

Seasonal differences in O₂ consumption and respiratory quotient in a hibernator (*Erinaceus europaeus* L.)¹

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O₂ consumption was measured in normothermic hedgehogs during the summer season and in hypothermic hedgehogs during the hibernation season.

O₂ consumption was lower in August than in May and June and decreased further at the approach of the hibernation season. The results suggest that O₂ consumption in normothermic hedgehogs is closely related to the area of the body surface. In all normothermic groups a significant negative correlation was observed between BW (body weight) and O₂ consumption calculated per unit of BW. There was a positive correlation (significant in October) between log BW and log total O₂ consumption. In hibernation hypothermia the dependence on the area of body surface disappeared, and instead O₂ consumption was dependent on body weight. The O₂ consumption of hypothermic hedgehogs was lower (10.6 ml/kg/h) in January and February than in April (14.8 ml/kg/h). The RQ (respiratory quotient), 0.7, in hibernation hypothermia indicated that the source of energy was fat. The differences between hibernation hypothermia in winter and induced hypothermia in August were suggestive.

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1. Introduction

Many regard hibernation as a manifestation of a primitive state of thermoregulation, which occurs only in a few genetically conservative lineages (EISENTRAUT 1956, KAYSER 1961). The view has also been presented that hibernation is not a manifestation of primitive thermoregulation, but an adaptive response to environmental stress which has occurred independently in several evolutionary lines (BLIGH 1973).

Hibernators maintain high, constant body temperatures during the active phase of their annual cycles, but during the hibernation season they undergo repeated bouts (periods) of hibernation hypothermia, during which the body temperature is only a little higher than the low ambient temperature. When the am-

bient temperature falls below 0°C the hibernator will respond with increased heat production, which may result in full arousal. Because of the spontaneous periodic arousals hibernation is not perfect as an energy conserving mechanism (TÄHTI & SOIVIO 1977).

KAYSER (1961) found that hibernators differ from other mammals in the correlations of body weight and metabolic rate. This observation is based on interspecific comparisons.

The purpose of the present study was to determine if there are annual differences in O₂ consumption and in the respiratory quotient in the hedgehog during the (homeothermic) summer season and the (heterothermic) hibernation season. Whether O₂ consumption during hypothermia induced in August differs from that measured during hibernation hypothermia (in winter) was also tested.

A further purpose was to find out whether differences in the correlations between body weight and O₂ consumption could be observed in different phases within a species.

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2. Material and methods

A. Material

The hedgehogs (*Erinaceus europaeus* L.) were caught in southern Finland. Their subsequent handling was dependent on their physiological status and the season of the year.

Animals caught between May and July ($n = 42$) were kept in separate cages in an animal room with natural daylight and a temperature of $+20$ – 22 °C. They were given fresh herrings and milk daily at about 11.00. Water was available ad libitum. These normothermic animals were studied in May–June and August.

The animals caught in September ($n = 36$) were kept in separate cages in an animal room with natural daylight and the temperature regulated so that the minimum temperature was $+12$ °C. They were transferred to a dark thermostatic room ($+4.2 \pm 0.5$ °C) at the beginning of November. They were given nothing to eat or drink during the hibernation season. These animals were studied in their normothermic state just before the hibernation season was started and then during the hibernation season.

Test groups

Group 1. Animals normothermic in May–June (26.V – 14.VI.1969). This group comprised 15 hedgehogs (8 ♂ and 7 ♀). In both males and females the body weights (BW) ranged from 400 to 1000 g. The animals had been caught at least one week before the experiments, which were conducted at $T_A +25$ – 26 °C.

Group 2. Animals normothermic in early August (3. – 14.VIII.1969). 14 animals (7 ♂ and 7 ♀) were studied. The BWs ranged from 600 to 1000 g in males and from 400 to 900 g in females. The experiments were conducted at $T_A +25$ – 26 °C.

