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# The impact of dietary fats, photoperiod, temperature and season on morphological variables, torpor patterns, and brown adipose tissue fatty acid composition of hamsters, *Phodopus sungorus*

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**Abstract** We investigated how dietary fats and oils of different fatty acid composition influence the seasonal change of body mass, fur colour, testes size and torpor in Djungarian hamsters, *Phodopus sungorus*, maintained from autumn to winter under different photoperiods and temperature regimes. Dietary fatty acids influenced the occurrence of spontaneous torpor (food and water ad libitum) in *P. sungorus* maintained at 18 °C under natural and artificial short photoperiods. Torpor was most pronounced in individuals on a diet containing 10% safflower oil (rich in polyunsaturated fatty acids), intermediate in individuals on a diet containing 10% olive oil (rich in monounsaturated fatty acids) and least pronounced in individuals on a diet containing 10% coconut fat (rich in saturated fatty acids). Torpor in *P. sungorus* on chow containing no added fat or oil was intermediate between those on coconut fat and olive oil. Dietary fatty acids had little effect on torpor in animals maintained at 23 °C. Body mass, fur colour and testes size were also little affected by dietary fatty acids. The fatty acid composition of brown fat from hamsters maintained at 18 °C and under natural photoperiod strongly reflected that of the dietary fatty acids. Our study suggests that the seasonal change of body mass, fur colour and testes size are not significantly affected by dietary fatty acids. However, dietary fats influence the occurrence of torpor in individuals maintained at low temperatures and that have been photoperiodically primed for the display of torpor.

**Key words** Seasonal temperature · Photoperiod · Dietary fatty acids · Torpor · Hamster, *Phodopus sungorus*

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**Abbreviations** *BAT* brown adipose tissue · *bm* body mass · *FA* fatty acid(s) · *MR* metabolic rate · *MUFA* monounsaturated fatty acid(s) · *PUFA* polyunsaturated fatty acid(s) · *SFA* saturated fatty acid(s) · $T_a$ air temperature · $T_b$ body temperature · $T_s$ body surface temperature(s) · *TNZ* thermoneutral zone · *UFA* unsaturated fatty acid(s)

## Introduction

The Djungarian hamster *Phodopus sungorus* undergoes a pronounced seasonal cycle in external appearance, reproductive physiology and thermal physiology. During summer, the animals are dark-furred, heavy, reproductive and homeothermic; in winter they are white-furred, light-weight, non-reproductive and display daily torpor (Hoffmann 1972; Figala et al. 1973; Heldmaier and Steinlechner 1981a: Goldman et al. 1986; Steinlechner et al. 1986). The seasonal change in the occurrence of torpor in *P. sungorus* appears to be controlled predominantly by photoperiod and a circannual rhythm, and less importantly by environmental temperature (Heldmaier and Steinlechner 1981a; Steinlechner et al. 1986; Ruf et al. 1993).

Experimental evidence on other mammalian species suggests that dietary FA are a further factor that can influence occurrence or patterns of torpor. Dietary PUFA have been shown to increase frequency of torpor and the duration of torpor bouts, and lower the $T_b$ and MR of torpid mammals (Geiser and Kenagy 1987; Geiser 1991, 1993; Frank 1992; Florant et al. 1993).

We were interested in how the FA composition of diet, energy content of diet, photoperiod, and $T_a$ influence seasonal changes of bm, fur colour, testes size and torpor in *P. sungorus*. For these experiments groups of hamsters were maintained from autumn until winter under natural photoperiod, short photoperiod (LD

8:16), or long photoperiod (LD 16:8). $T_a$ was either 23 °C, which is near the lower end of the TNZ or 18 °C, which is below the TNZ of this species (Heldmaier and Steinlechner 1981b). Animals were fed either hamster chow containing 4.7% fat or hamster chow with addition of 10% fat or oil that differed in composition of FA. Fats or oils that were added to the diet were coconut fat containing mainly SFA (12:0 to 16:0), olive oil containing predominantly oleic acid (18:1), and safflower oil containing predominantly the essential FA linoleic acid (18:2). At the end of the experiment we determined the FA composition of BAT to resolve whether they are affected by dietary fats and whether they correlate with physiological variables.

## Materials and methods

Sixty-six hamsters, born between 10 June and 8 August 1991, were held at a $T_a$ of 23 ± 1 °C, and a photoperiod that was adjusted weekly to the natural photoperiod of Marburg, Germany. They were maintained on water and hamster chow (Altromin 7014) ad libitum.

On 16 September 1991 they were divided into 11 groups ($n = 6$ each) of matched bm and sex ratio and exposed to different photoregimes and $T_a$s. From 19 September 1991 until 31 January 1992 the animals were fed different diets:

(1) Four groups were held under a photoperiod that was adjusted weekly to the natural photoperiod of Marburg and $T_a$ 23 °C, and from 20 November until the end of the experiment at $T_a$ 18 °C. The diets were (i) hamster chow (Altromin 7014), (ii) hamster chow with 10% addition by weight of coconut fat, (iii) hamster chow with 10% addition of olive oil, and (iv) hamster chow with 10% addition of safflower oil.
(2) Three groups were held under a short photoperiod of LD 8:16 and $T_a$ 18 °C from 16 September 1991. The diets were (i) hamster chow, (ii) hamster chow with 10% addition of coconut fat, and (iii) hamster chow with 10% addition of safflower oil. One individual on the safflower oil diet died on 16 October.
(3) Two groups were held under a short photoperiod of LD 8:16 and $T_a$ 23 °C. The diets were (i) hamster chow with 10% addition of coconut fat and (ii) hamster chow with 10% addition of safflower oil.
(4) Three groups were held under a long photoperiod of LD 16:8 and $T_a$ 23 °C. The diets were (i) hamster chow with 10% addition of coconut fat and (ii) hamster chow with 10% addition of safflower oil, and (iii) hamster chow.

Altromin hamster chow 7014 contained 22.5% protein, 4.7% fat, 4.5% fibre, 39% carbohydrates, 11% water, and minerals and vitamins. The fat of hamster chow contained 0.3% C14:0, 12.7% C16:0, 0.3% C16:1, 3.6% C18:0, 21.8% C18:1, 49.6% C18:2, 6.8% C18:3, 0.4% C20:0, 0.9% C20:1, 1.2% C20:4, and 0.5% C20:5 (Altromin Tier-Labor-Service, Lange). Coconut fat contained 45.4% C12:0, 18.0% C14:0, 10.5% C16:0, 2.3% C18:0, 14.6% other SFA, and 7.5% C18:1. Olive oil contained 6.9% C16:0, 2.3% C18:0, 84.4% C18:1 and 4.6% C18:2. Safflower oil contained < 1% of short-chain SFA, 6% C16:0, < 0.5% C16:1, 2.5% C18:0, 13% C18:1, 78% C18:2, 0.5% C18:3 and 1% long-chain FA (Akzo Chemicals, Emerich).

