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Effect of transfer from 4° to 0° C during midwinter on hibernation in the garden dormouse, Eliomys quercinus L.

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Garden dormice hibernating in constant and undisturbed conditions at a T_A of 4° C were exposed for 37—47 days in midwinter to 0°C. The animals were kept in darkness without food and water. The difference between the T_B and T_A was maximally 1° C during deep hibernation. At 0° C arousals were more frequent and the animals lost more weight during the whole season as compared with those hibernating constantly at 4° C. The breathing periods of periodic respiration grew longer, but not all animals had shorter apnoeic periods.

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I. Introduction

A previous paper (Pajunen 1974) on overwintering in the French garden dormouse described body temperature, heart rate, the periodic respiratory pattern, weight loss and periodicity of hibernation at a T_A of 4° C. Now, results of transference from 4° to 0° C in midwinter of the same hibernation season are presented.

II. Material and techniques

Experiments were made with six French garden dormice (2 ♀♀ and 4 ♂♂), several being the same individuals as in an experiment of the same season (Pajunen 1974). The animals were first transferred from room temperature to 4° C towards the end of October 1969. Then, during a normothermic period in midwinter (8.—13.I.), the animals were further transferred from 4° to 0.2 (± 0.5)° C. After 37—47 days at 0° C the animals were transferred back to 4° when some of the animals were in the active state and others hibernating. At 4° C they hibernated until transferred back to room temperature during April. The experimental conditions and handling of the hibernating animals were as described previously (Pajunen 1970, 1974, 1976a & b).

The sawdust technique was used for determining the durations of the hibernation periods. The depth of hypothermia was controlled by continuous subcutaneous temperature measurements. Heart rate was recorded with chronically implanted skin electrodes. The periodic respiratory pattern was recorded kymographically or/and measured from heart rate recordings. For a detailed description of techniques see Pajunen (1970, 1974).

III. Results

During deep hibernation the anterior body temperature (T_B) was maximally 1° C higher than the T_A. Fig. 1 shows mean values, standard errors of the means and standard deviations of the hibernation periods calculated at 10-day intervals throughout the hibernation season (cf. Pajunen 1974). The three means beginning from 17 January are for exposure to 0° C, the two following means include periods which were terminated at 4° C, because the transference back to 4° C did not induce arousal in the hibernating animals. The terms hibernation period and hibernation season are used as before (see Pajunen 1974).

The exposure to 0° C in midwinter led to more frequent arousals than constantly at 4°. There seemed to be no difference between the sexes. The mean weight loss during the whole winter was 48 % in intact animals; the animals with thermocouples and skin electrodes lost more than 50 %.

The mean durations of the apnoeic periods had a wide range, 7—74 min, and showed clear

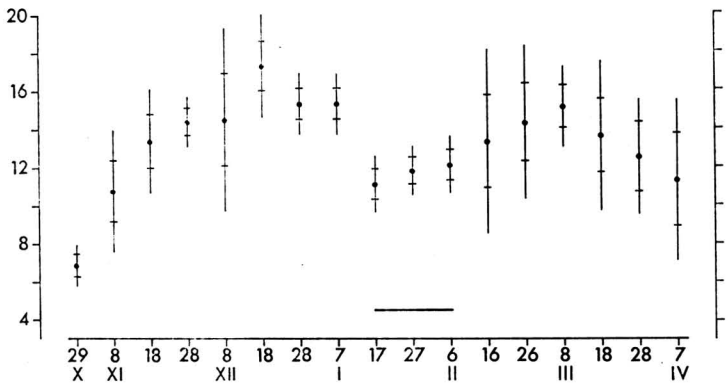

Fig. 1. Changes in the mean length of the hibernation periods at 10-day intervals, expressed as mean values (in days) of periods at that moment unfinished, starting from 29 October. The means at 0° C are indicated by a line above the abscissa. The standard errors of the means are marked off with short horizontal lines on the vertical lines denoting standard deviations.

individual variation (Table 1). Three of the five animals had shorter apnoeas at 0° C than constantly at 4°. Records for three of these animals in the beginning of the hibernation season at 4° C are given in a previous paper (Pajunen 1974). In the duration of the breathing periods, 4.9—7.7 min, individual differences were not so great. Breathing periods tended to be longer at 0° than at 4° C. Very short periods of apnoea were often recorded just before spontaneous arousal and also irregularly between phases of longer apnoeas in the course of a single hibernation period.

