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The Djungarian hamsters (*Phodopus sungorus*) have been studied in several species of marmot rodents [9, 19]. Past studies have established that nest-building behavior is limited to males [18, 31] and that both genetic and environmental factors influence the expression of nest-building behavior [20-24]. Taken together, these studies strongly suggest that building ambient temperatures in small rodents at low body temperature at low ambient temperatures.

For species inhabiting a harsh environment, such as the Siberian steppe, reducing energy expenditure by enhancing thermoregulation, should be of particular adaptive value. In this study we investigate two thermoregulatory behaviors, nestling and burrowing, in Djungarian hamsters which have been exposed to different cold exposure conditions. First, we determine the effect of cold exposure on these characters. Second, we investigate the effects of photoperiod and melatonin treatment on these thermoregulatory behaviors. In this study we investigate two thermoregulatory behaviors, nestling and burrowing, in Djungarian hamsters which have been exposed to different cold exposure conditions. First, we determine the effect of cold exposure on these characters. Second, we investigate the effects of photoperiod and melatonin treatment on these thermoregulatory behaviors.

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Dzungarian hamster, *Phodopus sungorus*, inhabits the Sibe-
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temperatures (-40°C) during winter [7]. In order to cope
with low environmental temperatures, this species has high
thermogenic (2 water) and insulative capacities [14]. How-
ever, hamsters acclimated to winter conditions tolerate
much lower ambient temperatures (-68°C) than hamsters
acclimated to summer conditions (-25°C). This sea-
sonality in cold tolerance is primarily caused by day length,
since exposure to short day conditions (less than 13 hr of
light; [5, 17]) can induce the syndrome of physiological winter
adjustments which includes body weight loss, molt to the
winter pelts, torpor, increased thermogenic capacity and re-
duced weight [6, 10, 11, 16, 25, 29]. Similar, short
day, adjustments are induced under a long day photoperiod if
hamsters are treated with melatonin, a hormone of the pineal
gland which relays photoperiodic information [3, 4, 12, 13,
15, 16].

This photoperiod-mediated adaptive syndrome makes
Phodopus sungorus an ideal experimental animal for investi-
gations which emphasize seasonal acclimation and thermo-
regulatory adaptation. However, past research has stressed
the seasonal control and biochemical basis for metabolic
heat production [2, 10, 11, 13, 27, 28]. Our knowledge of
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on thermoregulatory behavior in Dungarian hamsters, *PHYSIOL BEHAV* 42(2) 173-177, 1988.—Nests were measured in hamsters acclimated to either long or short day photoperiod in thermoneutrality. Both nests built larger nests under short day photoperiod or at 10°C as compared to long day photoperiod. Hamsters build larger nests under short day photoperiod about 50% to a total increase in nest size from 1.8 g control/day (long day thermoneutral cues) to 2.7 g control/day (short day at 10°C). Burrowing activity was suppressed by both cold or (long day) thermoneutral viruses short day at 10°C. Burrowing activity requires both day and night activity.

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Photoperiod, Temperature and Melatonin Effects on Thermoregulatory Behavior in Djungarian Hamsters

used in these studies were bred and raised in our laboratory at room temperature (20–23°C) under a long day photoperiod (16 hr light:8 hr dark; lights on at 4.30 hr). The original breeding stock was obtained by Dr. B. Goldman (Worcester Foundation, Shrewsbury, MA). Hamsters were weaned at 21 days of age and group-housed by sex. Water and food (Wayne Lab Blox) were supplied ad lib and wood shavings were used as bedding material. Adult hamsters (older than 80 days) were singly housed prior to the experiment.

Nesting was measured (see specific methods in the Measurement of Nesting section) on a total of 81 hamsters (50 males, 31 females) under long day conditions. Twenty males from this group were transferred to 10°C and the nesting scores recorded for the first 4 days of cold exposure. Measurement of nesting behavior was repeated after 10, 20 and 35 days of cold exposure and after hamsters had been returned to room temperature at 40 days. Burrowing activity (see specific methods in the Measurement of Burrowing section) was measured in these hamsters prior to cold exposure and after 28 days in the cold.

Another twenty hamsters (10 females, 10 males) were treated with melatonin. Hamsters were given a daily IP injection of melatonin (25 µg in 0.1 ml of 1% ethanol in saline) at 16.30 hr (12 hr after lights on). This treatment has been shown to be effective at inducing 'short day' adjustments for physiological characters under long days [15]. At the same time, 17 control hamsters (8 females, 9 males) were injected with ethanolic saline alone. Nesting scores were taken after 2, 6, 9, 12, and 17 weeks of melatonin injections. Body weight and fur color (after 6) were recorded each week and testis length was measured by external palpation every other week. These measurements served as an index for physiological response to the melatonin treatment.

