Daily torpor in the Djungarian hamster *(Phodopus sungorus)*: interactions with food intake, activity, and social behaviour

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Summary. In Djungarian hamsters, *Phodopus sungorus*, daily torpor occurs spontaneously in winter in the presence of abundant food, but individuals show different tendencies to enter torpor. The results show that in hamsters fed rodent chow ad libitum individual torpor frequencies were negatively correlated with both food consumption and the amount of nocturnal locomotor activity. Provision of cafeteria diet at ambient temperatures below thermoneutrality significantly lowered torpor frequencies and induced body weight gains. However, in hamsters fed seeds with a high fat or carbohydrate content (i.e., sunflower seeds or wheat, respectively) neither a decrease of torpor frequencies nor an increase of body weights was observed. The results suggest that in Djungarian hamsters, daily torpor is an intrinsic component of energy balance control and is functionally linked to individual physiological adjustments of food consumption and foraging activity. In addition, the employment of daily torpor can be affected by social interactions, since the long-term pattern of alternations between torpor and normothermia was found to be synchronized in breeding pairs caged together.

Key words: Body temperature – Cafeteria diet – Circadian rhythms – Locomotor activity – Sociality

Introduction

A variety of small mammals counter the problems of increased thermoregulatory energy demands and the shortage of food during winter by means of deep hibernation or shallow daily torpor. Both mechanisms result in significant energy savings and appear to differ only in the extent and duration of the torpid state (Hud-

Abbreviations: T_a ambient temperature; DIT diet-induced thermogenesis

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son 1978; Lyman 1982). Even though there is increasing evidence for considerable plasticity in the patterns of feeding and thermoregulation in deep hibernators (French 1986, 1989), there are at least two quite specific characteristics of daily torpor; individuals within a population differ largely in their predisposition for torpor, and daily torpor alternates with diurnal activity and food intake throughout the winter (Hill 1975; Hudson 1978; Heldmaier and Steinlechner 1981a; Vogt and Lynch 1982; Tannenbaum and Pivorun 1984, 1988).

In the white-footed mouse and the Djungarian hamster it was demonstrated that this daily alternation between episodes of activity and torpor is under direct control of the circadian system (Lynch et al. 1980; Ruf et al. 1989). On the other hand, the reliance on foraging throughout the winter implicates a close connection between the employment of torpor and the physiological systems controlling food intake. For example, in the genus *Peromyscus* food restriction has been widely used to induce torpor at different times of the year, even though in winter it can occur spontaneously in the presence of abundant food (e.g., Hill 1975; Vogt and Lynch 1982).

In Djungarian hamsters the seasonal occurrence of daily torpor is dominated by changes in photoperiod, which can be further facilitated by cold exposure (Heldmaier and Steinlechner 1981a; Elliott et al. 1987). However, the functional link between food intake and torpor in P. sungorus is complicated by a voluntary reduction of food consumption and consequently of body weight prior to the torpor season (Steinlechner et al. 1983). In summer, a forced limitation of food consumption resulted in irregular hypothermic episodes, but failed to elicit torpor with its characteristic depth, timing, and duration, as observed during spontaneous torpor in winter. Moreover, dramatic changes in circadian body temperature rhythms were caused by a very moderate food restriction (Steinlechner et al. 1986; Ruf and Heldmaier 1987). Equally strong effects on locomotor activity rhythms can also be induced by a slight reduction of food (Blank and Desjardins 1985). These studies highlight the

problem of drawing a clear distinction between a controlled thermoregulatory response and a possible failure of control mechanisms caused by the energy deficit, a problem inherent to any study employing food restriction to induce torpor.

In the study presented here, we adopt a new approach to investigate the interaction of food consumption and torpor in Djungarian hamsters. First, we attempt to correlate the individual tendency for torpor in animals fed ad libitum with their food intake and locomotor activity. Secondly, we examine the influence of diet composition, i.e., of lipid- or carbohydrate-rich seeds and cafeteria diet (Rothwell and Stock 1979), on the exhibition of torpor. Specifically we test the following hypotheses: (1) the individual proneness for torpor is a consequence of different foraging strategies during winter; (2) food quality and composition are environmental signals affecting the occurence of torpor; and (3) the exhibition of torpor is an intrinsic component of energy balance control and will be suppressed by an induced energy surplus.