Table 1. The mean durations of the breathing and apnoeic periods (min) with standard errors of the means ($s_{\bar{x}}$) and standard deviations (s).

Animal	Beginning date (Febr.) & length of record (days)		Breathing period Mean	$s_{\bar{x}}$	s	Apnoea Mean	$s_{\bar{x}}$	s
♀ 3	3	0.6	6.0	0.1	0.6	25.8	1.7	8.2
	4	0.2	5.2	0.1	0.5	7.5	0.6	2.9
	4	1.0	5.6	0.1	0.6	21.4	0.8	5.6
	5	0.3	5.0	0.1	0.4	12.9	0.9	4.2
♀ 21	7	1.9	7.3	0.2	1.1	72.3	3.8	22.3
♂ 12	6	0.5	5.9	0.1	0.4	20.4	0.8	3.9
	7	0.4	4.9	0.1	0.6	7.0	0.5	3.4
♂ 19	10	0.3	6.6	0.1	0.5	25.8	2.8	9.7
	11	0.9	6.5	0.1	0.4	26.2	2.2	13.6
	13	0.1	6.8	0.2	0.7	12.2	1.3	4.9
	18	1.3	7.4	0.1	0.5	36.2	1.7	10.8
	19	1.8	7.7	0.1	1.0	22.3	0.7	6.4
	21	0.4	7.1	0.2	1.0	11.8	0.9	5.0
	22	0.5	7.4	0.2	0.9	12.5	1.2	6.6
♂ 20	12	0.8	7.0	0.2	0.8	66.6	4.4	15.8
	13	0.3	7.1	0.5	1.0	74.1	4.0	8.0

Heart rate was recorded in two animals only. In one animal (♂ 20) the values ranged between 6—13 times/min during apnoea and 5—9 x/min during breathing periods, and in the other (♂ 19) 7—20 x/min during apnoea and 8—23 x/min during breathing periods. The values for the latter animal seemed to be higher at 0° than at 4° C; changes were also detected in its breathing rhythm. The former animal had apnoeas corresponding to those recorded in the other animals at 4° C.

IV. Discussion

Pajunen (1976b) suggested that 4° C is near the optimal T_A (or T_A range) for hibernation in the garden dormouse, i.e. the total energy loss (including arousals) is minimal. In the present study the 5- to 7- week exposure to 0° C in mid-winter led to more frequent arousals. When transferred back to 4° C hibernation periods again had lengths typical of animals kept constantly at 4° C (Pajunen 1974). The animals of the present study also seemed to lose more weight (48.0 %) than those kept constantly at 4° C (43.4 %). In all, hibernation seemed to be less economical at 0° C, but the results indicate that the animals would be able to survive a longer exposure to 0° C than the present.

In nature, garden dormice may occasionally be exposed to severe frost when hibernating in unprotected places, e.g. to —25° C, as measured by Bussy (1972) near Lyons in France. The animals may then leave their unprotected winter quarters.

In the literature, data concerning the total

maintenance energy required during the whole hibernation season at low T_As are scanty. Moreover, the results are difficult to interpret, because controls at other T_As are lacking.

