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SHORT COMMUNICATION

Photoperiod affects daily torpor and tissue fatty acid composition in deer mice

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Abstract Photoperiod and dietary lipids both influence thermal physiology and the pattern of torpor of heterothermic mammals. The aim of the present study was to test the hypothesis that photoperiod-induced physiological changes are linked to differences in tissue fatty acid composition of deer mice, *Peromyscus maniculatus* (~18-g body mass). Deer mice were acclimated for >8 weeks to one of three photoperiods (LD, light/dark): LD 8:16 (short photoperiod), LD 12:12 (equinox photoperiod), and LD 16:8 (long photoperiod). Deer mice under short and equinox photoperiods showed a greater occurrence of torpor than those under long photoperiods (71, 70, and 14%, respectively). The duration of torpor bouts was longest in deer mice under short photoperiod (9.3±2.6 h), intermediate under equinox photoperiod (5.1±0.3 h), and shortest under long photoperiod (3.7±0.6 h). Physiological differences in torpor use were associated with significant alterations of fatty acid composition in ~50% of the major fatty acids from leg muscle total lipids, whereas white adipose tissue fatty acid composition showed fewer changes. Our results provide the first evidence that physiological changes due to photoperiod exposure do result in changes in lipid composition in the muscle tissue of deer mice and suggest that these may play a role in survival of low body temperature and metabolic rate during torpor, thus, enhancing favourable energy balance over the course of the winter.

Keywords Torpor bouts · Fat · Heterothermy · Thermal energetics · Thermoregulation

Abbreviations

MUFA	monounsaturated fatty acids
PUFA	polyunsaturated fatty acids
SFA	saturated fatty acids
T_a	air temperature
T_b	body temperature
UFA	unsaturated fatty acids
$\dot{V}O_2$	rate of oxygen consumption
WAT	white adipose tissue

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Introduction

Seasonal changes in thermal physiology are widespread among mammals. In winter, many heterothermic species exhibit torpor, expressed as a periodic reduction in body temperature (T_b), metabolic rate, and other physiological functions to conserve energy (Wang 1989; Barnes and Carey 2004). In contrast, during summer, torpor is often less frequent or less pronounced, and in some species, appears to be absent altogether (Wang 1989; Geiser 2004). In many high latitude mammals, this seasonal cycle is to a

large extent controlled by photoperiod, a reliable predictor of seasonal changes in the environment. In general, short photoperiod (i.e. long daily exposure to darkness) enhances the occurrence and depth of torpor, whereas long photoperiod or long exposure to daylight has the opposite effect (Lynch et al. 1978; Steinlechner et al. 1986; Stamper et al. 1999; Körtner and Geiser 2000).

The occurrence, depth, and duration of torpor are also affected by dietary fatty acids (Dark 2005). Fatty acids play an important role in the acclimation to cold, which is generally accompanied by an increase in unsaturated fatty acids (UFA) and a decrease in saturated fatty acids (SFA) in tissues and cell membranes especially of ectotherms (Cossins and Wilkinson 1982). With regard to torpor, diets rich in UFA result in more frequent, deeper (lower T_b), and longer torpor bouts in several species. In contrast, diets rich in SFA result in shorter, shallower, and less frequent torpor bouts, and these physiological differences appear to be caused at least in part by diet-induced changes in the fatty acid composition of tissues and organs (Geiser and Kenagy 1987; Frank 1994; Geiser et al. 1994; Florant 1998; Fietz et al. 2003; Munro and Thomas 2004). Moreover, when hamsters (*Phodopus sungorus*) were exposed to a short photoperiod, which enhances torpor in this species, they selected a diet richer in UFA than those exposed to a long photoperiod (Hiebert et al. 2003a). These studies point to a functional link between body lipid composition and thermal physiology of heterothermic mammals.