The coconut fat diet therefore contained about 67% SFA, 12% C18:1, 16% C18:2, the olive oil diet contained about 12% SFA, 64% C18:1, and 19% C18:2, and the safflower oil diet contained about 13% SFA, 16% C18:1, and 69% C18:2. Chow contained about 17% SFA, 22% C18:1, 50% C18:2 and 8.5% other PUFA. The energy content of the chow was about 11.7 $kJ \cdot g^{-1}$ and that of the experimental diets about 14.5 $kJ \cdot g^{-1}$.

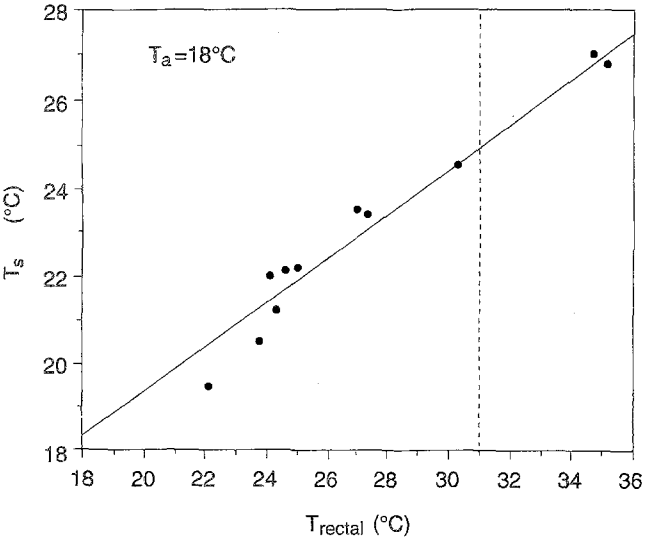


**Fig. 1** The relationship between body temperature measured rectally ($T_{rectal}$) and body surface temperature ($T_s$) measured by infrared thermometer in *P. sungorus* held at $T_a = 18$ °C. The *broken line* at 31 °C indicates the threshold temperature for torpor and corresponds with a $T_s$ of about 25 °C. Each data point represents one measurement. The solid line was fitted by a least squares regression and the equation is:

$$T_s(°C) = 9.31 + 0.50\ T_{rectal}(°C);\ r^2 = 0.96$$

Body mass was measured at regular intervals. The fur index was determined by a staging system using fur coloration (Figala et al. 1973). The extreme values in this staging system are "1" for dark-grey summer animals and "6" for white winter animals. Food uptake was measured twice over 2-day periods from 11–13 November and from 13–15 November by determining the difference in weight of food available to the animals before and after 2 days.

Testes size was measured in animals maintained under artificial short photoperiod and $T_a$ 18 °C. For these measurements animals were slightly anaesthetised with Halothane and width and length of both testes were measured with vernier callipers. Testes size was determined by multiplying the mean width by the mean length.

Spontaneous torpor (food and water ad libitum) was monitored by measuring, between 0930 and 1030 hours $T_s$ using an infrared radiation thermometer (Heiman KT 17; accuracy ± 0.2 °C at 1–40 cm; measured area 16–18 mm in diameter). For each $T_s$ measurement the back and head surface of each animal was scanned from 2–5 cm distance and the maximum $T_s$ was recorded (Ruf et al. 1991). Animals with a $T_s < 25.0$ °C at $T_a$ 18 °C were considered torpid because these $T_s$ correspond with rectally measured $T_b$ of < 31 °C determined with a calibrated digital thermocouple thermometer to the nearest 0.1 °C (Fig. 1). At $T_a$ 23 °C, animals with $T_s < 27.0$ °C were considered torpid because they were sluggish and were in the characteristic hunched position of torpid hamsters with eyelids narrowed to slits; these individuals began vigorous shivering after disturbance. Hamsters in long photoperiod and $T_a$ 23 °C were initially monitored by infrared thermometer as were the other groups, but since no indication of torpor was observed, the hamsters of both diet groups were no longer measured but observed between 5 December 1991 and 31 January 1992 for the behavioural torpor characteristics described above.

Hamsters under natural photoperiod at $T_a$ 18 °C were sacrificed on 3–5 February. Interscapular BAT was immediately removed and frozen. The total lipid FA of BAT were extracted within 2 weeks of storage using petroleum benzene/acetone (2:1). Fatty acids were methylated in sodium methylate and extracted with isooctane. FA

methyl esters were analysed in a Carlo Erba Instruments Vega 6130 gas chromatograph fitted with a Machery-Nagel (Düren, Germany) FS-FFAP-DF-2.00 capillary column.

Differences in the occurrence of torpor among and between experimental groups were determined by a $\chi^2$ test. Differences in $T_s$ between groups were determined by a one-way ANOVA. Fatty acid percentage values were arcsine-transformed before testing for differences by a one-way ANOVA followed by a Student-Newman-Keuls test (Sokal and Rohlf 1981). Numerical values are expressed as means $\pm$ 1 standard deviation (SD).

## Results

### Body mass and food uptake

Body mass changed with season in all groups of hamsters (Fig. 2). This seasonal change was influenced by photoperiod, temperature and somewhat by diet. Hamsters under natural photoperiod at $T_a$ 18 °C showed an initial increase of bm to about 34–35 g in September/October; bm then fell until January to about 26–30 g and rose again slightly in February. The decrease of bm was somewhat more pronounced in hamsters on olive and safflower oil diets than in hamsters on coconut fat diet and chow (Fig. 2).

Hamsters under artificial short photoperiod at $T_a$ 18 °C and experimental diets showed a similar seasonal cycle of bm as hamsters under natural photoperiod (Fig. 2). In contrast, hamsters on chow remained at a similar bm from October to January but bm rose in February.

The seasonal change of bm in hamsters under artificial short photoperiod at $T_a$ 23 °C was similar but weaker than that of hamsters at $T_a$ 18 °C (Fig. 2). As in hamsters under natural photoperiod, the seasonal change in bm was more pronounced in hamsters on safflower oil diet than in hamsters on coconut fat diet.