Materials and methods

Animal maintenance. Djungarian dwarf hamsters, *Phodopus s. sungorus*, from our breeding stock at the Philipps Universität Marburg were raised under natural photoperiodic conditions at an ambient temperature (T_a) of 23 ± 1 °C. At the age of 2 months, the animals were separated and housed individually in Makrolon cages. In late autumn 1989, 80 hamsters were sorted into 40 breeding pairs and housed together throughout winter (without having offspring during this season). All cages were provided with woodshavings as bedding material and water bottles. Depending on the experimental treatment, the animals were either fed solely on rodent chow (Altromin 7010; 18.3 kJ·g^{-1}), or additionally received wheat (16.9 kJ·g^{-1}), sunflower seeds (26.9 kJ·g^{-1}), or a varied mixture of nuts, cookies, chocolate, and seeds (26.7 kJ · g^{-1}), i.e., a cafeteria diet as described by Rothwell and Stock (1979).

Experiments and techniques

Experiment I: Individual variation of torpor, food intake, and locomotor activity. On January 2, seven male adult hamsters in winter condition, i.e., with body weights between 20.8 and 29.1 g and with winter fur [pelt index 5–6, see Figala et al. (1973)] were selected from the stock. On January 4, temperature-sensitive radio transmitters (Minimitter Model X; weight: 1.3 g; accuracy: ±0.1 °C) were surgically implanted into the visceral cavity of the animals. During surgery, the animals were under Ketamine/Rompun anaesthesia. From January 11–25 animals were kept at 23 ± 1 °C in artificial short days (LD 8:16) and body temperatures of all hamsters recorded at 6-min intervals by a microcomputer interfaced with radioreceivers [for details see Ruf and Heldmaier (1987)]. To determine the duration of torpor bouts the time spent at body temperatures below 32 °C was calculated.

Locomotor activity was monitored by passive-infrared motion detectors (SA 209; Conrad Electronic) placed on top of the cages. Each detector is capable of sensing temperature changes in an angle of 90° up to a distance of 12 m. An alarm output lasting 3 s is produced when an object significantly warmer than its environment passes one of 28 zones within the 90° angle. Thus, in the cages used ($22 \times 17 \times 15$ cm) an event was detected whenever an animal moved more than approximately 1.1 cm on the cage floor. Activity events were recorded continuously, summed, and stored by a computer at 6-min intervals.

The animals were fed solely on rodent chow ad libitum. Five days prior to the experiment removable food hoppers consisting of plexiglas tubes (i.d. 4 cm) were mounted onto the cage lids. Hamsters gained access to the food through 8-mm mesh wire. Food consumption was determined by weighing the food hoppers to the nearest 0.1 g. To avoid weight effects due to changes in humidity the food was stored in the animal chamber prior to and throughout the experiment. To minimize disturbances that could affect torpor frequencies, measurements of food intake were made every 5 days.

Experiment II. Effects of cafeteria diet and temperature on torpor. On December 15, 24 individually-caged hamsters of both sexes were divided into four groups ($n = 6$ each; mean body weights 25–27 g). All animals were placed on artificial short photoperiod (LD 8:16). Two groups each were kept at 23 ± 1 °C and 18 ± 1 °C, respectively. At each temperature, one group was fed rodent chow ad libitum and the other a cafeteria diet. During the following 4 weeks, body weight (to the nearest 0.1 g) and rectal temperatures were measured twice a week. Rectal temperatures were measured with a thermistor, inserted 2–3 cm into the rectum, and connected to a digital thermometer (AMR Therm 2264, accuracy ±0.1 °C). All temperature measurements were carried out between 10:00 and 14:00 hours, times at which Djungarian hamsters are most likely to be found torpid (see Ruf et al. 1989).

Experiment III. Torpor in breeding pairs: effects of seeds, cafeteria diet and sociality. From January 13 to February 19 torpor was monitored at 2-day intervals (between 10:00 and 14:00 hours) in 40 breeding pairs kept under natural photoperiod at 18 ± 1 °C. For ease of identification of individuals during torpor measurements, the male in each cage was marked with a spot of picric acid on the back prior to the experiment.