Group 3. Animals normothermic in October and November (27.X – 2.XI.1969). The group comprised 22 animals with BWs ranging from 350 to 1100 g in males and 540 to 1140 g in females. Sixteen animals (8 ♂ and 8 ♀) were studied at the same T_A ($+25$ – 26 °C) as in groups 1 and 2. Six animals (3 ♂ and 3 ♀) were studied at an T_A of $+15$ °C.

Group 4. Animals hypothermic in January and February (20.I – 15.II.1967). These 12 animals (7 ♂ and 5 ♀) had BWs ranging from 272 to 890 g. Copper constantan thermoelements were implanted under the skin of the neck region before the hibernation season (KRISTOFFERSSON & SOIVIO 1964), and T_A was monitored continuously with a laboratory recorder. Thus the periodicity of hibernation was followed.

Group 5. Animals hypothermic in April (11.IV – 22.IV.1967). These 9 animals (4 ♂ and 5 ♀) had BWs ranging from 325 to 505 g. The periodicity was followed with the sawdust technique (JOHNSON 1931).

Group 6. German hedgehogs hypothermic in March (5. – 15.III.1967). These 3 animals (2 ♂ and 1 ♀) from the material of KRISTOFFERSSON & SOIVIO (1967) had BWs ranging from 530 to 780 g. The periodicity was followed as in group 4.

Group 7. Animals hypothermic in August (15. – 30.VIII.1969). The 6 animals (3 ♂ and 3 ♀) had BWs ranging from 442 to 780 g. They were studied at $T_A +4.2 \pm 0.5$ °C. The animals had access to water but not to food. They became hypothermic in 1–3 days in the cold room. The sawdust technique showed that the hypothermic periods varied in length from 1 to 6 days. The hedgehogs had been caught during June and July.

B. Methods

Measurements in normothermic hedgehogs

O₂ consumption and CO₂ production were measured in an open system. The respiration chamber (plexiglass, vol. 5 l) was placed in a thermostatically controlled refrigerator ($+25$ – 26 °C). The air (50 l/h) was introduced into the chamber with a diaphragm pump and the flow was measured with a rotameter. Before entering the respiration chamber the air passed through spiral copper tubes, reaching the temperature of the refrigerator. The outflow was conducted through drying tubes. The O₂ concentrations were measured with a paramagnetic O₂ analyser (Beckman E₂) and with a Scholander micro-gas analyser (SCHOLANDER 1947). The CO₂ was analysed with the Scholander micro-gas analyser. Before the experiments the animals were fasted for 20 h. They were placed in the respiration chamber 2 h before the experiments. The O₂ consumption and CO₂ production were measured at 15-min intervals during 1–2 h. Only values measured when the animals were resting were accepted. The experiments were performed between 12.00 and 16.00. The CO₂ concentration in the chamber air did not exceed 1 %. The temperature of the chamber was registered with copper constantan thermoelements and a multipoint laboratory recorder.

The respiratory rate (RR) was determined visually by observing the fluctuations of the air flow in the rotameter. Groups 1–3 were studied in this way.

Measurements in hypothermic hedgehogs

O₂ consumption and CO₂ production were measured in a closed system. The hedgehog in hibernation hypothermia was transferred to the respiration chamber at the beginning of the hibernation period. After transfer the animal was left in the (uncovered) chamber until the following day, when the experiment was begun.

Samples for analysis were taken 20 h after the chamber was closed. Before sampling, the air in the respiration chamber was mixed with an electrically driven stirrer. Air was then withdrawn into an airtight syringe and the sample was analysed immediately with a Scholander micro-gas analyser. The total volume of the air was measured by filling the respiration chamber with water. The volumes were corrected for STPD conditions. The respiratory movements of an animal in the closed chamber were recorded either kymographically (TÄHTI 1975) or with a copper constantan thermocouple placed before the animal's nose and an electronic laboratory recorder (TÄHTI & SOIVIO 1977). The duration of apnoeas and the number of respiration periods were observed.