Because we know that dietary lipids can affect torpor via body lipid composition, and photoperiod affects diet selection as well as torpor use and duration, we tested the hypothesis that body fatty acid composition is linked to the animals' photoperiod exposure. Specifically, we aimed to determine to what extent exposure to different photoperiods affects the use, duration, and depth of torpor in deer mice, *Peromyscus maniculatus*, fed the same diet. We also tested whether photoperiod-induced changes in thermal physiology were reflected in changes of tissue fatty acid composition in the absence of a choice between SFA-rich and UFA-rich diets. Specifically, we tested the expectation, based on previous experiments, that short photoperiod exposure would favour increases in UFAs and decreases in SFAs in tissues relative to long photoperiod exposure. Deer mice were selected as experimental animals because, with regard to torpor physiology, members of the genus *Peromyscus* are known to be responsive to dietary lipid treatment (Geiser 1991) and are strongly photoperiodic (Lynch et al. 1978).

Material and methods

Deer mice (n=24) were trapped in early September 1986 in the Cascade Mountains, Chelan County, Washington (47° 49′N, 120°40′W). They were transported to the University of Washington, Seattle, divided into three groups with equivalent sex ratios and distributions of body mass, and were kept individually in cages at an air temperature (T_a) of 22±1°C. Deer mice were maintained throughout the experimental period under three photoperiods: LD 8:16 (short photoperiod, light from 0800 to 1600 hours PST; n=7), LD 12:12 (equinox photoperiod, light from 0600 to 1800 hours; n=10), and LD 16:8 (long photoperiod, light from 0400 to 2000 hours; n=7) and fed ad libitum with water and a single diet consisting of rodent laboratory chow (Ralston Purina 5001, 4.5% fat) throughout the experiment. Physiological measurements began after the animals had been exposed to their respective photoperiods for 8 weeks.

We employed two methods to quantify the use of torpor. First, torpor occurrence was measured once for each deer mouse at a T_a of 19±1°C, a temperature known from previous work to enhance the occurrence of torpor. In this procedure, deer mice were transferred in their home cages to a temperature-controlled room at 1500 hours; food and water were withheld. Animals were checked at 0900 hours on the following morning, known from our previous work to be the most likely time of day for torpor to occur in this species. Because deer mice are stiff and immobile at T_b characteristic of torpor (Lynch et al. 1978; Geiser 1991), observations of such behaviour were used to identify torpor bouts. If no clear decision could be derived from such observations (i.e. in 7 out of 24 individuals), T_b was measured to the nearest 0.1°C by 2-cm rectal insertion of a thermocouple probe read from a digital thermometer; animals with T_b<31.0°C were considered to be torpid (Hudson and Scott 1979).

A second method was employed to obtain further information about the use, depth, and duration of torpor after the animals had been exposed to their photoperiod treatment for 10 weeks. Once for each animal, the rate of oxygen consumption ($\dot{V}O_2$), which is directly proportional to metabolic rate, was measured continuously for 23 h between 1500 and 1400 hours the next day at a T_a of 17.0± 0.5°C. For this measurement, we lowered T_a slightly in comparison to the previous experiment because animals had to be transferred to a 2-l respirometer within a temperature-controlled cabinet in which animals would have been less likely to enter torpor than if they had been tested in their home cages; lowering T_a to 17°C enhanced the likeliness that animals would display torpor under these conditions. As in the previous protocol, food and water were withheld. Flow rates of dry air of 400 ml/min were regulated by a Brooks thermal mass flow controller. Oxygen consumption was measured with an Applied Electrochemistry S-3A oxygen analyser. The occurrence of torpor, the duration of torpor, and daily $\dot{V}O_2$ minimum, determined over an interval of at least 30 min, were derived from these measurements. Animals were weighed at the

beginning and end of each measurement period, and a linear decline of body mass was assumed for the calculation of mass-specific $\dot{V}O_2$. Deer mice were considered to be torpid when $\dot{V}O_2$ fell below 75% of the normothermic resting $\dot{V}O_2$ at T_a of 17°C, but usually, $\dot{V}O_2$ during torpor fell well below this level (usually to between 10 and 20% of resting $\dot{V}O_2$). Torpor induction experiments were conducted only twice/individual to minimize the potential effect of torpor rather than photoperiod acclimation on tissue fatty acid composition.