Torpor was determined by the measurement of body surface temperatures using an infrared radiation thermometer (Heimann KT17). This device is capable of measuring temperatures of small surface areas ($\varnothing$ 16–18 mm at distances between 1 and 40 cm) with an accuracy of ±0.2 °C. For each measurement, the animals' back and head surface was scanned from a distance of 2–5 cm and the maximal temperature recorded. The frequency distribution of the surface temperatures of torpid and normothermic hamsters (Fig. 1) shows a pattern similar to that of rectal temperatures (see Heldmaier and Steinlechner 1981a). Even though the surface temperatures of normothermic animals are lower than rectal temperatures, the bimodal frequency distribution allows a clear distinction to be made between active and torpid hamsters. Hamsters with surface temperatures of less than 25 °C were considered to be torpid.

During the first 8 days of the experiment (January 13–21) all hamsters were fed on rodent chow ad libitum. For the next 16 days (January 22–February 7) 13 pairs were additionally supplied with wheat seeds ad libitum and another 13 pairs with sunflower seeds ad libitum. The remaining 14 pairs were continuously provided with rodent chow only. On February 7 all hamsters were randomly separated into two new groups (20 pairs each) which included animals from all previous treatments. From February 8–19 one group received rodent chow only, whereas the other group was fed the cafeteria diet described earlier. Body weights of all hamsters were measured at the end of each dietary treatment, i.e., on January 21, February 7, and February 19.

Statistical analyses. Results are expressed as total numbers or means ± SEM. The significance of body mass changes was tested by the use of the sign test. The comparison of torpor frequencies is complicated by a non-normal distribution of the occurrence of torpor in the population (see results) and by the change of torpor frequencies during winter (see Heldmaier and Steinlechner 1981a). Consequently, the comparison of torpor frequencies was restricted to data recorded during the same experimental period. Also, nonparametric tests were used, i.e., the Mann-Whitney U-test for two samples, and Kruskal-Wallace ANOVA for more than two samples. To test for deviations of the observed torpor frequencies from

normal distributions or from expected distributions (Exp. III), the Chi-square goodness of fit analysis was applied.

Results

Experiment I. Individual variation of torpor, food intake, and locomotor activity

Body weights were similar in all animals (24.8 ± 1.09 g on January 11) and did not change significantly during the experiment (25.3 ± 0.91 g on January 25) with the exception of one animal. In hamster #FK7 body weight decreased from 24.5 to 19.6 g within the 15-day recording period, then increased again to reach 24.9 g during the following 10 days under identical dietary and environmental conditions.

Figure 2 shows body temperature recordings and average daily food intake of all individuals in this experiment. In those animals exhibiting torpor, mean torpor duration ranged from 3.54 ± 0.48 to 7.40 ± 0.35 h (mean: 5.14 ± 0.33; $n = 41$). Minimal body temperatures during torpor varied from 25.6 ± 0.19 to 29.1 ± 0.21 °C (mean: 27.6 ± 0.28 °C). As expected, duration and depth (i.e., minimal body temperature) of torpor bouts were correlated (Spearman rank correlation coefficient $r = -0.67$, $P < 0.05$).

Also, individual daily food intake and torpor frequency were closely correlated ($r = -0.88$; $P < 0.05$). During the 14 days of complete 24-h recordings of body temperatures, animal #FK7 spent 96.2 h in torpor (i.e., 6.87 h · day^{-1}) whereas hamster #FK8 never exhibited torpor. The average daily time spent torpid in this group was 3.49 ± 0.59 h. In the same 2-week period mean daily food intake ranged from 0.66 g · d^{-1} in animal #FK7 to 2.71 g · d^{-1} in animal # FK8 (mean: 1.93 ± 0.26 g · d^{-1}).