Hamsters under long photoperiod at $T_a$ 23 °C differed completely from the other groups (Fig. 2). All individuals on all diets raised their bm from about 32 g in September to about 40 g in October and remained at that value until December.

Food uptake measured in November was indistinguishable among diet groups held at the same $T_a$. Food uptake at $T_a$ 23 °C ranged between $2.12 \pm 0.44$ g·day$^{-1}$ (30.7 kJ·day$^{-1}$) in animals on safflower oil diet and $2.73 \pm 0.82$ g·day$^{-1}$ (39.6 kJ·day$^{-1}$) in animals on the olive oil diet. At $T_a$ 18 °C food intake was slightly higher and ranged from $3.05 \pm 0.49$ g·day$^{-1}$ (44.2 kJ·day$^{-1}$) in animals on the coconut diet to $3.72 \pm 1.05$ g·day$^{-1}$ (43.5 kJ·day$^{-1}$) in animals on chow.

### Fur index

The fur index was similar among groups of hamsters under natural and short photoperiods irrespective of $T_a$ and diets (Fig. 3). The fur index rose from about 1 (dark-grey) in September to about 5–6 (white)

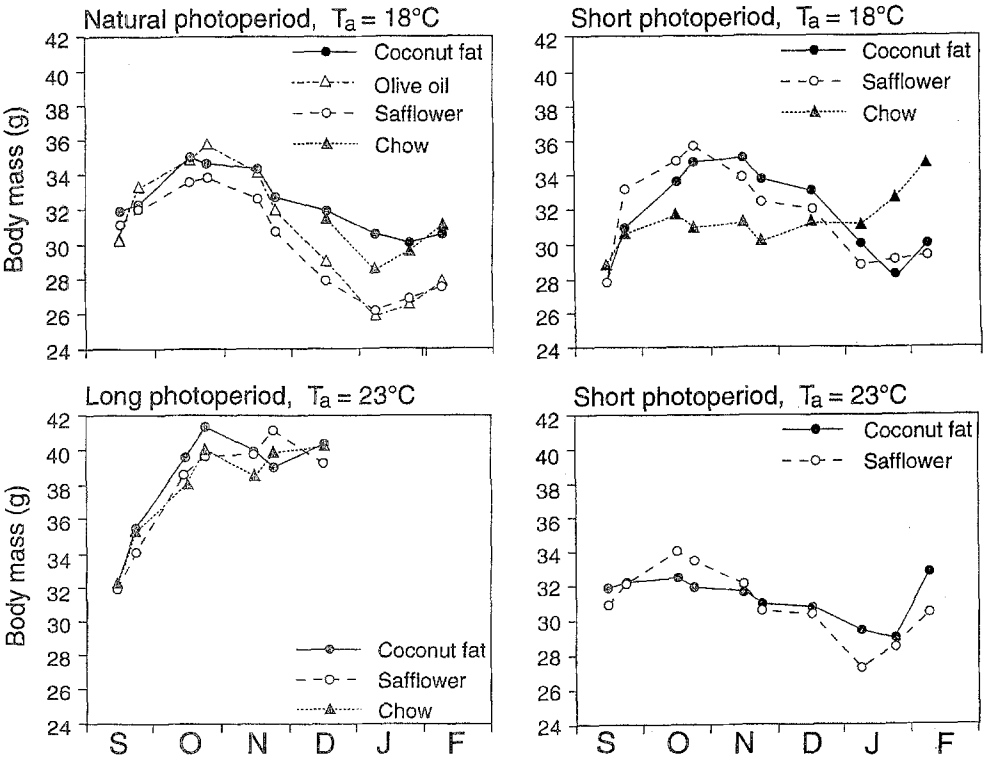


**Fig. 2** Seasonal change of body mass in *P. sungorus* maintained under different environmental conditions and on different diets. *Solid circle*, coconut fat diet; *open triangle*, olive oil diet; *open circle*, safflower oil diet; *closed triangle*, chow without added fat or oil. Each data point represents the mean of 6 individuals with the exception of the safflower oil diet under short photoperiod at $T_a$ 18 °C where they represent the mean of 5 individuals. In the interest of clarity standard deviation, which ranged between 1.7–13.0 g, were omitted

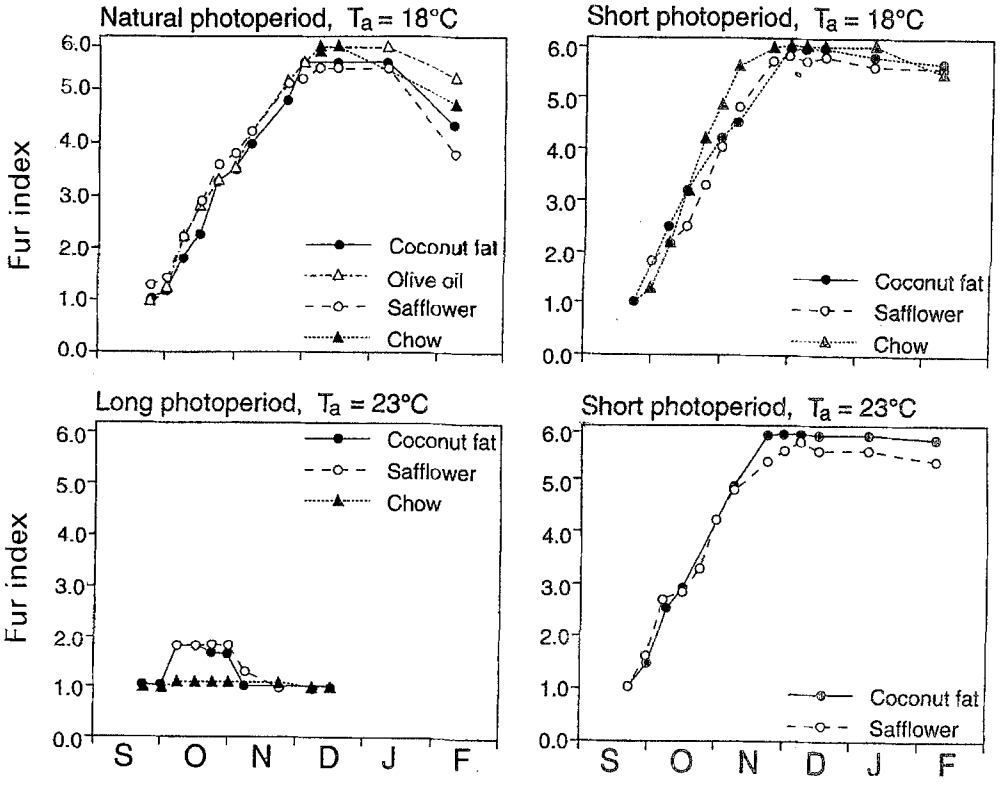


**Fig. 3** Seasonal change of fur index (1 = dark-grey, 6 = white) in *P. sungorus* maintained under different environmental conditions and on different diets. *Solid circle*, coconut fat diet; *open triangle*, olive oil diet; *open circle*, safflower oil diet, *closed triangle*, chow without added fat or oil. Each data point represents the mean of 6 individuals with the exsception of the safflower oil diet under short photoperiod at $T_a$ 18 °C where they represent the mean of 5 individuals. In the interest of clarity standard deviations, which ranged between 0 and 1, were omitted