After physiological experiments were completed, experimental animals were sacrificed. Upper hind leg muscle and white adipose tissue (WAT) from the perirenal fat pad were immediately removed and frozen at −30°C. Before lipid extraction, tissues were defrosted and homogenized with a glass–Teflon homogenizer. Total lipids of tissues were extracted and transesterified using methanol–benzene 4:1 with acetyl chloride in sealed glass vials at 100°C for 1 h as described by Lepage and Roy (1986). Vials were cooled and fatty acid methyl esters were extracted in hexane (Lepage and Roy 1986), concentrated under nitrogen, and analysed by gas–liquid chromatography in a Hewlett-Packard 5790A gas chromatograph fitted with a Supelco SP-2330 capillary column and a flame ionization detector. The percent fatty acid concentration was determined with a Hewlett-Packard 3390A integrator (further details in Geiser et al. 1994). Lipid analyses were carried out within 2 months of tissue preparation.

Numeric values are expressed as mean±standard error. The effect of photoperiod on torpor occurrence was tested by a Fisher exact test, with probability representing the sums of the probabilities of the observed array plus the probabilities of all other arrays that are equal to or smaller than the observed array. One-way analysis of variance (ANOVA) was followed by linear planned comparisons (torpor bout duration) or Fisher's least significant difference (LSD) for post-hoc pairwise comparisons (fatty acid composition) to determine differences among mean values from different photoperiod treatment groups. Percentage values of fatty acids were arcsine-transformed before testing.

Results

The mean body mass of deer mice after 8 weeks of acclimation was indistinguishable (ANOVA $F_{2,21}=0.23$, $p=0.79$) among photoperiod groups at 17.8±1.2 g (short photoperiod, $n=7$), 18.2±0.6 g (equinox photoperiod, $n=10$), and 18.7±0.8 g (long photoperiod, $n=7$).

At $T_a=19$°C, expression of daily torpor in deer mice was affected by photoperiod. Torpor occurrence was 71% (5/7 individuals) in deer mice under short photoperiod, 70% (7/10 individuals) under equinox photoperiod, and 14% (1/7 individuals) under long photoperiod and differed significantly among photoperiod treatment groups (Fisher exact, $p<0.05$). At $T_a=17$°C, a similar trend was observed during measurements of $\dot{V}O_2$: Torpor occurred in 67% of deer mice (4/6 individuals) exposed to short photoperiod, in 60% (6/10 individuals) under equinox photoperiod, and in 50% (3/6) under long photoperiod. Photoperiod had a significant overall effect on torpor bout duration at $T_a=17$°C (ANOVA $F_{2,10}=4.22$, $p=0.047$), and linear contrasts confirmed the a priori prediction that torpor bout duration should be greatest under short photoperiod (9.3±2.6 h, $n=4$), intermediate under equinox photoperiod (5.1±0.3 h, $n=6$), and smallest under long photoperiod (3.7±0.6 h, $n=3$; $p<0.05$; Fig. 1).

Mean minimum $\dot{V}O_2$ of torpid individuals during the 23-h measurements at $T_a=17$°C (0.56±0.08 ml $g^{-1}h^{-1}$ under short photoperiod, 0.61±0.05 ml $g^{-1}h^{-1}$ under equinox photoperiod, and 0.55±0.13 ml $g^{-1}h^{-1}$ under long photoperiod) did not differ among photoperiod treatment groups (ANOVA $F_{2,10}=0.13$, $p=0.9$). Moreover, the minimum $\dot{V}O_2$ of all individuals, including those that did not enter torpor, did not differ among photoperiod groups (ANOVA $F_{2,19}=0.26$, $p=0.8$; short photoperiod 1.24±0.44 ml $g^{-1}h^{-1}$ $n=6$, equinox photoperiod 1.19±0.37 ml $g^{-1}h^{-1}$ $n=10$, long photoperiod 1.75±0.55 ml $g^{-1}h^{-1}$ $n=6$).