Furthermore, the individual number of torpor episodes was negatively correlated with the amount of

Fig. 2. Body temperature and average daily food intake in seven Djungarian hamsters during 15 consecutive days (LD 8:16; 23 °C). Body temperatures are shown as *black areas* between 34 °C and the actual core temperature
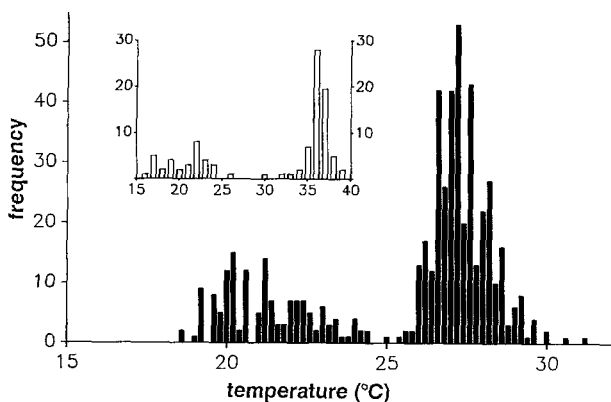
Fig. 1. Frequency distributions of surface temperatures showing a clear distinction between torpid and non-torpid *Phodopus sungorus*. Surface temperatures were measured with an infrared radiation thermometer in 80 hamsters kept at 18 ± 1 °C in natural photoperiod in January and February. The inset graph shows rectal temperatures of 33 animals housed in outside cages in December and was redrawn from Heldmaier and Steinlechner (1981a). Notice the similar bimodal distribution but the different scales
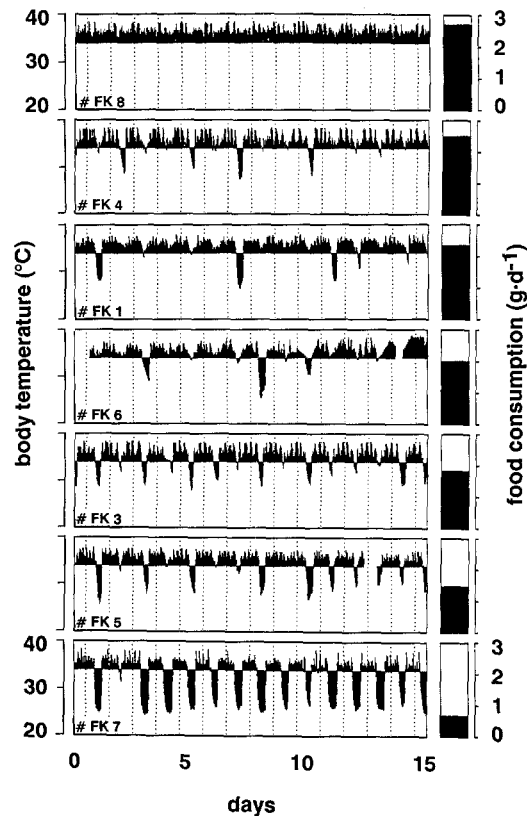
nocturnal locomotor activity ($r = -0.79$; $P < 0.05$). Three examples of activity recordings in hamsters showing no torpor, intermediate torpor frequency, and a very high torpor frequency are shown in Fig. 3. Since the employment of torpor obviously excludes activity during the day, the correlation was restricted to the total number of events recorded during the nightime hours only. It is possible that the amplitude of activity recordings reflects individual patterns of locomotion rather than the actual amount of activity. Therefore, the time spent active during the night was calculated by counting the number of intervals in which at least one event was detected. Again, this nocturnal activity time (2.64–5.92 h) was found to be negatively correlated with torpor frequency ($r = -0.84$; $P < 0.05$).

Experiment II. Effects of cafeteria diet and temperature on torpor

During the 28 days of treatment body weights in the control groups showed only minor changes (Fig. 4, upper panel) both at 23 °C and at 18 °C. In the cafeteria groups body weights increased by 1.2 ± 0.04 g at 23 °C ($P < 0.05$) and by 3.4 ± 0.11 g ($P < 0.01$) at 18 °C.