in November/December. Hamsters under short photoperiod at $T_a$ 18 °C changed fur colouration to white shortly before those at $T_a$ 23 °C in November; animals under natural photoperiod became white in December. The fur index remained at about 5–6 until February in hamsters under artificial short photoperiod, but fell to about 4–5 in hamsters under natural photoperiod. The fur index of hamsters under long photoperiod remained between 1 and 2 throughout the period of observation, irrespective of the diet or season (Fig. 3).

## Testes size

At the beginning of the experiment on 19 September, testes size in males maintained at $T_a$ 18 °C and under artificial short photoperiod was 64.6 ± 24.6 mm$^2$ ($n$ = 3; chow), 49.7 ± 13.2 mm$^2$ ($n$ = 3; coconut diet), and 49.5 ± 19.1 mm$^2$ ($n$ = 2; safflower oil diet); these means were indistinguishable. Testes size decreased over the next months and on 12 December testes size was still similar among diet groups: 23.0 ± 5.2 mm$^2$ ($n$ = 3; chow), 25.2 ± 2.0 mm$^2$ ($n$ = 3; coconut diet), and 26.6 ± 5.0 mm$^2$ ($n$ = 2; safflower oil diet).

## Diet and torpor

### *Natural photoperiod*

Spontaneous torpor (food and water available) in animals held under natural photoperiod was affected by dietary FA. Torpor was first observed in a hamster on the safflower oil diet on 12 November ($T_a$ 23 °C; $T_s$ 26 °C; not shown) – all other individuals remained normothermic. After $T_a$ was lowered to 18 °C on 20 November, torpor was first observed on 21 November (safflower oil diet), 3 December (hamster chow and olive oil diets), and 12 December (coconut fat diet) (Fig. 4). In November 41.7% on animals on the safflower oil diet displayed torpor in contrast to 0% torpor in the other diet groups (Table 1). In December the occurrence of torpor increased in all diet groups and was highest in animals on safflower oil (54.5%) and olive oil (43.8%) diets and lowest in animals on coconut fat diet (14.8%) and chow (16.7%). A further increase in torpor occurrence was observed in January, except in animals on the olive oil diet (Fig. 4; Table 1). When all measurements throughout the period of observation at $T_a$ 18 °C were combined, the mean occurrence of torpor was low in animals on coconut fat diet and chow (17–19%), more pronounced in animals on olive oil diet (32%), and most pronounced in animals on the safflower oil diet (53%; Table 1).

The mean $T_s$ also showed some diet-induced differences (Table 2; Fig. 4). Significant differences among diet group means were observed in November (ANOVA $P < 0.01$) and December (ANOVA $P < 0.01$) and when means were calculated from all measurements taken throughout the experimental period (ANOVA $P < 0.01$). The lowest mean $T_s$ of 24.0 ± 0.7 °C was observed for animals on the safflower oil diet in December and the highest mean $T_s$ of

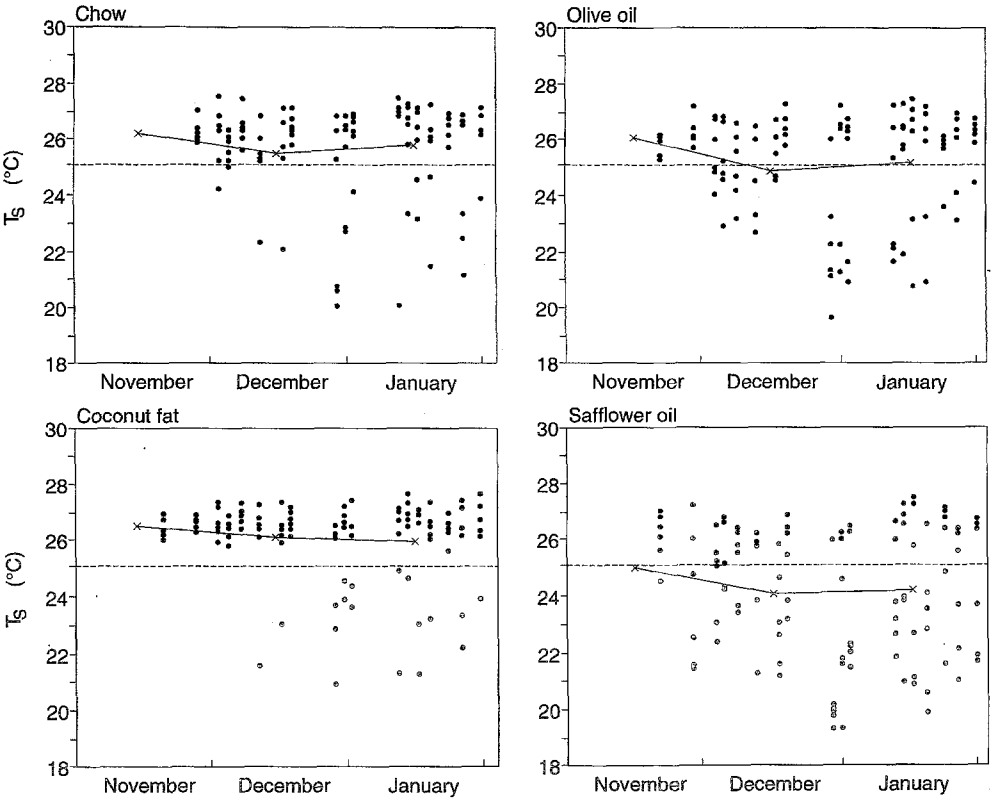


**Fig. 4** Seasonal change of body surface temperature ($T_s$) in *P. sungorus* maintained under natural photoperiod and a $T_a$ of 18 °C. Food and water were available ad libitum. The four groups of $n = 6$ were fed: 1. chow without added fat or oil, 2. chow containing 10% coconut fat, 3. chow containing 10% olive oil, and 4. chow containing 10% safflower oil. Each solid point represents one measurement. The *broken line* indicates the threshold temperature for torpor, crosses represent the mean $T_s$ for the particular month. The overall mean $T_s$ of the groups are shown in Table 2

26.5 ± 0.2 °C for animals on the coconut fat diet in November (Fig. 4).