Photoperiod significantly affected the content of total lipid extracted from leg muscle of deer mice. In four measures of fatty acid composition, the following significant differences (ANOVA $F_{2,7}=4.8$, 5.2, 5.3, 5.3, 5.7, 7.9, 9.1, 9.2, and 26.0, $p<0.05$ in each case; Fig. 2) were observed: First, total polyunsaturated fatty acids (PUFA) were significantly more abundant in long photoperiod (45.81±0.99%) than in short photoperiod (33.63±3.05%; Fisher's LSD, $p<0.05$). Second, the sums of n3 and n6 fatty acids differed significantly among photoperiod treatment groups, but in opposite directions. The n3 fatty acids were most abundant in long

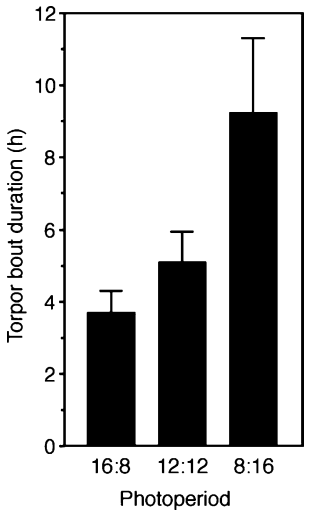

Fig. 1 Duration of torpor bouts (h) in deer mice under short (LD 8:16, $n=4$), equinox (LD 12:12, $n=6$), and long photoperiods (LD 16:8, $n=3$) was significantly affected by photoperiod

photoperiod (34.52±1.33%) and least abundant in short photoperiod (16.03±4.14%), whereas n6 fatty acids were most abundant in short photoperiod (17.77±1.08%) and least abundant in long photoperiod (11.30±0.34%; Fisher's LSD, $p<0.05$ in both cases). Third, the ratio of SFA and monounsaturated fatty acids (MUFA) was greater in long photoperiod (1.77±0.13) than in either equinox (0.87±0.24) or short photoperiod (0.87±0.12). Fourth, 6 of the 12 major fatty acids that constituted greater than 0.5% of the lipid sample differed significantly among photoperiod treatment groups. All fatty acids that differed overall among photoperiod groups also differed significantly between short and long photoperiod, and in some cases, also between long and equinox photoperiods (Fisher's LSD, $p<0.05$; Fig. 2).

Of the major fatty acids identified, the SFA myristic acid (14:0), the MUFA palmitoleic acid (16:1), and the essential fatty acids linoleic acid (18:2n6) and linolenic acid (18:3n3) were most abundant in the short photoperiod group and least abundant in deer mice held under long photoperiod; those under equinox photoperiod exhibited an intermediate abundance. Photoperiod had a significant effect in the expected direction on the sum of C16 and C18 UFA, which made up 54.04±5.04% (short photoperiod), 44.65±5.88% (equinox photoperiod), and 30.76±1.45% (long photoperiod) of total lipids (ANOVA $F_{2,7}=5.10$, $p=0.043$). Also consistent with expectation, the SFA stearic acid (18:0) was most abundant in deer mice under long photoperiod (14.24±0.96%), least abundant in those under short photoperiod (7.73±1.24%), and intermediate in those under equinox photoperiod (9.43±1.38%). Unexpectedly, however, the long-chain polyunsaturate docosahexaenoic acid (22:6n3) was most abundant (29.05±1.47%) in deer mice exposed to long photoperiod, least abundant in those on short photoperiod (12.68±3.61%), and intermediate in those under equinox photoperiod (16.75±3.57%).