Statistics

To test the significances of differences, Student's *t* test and analysis of variance were used. To test the validity of the "surface law", correlations were calculated between log BW and log O_2 consumption (ml/h) (ULTSCH 1973).

3. Results

A. O_2 consumption, respiratory quotient (RQ) and respiratory rate (RR) in summer and autumn at $T_A +25-26^\circ\text{C}$

O_2 consumption (ml/kg/h) was lower in August than in May and June ($P < 0.02$, Table 1, Fig. 1). The values measured were significantly lower just before the hibernation season than in early summer ($P < 0.01$) or in August ($P < 0.02$).

The RQ was significantly greater in August than in May and June ($P < 0.01$). The RQ just before the hibernation season did not differ significantly from the RQs measured in May and June or in August.

The RR was significantly greater in October than in August. The sex differences (Fig. 1) were not statistically significant ($0.5 > P > 0.05$). To test the validity of the surface law correlations were calculated between log BW and log O_2 consumption (ml/h) (Table 3). In June and August the positive correlation obtained was not significant ($P < 0.1$). In October this correlation (Fig. 3) was highly significant ($P < 0.001$). The exponent of BW (*b*) in the correlation equation $O_2 \text{ ml/h} = a \times BW^b$ was 0.37,

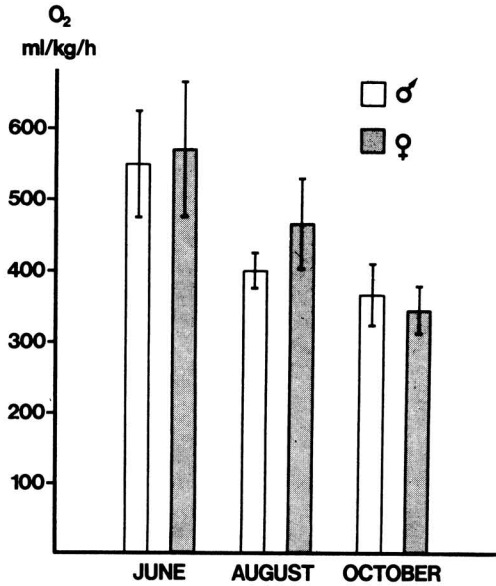


Fig. 1. O_2 consumption in normothermic hedgehogs in summer and autumn. The differences between males and females are not statistically significant.

which is lower than the value 0.75 in non-hibernating homeotherms. The result suggests that O_2 consumption in hedgehogs is highly dependent on the area of body surface.

In all normothermic groups a significant negative correlation was observed between BW and O_2 consumption calculated per unit of BW ($O_2 \text{ ml/kg/h}$) (Fig. 2, Table 3), indicating that the O_2 consumption in a small animal is much more rapid than in a large animal.

Table 1. The O_2 consumption, respiratory quotient (RQ) and respiratory rate (RR, resp./min) of normothermic hedgehogs in summer and autumn at $T_A +25-26^\circ\text{C}$ and autumn at $T_A +15^\circ\text{C}$. Values are means with SEMs and numbers of animals in parentheses.

	June +25–26°C	<i>P</i>	August +25–26°C	<i>P</i>	October +25–26°C	<i>P</i>	October +15°C
$O_2 \text{ ml/h}$	341 ± 15 (15)	<0.01	285 ± 19 (14)	<0.01	252 ± 8 (16)	<0.001	564 ± 30 (16)
$O_2 \text{ ml/kg/h}$	557 ± 42 (15)	<0.02	433 ± 104 (14)	<0.02	357 ± 74 (16)	<0.05	736 ± 54 (6)
RQ	0.82 ± 0.01 (8)	<0.01	0.94 ± 0.03 (13)	NS	0.84 ± 0.08 (8)	<0.05	0.94 ± 0.02 (2)
RR	24 ± 1.7 (14)	NS	22 ± 1.1 (13)	<0.01	26 ± 0.8 (15)	<0.001	45 ± 4 (6)

June – October: $O_2 \text{ ml/h}$ $P < 0.001$, $O_2 \text{ ml/kg/h}$ $P < 0.001$, RQ NS, RR NS.