In a second study, sixty hamsters (21 females, 39 males) were transferred to a short day photoperiod (9 hr light:15 hr dark; lights on 8.00 hr). Body weight, fur color and testis length were recorded continuously in these hamsters and served as an index for their photoperiodic response. After at least 18 weeks of short day exposure nesting and burrowing activity was measured. Twenty male hamsters which had responded to the short day treatment were then transferred to the cold (10°C) and treated as the long day cold acclimated hamsters described above.

Measurement of Nesting

Hamsters were provided with a 30–40 g roll of cotton which was placed on top of the cage. The hamsters used this cotton immediately to build nests. After 24 hr these nests were removed and the remaining cotton weighed to determine the amount which was used for nest construction. This procedure was repeated for 5 consecutive days. Data for the first day were discarded to avoid the effects of a novel environment on the nesting score. Since no consistent difference in the nesting scores between days 2 and 5 were found, data were averaged across these days. A roll of cotton, placed next to the cage, served as a control to determine the effect of environmental factors such as humidity on cotton weight. If necessary, nest size was corrected according to the weight change in the control roll.

Measurement of Burrowing

To assess burrowing behavior a plastic chamber (30×30×30 cm) was filled with a mixture of two parts Premium brand sphagnum peat moss and one part of play sand.

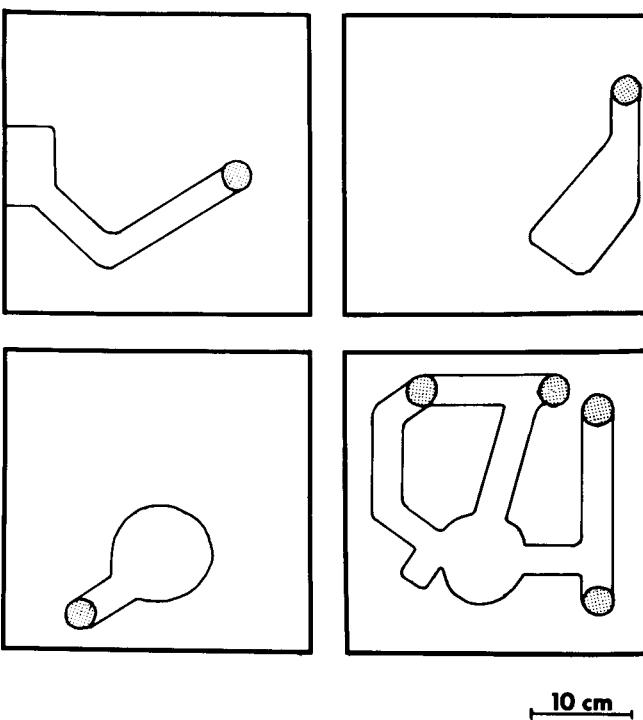


FIG. 1. Representative burrow systems of 4 hamsters kept at room temperature under long day conditions. Dimensions of the burrow system are given in cm, and a shaded area indicates a burrow entrance.

To make this peat moss-sand mixture workable, approximately 5 l of water was added. The mixture was then packed by hand to approximately two-thirds the height of the chamber. Three pieces of Lab Blox and a quarter of an apple were provided at the start of each test. An individual hamster was placed in a chamber at noon and removed 24 hr later. Burrows were excavated and sketches were made of each burrow system (Fig. 1). The following measures were taken: Number of surface holes, number of tunnel segments, number of chambers, average tunnel diameter, chamber dimensions, and total volume of the burrow system. Only horizontal distances were measured and consequently vertical holes without any horizontal extension were not taken as a burrow. At the end of each test the dirt was remixed and remoisturized.

Data Analysis

Data are expressed as means \pm SEM. Analysis of variance was performed to test for differences in continuously varying traits such as nesting. When a significant treatment effect was found, comparisons between means were made using the error term from the analysis of variance and the *t*-distribution. A chi-square test for independence was used to establish differences in the percentage of hamsters exhibiting burrowing activity.

RESULTS

Photoperiodic Effect

The nesting score for long day hamsters was 1.9 ± 0.1 g cotton per day for males and 1.4 ± 0.2 g cotton per day for females (Fig. 2). Hamsters exposed to short day conditions

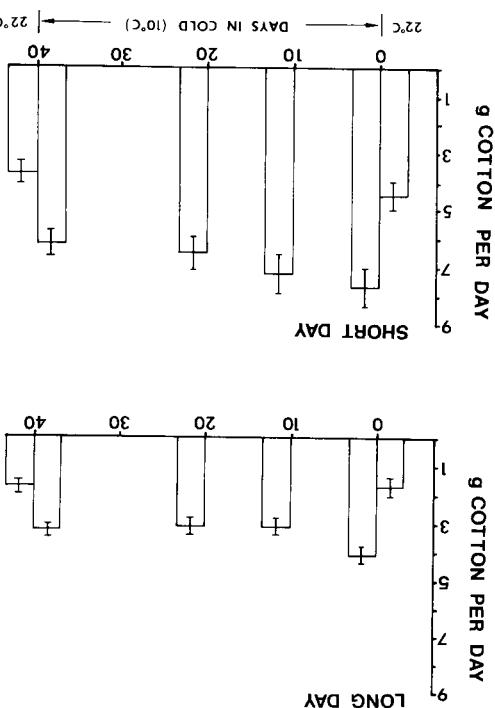
In contrast to hamsters which responded physiologically to Melatonin treatment, melatonin insensitive individuals and saline-injected controls did not build larger nests after 17 days per in this group.

