ACTA THERIOLOGICA
Vol. 33, 20: 293—291, 1988

Basal and Cold-Induced Metabolic Rates in the Harvest Mouse Micromys minutus

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Grodziński W., Böckler H. & Heldmaier G., 1988: Basal and cold-induced metabolic rates in the harvest mouse *Micromys minutus*. Acta theriol., 33, 20 : 283—291 [With 2 Tables & 2 Figs]

The oxygen consumption in European harvest mice *Micromys minutus* (Pallas, 1771) was measured using a computerized open flow respirometr, at ambient temperatures ranging from +30 to −10°C. For warm adapted spring animals, a temperature of −10°C lies below their cold limit. The basal metabolic rate (BMR) determined at +30°C was 2.86 ml $O_2g^{-1}h^{-1}$, which is very close to that predicted (2.55 ml $O_2g^{-1}h^{-1}$) from the allometric function scaling rodents' BMR/body weights. The relationship of the resting metabolic rate of the harvest mice (RMR in ml $O_2g^{-1}h^{-1}$, and ambient temperature (T_a) from 0°C through +30°C can be described by the regression: $RMR = 12.063 - 0.305 \times T_a$. All the BMR and RMR values are much lower (1.8—2.2 and 1.4—1.8 times lower) than in previous studies with nonrecording closed circuit respirometers. The energy strategy of the five smallest rodent species (7—10 g) is discussed, including torpor, hibernation, and behavioural adaptations.

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1. INTRODUCTION

The harvest mouse *Micromys minutus* (Pallas, 1771), one of the smallest rodent species in Europe, has long been a subject of interest in field and laboratory studies (for a review see Trout, 1978 a, b). Metabolic rates of the harvest mouse were previously investigated by measuring oxygen consumption at various ambient temperatures (Smirnov 1957, Górecki 1971). Both Smirnov and Górecki found exceptionally high values of basal and resting metabolic rates in this small mouse; however, both employed respirometers with closed circuit systems. Smirnov used 5-litre closed chambers and then analysed the oxygen content using Haldane's method, while Górecki used the Kalabukhov-Skvortzov monometric respirometer (Górecki 1975). The aim of this small methodological contribution is to re-examine the metabolic rates of the harvest mouse using an automatic open flow gas analyzer.

2. MATERIAL AND METHODS

Three harvest mice, acquired from the Niepołomice Forest in southern Poland (50°07'N, 20°23'E) and the Białowieża Forest in northeastern Poland (52°40'N, 23°30'E), were used in this experiment. They were housed individually in cages under natural photoperiod and room temperature (about 20°C), and fed on seeds, grain, and apples (according to the diet of Piechocki, 1958; Smirnov, 1959). All oxygen consumption measurements were made during April and May. During this period, the mean body weights of the three harvest mice were 6.50 g, 6.80 g, and 8.80 g. Oxygen consumption was measured using an open respirometric system (Heldmaier & Steinlechner, 1981) (S-3A oxygen analyzer, Zirconium oxide cell, two channel system, Applied Electrochemistry Inc.) each run lasting 7—8 hours (9.00—16.00—17.00). A single mouse was put in a 1.8 l plastic cuvette with a small supply of oats and apple pieces. The metabolic cuvettes were placed in a climatic chamber and the mice were exposed to step-wise decreasing ambient temperatures, starting from 30 and 28°C, and going through 20, 10, 0°C, or in some runs down to −10°C. The behaviour of the harvest mice was carefully observed during the runs. Data were collected at 1 minute intervals by a computer system, and recorded both on line and on tape. These were analysed later using computer programmes which plotted the original data, and calculated regression by the least squares method on the basis of the five lowest or mean values at each ambient temperature (Böckler, 1985).

3. RESULTS AND DISCUSSION

An example of resting metabolic rate in a harvest mouse for a wide range of ambient temperatures (+30 to −10°C) is shown in Fig. 1. Plotted here are the data points for every 3 minutes of the entire 8-hour run. Minus 10°C is below the cold limit of the harvest mouse. This is indicated by the inability of the mouse to increase its heat production at this temperature. The relationship between the resting metabolic rate and ambient temperature from 0 to 30°C showed a high correlation ($r^2 = 0.967$) and can be described by the following regression: $RMR = 12.063 - 0.305 \times T_a$ (RMR in ml $O_2 g^{-1} h^{-1}$, T_a in °C). At each temperature this computation applies to the mean values for three animals (Fig. 2). Likewise, the maximum level of metabolic rate (vO_2 max) was calculated for these harvest mice and averaged 17.82, 14.64, 9.50, 7.76, 7.52, and 3.76 ml $O_2 g^{-1} h^{-1}$ at temperatures of 0, 10, 20, 25, 28 and 30°C, respectively. These measurements, however, include the additional cost of activity.