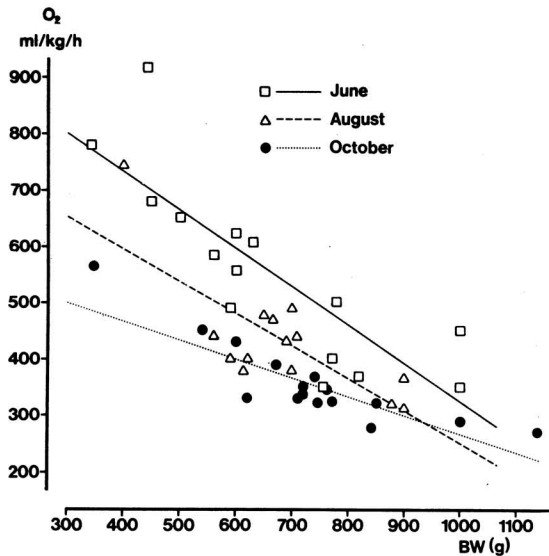


Fig. 2. Regression lines showing the negative correlations between body weight and O_2 consumption (ml/kg/h) in normothermic hedgehogs in summer and autumn.

B. O_2 consumption, RQ and RR in autumn at $T_A +15^\circ\text{C}$ (Table 1)

In October O_2 consumption and RR were much higher at $T_A +15^\circ\text{C}$ than at $T_A +25$ – 26°C , and even higher than those at the latter temperature in May–June and in August. The RQ (measured from two animals) was higher at $T_A +15^\circ\text{C}$ than at $T_A +25$ – 26°C . Thus the thermoregulatory ability is still functional just before the onset of the hibernation season.

C. The O_2 consumption, RQ and RR of hypothermic hedgehogs during the hibernation season (Table 2)

O_2 consumption, RQ and RR in the middle of the hibernation season (January and February) were compared with these values measured in April at the same T_A . The O_2 consumption (10.6 ml/kg/h) was lower in January and February ($P < 0.01$) than in April (14.8 ml/kg/h). The O_2 consumption during one respiration period (7.0 ml/kg/RP) was not significantly ($P < 0.3$) greater in April than in January (5.2 ml/kg/RP). Apnoeic periods had a mean duration of 58 min in January and February and 65 min in April. The mean RQ, 0.72 in both groups, indicates that during hibernation the main source of energy is fat. There was a significant positive correlation between log BW and log O_2 consumption (ml/h) ($r = 0.76$, $P < 0.01$) (Fig. 3). The exponent of BW (b) in the correlation equation $O_2 \text{ ml/h} = a \times BW^b$ was 1.00. This indicates that O_2 consumption is dependent on BW and not on body surface in these intra-specific comparisons.

D. O_2 consumption, RQ and RR in three German hedgehogs (Table 2)

The experiments were conducted in early March. The O_2 consumption (8.6 ml/kg/h) was lower than in Finnish hedgehogs in January and February. The O_2 consumption during one respiration period (9.0 ml/kg/RP) was greater

Table 2. O_2 consumption, respiratory quotient (RQ) and duration of apnoea AD, in minutes in hedgehogs in hypothermia during the hibernation season and in hypothermia induced in August. Values are means with SEMs. Numbers of animals in parentheses. RP=respiratory period.