Melatonin-injected hamsters were separated into two groups because 6 of the 20 hamsters did not exhibit weight loss, gonadal regression or molt following 8 weeks of melatonin injections. During this 8 week period these hamsters gained weight (from 38.9 ± 2.7 to 44.2 ± 3.5 g). The remaining melatonin-injected hamsters lost body weight during this period of time (from 37.3 ± 1.2 to 34.4 ± 1.4 g; $p < 0.05$). The male hamsters exhibited gonadal regression during this time (initial testis length was 12.5 ± 0.8 mm and after week 8 it was 9.7 ± 0.2 mm; $p < 0.01$). All but one of these hamsters molted to a winter pelts during the course of the 17 week study. Saline-injected hamsters gained weight over the first 8 weeks of the study (from 37.4 ± 1.3 to 42.1 ± 1.2 g; $p < 0.01$). No hamster exhibited gonadal regression or molted to the winter pelts in this group.

Effect of Melatonin Injections

test was significant ($F(1,24) = 5.2$, $p < 0.05$). There was a significant difference between the initial nesting scores at 10°C ($p < 0.05$) for long day and short day hamsters ($p < 0.02$). When hamsters were re-exposed to cold burrowing activity to 65% ($p < 0.05$), hamsters from long day also showed a significant increase in their nesting scores ($F(1,24) = 5.2$, $p < 0.05$). The mean nesting scores at 10°C were significantly lower than those built before cold acclimation. Cold exposure reduced burrowing activity in long day hamsters from 85% to 65% ($p < 0.05$). Short day hamsters also tended to dig less after cold exposure (20% after cold exposure versus 33% in thermoneutral, $p = n.s.$). No change in the size or shape of the burrow system due to cold acclimation was found.

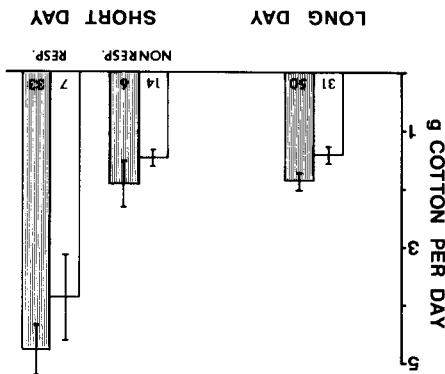
FIG. 3. Effect of cold exposure on nest-building behavior. Ladd day at 22°C and week short day (lower panel) male hamsters were kept at 22°C and were then transferred to 10°C for 40 days. They were then returned to 22°C.



Hamsfors built significantly larger nests when transferred from thermoneutrality to 10°C (long day from 1.81 ± 0.3 to 4.1 ± 0.3 ; short day from 4.5 ± 0.5 to 7.7 ± 0.7 , $p < 0.001$) for both groups. This increase was more pronounced in short day than in long day hamsfors ($p < 0.05$). These high initial nestling scores declined during the course of cold acclimation in both groups. While long day hamsfors reached a lower level after 10 days of cold exposure and maintained this level throughout the experiment, the nestling score of short day hamsfors continued to decline during the whole period of the experiment.

Cold Acculturation

Fig. 2. Photoperiodic control of nest-building behavior. Male (striped bars) and female (clear bars) hamsters were either kept under a long day photoperiod (LD16:8) or a short day photoperiod (LD9:15). Hamsters which did not exhibit weight loss, gonadal regression and molt to the winter pelts after 18 weeks of LD9:15 exposure were defined as 'nonresponders'. Sample size is given within each bar.



