Torpor in the European white-toothed shrews

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Summary. 4 species of European white-toothed shrews enter torpor with extremely low metabolic rate. Newborn shrews (*Crocidura russula*) react as homeotherms during their first week before they develop the ability of torpor.

It has been shown by Vogel[2] that white-toothed shrews (Crocidurinae) are characterized by an unexpectedly low metabolic rate compared with the red-toothed shrews (Soricinae). He related this difference to their evolution in geographic isolation. However, most data on metabolism come from studies of African species. I report here results of experiments with European white-toothed shrews, which show the adaptive character of an extremely low metabolic rate (torpor) to climatic conditions.

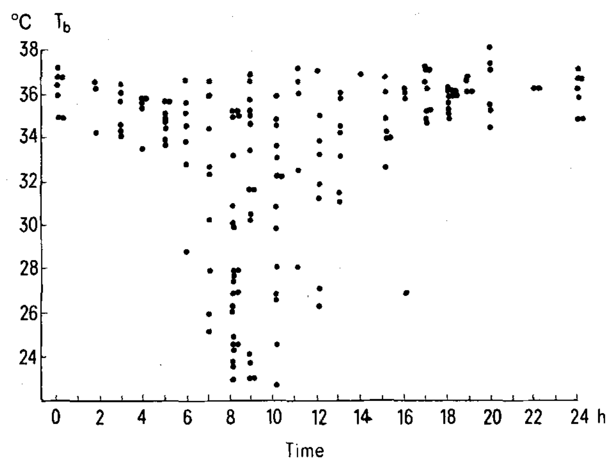

Fig. 1. Alteration in body temperature of 4 *Crocidura russula* during 24 h (T_a 22 °C), each point represents one rectal measurement.

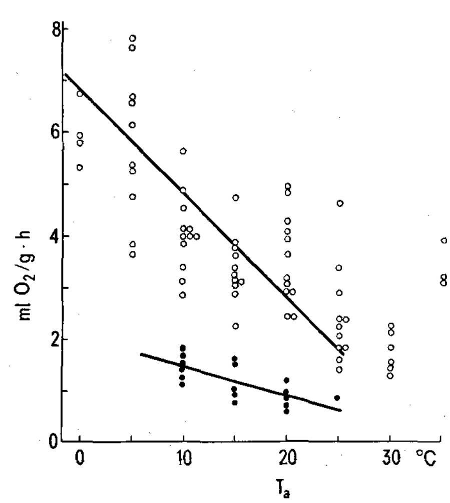

Fig. 2. O_2-consumption (*Crocidura russula*) at different T_a. The relation between oxygen consumption and T_a below the lower critical temperature are: Nontorpid shrews $Y = -0.20\,T_a + 6.9$ (ml O_2/g · h °C) and torpid shrews $Y = -0.06\,T_a + 2.1$ (ml O_2/g · h °C). The open circles are values of shrews which are awake, the closed circles are values of torpid shrews.

Materials and methods. The European species *Crocidura russula*, *Crocidura leucodon*, *Crocidura suaveolens* and *Suncus etruscus* were kept under seminatural conditions in our laboratory [natural light-dark cycle and ambient temperature (T_a), 22 °C]. The shrews were completely tame and could be handled well for measuring rectal temperature (T_b) with a thermistor, which was inserted about 18 mm into the rectum. With the young of *Crocidura russula* and with the adults of *Suncus etruscus*, only T_b was measured on the neck. Oxygen consumption was measured in periods lasting from 2 h to 2 days using a Beckman Analyzer G2. All values were calculated to STPD[3]; no correction was made with respect to CO_2-production. To measure the metabolic rate, the shrews were acclimated to 22 °C for at least 4 weeks. All experiments with young animals lasted 30 min at T_a 30 °C and 20 °C. The young of each of 3 litters were put together in a metabolism chamber (glass tube, 100 cm³). During a period of 4 weeks, the daily food consumption (mealworms) was reduced step by step to 20% of b.wt in *Crocidura russula* and *C. leucodon*, to 40% in *C. suaveolens* and to 100% in *Suncus etruscus*.

1 This work was undertaken with the aid of the Deutsche Forschungsgemeinschaft and Prof. Dr E. Kulzer.

2 P. Vogel, Acta Theriol. *21*, 13, 195 (1976).

3 F. Depocas, J. S. Hart and O. Heroux, J. appl. Physiol. *10*, 388 (1957).

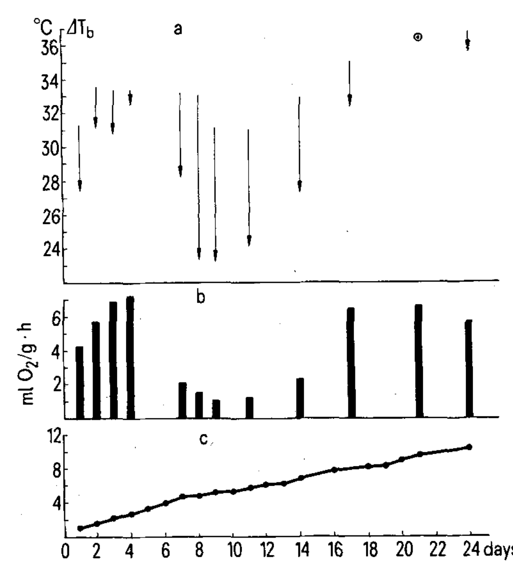

Fig. 3. Development of temperature regulation in one litter (4 pups) of *Crocidura russula* (T_a 20 °C). *a* ΔT_b between the beginning and the end of each experiment. The arrow points in the direction of the alteration. On the 21st day $\Delta T_b = 0$. *b* Oxygen consumption during the last 15 min of each experiment. *c* Average b.wt of the shrews. The hair grew from the 7th to the 16th day to the adult length.