	Finnish hedgehogs January February	<i>P</i>	April	August	German hedgehogs March
O_2 ml/h	5.2 ± 0.6 (12)	< 0.01	6.3 ± 0.7 (9)	9.3 ± 0.9 (6)	6.1 ± 1.4 (3)
O_2 ml/kg/h	10.6 ± 0.5 (12)	< 0.01	14.8 ± 1.4 (9)	16.4 ± 1.1 (6)	8.6 ± 1.2 (3)
O_2 ml/kg/RP	5.2 ± 0.02 (9)	NS	7.0 ± 0.8 (9)	7.3 (2)	9.0 ± 2.5 (3)
RQ	0.72 ± 0.02 (8)	NS	0.72 ± 0.01 (7)	0.78 ± 0.04 (3)	0.73 ± 0.03 (3)
AD min	58 ± 6 (9)	NS	66 ± 4 (9)	47 (2)	87 ± 5 (3)

Table 3. A: Correlations between log BW (body weight, kg) and log O₂ consumption (ml/h). — B: Correlations between BW and O₂ consumption (ml/kg/h.) — r = correlation coefficient, b = the slope of the regression curve, a = the Y intercept.

	A) $\log O_2 \text{ (ml/h)} = \log a + b \times \log BW$ (or $O_2 \text{ ml/h} = a \times BW^b$)				B) $O_2 \text{ ml/kg/h} = a - b \times BW$			
	a	b	r	P	a	b	r	P
Normothermic								
June	113	0.17	0.41	NS	1004	-0.68	-0.83	<0.001
August	195	0.18	0.31	NS	829	-0.58	-0.77	<0.001
October	23	0.37	0.80	<0.001	603	-0.33	-0.86	<0.001
Hypothermic								
in winter	12	1.00	0.76	<0.01				
in August	45	0.84	0.68	NS				

than in Finnish hedgehogs (5.2 ml/kg/RP). The apnoeic period was correspondingly longer. The mean RQ, 0.73, again indicates fat metabolism.

E. The O₂ consumption, RQ and RR in induced hypothermia in August (Table 2)

In this state O₂ consumption was faster (16.4 ml/kg/h) than in spontaneous hypothermia during the hibernation season, but the difference was only suggestive ($P < 0.10$). The RQ was greater than during the hibernation season, but not significantly so ($P < 0.10$). There was a positive correlation ($r = 0.68$, $P < 0.1$), but not significant, between log BW and log O₂ ml/h. Periodic respiration was observed in all animals. Apnoeas recorded for two animals lasted 30–60 min.

4. Discussion

The O₂ consumption of hedgehogs was measured in June, August and October at the same ambient temperature of +25–26 °C. This temperature is regarded as the lower limit of the thermoneutral zone (+25–30 °C) for normothermic hedgehogs (HILDWEIN & MALAN 1970).

There were marked seasonal differences in O₂ consumption between normothermic animals. Their O₂ consumption was high in June; it decreased significantly before the onset of hibernation in October—November, and the trend could already be discerned in August.

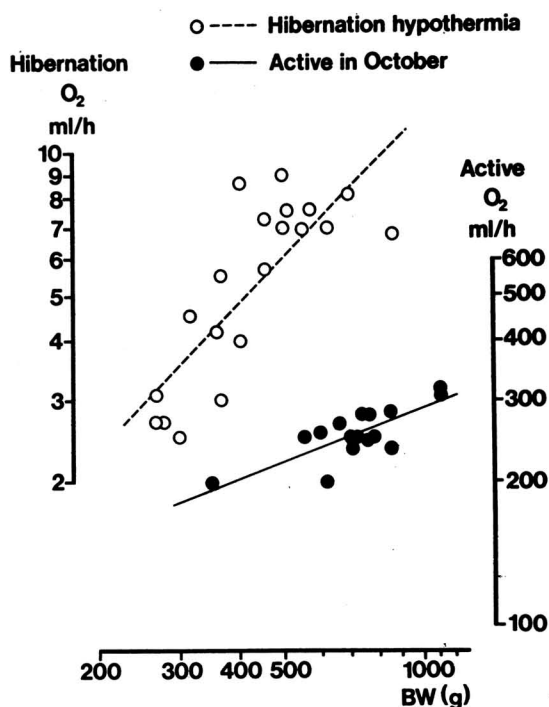


Fig. 3. Regression lines showing the positive correlations between log body weight and log O₂ consumption (ml/h) in hibernation hypothermia and in normothermic (active) hedgehogs in October.