In contrast to muscle, fatty acids of WAT were little affected by photoperiod, and significant differences (ANOVA $F_{2,9}=4.7$ and 6.1, $p<0.05$) were restricted to two fatty acids. Palmitoleic acid (16:1) was least abundant in short photoperiod (3.24±0.31%), most abundant in equinox photoperiod (5.48±0.74%), and intermediate in long photoperiod (4.81±0.32%). An overall significant effect of photoperiod was also found for the abundance of the unusual margaric acid (17:0) in WAT, for which means ranged between 0.5 and 0.6% in all groups.

Discussion

Our study provides the first evidence that photoperiod-induced functional changes in heterothermic mammals are accompanied by changes in the fatty acid composition of muscle tissue in the absence of differences in the composition of dietary lipids. It suggests that some of the differences in thermal physiology induced by photoperiod or season are linked to changes in the

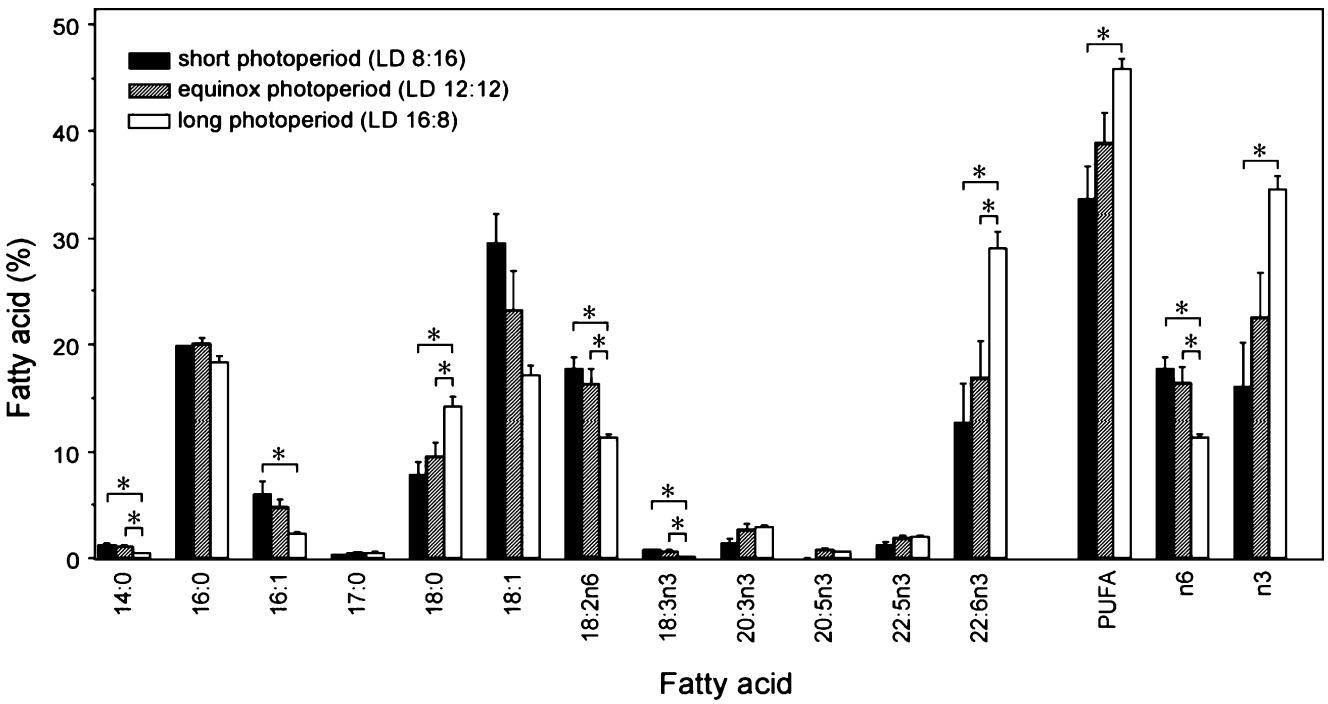

Fig. 2 Lipid composition of leg muscle for deer mice represented as percent composition of fatty acids representing at least 0.5% of total fatty acids and sums of PUFA, n3, and n6 fatty acids. All measures that showed overall effects of photoperiod (ANOVA, $p<0.05$) also showed a significant pairwise difference (Fisher's LSD, $p<0.05$, indicated by an *asterisk* above the *horizontal bar*) between short ($n=3$) and long photoperiods ($n=3$), and between equinox ($n=4$) and long photoperiods

composition of somatic fatty acids, unrelated to dietary selection.

