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Author(s): St. Steinlechner, G. Heldmaier, H. Becker

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The seasonal cycle of body weight in the Djungarian hamster: photoperiodic control and the influence of starvation and melatonin

St. Steinlechner, G. Heldmaier, and H. Becker

Department of Biology, Philipps-University, D-3550 Marburg, Federal Republic of Germany

Summary. Photoperiod is the primary environmental cue for seasonality in the Djungarian hamster (*Phodopus sungorus*). This species reduces its body weight by 30% during winter to reduce its energy requirements. The aim of this study was (1) to examine the influence of food intake on the body weight cycle and (2) to evaluate the role of photoperiod and melatonin in determining this seasonal cycle.

While body weight increased slightly (7%) from August through December in long photoperiod, it dropped significantly (32%) in the natural photoperiod group and food intake gradually decreased in this group by about 20%. After two periods of 40% food restriction, the hamsters in long photoperiod rapidly returned to their initial body weight. In contrast, hamsters under natural photoperiod only gained weight until they had reached the body weight of the controls at that particular time.

In a second experiment, hamsters were kept under natural photoperiod throughout the year. At 6 different intervals two groups of hamsters were implanted with melatonin capsules and transferred to either short (LD 8:16) or long photoperiod (LD 16:8). The results show that the seasonal change in body weight is caused by a combined action of photoperiod and a change in the animals' sensitivity towards photoperiod and melatonin.

Introduction

Many small mammals of the temperate zones and higher latitudes show seasonal cycles in body weight. The Djungarian hamster, in particular, exhibits rather exaggerate seasonal changes in body weight with a maximum of about 45 g in summer and a minimum near 25 g during winter (Figala et al. 1973; Hoffmann 1973, 1979). In a previous study (Heldmaier and Steinlechner 1981) we could demonstrate the energetic advantages of a reduced body weight during winter.

Seasonal rhythms are either induced by exogenous, environmental signals or they are generated by endogenous oscillators with a period of approximately one year, requiring environmental zeitgeber to entrain these circannual rhythms with the change of seasons. In many hibernators seasonality seems to be established by such circannual rhythms (for reviews see Mrosowsky 1977, Gwinner 1981), whereas in most non-hibernating mammals environmental cues like

temperature, food availability or photoperiod are necessary to sustain seasonality. The Djungarian hamster belongs to the latter group. A true endogenous circannual rhythm seems to be lacking in this species (Hoffmann 1979) but it exhibits marked annual cycles in a number of parameters like testicular weight, fur colouration, thermoregulatory capacities and body weight (Figala et al. 1973; Hoffmann 1973, 1979; Heldmaier and Steinlechner 1981a, b; Heldmaier et al. 1982). All these parameters change in parallel or in a very close phase relationship throughout the year and appear to be controlled primarily by the photoperiod, although temperature can accentuate the photoperiodic effects, e.g. with respect to thermogenic capacities or fur colouration.

Photoperiodic effects are believed to be transduced by the pineal gland and one of its compounds, melatonin, by converting the neuronal signals of light perception into endocrine signals. In order to examine more closely the effects of photoperiod and to analyse the significance of the pineal hormone melatonin for photoperiodic control of the seasonal body weight cycle, Djungarian hamsters were exposed to long and short photoperiods and treated with melatonin at different times of the year. In further experiments we tried to evaluate the nature of weight regulation during seasonal reduction of body weight. In order to demonstrate whether seasonal changes in body weight are based on a continually changing set point for weight regulation, or whether they can be anticipated by starvation, we tested the influence of photoperiod and of food restriction on the body weight during late summer and fall. Do the animals need less food because they are smaller, or does the animals' body weight decrease because they eat less? Any reduction of food consumption during the winter should be of great advantage for survival of both the individual and the population.

Materials and methods

Djungarian hamsters, *Phodopus sungorus sungorus*, were bred and raised in an air-conditioned room ($23 \pm 1.5^\circ \text{C}$) under natural, seasonally changing photoperiod (Frankfurt $50^\circ 08'$ northern latitude). At the age of two months the animals were separated into single cages and kept individually during all experimental treatments. Woodshavings served as bedding material except for animals in experiment I. Food (Altromin 7010, hamster breeding pellets, supplemented weekly with fresh apples) and water were available *ad libitum*, unless otherwise stated.