The results of Kristoffersson & Soivio (1964) and Soivio et al. (1968) indicate the same trends as were seen in the garden dormice in the present study. These authors studied the effect of lowering T_A from 4° to — 5 °C in the hedgehog, *Erinaceus europaeus*. At —5° C hibernation periods were significantly shorter, the subcutaneous T_B fell to 0.3—0.9° C (Soivio et al. 1968), the heart rate and metabolic rate accelerated, and respiration changed from Cheyne-Stokes rhythm at 4° to continuous respiration. Twente & Twente (1970) studied the effect of a corresponding lowering in T_A on the golden-mantled ground squirrel, *Citellus lateralis*, but the animals died. However, they tolerated a lowering first to +2° and then further to —2° C. Luecke & South (1972) lowered the T_A from 5° to 0.5° C in the yellow-bellied marmot, *Marmota flaviventris*. They proposed that the normothermic regulatory responses are actively inhibited during low-temperature hibernation and further hypothesized that this inhibition fails near freezing when heat-producing responses are reactivated as shown, for example, by the occurrence of peaks with elevated heart rates. According to Erikson (1956) and Lyman (1963), very low T_A often kills the animal or awakens it. In the study of Popovic & Popovic (1956) *Citellus citellus* hibernated at 0.5°, but at T_As below —0.5° C most of the animals died. The preceding studies show that differences exist between different species; garden dormice have tolerated exposure to —2° C (Pajunen, unpublished).

As hibernation periods are shorter at higher T_As, they might also be expected to be shorter near the lower average temperature limit for hibernation, as the results of the present study in garden dormice are suggested to show in this species. At a T_A of 2.5° garden dormice still hibernated for long periods (Pajunen, unpublished), but 0° C had a clear shortening effect. Twente & Twente (1965) have shown that at T_As ranging from 2 to 25° C the log of the length of the hibernation periods in *Citellus lateralis* is a function of T_B. The results of Pengelley & Fisher (1961) in *C. lateralis* at 0° C are broadly in agreement with those of Twente & Twente (1965). Thus, in this species a T_A of 0° is not low enough to shorten the hibernation periods.

Scott & Fisher (1970, 1976) obtained inconsistent results on exposing *Glis glis* to 0° C. First they found this T_A to be critically low for hibernation in this animal, and later they recorded hibernation periods of maximally 40 days in length, confirming the observations of Pengelley & Fisher (1961). The periods were long as compared with those recorded in garden dormice. Scott & Fisher (1976), however, were suspicious of the reliability of the sawdust technique in *Glis glis*, because the animals possibly moved so little during the normothermic periods that arousal was not detected. In garden dormice this technique can be considered safe; the reliability of the technique was tested with simultaneous continuous T_B measurements (1970, 1974, the present study).

The garden dormouse can be considered a good hibernator at 0° C, with hibernation periods averaging 11—12 days in the present study and a gradient of maximally 1° C between the T_B and T_A during deep hibernation. An example of a poor hibernator is the eastern chipmunk, *Tamias striatus*, in which Neuman (1967) observed torpid periods of less than 24 h at T_As of 0—22° C and of some days at T_As near zero (Panuska 1959, Wang & Hudson 1971, Scott & Fisher 1972). *Tamias striatus* and *Eliomys quercinus* differ in their ability to regulate the T_B to the level of the T_A; in *Tamias striatus* the gradient was several degrees during torpid periods (Neuman 1967, Wang & Hudson 1971). Only above a T_A of 15° C were T_Bs close to the T_A (Neuman 1967).

Few records exist on breathing or heart rate at very low T_As. In the hedgehog Kristoffersson & Soivio (1964) and Soivio et al. (1968) recorded the change from the Cheyne-Stokes rhythm at 4° to continuous respiration at — 5° C. In the present study breathing periods lasted longer in all animals at 0° C, and in some animals apnoeas were shorter.

Kristoffersson & Soivio (1964) and Soivio et al. (1968) recorded an acceleration of the heart rate and of the metabolic rate at —5° as compared with the values at 4° C. According to Lyman (1963, 1965), the hibernator increases its metabolic rate below 5° or 3° C and the heart rate increases also. In the present study the heart rate of one animal accelerated, and that of the other remained at the same level as at 4° C. Periodic respiration is the most reliable indicator of undisturbed deep hibernation (Pajunen 1974)

and heart rate does not seem to react as quickly to changes in T_A.

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