In the control groups, torpor frequency was greater at 18 °C than at an T_a of 23 °C ($P < 0.01$; Fig. 4). In contrast, torpor frequency in cafeteria diet hamsters at
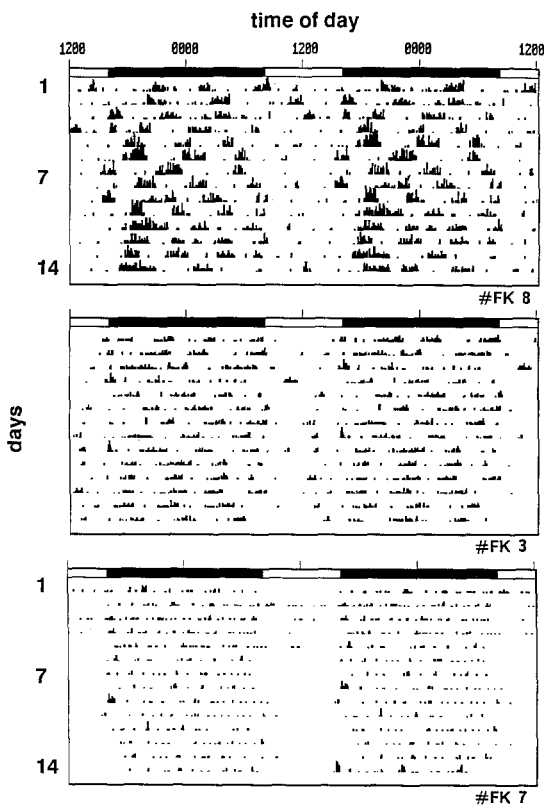
Fig. 3. Representative activity records of three Djungarian hamsters over 15 consecutive days at LD 8:16 and 23 °C. During the recording period hamster # FK8 showed no torpor, hamster # FK3 was found torpid on 8 days, and hamster # FK7 on 13 days. Locomotor activity was recorded with infrared motion detectors

Fig. 4. Changes in body weight (*upper panel*) and the number of torpor bouts (*lower panel*) occuring in four groups of hamsters ($n = 6$). The animals were kept at 23 ± 1 °C or 18 ± 1 °C for 28 days and fed either rodent chow (controls) or a cafeteria diet

18 °C – was not different from the 23 °C – group, but significantly less than in the controls at 18 °C ($P < 0.01$).

Experiment III. Torpor in breeding pairs: effects of seeds, cafeteria diet, and sociality

Cafeteria diet caused the most prominent changes in body weight. Within 12 days on cafeteria diet mean body weights increased from 30.5 ± 0.82 to 33.8 ± 0.93 g. As a weight gain was observed in 37 of 40 animals, this increase is highly significant ($P < 0.001$). During the same time period, body weights in the control groups remained
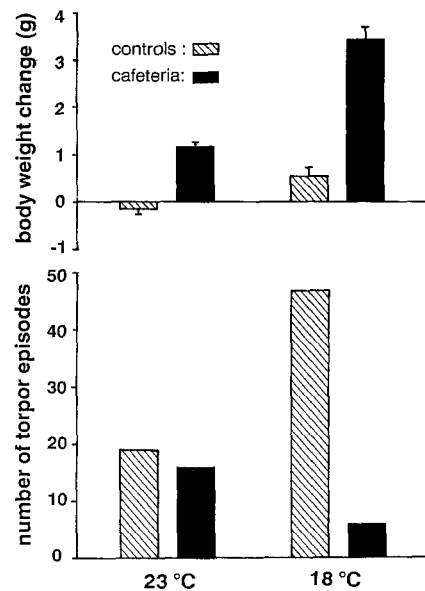
constant (see Table 1). Unexpectedly, the provision of wheat during the second experimental period resulted in an average weight loss of 2.2 g and was observed in 24 of 26 hamsters fed on this diet ($P < 0.001$).

The provision of sunflower seeds and wheat had no influence on mean torpor frequencies. However, as expected from experiment II, cafeteria diet significantly lowered torpor frequencies irrespective of the previous diet ($P < 0.01$ for all animals fed cafeteria diet vs controls). Details of torpor frequencies and body weight changes during all treatments are given in Table 1.

During the first two experimental periods where spontaneous torpor occurred unaffected by the dietary treatment, the mean daily fraction of animals exhibiting torpor was $20.8 \pm 2.3\%$. As expected from experiment I, this value is derived from a frequency distribution that is strongly skewed towards the left (standardized skewness 3.54) and significantly different from a normal distribution ($P < 0.001$). Thus, there was a large fraction of animals showing much lower than expected torpor fre-

Table 1. Effects of different diets on torpor and body weight in Djungarian hamsters. Torpor frequencies in mean (% ± SEM) animals torpid per day. Treatment labels indicate the diets for each group during the three periods of the experiment. C: rodent chow; S: +sunflower seeds; W: +wheat seeds; CA: cafeteria diet. Body weights were measured at the end of each treatment period