Experiment I

On August 1st, 32 hamsters were divided into four groups of eight animals, each group having a mean body weight of 40 to 42 g. All groups remained in natural photoperiod until September 8; thereafter two of the groups were transferred to artificial long photoperiod (LD 16:8). Each hamster was weighed to the nearest 0.1 g every other day from August through December. Twice during this period (starting Aug 27 and Oct 18) two groups of hamsters were allowed only 60% of the amount of food consumed by the control groups. This food restriction caused a marked reduction in body weight without the disadvantages of permanent starvation. During these periods of food restriction (10 and 16 days respectively) water was available *ad libitum*. One hamster (long photoperiod group) died on the last day of the second food restriction (Nov 3) although food was still available. One control hamster of the natural photoperiod group continuously gained weight until December and was therefore not included in the calculations of mean body weights. During these experiments hamsters were kept on wire mesh grids to allow separation of food and feces. To estimate food consumption, a weighed amount of food was placed in each cage and 48 h later remaining pellets and crumbs were reweighed.

Experiment II

At six times throughout the year adult hamsters of both sexes were transferred to artificial long photoperiod (LD 16:8) or short photoperiod (LD 8:16) with the same T_a (23°C) for a period of eight weeks. In each group 9 hamsters were left untreated and 9 were implanted with two silastic capsules containing crystalline melatonin. The implants were prepared according to Turek et al. (1975) and implanted subcutaneously through a small skin incision on the back. Each animal was weighed weekly to the nearest 0.1 g.

Statistics

All data are expressed as means \pm 1 standard error of the mean ($\bar{x} \pm 1$ SEM). Comparisons between means were made using analysis of variance or paired t-test where appropriate.

Results

Experiment I

The results of this experiment are illustrated in Fig. 1. During the first week in naturally decreasing photoperiod both control groups have a constant body weight of 41 to 42 g. Thereafter in both groups a trend for decreasing body weight is apparent which becomes fully evident in the natural photoperiod group by the end of the experiment in December. In contrast to this decrease, hamsters are slowly gaining weight after exposure to long photoperiod; reaching a mean of 44 g upon termination of the experiment. Food restriction caused exponential reductions in body weights of both groups. After the period of food restriction the long photoperiod group quickly returned to the initial body weight whereas the natural photoperiod group only regained weight up to the body weight of its control group and subsequently reduced the body weight parallel to the

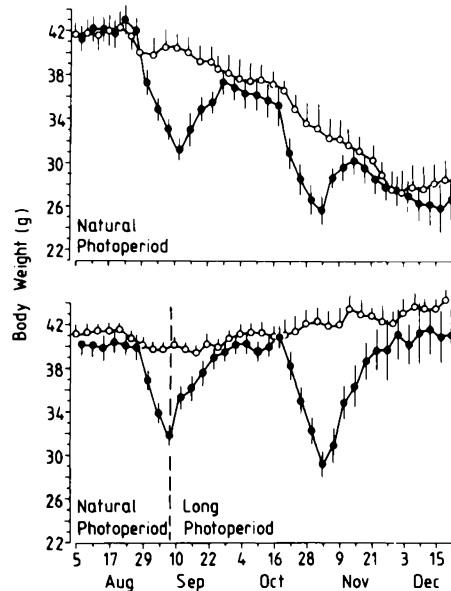


Fig. 1. Body weight of *Phodopus* living either in natural photoperiod (upper panel) or in long photoperiod (starting Nov 6; lower panel). Animals were weighed every other day; however, for ease of visualization only every other weighing is illustrated (means \pm SEM). \circ — \circ control groups, \bullet — \bullet subjected twice to 40% food restriction for 10 or 16 days

control group in natural photoperiod. At the beginning of this experiment the food consumption per animal was about 3.5 g/day in all groups. In the natural photoperiod group it continually dropped to a minimum of 2.8 g/day by the end of December, but it increased to about 4 g/day in the long photoperiod group ($P < 0.01$, long photoperiod vs natural photoperiod).

Experiment II

The control animals living in natural photoperiod showed a clear annual cycle in body weight with about 28 g in winter and a maximum of about 45 g in summer (Fig. 2). If the hamsters are exposed to long photoperiod in fall and winter they react with an immediate increase of their low body weights (35 g and 28 g, respectively) up to summer values (40 g and 42 g, respectively). The increase in body weight during spring is not different in slope from the increase occurring in natural photoperiod at this time of year. Exposure to constant long photoperiod during summer has no effects on the high body weights of *Phodopus*. In late summer (Aug 21) the initial mean body weight of the experimental groups was lower than the mean body weight of control hamsters at this time of year (37 g vs. 41 g, see Fig. 2). This was due to a higher proportion of young animals and females (which are about 3 g lighter than males, Figala et al. 1973). Nevertheless, the hamsters in long photoperiod retained their body weight which was not significantly lower than the body weights of hamsters living in long photoperiods at other times of the year. Thus, the consequence of exposure to long photoperiod is the same throughout the year: Two months after exposure to long photoperiod all hamsters have high body weights comparable to the values of control animals during summer (Fig. 2a). On the other hand, the consequence of exposure to short photoperiod is different at each time of the year:

