower panel). For example, while in this model a hamster that always stays normothermic can survive at  $T_a$   $0^{\circ}\text{C}$  with energy gains above  $8 \text{ kJ h}^{-1}$ , at  $T_a$   $-30^{\circ}\text{C}$  outside the nest energy balance turns negative if energy gain falls below  $18 \text{ kJ h}^{-1}$ .

Figure 12.6 also shows that, although it might be advantageous in terms of energy expenditure to minimise locomotion at any given  $T_a$ , a significant increase of foraging activity in response to scarcity of food is possible only under conditions of fairly moderate temperatures. At very low  $T_a$ s, energy expenditure reaches the maximum sustained metabolic rate within short periods of foraging activity, and any further time spent outside the burrow would only facilitate depletion of fat and other internal energy stores.

Finally, Fig. 12.6 illustrates the principal effect of daily torpor, namely to extend the range of environmental conditions that can be tolerated with a

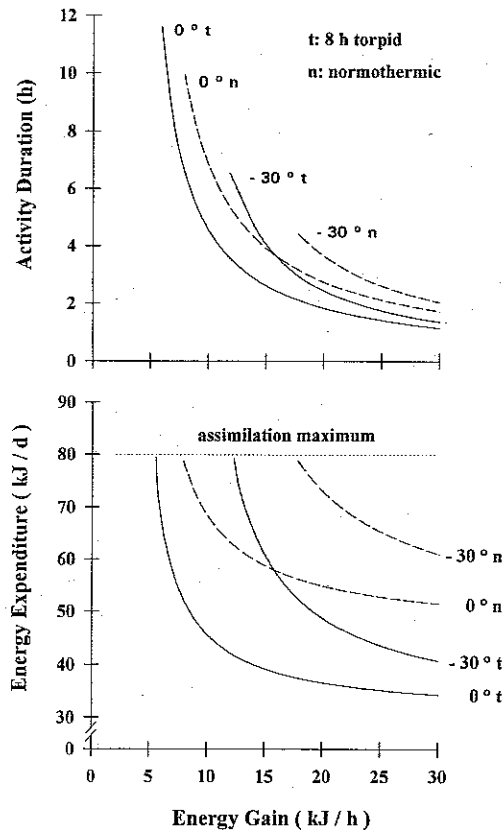


Fig. 12.6. A model for the effect of daily torpor on the relations between energy gain during foraging and minimum required daily activity duration (upper graph), as well as daily energy expenditure (lower graph). Calculations were carried out for hamsters staying either normothermic (n) or exhibiting 8-h episodes of daily torpor (t), and encountering temperatures outside their burrow of 0 or  $-30^{\circ}\text{C}$ .

positive energy balance towards lower temperatures and decreased food accessibility. At any given  $T_a$  and energy gain, torpor significantly lowers both the minimum required foraging time and resulting daily metabolic costs. As indicated by the two crossing lines in the lower panel of Fig. 12.6, these energy savings may compensate for a  $30^{\circ}\text{C}$  drop in environmental temperature. Most importantly, however, as food sources decrease, only the use of daily torpor will in turn allow for an increase of foraging activity and thus guarantee survival in extremely harsh winters (see also Weiner in Chap. 3). Daily torpor thus helps not only to cope with high metabolic costs and scarcity of food but also enables hamsters to flexibly respond to varying and unpredictable energy resources in the environment.

Taken together, these results underline that activity, food intake, and energy expenditure during locomotion, rest, and torpor, represent linked variables of energy balance, that continuously feed back on each other. This feedback is, of course, not unidirectional. For instance, while torpor affects the duration of required nocturnal activity, foraging success and energy up-

take during this period will in turn also influence the subsequent exhibition of daily torpor.

## 12.8 Constraints, Unknowns, and Alternative Strategies

The above discussion of seasonal strategies in Djungarian hamsters leaves several open questions that require the incorporation of additional factors and physiological constraints. For instance, with respect to torpor, why, if food is abundant, not all hamsters exhibit episodes of hypothermia and reduce energy turnover? The following argument may explain this phenomenon: deep abdominal temperatures during hypothermia probably reduce nutrient assimilation in the intestine and thereby lower total daily energy assimilation rates (Carey 1989). If food resources are high, torpor will therefore counteract maximum energy intake and particularly hinder the formation of fat and other energy stores in the body. There is evidence from other species that large energy stores and increased body weights, in particular in males, can provide a better 'starting position' for sexual activity and competition when environmental conditions improve in spring (e.g. Kenagy 1986). Hence, hamsters employing a torpor-avoidance, high-energy-turnover strategy of winter survival may well represent a 'high-risk' phenotype, that has selective advantages after survival of mild winters with abundant food.