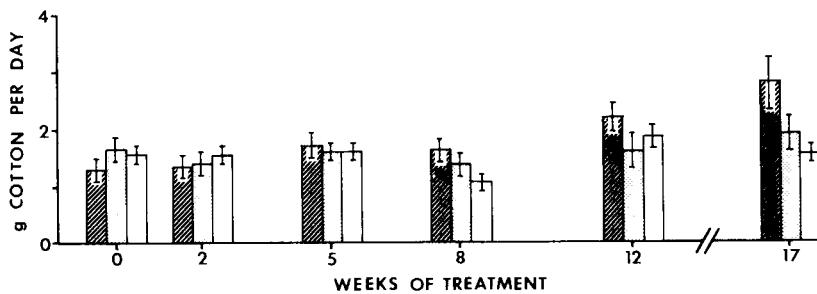


FIG. 4. Effect of daily afternoon melatonin injections (25 µg IP) on nest-building behavior. Striped bars represent hamsters which exhibited melatonin-induced weight loss, gonadal regression and molt to the winter pelt. The stippled bars represent hamsters which were insensitive to melatonin for these characters. Clear bars represent saline-injected controls.

weeks of treatment (increase in nest size relative to initial scores: responsive = 1.49 ± 0.44 g, $p < 0.01$; nonresponsive = 0.03 ± 0.22 g, $p = \text{n.s.}$; saline = 0.03 ± 0.16 g, $p = \text{n.s.}$). This increase in nest size was not a continuous process, but started between 8 and 12 weeks of injections (increase in nest size: $p < 0.01$; week 0 versus week 12).

DISCUSSION

In *Phodopus sungorus* physiological adjustments in thermoregulation, such as fur insulation, basal metabolism and capacity for nonshivering thermogenesis, are controlled by both photoperiod and ambient temperature [11,14]. In this species acute cold exposure also elicits an immediate increase in nest size (Fig. 3). However, during the course of cold acclimation nest size decreases, which indicates that a subsequent increase in thermogenesis or decrease in heat loss might reduce the need for large nests. Behavioral thermoregulation and metabolic heat production are additive with regard to cold tolerance, and 2–3 weeks of cold exposure induces enhanced thermogenesis [2,27]. Photoperiodic control of nesting behavior is evident as well (Fig. 2). At both test temperatures, short day hamsters consistently built larger nests than long day hamsters. The combined action of photoperiod and cold exposure caused an increase in nest size from 1.8 to 7.7 g (long day at 22°C versus short day at 10°C). Fifty-four percent of this increase can be attributed to the effect of photoperiod, while 46% is an adaptive response to temperature. Similar contributions of photoperiod and temperature have been reported for the seasonal control of nonshivering thermogenesis [14]. Hamsters which were physiologically insensitive to the short day conditions also lacked an increase in nesting. These data on short day-insensitive hamsters further demonstrate that nest size is not a function of night length *per se*. Nests are not larger under short day conditions because the period of activity is longer for nocturnal rodents under short day conditions. Nesting behavior should be viewed as closely associated with the adaptive syndrome of seasonal photoperiodism.

Physiological short day adjustment is mediated by the pineal hormone melatonin [2, 4, 12, 13, 15, 16]. The data demonstrate that melatonin injections, which were effective at inducing weight loss, gonadal regression and a molt, also increased nesting scores. Hamsters which did not respond to melatonin with decreased body weight, etc., also built small nests (Fig. 4). These data further support the close association between behavioral and physiological thermoregulatory

adjustments.

As in the house mouse [21], we found that male hamsters build larger nests than females. In the house mouse this sex difference may be related to the social organization of the species. Due to the pronounced aggressiveness between male mice, they do not use huddling behavior to the same extent as females [1] to combat cold. Males must therefore rely more on nest building to combat cold. In the Djungarian hamster a different social structure exists. Laboratory studies indicate that this species lives in groups consisting only of the parents and their offspring [26], and not in large social groups as in the house mouse. A biological explanation for the sex difference in nesting behavior in Djungarian hamsters remains unclear.

Burrowing activity is also controlled by day length and ambient temperature. However, the thermoregulatory significance of burrowing behavior is less clear, since both environmental cues for winter conditions (short day photoperiod and cold) reduce burrowing activity. From these data it appears that burrowing activity may be depressed during winter. However, depressed burrowing activity during winter could be advantageous. By overwintering in the last burrow dug in summer, a hamster avoids the energetic expenditure necessary to dig in frozen soil. Short day or cold exposure might not only affect the degree of burrowing activity, estimated in this study by the percentage of hamsters digging a burrow, but might also affect the shape, complexity or depth of the burrow system. However, changes in such characters are difficult to determine in captivity since space available for a burrow system is usually restricted. Data from the literature however, suggest that these characteristics are not affected by ambient temperature or photoperiodic conditions in *P. sungorus*. No differences between summer and winter burrows are known for Djungarian hamsters in its natural habitat [7], although related species of dwarf hamster living in a similar habitat build a more complex burrow system during winter [7].

Data concerning the social behavior of *Phodopus sungorus* agree with our finding that burrowing activity is higher under long day than under short day conditions. Adult Djungarian hamsters leave the burrow system after their offspring are reproductively competent and dig a new burrow for the next litter [26], which suggests that burrowing activity may be associated with breeding. Given these data we conclude burrowing activity is probably more closely related to reproductive needs than to thermoregulation.

REFERENCES

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