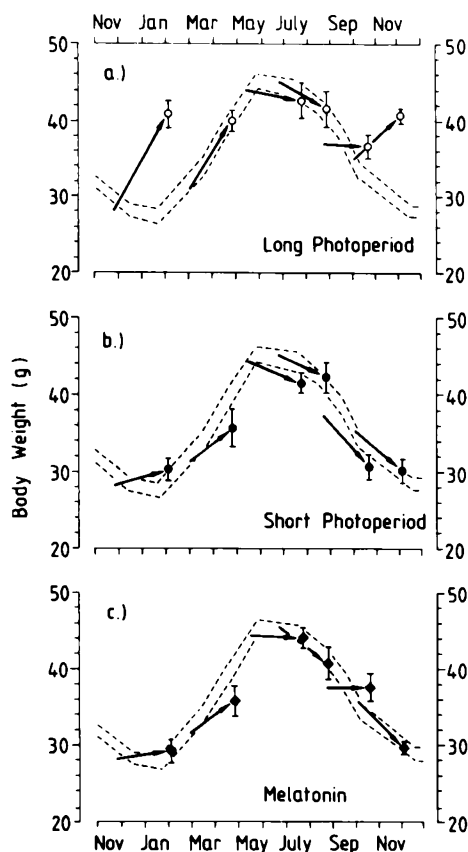


Fig. 2a-c. Influence of exposure to a long photoperiod, b short photoperiod, or c implantation of melatonin on the body weight of *Phodopus* at different times of the year. Start and duration of the single experiments are indicated by arrows. The area enclosed between the two broken lines represents the mean body weight \pm 1 SEM of a control group living in natural photoperiod throughout the year ($n=9$)

During late summer and fall short photoperiod causes a drop in body weight and during winter the body weight is fixed at the low level by short photoperiod. During spring an increase in body weight is to be observed despite exposure to short photoperiod and in summer short photoperiods do not have any influence on the high summer weights (Fig. 2b). Very similar results are obtained by implantation of melatonin regardless whether the animals are exposed to long or short photoperiods after implantation. Only in late summer chronic melatonin implantation does not mimic short photoperiod but rather prevents the action of short photoperiod (Fig. 2c).

Discussion

The cold and long lasting winters in higher latitudes require special adaptations of an animals' thermoregulatory system. For a small mammal living in such a harsh environment it is essential to economize on the energy required for both reproduction and thermoregulation. By reducing in fall the high energy demands needed during spring and summer for reproduction, the animal can cope with the high energy demands required for thermoregulation during winter. In previous studies (Heldmaier and Steinlechner 1981; Heldmaier et al. 1982) we described the improvements of thermogenic capacities and thermal insulation in

Phodopus and discussed the thermoregulatory advantages of a reduced body weight. The disadvantage of an increased heat loss due to an increased relative surface area of a smaller body is compensated in *Phodopus* by an improved thermal insulation. In spite of the energetically more efficient thermoregulatory system of winter acclimatized *Phodopus* as compared to summer acclimatized hamsters, we have to bear in mind that the season of increased energy requirements for thermoregulation coincides with times when food availability is reduced and accessibility of food is hindered by snow cover and a frozen ground. The root vole (*Microtus oeconomus*) depends heavily on the 1st-year rhizomes of *Eriophorum angustifolium* for food and the winter minimum body weight of the vole correlates with the availability of rhizomes. Tast (1972), therefore, suggests that the vole's body weight is primarily dependent on food supply. However, Iverson and Turner (1974) showed in a thorough field study of *Microtus pennsylvanicus* that in this species significant weight losses occurred during August through October when food was apparently near maximum and weight gains began in early spring when food supplies should have been near minimum. This agrees well with our findings in *Phodopus* where body weight started to decrease in late August despite the fact that food was available ad libitum. A reduction of body weight during fall and winter has also been described in a number of other small mammals (Mezhzherin 1964; Fuller et al. 1969; Rigaudiere 1969; Hyvärinen and Heikura 1971; Wunder et al. 1977; Stebbins 1978). One proposed explanation for this phenomenon is a reduction of total energy requirements during winter, since there is a considerable decrease in the amount of food needed with the reduction of body weight of the animals (Mezhzherin 1964). This assumption can be confirmed by our present study. The hamsters living in natural photoperiod decreased their body weight by 13.3 g (-32%) and reduced their food consumption at the same time by 20%. Relative food consumption (g food consumed/g body weight) per day increased from 0.084 to 0.102. Thus, reduction in body weight enables relative food requirements to be increased (which is necessary for the increased metabolic rate of *Phodopus* during winter), without increasing its food requirements in absolute values.