*Short photoperiod, $T_a$ 18 °C*

Hamsters held under short photoperiod and $T_a$ 18 °C showed a similar seasonal pattern, but differed somewhat from animals under natural photoperiod in their response to diet. Torpor was first observed on 7 November in animals on hamster chow and safflower oil diets and on 21 November in an animal on coconut fat diet. In November, torpor was most frequent in animals on safflower oil diet, intermediate in animals on hamster chow, and least frequent in animals on coconut fat diet (Fig. 5; Table 1). In December incidence of torpor increased in all groups and was 20.2% in hamsters on coconut fat diet > 44% in hamsters on safflower oil and hamster chow diets. In both months significant differences were observed between coconut fat and hamster chow diets and between coconut fat and safflower oil diets, but not between hamster chow and safflower oil diets (Table 1). In January, torpor occurrence increased further in animals on coconut fat and safflower oil diets, but decreased in animals on chow (Table 1). Throughout the period of observation, torpor was least frequent in animals on the coconut fat diet, intermediate in animals on chow and most frequent in animals on the safflower oil diet (Table 1).

$T_s$ did not differ among the diet groups during the 3 months of investigation. However, when the group means were calculated from all measurements taken throughout the experimental period the mean $T_s$ differed significantly among the three diet groups (ANOVA $P < 0.05$; Table 2).

*Short photoperiod, $T_a$ 23 °C*

At $T_a$ 23 °C torpor commenced later in the year than at $T_a$ 18 °C (Fig. 6). Torpor was first observed on 5 December in hamsters on safflower oil diet and on 12 December in hamsters on coconut fat diet. In December, torpor occurred in 11.8% in hamsters on coconut fat and in 18.8% of hamsters on safflower oil diet (Table 1). In January, the occurrence of torpor was similar in animals on coconut fat (16.7%) and safflower oil (22.2%) diets. When all measurements were combined for calculation of an overall mean occurrence of torpor the group means remained indistinguishable (Table 1), although a trend towards more frequent torpor was observed in the animals on safflower oil diet. $T_s$ was indistinguishable between the two diet groups.

**Table 1** Percent spontaneous torpor (food and water ad libitum) in *Phodopus sungorus*. Group means ± SD were calculated from the mean %torpor in each individuals. Values in parentheses are number of observations

| *Natural Photoperiod, $T_a$ 18 °C* Diet | November | December | January | All |
|---|---|---|---|---|
| Coconut fat (1) | 0.0 ± 0.0 | 14.8 ± 14.7 | 23.0 ± 35.3 | 16.7 ± 18.3 |
| $n = 6$ | (12) | (48) | (48) | (108) |
| Olive oil (2) | 0.0 ± 0.0 | 43.8 ± 27.2 | 29.3 ± 25.8 | 32.4 ± 19.7 |
| $n = 6$ | (12) | (48) | (48) | (108) |
| Safflower oil (3) | 41.7 ± 20.4 | 54.5 ± 21.8 | 56.5 ± 28.1 | 52.8 ± 16.8 |
| $n = 6$ | (12) | (48) | (48) | (108) |
| Hamster chow (4) | 0.0 ± 0.0 | 16.7 ± 20.4 | 23.2 ± 18.4 | 18.6 ± 17.2 |
| $n = 6$ | (6) | (48) | (48) | (102) |
| $\chi^2$ all | $P < 0.005$ | $P < 0.0001$ | $P < 0.001$ | $P < 0.0001$ |
| $\chi^2$ 1 vs 2 | ns | $P < 0.01$ | ns | $P < 0.01$ |
| 1 vs 3 | $P < 0.05$ | $P < 0.0001$ | $P < 0.001$ | $P < 0.0001$ |
| 1 vs 4 | ns | ns | ns | ns |
| 2 vs 3 | $P < 0.05$ | ns | $P < 0.01$ | $P < 0.01$ |
| 2 vs 4 | ns | $P < 0.01$ | ns | $P < 0.05$ |
| 3 vs 4 | ns | $P < 0.0001$ | $P < 0.001$ | $P < 0.0001$ |
| *Short Photoperiod, $T_a$ 18 °C* Diet | November | December | January | All |
| Coconut fat (1) | 3.7 ± 5.7 | 20.2 ± 16.2 | 33.3 ± 23.3 | 18.6 ± 14.3 |
| $n = 6$ | (54) | (54) | (48) | (156) |
| Safflower oil (2) | 22.2 ± 26.2 | 46.6 ± 31.0 | 60.0 ± 32.4 | 42.3 ± 23.9 |
| $n = 5$ | (45) | (45) | (40) | (130) |
| Hamster chow (3) | 16.5 ± 19.4 | 44.3 ± 29.1 | 31.3 ± 27.1 | 30.8 ± 19.9 |
| $n = 6$ | (54) | (54) | (48) | (156) |
| $\chi^2$all | $P < 0.025$ | $P < 0.01$ | $P < 0.025$ | $P < 0.0001$ |
| $\chi^2$ 1 vs 2 | $P < 0.01$ | $P < 0.01$ | $P < 0.025$ | $P < 0.0001$ |
| 1 vs 3 | $P < 0.05$ | $P < 0.01$ | ns | $P < 0.025$ |
| 2 vs 3 | ns | ns | $P < 0.01$ | $P < 0.05$ |
| *Short Photopriod, $T_a$ 23 °C* Diet | December | January | All | |
| Coconut fat | 11.8 ± 10.8 | 16.7 ± 22.0 | 14.6 ± 15.7 | |
| $n = 6$ | (42) | (54) | (96) | |
| Safflower oil | 18.8 ± 19.5 | 22.2 ± 28.1 | 20.9 ± 23.9 | |
| $n = 6$ | (42) | 45 | (96) | |
| $\chi^2$ all | ns | ns | ns | |
| *Long Photoperiod, $T_a$ 23 °C* Diet | December | January | | |
| Coconut fat | 0.0 ± 0.0 | 0.0 ± 0.0 | | |
| $n = 6$ | (48) | (54) | | |
| Safflower oil | 0.0 ± 0.0 | 0.0 ± 0.0 | | |
| $n = 6$ | (48) | (45) | | |

*Long photoperiod, $T_a$ 23 °C*

Animals maintained under long photoperiod and $T_a$ 23 °C never were observed in torpor irrespective of the diet. $T_s$ measured in December was slightly higher than those in animals maintained under short photoperiod at the same $T_a$ and on the same diets (Table 2).