Treatment	n	% animals torpid per day			Body weight (g)		
		Period 1	Period 2	Period 3	Period 1	Period 2	Period 3
C–C–C	14	21.4 ± 3.5	28.6 ± 5.1	20.0 ± 2.6	28.9 ± 1.5	31.4 ± 1.5	31.0 ± 1.4
C–S–C	16	21.3 ± 2.5	12.6 ± 2.0	16.3 ± 2.8	29.4 ± 1.7	30.3 ± 1.7	30.4 ± 1.9
C–W–C	10	20.0 ± 4.4	21.4 ± 3.8	14.0 ± 2.5	30.3 ± 0.9	28.5 ± 1.1	28.7 ± 1.3
C–C–CA	14	15.7 ± 1.1	27.6 ± 3.2	2.9 ± 1.6[a]	29.4 ± 1.0	31.0 ± 0.9	33.6 ± 1.4[a]
C–S–CA	10	26.0 ± 1.6	28.6 ± 7.6	4.0 ± 2.5[a]	29.2 ± 1.8	30.1 ± 2.1	33.2 ± 2.0[b]
C–W–CA	16	16.3 ± 1.8	15.2 ± 2.8	0[b]	32.7 ± 1.7	30.2 ± 1.5[b]	34.4 ± 1.7[b]

[a] $P < 0.05$
[b] $P < 0.01$ relative to torpor frequencies of controls or to body weights in the previous period
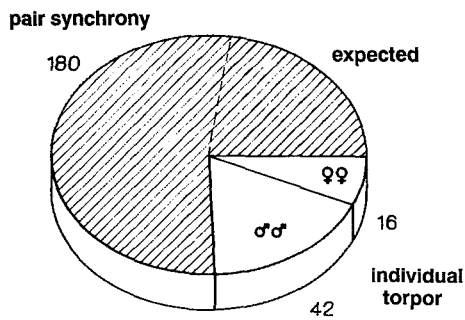
pair synchrony

Fig. 5. Synchronization of torpor episodes in 40 breeding pairs of Djungarian hamsters. Torpor episodes were synchronized between males and females caged together (i.e., both animals were torpid on the same day) in 180 out of 238 cases (*shaded segment*). This degree of synchrony is significantly higher ($P < 0.001$) than expected from the average coincidental synchrony between hamsters from different cages (54 cases, *dashed line*). Males showed significantly more individual, not synchronized torpor episodes than females (*blank segments*; $P < 0.001$)

quencies whereas certain individuals exhibited torpor very regularly.

The employment of torpor was synchronized in the breeding pairs housed together (Fig. 5). In 180 of 238 torpor episodes (i.e., 75%) the male and female in each cage were both found torpid on the same day. This synchrony between the actual pairs caged together is significantly higher than expected from the average coincidental synchrony in the population (calculated from 4000 random pair combinations of animals from different cages; $P < 0.001$). In 19 of 40 breeding pairs completely identical patterns of alternations between torpor and normothermia were observed throughout the experiment. During torpor episodes the breeding pairs were always found huddled together closely. In 58 cases only one hamster in a cage was found torpid (Fig. 5). Males showed significantly more of these individual torpor episodes than females ($P < 0.001$). However, the total ratio of 132 vs 106 torpor episodes in male vs female hamsters gives no evidence for a significant sex difference ($0.05 < P < 0.10$).

Discussion

In view of the present findings, individual tendencies for torpor seem to be one of the various components of combined physiological adjustments differing largely between individuals. The coupling of different behavioural systems as indicated by the correlation between the use of torpor, nocturnal activity, and food intake, implies markedly different strategies adopted to overcome similar environmental constraints. If we assume that the measured locomotor activity reflects foraging behaviour in free-living hamsters, then our results suggest that certain individuals counter the shortage of food during winter by high nocturnal foraging activities, whereas others voluntarily reduce foraging and food intake but compensate for the lower energy input by the use of daily torpor. Thus, energy balance might be maintained by various combinations of input and output levels. Hudson

(1978) was the first to emphasize the ecological advantage of an individual variation of torpor tendency, since it allows for a flexible response of the population towards yearly fluctuations in the harshness of winter conditions. Hence, the use of torpor would be most advantageous when the costs of foraging are amplified during periods of extreme cold or shortage of food. From this point of view, torpor frequency seems to be adjusted to variations in the environment, in particular to food availability. However, in our experiments those individuals which exhibited torpor obviously did not respond to the presence of abundant food. Thus, it remains unclear whether in fact low food intake causes high torpor frequencies or vice versa, or if energy savings due to (endogenously preprogrammed) high torpor frequencies enable the animal to reduce its food consumption.