Also, while this chapter has centered around short-term behavioural adjustments, the regulation of energy budgets in a small mammal obviously involves an entire set of additional factors. In particular, a variety of more static seasonal adaptations, such as changes of body weight and fur insulation, certainly play an important role for the energetic costs of locomotor activity. Further, both internal and external energy stores, i.e., body fat and food caches, certainly can have a strong impact on budgeting of time and energy, and deserve further attention. As far as external energy stores are concerned we have, however, evidence that hoarding behaviour also largely differs between individual hamsters, and that intense food caching is again closely correlated with an individual's disposition for intense locomotor activity and low torpor tendency (Ruf and Heldmaier 1993). Thus, while hoarding of food certainly can provide an important energetic buffer and therefore represents an alternative to energy savings via daily torpor, it does not seem to principally alter the relations between locomotion, energy uptake and metabolic costs outlined above. Basically, hoarding is merely another behavioural adaptation designed to avoid or minimise foraging under unfavourable conditions. It is interesting, though, that even in the presence of large food caches the frequency of daily torpor keeps closely correlated to total food uptake (that is, to both digested and hoarded food; Ruf and Heldmaier 1993; see also Tannenbaum 1993). This observation indicates that the 'decision making' processes involved in balancing of energy budgets as

described above, can rely on surprisingly precise mechanisms for the assessment of not only time, actual environmental conditions, and the animal's present energetic state, but is also able to keep track of, and incorporate, past variations of foraging success.

In view of these complex regulatory mechanisms required for a seasonal strategy of sustained foraging and its inherent risks, one might be tempted to ask why natural selection in Djungarian hamsters has not resulted in the seemingly simpler solution of prolonged, deep hibernation during winter? It could be argued that possibly, for a small graminivore, the subarid plains of Djungaria, Siberia and Mongolia – if the entire year is considered – are simply too harsh for a hibernation strategy that relies on gathering of substantial energy stores prior to winter (cf. Weiner 1987a). It is conceivable that both their body size, which excludes large fat depots, and the distribution and accessibility of small seeds in their natural habitat prevent Djungarian hamsters from storing quantities of energy that are sufficient to survive long winters, even at hibernation-typical metabolic rates. Even more so since *P. sungorus* lives in shallow burrows at depths of 25 to 30 cm only (Flint 1966). Therefore, cold nest temperatures (Weiner 1987a) would require relatively high rates of heat production during hibernation to avoid freezing of the body, which again increases the need for large energy stores. On the other hand, these factors may just as well be completely irrelevant, since there are several examples of mammals of similar size, feeding habit, and apparent general ecology that may hibernate or stay normothermic throughout winter in the same habitat. Our lack of understanding of these differences, or of the specific evolutionary processes leading to intermediate patterns such as the rapid shifts between hypothermia and foraging observed in Djungarian hamsters, indicates that we are still largely ignorant as to the actual selective forces and constraints that have shaped different strategies of winter survival in small mammals.

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## 13 Shrews – Small Insectivores with Polyphasic Patterns

Joseph F. Merritt and Stephen H. Vessey

### 13.1 Introduction

Daily activity patterns of shrews are controlled by metabolic requirements commensurate with their diminutive body mass and resultant high surface-to-mass ratios: they must forage often to avoid exhaustion of their energy stores. To remain homeothermic, shrews must partition a 24-h period into multiple bouts of foraging, rest, and sleep.

Shrews typically display polyphasic activity patterns shorter than 24 h (ultradian rhythms, Aschoff 1981). A variety of field and laboratory studies during the past 50 years elucidated the polyphasic rhythm of shrews (Table 13.1). Comparing experiments is compromised by differences in techniques and biological attributes of individuals and species. However, we present a diagram of a 'typical' activity pattern in order to discuss variations within the family Soricidae.

The classic laboratory study of Crowcroft (1954), working with *Sorex araneus*, *S. minutus*, and *Neomys fodiens*, is commonly cited as a reference point in studies of diel activity. His diagram of the daily activity of *S. araneus* is representative for our discussion (Fig. 13.1). The activity pattern of one *S. araneus* consisted of about ten active periods lasting from 1–2 h (Fig. 13.1a). Two periods of maximum activity occurred with the major peak between 20:00 and 4:00 and a lesser peak between 7:00 and 11:00. (Fig. 13.1b). Peaks are reported to represent the periods of sunrise and sunset (Crowcroft 1954). Shrews demonstrated periods of rest and sleep, with most active foraging in darkness and with an afternoon lull in activity. This depiction of the 24-h activity pattern of *S. araneus* permits resolution of the number and duration of foraging bouts plus calculation of the percent of activity occurring per day. Most studies of soricid activity presented in Table 13.1 have employed the technique of Crowcroft (1954) or a comparable one. Our discussion will focus initially on a survey of the different methods employed to study activity periods and then address the factors influencing variation in the polyphasic activity patterns of shrews.