## FA composition of BAT

Total lipid FA in BAT from hamsters maintained under natural photoperiod at $T_a$ 18 °C differed significantly among the diet groups (Table 3). Of the nine FA that were identified, eight differed significantly (ANOVA; $P < 0.001$). Moreover, the sums of SFA, UFA and PUFA and the SFA/UFA ratio differed among the diet groups (ANOVA; $P < 0.0001$). The FA composition of BAT reflected that of the respective diets. In comparison with the other diet groups, BAT of animals on the coconut fat diet was particularly rich in the saturated myristic acid (14:0) and palmitic acid (16:0), those on the olive oil diet was particularly rich in the monounsaturated oleic acid (18:1), and those on the safflower oil diet was rich in the essential PUFA linoleic acid (18:2). Most FA from BAT of

**Table 2** Surface temperature ($T_s$) of *Phodopus sungorus*. Group means ± SD were calculated from the mean $T_s$ of each individual. $N$ = number of individuals, $n$ = number of determinations. Food and water were available and libitum

| *Natural Photoperiod, $T_a$ 18°C* | | | |
|---|---|---|---|
| | $T_s$ (°C) | | |
| Diet | All | $N$ | $n$ |
| Coconut fat | 26.0 ± 0.6 | 6 | 108 |
| Olive oil | 25.2 ± 0.7 | 6 | 108 |
| Safflower oil | 24.2 ± 0.9 | 6 | 108 |
| Hamster chow | 25.6 ± 0.6 | 6 | 108 |
| ANOVA | $P < 0.01$ | | |
| *Short Photoperiod, $T_a$ 18°C* | | | |
| | $T_s$ (°C) | | |
| Diet | All | $N$ | $n$ |
| Coconut fat | 25.7 ± 0.5 | 6 | 150 |
| Safflower oil | 24.3 ± 1.1 | 5 | 125 |
| Hamster chow | 25.1 ± 0.9 | 6 | 150 |
| ANOVA | $P < 0.05$ | | |
| *Short Photoperiod, $T_a$ 23°C* | | | |
| | $T_s$ (°C) | | |
| Diet | All | $N$ | $n$ |
| Coconut fat | 28.2 ± 0.7 | 6 | 96 |
| Safflower oil | 27.8 ± 0.6 | 6 | 96 |
| ANOVA | ns | | |
| *Long Photoperiod, $T_a$ 23°C* | | | |
| | $T_s$ (°C) | | |
| Diet | All | $N$ | $n$ |
| Coconut fat | 30.0 ± 0.3 | 6 | 12 |
| Safflower oil | 29.8 ± 0.3 | 6 | 12 |
| ANOVA | ns | | |

animals on the control diet showed concentrations that were intermediate between those from the experimental diets.

## Discussion

Our study shows that the composition of dietary fats can modify the occurrence and depth of torpor in *P. sungorus*. However, the seasonal change of morphological variables and thermal physiology are largely controlled by photoperiod and a circannual rhythm. Dietary influences on physiological variables were only observed in animals which were photoperiodically primed for the display of torpor and were exposed to cold.

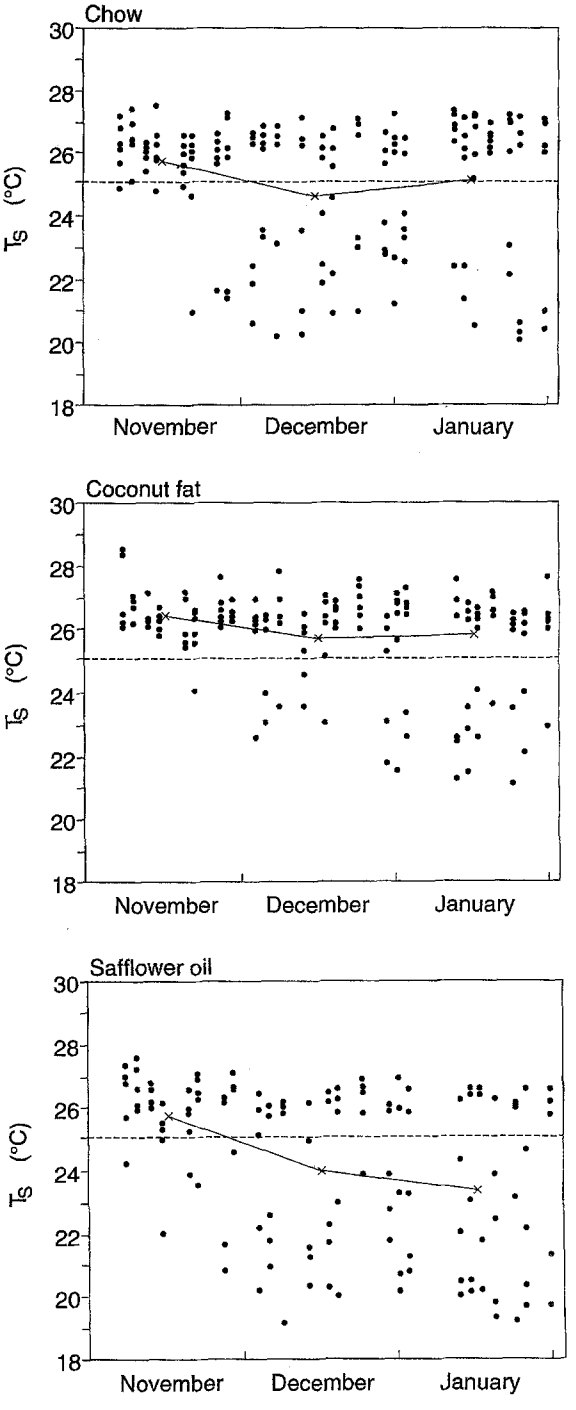


**Fig. 5** Seasonal change of body surface temperature ($T_s$) in *P. sungorus* maintained under short photoperiod and a $T_a$ of 18 °C. Food and water were available ad libitum. The three groups were fed: 1. chow without added fat or oil ($n$ = 6), 2. chow containing 10% coconut fat ($n$ = 6) and 3. chow containing 10% safflower oil ($n$ = 5). Each solid point represents one measurement. The *broken line* indicates the threshold temperature for torpor, crosses represent the mean $T_s$ for the particular month. The overall mean $T_s$ of the groups are shown in Table 2