Comparative data on O_2-consumption and temperature regulation (minimal thermal conductance) in the 4 species of white-toothed shrews

	n	B.wt (g)	Average O_2-consumption at T_a 20 °C (ml O_2/g · h)		Minimal thermal conductance T_a 0–25 °C (ml O_2/g · h °C)	
			Awake	Torpid	Awake	Torpid
C. russula	18	13.7	3.50	0.88	0.20	0.06
C. leucodon	7	12.0	4.23	0.70	0.20	0.08
C. suaveolens	6	7.5	5.03	1.61	0.37	0.10
Suncus etruscus	2	2.4	10.58	3.58	0.59	0.29

Minimal thermal conductance corresponds to the slope of the line representing O_2-consumption at different T_a (0–25 °C). Thermal conductance in awake shrews is considerably greater than in torporous shrews.

Results. The body temperatures in shrews which were resting but awake usually varied between 34° and 38 °C. However, early in the morning, in all species, T_b was often almost as low as T_a (figure 1). In this case the shrews entered into torpor and were unable to leave their nests. Their movements were uncoordinated, the animals did not show the typical sniffing behaviour. It was difficult for them to change from a forced upside down position. Disturbance during torpor always caused a series of shrieking sounds and biting reactions. Disturbance also immediately led to an increase in T_b and oxygen consumption; strong shivering lasted till the normal T_b was reached. During rewarming T_b rose at a rate of 0.5–0.9 °C/min in *Crocidura russula, C. leucodon* and *C. suaveolens* and 1–2 °C/min in *Suncus etruscus*.

2 distinct levels of oxygen consumption were found in all species. For example in *Crocidura russula* (figure 2) in a resting but nontorpid state (T_a 20 °C), the metabolic rate varied due to the different T_b (T_b 34–38 °C) from a maximum of 5.0 to a minimum of 2.5 ml O_2/g · h. This means that the resting but not torpid shrews are able to reduce their metabolism about 50% parallel to a lowered T_b. Figure 2 shows that ambient temperatures between 25 °C and 10 °C either lead to an increase in the metabolic rate in nontorpid shrews or to extremely low levels during periods of torpor. But even during torpor, low T_a induce an increase in oxygen consumption enough to prevent a further decrease in T_b. We have not recorded a body temperature below 18.5 °C. However, entering into torpor was prohibited at ambient temperatures below 10 °C. In this case all shrews maintained their normal T_b. Continuously measured oxygen consumption during 24 h showed that the torpor period has an average duration of about 3 h, during which the metabolic rate is reduced to about 25–35% of the normal resting level of shrews which are awake (T_b 34–38 °C). Comparative data on temperature regulation are shown in the table.

An unexpected development of temperature regulation was found in the newborn and growing shrews of *Crocidura russula* by measuring oxygen consumption and T_b. Up to an age of 17 days, the T_b varied beteen 30.5 °C and 35 °C at T_a 30 °C. This thermal situation was similar to that in the nest. After the age of 17 days, T_b rose to the adult level or was even higher (37–38 °C). The oxygen consumption decreased after a first period (first 5 days after birth) till about the 15th day. During the following days, it increased again. At T_a 20 °C (figure 3), which acts as a cold stress on the newborn and naked shrews, the difference in T_b between the beginning and the end of an experiment gradually decreased from the 1st to the 4th day (ΔT_b: 4 °C to 0.4 °C). This indicates the maturing of the *homeothermic* reaction in the still naked and blind animals. Corresponding to this reaction, the oxygen consumption during the first 4 days rose definitely and was much higher at T_a 20 °C than at T_a 30 °C. But from the 5th to the 17th day ΔT_b in each experiment increased to a maximum of 10 °C. T_b and oxygen consumption simultaneously decreased to the level measured in torporous adults. Any disturbance immediately led to rewarming. There is no doubt that all young shrews in this phase were able to enter torpor. Between the 17th and 24th day after birth, T_b and metabolic rate were stabilized at higher levels again; the young ones now reacted similarly to the adults.

Discussion. I can discuss these results only as an adaptation to the climatic conditions in the temperate zone. Periods of cool weather and shortage of food are compensated by a low normal metabolism and by hours of torpor with an extremely low metabolism. In this way, some fat *Crocidura russula* could starve for 5 days (T_a 22 °C) with a weight reduction of 1 g/day. The fact that only a few days after birth first *homeothermic* reactions exist while the ability to enter torpor develops a few days later, shows the adaptive character of torpor or the *heterothermic* reaction of these shrews. A comparison with the results of Vogel[2] leads to the conclusion that the whole family (Soricidae) must have developed very different abilities in temperature regulation, perhaps most comparable to some of the subtropical bat families, where many species make use of an energy-saving daily lethargic period but are unable to partake in real hibernation[4,5].

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