Estimations of energy savings by torpor based on comparisons with animals that maintain normothermic body temperatures usually range from 5 to 30% (Hill 1975; Heldmaier and Steinlechner 1981a; Vogt and Lynch 1982). In experiment I, the animal with the highest torpor frequency had a 75% lower food intake over a 15-day period than an animal which remained always normothermic. Although energy assimilation was not determined, this difference suggests that the use of torpor, at least for limited time periods, might account for very large differences in the energy expenditure of certain individuals. The striking individual differences in food consumption and torpor frequency could be partly due to the special type of food hoppers used in our experiment. These hoppers may have "forced" the animals to expend more effort in accessing food than in the usual cages. Consequently, the significance of torpor may be underestimated in typical laboratory situations where the costs of "foraging" could be much lower than in free-ranging animals. Using the double-labeled water method to obtain field metabolic rates, Mullen and Chew (1971, 1972) demonstrated in several rodent species that, "laboratory metabolic studies may not reflect the metabolism of animals in the field". These studies strongly indicated the frequent use of torpor in free ranging *Dipodomys merriami*, a species known to enter torpor in the laboratory only following a prolonged withdrawal of food (Dawson 1955; Carpenter 1966; Lyman 1982).

As mentioned before, in Djungarian hamsters the seasonal adjustment of body weight, pelage color, gonadal function, and the use of torpor are controlled by the changing photoperiod (Hoffmann 1972; Heldmaier and Steinlechner 1981a; Elliott et al. 1987). However, even in this highly photoperiodic species, a certain fraction of animals show no response to short days and consequently lack seasonal physiological adjustments (Puchalski and Lynch 1986). This non-responsive phenotype is characterized by a deficiency in circadian functions and the neuroendocrine transduction of photoperiodic signals (Puchalski and Lynch 1988). However, all animals used in experiment I of this study had undergone winter molt and the typical seasonal reduction of body weight. Thus, our observations of individual variations of torpor, activity, and food intake are clearly not due to a phenotypic lack of short day response but should be

interpreted as a variablity of photoperiodically controlled adaptations which could occur in natural, free-living populations. A similar plasticity of photoresponsiveness has been observed for reproductive functions in deer mice, accompanied by individual differences in the secretion of hormones from the hypothalamic-pituitary axis (Desjardins and Lopez 1983; Blank and Desjardins 1986).

In contrast to long-term, continuous, seasonal adjustments such as the changes in body mass and fur insulation, diurnal patterns of feeding and thermoregulation are particularly suitable for fast and flexible responses to changes in food availabilty or quality. This is demonstrated by the immediate, almost complete suppression of torpor in animals fed on cafeteria diet. Thus, food composition can influence the employment of torpor in *P. sungorus* thereby counteracting the torpor-inducing effects of short days and lowered ambient temperature. The observed response to cafeteria diet clearly shows a tight coupling between the physiological systems responsible for food intake and body temperature control. This functional link is not only restricted to thermoregulatory emergency reactions during food deprivation but generally supports the maintenance of energy balance.

We observed effects of cafeteria diet on torpor frequencies and body weights only at T_a 18 °C, i.e., below the thermoneutral zone of Djungarian hamsters (see Heldmaier and Steinlechner 1981b). This result is in accordance with earlier reports demonstrating that the effects of cafeteria diet on food consumption and energy output via diet-induced thermogenesis in the brown adipose tissue were significantly enhanced in rats kept below thermoneutrality (Rothwell and Stock 1986). According to Mc Elroy et al. (1986), in Djungarian hamsters a high energy diet can also lead to a four- to eight-fold increase in the thermogenetic activity of the brown fat. This effect was observed only in hamsters exposed to long photoperiods, but not in short days. This lack of a response might be partly due to the fact that the experiments were carried out at 22 °C. This is below thermoneutrality of *P. sungorus* in long days, but above the lower critical temperature in short days (Heldmaier and Steinlechner 1981b).