Torpor was most frequent and pronounced in deer mice under short photoperiod, as has been observed in other members of the genus *Peromyscus* (Lynch et al. 1978). Functional differences of the animals measured here were most strongly expressed for torpor bout duration. Under short photoperiod, torpor bout duration was 2.5-fold longer than in deer mice under long photoperiod. The other difference among the photoperiod treatment groups was observed in the occurrence of torpor, which was greater in the short than long photoperiod groups and intermediate in the equinox group. Surprisingly, minimum $\dot{V}O_2$ did not differ among photoperiod groups, as would have been predicted from the findings of Geiser (1991). However, a similar lack of difference in torpor depth after differing photoperiodic exposure has been observed in other small mammals (Holloway and Geiser 1996; Lovegrove et al. 2001).

Functional changes in torpor occurrence and length were accompanied by changes in fatty acid composition. Whereas our study suggests that photoperiod could have affected tissue fatty acid composition directly, it is also possible that differences in torpor occurrence were responsible, and we cannot rule out the possibility that increased use of torpor stimulated the change in fatty acid composition. However, as we induced torpor only twice/individual, it is likely that acclimation to photoperiod was directly responsible for the compositional differences.

For leg muscle total lipids, about half of the detected major fatty acids exhibited significant differences among photoperiod groups. The response of WAT fatty acids to photoperiod was much less pronounced, with only two fatty acids showing significant differences. This suggests that changes in tissues due to photoperiod exposure may be related to tissue function. One possibility is that because WAT is an inactive tissue incapable of active movement, whereas muscle is a very active tissue capable of contraction, adjustment of fatty acid composition may be required for maintenance of some motility at low T_b during bouts of torpor, which in the short photoperiod group lasted for almost 40% of a day. Differences in tissue fatty acid composition in a diet experiment where deer mice were maintained on diets enriched with SFA and UFA were also more pronounced for muscle tissue than WAT (Geiser 1991). In that study, differences between deer mice on SAT vs UFA diets were observed for more fatty acids in muscle (85% of detected fatty acids) than in WAT (66% of detected fatty acids). However, the overall compositional differences among diet groups (Geiser 1991) were substantially bigger than those found among photoperiod groups in the present study.

A second possibility is that UFAs are important for muscle function or exercise in general, even in the absence of heterothermy. During migration, UFAs are typically more abundant than are SFAs in avian fat stores, and migratory birds given a choice of diets preferred a diet rich in oleic acid (18:1) over a diet rich in stearic acid (18:0) (reviewed in McWilliams et al. 2004). In the glycolytic muscles of rats, exercise results in a decrease in membrane phospholipids containing stearic acid (18:0) residues and an increase in phospholipids containing oleic (18:1) and linoleic acid (18:2) residues (Mitchell et al. 2004). In the phospholipids of skeletal muscle in hares, another group of extremely active vertebrates, Valencak et al. (2003) found the highest proportion of PUFA reported for any mammalian tissue. Interestingly, and consistent with the current and previous findings for deer mice, these authors also found that PUFA content was significantly higher during winter than during summer. Even for homeothermic mammals, tissue temperature in the extremities decreases at low T_a, such that thermal adjustments in tissue composition may be needed even in the absence of torpor (Valencak et al. 2003). The significant increase in preference for dietary UFAs by hamsters that do not exhibit torpor supports this interpretation (Hiebert et al. 2000, 2003b).