Depending on the ambient temperature, the harvest mice drastically altered in behaviour and activity. At temperatures close to their thermoneutral zone (+28°C—30°C) the mice were moderately active; after a 1 hr acclimation period they remained quiet and stretched their bodies. At temperatures of +10°C and +20°C they were alternately active or quiescent, if they rested it was in a "mouse-like" posture, however, they spent most of the time in a curled posture.

The lowest levels of oxygen consumption were found in the harvest mice at +30°C, and averaged 2.86 ± 0.51 ml $O_2 g^{-1} h^{-1}$. This can be considered to be the standard or basal metabolic rate (BMR), (Grodziński & Wunder, 1975) for this small rodent. The mice showed the maximum cold induced oxygen consumption (vO_2), at 0°C, which amounted to 12.12 ± 0.98 ml $O_2 g^{-1} h^{-1}$. At −10°C the harvest mouse cannot maintain a positive

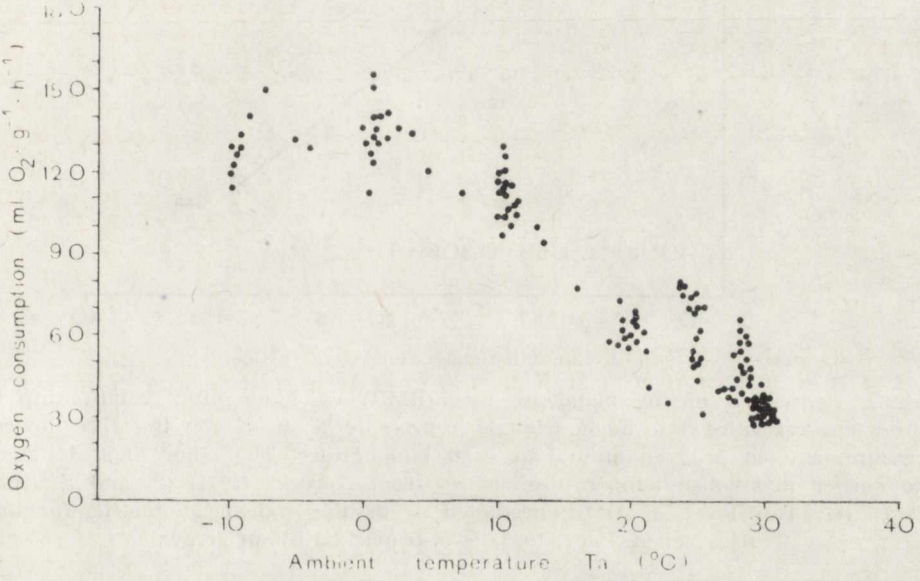

Fig. 1. Individual records of oxygen consumption of an 8.8 g harvest mouse (*Micromys minutus*) at various ambient temperatures. The data points represent records monitored by computer at three minute intervals. (Note that at temperatures below 0°C the cold limit for this mouse was reached).

heat balance and its oxygen consumption drops to an average of 11.49 ml during the first 30 minutes. The mean rectal body temperature, measured in only two animals before and after several 7—8 hour runs was 36.2°C.

The metabolic rates of the harvest mice studied, from the thermoneutral zone up to the cold limit, have been summarized in Table 1. This table also presents the previous metabolic measurements, compiled