In hedgehogs body weight starts to increase in August (KRISTOFFERSSON & SOIVIO 1964). The low O₂ consumption and high RQ indicate that fat deposits are being laid down. The mating season starts almost immediately after hibernation and ends during the first half of July (SAURE 1969). The early ending of the breeding

season (compared with other mammals) suggests that hibernation will succeed only after adequate preparation. The activity of the thyroid gland decreases at midsummer and reaches a minimum in autumn before the onset of hibernation (SUOMALAINEN 1964). This inactivation of the thyroid gland correlates very well with the present results for O_2 consumption. A similar decrease in metabolic rate before the hibernation season occurs in the ground squirrel (*Citellus citellus*) and the marmot (*Marmota flaviventris*) (HOCK 1969).

The lack of significant positive correlations between $\log BW$ and $\log O_2$ ml/h and the very significant negative correlations between BW and O_2 ml/kg/h may be due to different amounts of inactive adipose tissue in small and large animals in June and August. The weight differences may be caused by the adipose tissue. The age differences (not known) may also have influenced the results. However, these results indicate that body size has a marked effect on the intensity of metabolism in hedgehogs during summer season. This dependence on body size seems to be greater than in mammals which do not hibernate. In the present study, the exponent for BW in the correlation equation O_2 (ml/h) = $a + BW^b$ was 0.37 just before the hibernation season, which is lower than the exponent (0.62) found by KAYSER (1961) for hibernators in interspecific comparisons, or the value (0.75) estimated for other mammals by KLEIBER (1947).

Intraspecific studies on the correlations between body weight and metabolic rate in hibernators have not been presented previously. The size differences may be too small to give good correlations between $\log BW$ and $\log O_2$ ml/h. According to the "surface law", a small animal has a higher metabolic rate per unit of weight than a large animal, but the present study showed that in hibernation hypothermia this law does not hold good. The exponent (b) in the correlation equation was then 1.00. KAYSER (1961) obtained the same result in interspecific comparisons.

The O_2 consumption (10.6 ml/kg/h) in hedgehogs in hibernation hypothermia at $T_A +4.2 \pm 0.5$ °C was about 1/50 of the O_2 consumption in normothermic animals at T_A

+25–26 °C just before hibernation. It was about 1/100 of the O_2 consumption in active hedgehogs after periodic arousal during hibernation at $T_A +4.2 \pm 0.5$ °C, and only 1/200 of the peak O_2 consumption during spontaneous periodic arousals (TÄHTI & SOIVIO 1977). The O_2 consumption during hypothermia is dependent on the T_A . In hedgehogs hibernating at $T_A -5.0$ °C, the O_2 consumption was much greater, 277 ± 14 ml/kg/h (SOIVIO *et al.* 1968).

Towards the end of the hibernation season the O_2 consumption increased. At this period hibernating hedgehogs lose weight at an increasing rate (KRISTOFFERSSON & SUOMALAINEN 1964). The increase in O_2 consumption fits in with the observations that sexual activation starts during the hibernation season (SAURE 1969). The mating period starts immediately after the terminal awakening.

German hedgehogs lose less weight during hibernation (mainly because of less frequent arousals) than do Finnish hedgehogs (KRISTOFFERSSON & SOIVIO 1967). In the present study their O_2 consumption during hibernation hypothermia was also slower than in the Finnish hedgehogs. The O_2 consumption during one respiration period was higher in the German hedgehogs, because they had longer apnoeas (80–95 min vs. 60 min).

The RQ (0.7) in hibernation hypothermia indicates fat metabolism, as in many other hibernating mammals (Kayser 1961). The proportion of saturated fatty acids in depot fat decreases during the hibernation season (LAUKOLA & SUOMALAINEN 1971).

The seasonal differences in O_2 consumption and RQ found in the present study confirm that the ability to hibernate is a precisely controlled metabolic adaptation, and hibernation can be considered as a derived and highly adaptive physiological condition.

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