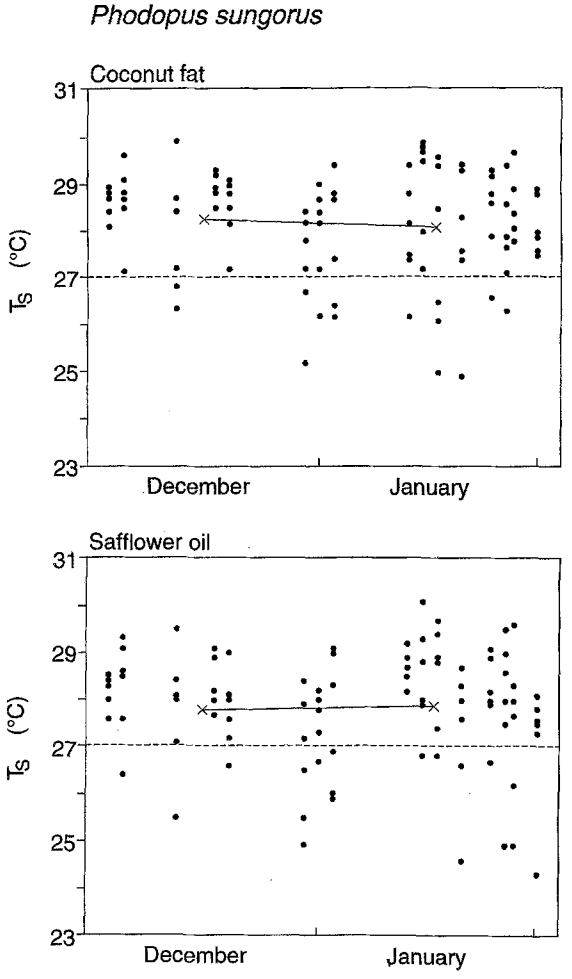


**Fig. 6** Seasonal change of body surface temperature ($T_s$) in *P. sungorus* maintained under short photoperiod and a $T_a$ of 23 °C. Food and water were available ad libitum. The two groups of $n = 6$ were fed: 1. chow containing 10% coconut fat, and 2. chow containing 10% safflower oil. Each solid point represents one measurement. The *broken line* indicates the threshold temperature for torpor, crosses represent the mean $T_s$ for the particular month. The overall mean $T_s$ of the groups are shown in Table 2

## Body mass, food uptake, fur index and testes size

Dietary fats had little effect on seasonally changing bm of *P. sungorus*. Such changes in bm are primarily controlled by photoperiod, but are accelerated by cold exposure as indicated by the differences between animals under the different environmental conditions, but not by dietary FA. Food uptake was also similar among diet groups. Animals on control diet consumed slightly more food; however, their uptake of energy was similar to that of animals on the experimental diets.

Fur index and testes size were also little affected by dietary fats. As with bm, fur colour and testes size appear to be controlled primarily by photoperiod, while temperature and other exogenous factors appear to have little influence.

## Torpor and dietary fats

While morphological variables showed little response, torpor in *P. sungorus* was affected by dietary FA. This is in agreement with studies on other heterothermic mammals (Geiser and Kenagy 1987; Geiser 1991, 1993; Frank 1992; Florant et al. 1993), which did, however, not provide data on the time-course of the effect of dietary FA on torpor occurrence and depth (present study). Particularly dietary UFA and PUFA enhanced torpor in comparison to dietary SFA. However, this effect was only observed when the animals were maintained under natural or artificial short photoperiods and at $T_a$ 18 °C. Torpor in animals maintained under short photoperiod and at $T_a$ 23 °C, which is at the lower end of the TNZ (Heldmaier and Steinlechner 1981b), did not appear to be affected by the composition of the dietary fat provided. This observation suggests that the effects of dietary fats are only observed when the animals are under some thermal stress and when $T_b$ during torpor can fall to low values because of exposure to low $T_a$. Animals maintained under long photoperiod never displayed spontaneous torpor in agreement to previous studies (Steinlechner et al. 1986) and dietary UFA did not alter that thermoregulatory pattern.

Not all dietary UFA had the same effect on torpor. Animals on the olive oil diet, which is rich in oleic acid (18:1), a MUFA, showed more frequent and deeper torpor than animals on coconut fat, which is rich in SFA. However, torpor in animals on the safflower oil diet, which is rich in linoleic acid (18:2), an essential PUFA, showed more pronounced torpor than animals on the olive oil diet. These observations suggest that although MUFA may enhance torpor, their effect is less effective than that of essential PUFA (Geiser et al. 1994).

In a study on Turkish hamsters, *Mesocricetus brandti*, Bartness et al. (1991) concluded that content of dietary fats (i.e. energy content), rather than its FA composition, affects torpor. This is in contrast to our present study, which shows that in *P. sungorus* the FA composition of dietary fat influences patterns of torpor. Torpor in *P. sungorus* maintained under natural, short photoperiod and on chow, without added fat or oil and thus low energy content, was infrequent and shallow and most similar to that of animals maintained on the coconut fat diet with high energy content. However, torpor in hamsters on chow with low energy content was less pronounced than that in the groups maintained on oil diets which had a high energy content. Torpor in *P. sungorus* maintained under artificial, short photoperiod and on chow without added fat or oil was intermediate between individuals fed isocaloric diets containing 10% added coconut fat or safflower oil. These observations support the view that composition of dietary fats rather than or in addition to fat content affects occurrence and depth of torpor. It is likely that