The fatty acid composition of total leg muscle lipid showed several interesting patterns among photoperiod treatment groups. Medium-chain (C16 and C18) UFA (including PUFA) increased in the short photoperiod group in comparison with the equinox and long photoperiod groups. These fatty acids have melting points in the range of −1 to −15°C. Importantly, C16 and C18 UFA add up to ~54% in the short photoperiod group, ~45% in the equinox photoperiod group, and only ~31% in the long photoperiod group. On the other hand, the SFA stearic acid (18:0), which has a melting point of +70°C, was almost twice as abundant in deer mice under long photoperiod than under short photoperiod. Whereas these observations are consistent with the notion that general homeoviscous adaptations may play an important role in enhancing torpor in short photoperiod, the significantly higher proportion of PUFA in the long photoperiod group, largely due to the large proportion of docosahexaenoic acid (22:6n3), suggests that it is individual fatty acids or groups of fatty acids, rather than an adjustment of membrane fluidity in general as suggested by Cossins and Wilkinson (1982), that are responsible for whole-animal functional differences. It has been shown previously that only small additions (5%) of C18 SFA, MUFA, and di-unsaturated fatty acids to the diet resulted in substantial differences in torpor physiology (Geiser et al. 1994). This suggests that it may be the large differences among C18 fatty acids of differing unsaturation (zero, one, two, and three double bonds) found in animal tissues in the photoperiod groups that may be responsible for the functional differences. It must also be remembered, however, that whereas homeoviscous adaptation is perhaps the most frequently invoked explanation for alterations in

tissue lipid composition in response to changes in temperature, optimal lipid composition for any set of environmental conditions and physiological states is likely to result from a complex interaction among factors including: (1) the effects of membrane lipids on membrane fluidity (Cossins and Wilkinson 1982), (2) the effects of membrane lipids on membrane leakiness and its consequences for metabolic heat production (Hulbert et al. 2005), (3) interactions between individual membrane proteins and their immediate lipid environment (Opekarová and Tanner 2003), and (4) a balance between the desirable effects of UFAs at low temperatures and the increased peroxidation risk associated with UFAs (Frank et al. 1998). Further study is necessary to ascertain the underlying functions of changes in tissue lipid composition.

How could the compositional differences due to photoperiod exposure be achieved? An increase in Δ9-desaturase activity in short photoperiod relative to long photoperiod could account for the simultaneous increase in oleic acid (18:1) and decrease in stearic acid (18:0) in leg muscle from deer mice in short photoperiod. The essential polyunsaturated C18 fatty acids (18:2 and 18:3) cannot be synthesized by mammals and, as the diet composition for all photoperiod groups was identical, these compositional differences cannot have been due to changes in endogenous desaturase activity. However, selective absorption in the gut is a further mechanism by which the composition of the somatic fatty acid pool might be altered (Olsen et al. 1998; Zhou and Nilsson 2001). In addition, fatty acyl composition is known to differ among tissues within the body and even among organelles within the same cell (Geiser 1990; Thompson 1992), indicating that mechanisms, possibly selective deposition and/or selective retention in muscle tissue, could supplement (in the case of Δ9-desaturases) or replace (in the case of the missing PUFA-synthesizing desaturases) the ability of endogenous desaturases to increase the UFA/SFA ratio. In nature, where multiple food sources are available, diet selection may facilitate further alterations in tissue lipid composition (Hiebert et al. 2000, 2003a,b). It is likely that these processes are in some way linked to the daily profile of melatonin production, as the duration of circulating melatonin increases during exposure to short photoperiods (Lynch et al. 1978; Hiebert et al. 2003a).

Our study suggests that exposure to short photoperiod in heterothermic mammals causes changes in whole animal thermoregulatory physiology (torpor occurrence and duration) as well as in tissue lipid composition. These compositional changes may be involved in seasonal functional adjustments, especially in high-latitude mammalian heterotherms, which employ photoperiod as a reliable cue for predicting seasonal changes in weather and food availability.

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