As underlined by the present study, under short day photoperiods substantial energy dissipation could be achieved not only by diet-induced thermogenesis, but simply by decreasing torpor frequency. Considering that core temperatures of Djungarian hamsters during torpor can be as low as 12.3 °C (unpublished observations), it can be concluded that cafeteria diets influence mean daily body temperatures (and consequently metabolic rates) in *P. sungorus* dramatically, compared, for example, to the slight increase of body temperatures observed in rats (see Rothwell and Stock 1979). Hence, in Djungarian hamsters, the inhibition of torpor could serve to partly counteract the effects of overfeeding and support maintenance of the endogeneous set-point of body weight (cf. Steinlechner et al. 1983).

The use of cafeteria diet not only alters the energy level of the food, but also the relative proportions of carbohydrates, fats, and proteins (Rothwell and Stock 1987). The objective of examining the influence of feeding seeds was to determine whether the effects of cafeteria diet could be simulated by diets with high fat (47% in sunflower seeds) or carbohydrate [71% in wheat seeds, Ciba Geigy (1981)] content only. In spite of its high carbohydrate content, the wheat diet (with a lower energy content than rodent chow) obviously had a negative influence on the animals energy balance, leading to the slight but significant body weight losses in this group. In the case of the animals fed sunflower seeds, the lack of an inhibition of torpor as observed during cafeteria diet was not completely unexpected. It has been demonstrated in chipmunks that diets with a high content of polyunsaturated lipids, as found in sunflower oil, can even facilitate torpor episodes during hibernation (Geiser and Kenagy 1987). In our experiments the sunflower seed diet not only failed to affect torpor frequencies, but also had no influence on body weights (despite the high caloric density). Taken together, these results imply that the suppression of torpor during cafeteria diet is closely linked to the simultaneous induction of an excessive energy intake by the variation of food items. This might lead to the assumption that a sensory input of food quality or energy content directly affects body temperature control. However, inhibition of torpor by cafeteria diet could be also mediated via an indirect, behavioural pathway which involves the induction of increased feeding activity. The latter possibility would correspond to our observation of activity/torpor interactions in exp. I. Moreover, it could explain the tight link between torpor frequencies and circadian system properties in *P. sungorus* demonstrated earlier (Ruf et al. 1989).

Apart from abiotic environmental factors, such as food accessibility and ambient temperature, the energetic benefits and costs of a certain thermoregulatory pattern can be strongly influenced by social interactions. Vogt and Lynch (1982) found individual energy savings by torpor in *Peromyscus leucopus* to be significantly improved when mice huddled together in groups. Unfortunately, in the case of *P. sungorus*, very little is known about its social behaviour in the field, but sharing of burrows by groups of animals and huddling during winter has been observed occasionally in the laboratory (Müller 1982; Ruf and Steinlechner, unpublished results). Evidently, social thermoregulation requires temporal synchronisation. Since daily torpor differs from deep hibernation in that it occurs as a strongly diurnal phenomenon, some temporal conformity of the body temperature rhythms between individuals is inevitable. However, apart from this inherent temporal synchrony, the present results show that Djungarian hamsters also have the abilty to synchronize their long-term general pattern of alternations between torpor and normothermia. The mechanisms underlying this thermoregulatory synchrony remain unclear, but as Arnold (1988) has demonstrated with hibernating marmots, social thermoregulation could be based on the direct perception of peripheral thermal stimuli in animals huddled together.

In the context of effects of sociality on the exhibiton of torpor it should be noticed that no significantly dif-

ferent torpor frequencies were observed in male and female hamsters when kept as pairs. Previous reports have shown (Elliott et al. 1987; and our unpublished observations), that individually-caged Djungarian hamster males are clearly more prone to enter torpor than females. Considering also that in this study males showed significantly more individual (not synchronized) torpor episodes than females, it can be concluded that a sex-dependent torpor tendency is overcome by the synchronisation of torpidity in animals housed together. With our present knowledge of the biology of free-living Djungarian hamsters the significance of sex differences in torpor control and the functional links between thermoregulation and social interactions remain obscure.

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