**Table 3** Fatty acid composition of *Phodopus sungorus* brown adipose tissue (BAT). Mean FA% ± SD of hamsters maintained under natural photoperiod and at $T_a$ 18 °C are shown

| Fatty Acid | Coconut Fat (1) ($n = 6$) | Olive Oil (2) ($n = 6$) | Safflower Oil (3) ($n = 6$) | Hamster Chow (4) ($n = 6$) | ANOVA $P$ value | SNK 1–2 | 1–3 | 1–4 | 2–3 | 2–4 | 3–4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 12:0 | 3.4 ± 0.8 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.0001 | * | * | * | ns | ns | ns |
| 14:0 | 7.1 ± 1.3 | 0.3 ± 0.0 | 0.4 ± 0.1 | 0.7 ± 0.2 | 0.0001 | * | * | * | ns | * | * |
| 16:0 | 19.4 ± 1.0 | 11.8 ± 0.6 | 11.0 ± 0.8 | 15.9 ± 1.5 | 0.0001 | * | * | * | ns | * | * |
| 16:1 | 1.6 ± 0.7 | 1.1 ± 0.2 | 0.6 ± 0.1 | 1.6 ± 0.4 | 0.001 | ns | * | ns | * | ns | * |
| 18:0 | 12.8 ± 1.4 | 11.9 ± 0.9 | 12.4 ± 0.9 | 17.6 ± 1.7 | 0.0001 | ns | ns | * | ns | * | * |
| 18:1 | 27.8 ± 3.5 | 53.6 ± 0.5 | 18.1 ± 0.9 | 31.0 ± 2.4 | 0.0001 | * | * | * | * | * | * |
| 18:2 | 25.9 ± 2.2 | 19.6 ± 0.4 | 55.5 ± 1.2 | 30.7 ± 2.0 | 0.0001 | * | * | * | * | * | * |
| 18:3 | 1.2 ± 0.1 | 0.7 ± 0.1 | 0.7 ± 0.1 | 1.5 ± 0.2 | 0.0001 | * | * | * | ns | * | * |
| 20:1 | 0.4 ± 0.2 | 0.4 ± 0.1 | 0.3 ± 0.1 | 0.3 ± 0.1 | ns | ns | ns | ns | ns | ns | ns |
| Unknown | 0.5 ± 0.3 | 0.7 ± 0.1 | 1.0 ± 0.3 | 0.8 ± 0.7 | – | – | – | – | – | – | – |
| SFA | 42.8 ± 2.5 | 24.0 ± 0.3 | 23.8 ± 0.9 | 34.2 ± 2.0 | 0.0001 | * | * | * | ns | * | * |
| UFA | 56.8 ± 2.6 | 75.4 ± 0.3 | 75.2 ± 1.0 | 65.1 ± 2.2 | 0.0001 | * | * | * | ns | * | * |
| SFA/UFA | 0.8 ± 0.1 | 0.3 ± 0.0 | 0.3 ± 0.0 | 0.5 ± 0.1 | 0.0001 | * | * | * | ns | * | * |
| PUFA | 27.1 ± 2.3 | 20.3 ± 0.5 | 56.3 ± 1.1 | 32.2 ± 2.1 | 0.0001 | * | * | * | * | * | * |

SNK Student-Newmans-Keuls test; * $P < 0.05$, ns = not significant

in the study by Bartness et al. (1991) the difference in PUFA content between diets was too small to elicit a physiological response.

Since torpor patterns in *P. sungorus* was affected by dietary fats, whereas morphological variables such as bm, fur colour and testes size were only little affected, it appears that specific physiological traits not entire individuals respond to dietary FA. In this aspect dietary fats seem to act similarly to photoperiod, which also influences physiological or morphological traits rather than the organism as a whole (Zucker 1988).

## FA of BAT and torpor

Torpor occurrence was correlated with the content of several of the major FA in BAT that were identified and also with the sum of FA groups. Significant correlations were observed for palmitic acid (16:0; $P < 0.01$; $r^2 = 0.41$). palmitoleic (16:1; $P < 0.001$; $r^2 = 0.47$, linoleic acid (18:2; $P < 0.01$; $r^2 = 0.26$), linolenic acid (18:3; $P < 0.005$; $r^2 = 0.32$), and the sum of saturated (SFA; $P < 0.025$; $r^2 = 0.25$), unsaturated (UFA; $P < 0.025$; $r^2 = 0.23$) and polyunsaturated (PUFA; $P < 0.025$; $r^2 = 0.25$) FA. The mean $T_s$ of individual *P. sungorus* also correlated with content of several FA: palmitic acid (16:0; $P < 0.025$; $r^2 = 0.25$), palmitoleic (16:1; $P < 0.01$; $r^2 = 0.32$, linoleic acid (18:2, $P < 0.05$; $r^2 = 0.18$) linolenic acid (18:3; $P < 0.025$; $r^2 = 0.22$). These correlations suggest that torpor occurrence and the FA composition of BAT may be functionally linked. Carneheim et al. (1989) observed a differential use of FA during different states of hibernation in hamsters (*Mesocricetus auratus*) and concluded that some FA may be of quantitative significance during hibernation and arousal. This interpretation is supported by the observation of sparing of PUFA in depot fat during hibernation (Florant et al. 1990) and by the selective retention of PUFA in tissues of marmots. *Marmota flaviventris* (Coleman et al. 1993).

But how could the composition of BAT affect thermal physiology of hamsters? It is possible that neural connections from BAT report on fluidity of this tissue to the brain which could affect torpor patterns. Another likely possibility is that diet-induced changes in BAT reflect changes in other parts of the body as, for example neural tissues (Geiser 1990), which may in turn influence thermoregulatory behaviour. The lipid environment surrounding neural receptors can affect their affinity (Loh and Law 1980) in a similar manner as membrane-associated enzymes are influenced by the membrane FA composition (McMurchie 1988; Aloia and Raison 1989).

## Selection of diet?

If dietary UFA and PUFA enhance torpor and survival of the hibernation season in heterothermic mammals (Geiser and Kenagy 1987; Frank 1992), it would be advantageous if they would select food items rich in these FA before the hibernation season. There is some evidence that suggests that diet selection according to FA composition may occur during autumn, in both the field and the laboratory. Several heterothermic rodents appear to increase the intake of oily seeds, which are generally rich in essential FA in autumn (Tevis 1953; Howard 1961). Chipmunks, *Tamias striatus*, collect sunflower seeds and almonds, both rich in PUFA, irrespective from the distance to their burrow, whereas other food items are only collected when they were found close to their burrow (Wood 1993). The mountain pygmy possums, *Burramys parvus*, a marsupial

hibernator, shifts its food intake from largely arthropods in spring and summer to predominantly seeds and berries in autumn (Smith and Broome 1992). Similarly, *P. sungorus* shows a seasonal change of preferred food items (Flint 1966) and stores composite seeds which are rich in oil and linoleic acid (Hitchcock and Nichols 1971) in their winter burrow (Flint 1966). While such seasonal changes may be interpreted as a reflection of a change in availability in food items, it has been demonstrated experimentally in both captivity and the wild that ground squirrels, *Spermophilus lateralis*, select food items that are rich in PUFA independent of availability (Frank 1994). These observations strongly suggest a seasonally changing diet selection according to FA composition rather than, or in addition to, seasonally changing availability of food items. Thus selective uptake of UFA and PUFA may form part of the winter preparation in heterothermic mammals.

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