The weight loss of *Phodopus* during fall is primarily triggered by the decreasing photoperiod. A surplus of food cannot prevent or even diminish this drop in body weight; nor is the rate and amplitude of weight loss affected by ambient temperature (Heldmaier and Steinlechner 1981). On the other hand, exposure to long photoperiod can interrupt the weight loss at any stage and induce a weight gain until the high body weight of summer animals is reached (Hoffmann 1973, 1979; this study). Exposure to short photoperiod does not accelerate the rate of weight loss (see Fig. 2b) showing that both short photoperiod and natural photoperiod in fall are equivalent signals once a critical photoperiod is reached. The critical photoperiod, i.e. the photoperiod dividing long day from short day responses, is roughly 13 hrs light/day in *Phodopus* (Hoffmann 1981). This corresponds to the photoperiod in mid-August, the same time when body weight starts to decrease.

The decrease of body weight however, is not a simple on-off reaction induced by the critical photoperiod but rather a continuous transition from high to low body weight in the sense of a sliding set-point (Mrosovsky and Fisher 1969). The weight loss can be accelerated by food restriction

but it is compensated by increased food intake after resumption of *ad libitum* feeding. This increase again is dependent on the photoperiod. The hamsters always "know" the proper body weight for the corresponding time spent at transition from long to short photoperiod and control their food intake accordingly. However, the question whether the hamsters eat less because they become smaller, or whether they become smaller because they eat less cannot be answered by our data. The onset of body weight decrease was too variable between individuals and the temporal span between measurements of body weight and food consumption was too long to allow differentiation of cause and consequence.

Besides the decrease in food intake a number of other factors like increased motor activity, higher body temperature, or decreased feeding efficiency can cause a decrease in body weight. Melnyk and Boshes (1980) showed that a cycle of feeding efficiency is responsible for the weight gain phase of the body weight cycle in the dormouse. The exact mechanism of how the hamsters know their proper body weight is still unknown, but our data clearly show that the photoperiod is the primary environmental cue to inform the animals about the time of year. This seems reasonable since the photoperiod is the most noise-free and therefore most reliable signal for the change of seasons. It allows the animals to adapt well in advance of unfavorable weather conditions. A large number of experiments have demonstrated that the pineal gland is essential in conveying the photoperiodic information (for reviews see Hoffmann 1981, Reiter 1981). In our experiments, implantation of melatonin in fall and winter mimicked the action of short photoperiod showing that melatonin is indeed an important humoral factor of the pineal gland and involved in transduction of the photoperiodic message.

The weight gain during spring seems to be based on an endogenous component of the annual cycle. Neither short photoperiod nor melatonin can prevent this spontaneous regrowth, but it can be advanced and accelerated by long photoperiod (Hoffmann 1973, this study). Since the regrowth in spring goes parallel with the recrudescence of the testes (Hoffmann 1973) it was argued that the increase in testosterone level might be responsible for the increase in body weight. However, Hoffmann (1978) has shown that even in castrated hamsters there is a spontaneous increase in body weight during spring and a decrease of body weight after exposure to short photoperiod, although the amplitude of body weight changes is diminished. Thus, androgens seem to exert an amplifying influence on the seasonal body weight cycle by means of their anabolic effects, but they are not a prerequisite for the annual cycle.

After the high body weight is regained in late spring a prolonged exposure to long photoperiods is necessary to render the animals sensitive towards the effects of short photoperiod or melatonin. A similar refractoriness has been described for the thermoregulatory system of *Phodopus* (Steinlechner and Heldmaier 1982) and for the gonadal system of the golden hamster (Reiter 1972). Stetson et al. (1977) showed in the golden hamster that 11 weeks of long photoperiod are necessary to terminate photorefractoriness. The mechanism by which hamsters measure the duration of long photoperiod exposure is based on a circadian cycle of photosensitivity (Stetson et al. 1976). The refractoriness for melatonin seems to last longer since in late summer (Aug 21), at a time when the hamsters are already sensitive

for short photoperiod, melatonin does not induce a decrease in body weight. The puzzling fact that melatonin can either mimic or interfere with short photoperiod may be due to the mode of melatonin application. Melatonin is synthesized and released by the pineal gland mainly during the night, resulting in a well defined day/night rhythm of the melatonin level. Thus the continuous release of melatonin from implants may not exactly reflect the physiological conditions. This is supported by the finding that after implantation the hamsters are unable to discriminate between either long or short photoperiod, suggesting that this exogenous melatonin interfered with the naturally occurring level of this indole. Nevertheless, it is quite obvious that the pineal gland and melatonin are important for conveying the photoperiodic message for seasonal adaptation. The further pathway of information transmission leading finally to a change in body weight is still unknown. However, all seasonally changing functions of *Phodopus* investigated to date are linked in a very close phase relationship, indicating the prevalence of a single photoperiodic master switch. These interconnections make it more plausible that melatonin acts on a higher integrative center, such as the hypothalamus, rather than at the peripheral organ level.

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