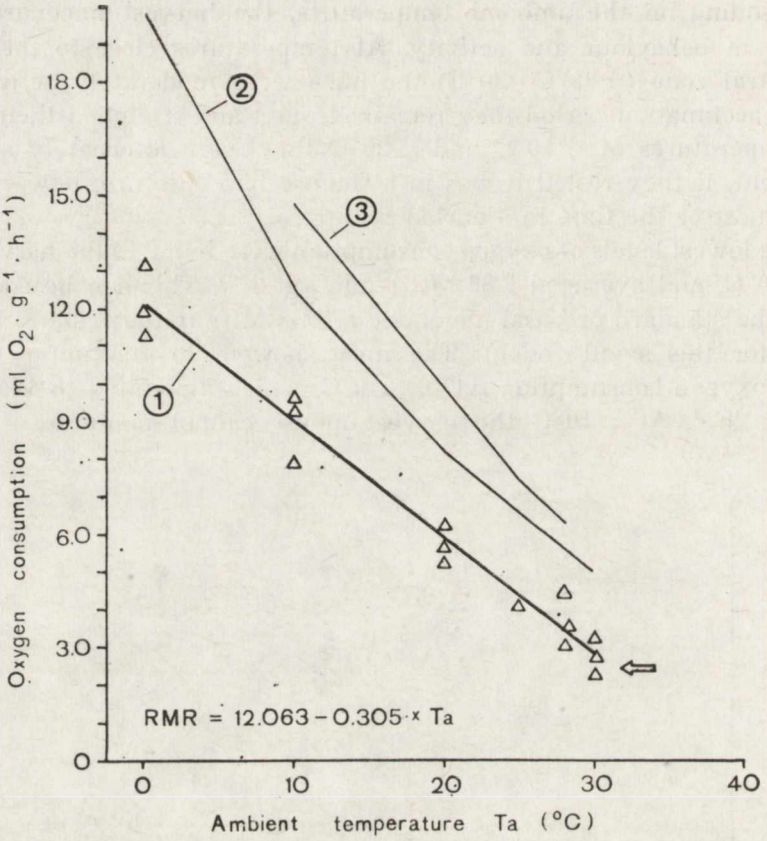

Fig. 2. Regression of the metabolic rate (RMR) vs. temperature relationship in three harvest mice (1). Each triangle represents a mean for the five lowest measurements of a given animal at each temperature. The other lines designate the earlier metabolism/temperature curves from Górecki (1971) (2) and Smirnov (1957) (3). The level of BMR predicted from the rodent allometric function (Hayssen & Lacy, 1985) is also marked by an arrow.

Table 1

Resting metabolic rate (RMR in ml $O_2 g^{-1} h^{-1}$) of harvest mice (*Micromys minutus*) at various ambient temperatures. For comparison with this study the values determined by Smirnov (1957) and Górecki (1951) are also given. Smirnov's data were taken from a table in his paper, those of Górecki (1971) being taken from the abstract (and/or read from a figure). BMR values are boldfaced.

Source of data	Ambient temperature (°C)					
	0	10	20	25	28	30
This study (mean±SD)	12.12 ±0.98	8.97 ±0.93	5.82 ±0.52	4.20	3.20 ±0.78	**2.86** ±0.51
Smirnov (1957)	—	14.74	9.94	7.47	**6.42**	
Górecki (1971)	19.8	12.5	8.3	—	—	**5.0**

by Smirnov (1957) and Górecki (1971). Smirnov's data represent metabolic rates of spring animals (May), measured between 10—28°C, while Górecki's data were obtained from autumn animals (October, November), studied at ambient temperatures from 0°C to 30°C. These studies were based on measurements made using more than 20 animals, whereas in this investigation only three harvest mice were studied. All of both Smirnov's (1957) and Górecki's data (1971) are much higher than those found in this study (see also Fig. 2). This is particularly true of basal metabolic rate, which Smirnov and Górecki determined to be 6.42 and 5.0 ml $O_2g^{-1}h^{-1}$, while in the present work a value of 2.86 ml $O_2g^{-1}h^{-1}$, *i.e.* about half that, was obtained. At lower temperatures the oxygen consumption measured by both Smirnov and Górecki was 43—78% higher than those we determined.

Such a drastic discrepancy between measurements made 30 and 16 years ago and the current ones is probably associated with the method of measurement. It is probably not solely dependent on the fact that Smirnov and Górecki used closed circuit respirometers, while an open flow one was used in the present study. The differences most probably result from the frequency with which oxygen consumption is recorded. A computerized open flow gas analyzer permits continuous recording (with a printout for each minute), while in simple cuvettes oxygen consumption could not be recorded more often than every 60 minutes (Smirnov 1957), or, in the case of the closed circuit manometric respirometer, every 5—10 minutes (Górecki 1971). During such long periods the animals may be active, thereby increasing the cumulative amount of oxygen consumed.

This study allows two more general conclusions. When comparing metabolic rates (BMR, RMR) of small mammals and scaling them as a function of body size we must be very careful and critical in selecting data, taking into account differences in the equipment and techniques of measurement. There have been several attempts to scale rodent basal or standard metabolic rate to their body size (*e.g.* Grodziński & Górecki, 1967; Hart, 1971; Grodziński & Wunder, 1975; Hayssen & Lacy, 1985; Elgar & Tarvey, 1987). The regressions usually began with the very high metabolic rates of the tiny European harvest mouse (*Micromys minutus*). The BMR determined for the harvest mouse in this paper (2.86 ml $O_2g^{-1}h^{-1}$) is rather low, but close to that which can be predicted from the general allometric regression for small mammals (Grodziński & Wunder, 1975) or from a more specific regression exclusively for rodents (Hayssen & Lacy, 1985). The BMR calculated from these equations for animals with a body weight of 7.5 g equals 2.30 and 2.5 ml $O_2^{-1}h^{-1}$, respectively. Thus, the level of basal metabolism

Table 2

Basal (BMR) and average daily (ADMR) metabolic rates in five species of very small rodents. T — torpor, H — hibernation, G — granivore, O — omnivore.

Species, Family, common name	Body weight (g)	BMR ml $O_2 g^{-1} h^{-1}$	ADMR ml $O_2 g^{-1} h^{-1}$	Ecol. charact.	Reference
Baiomys tailori (Osgood) (*Cricetidae*), pygmy mouse	7.3	1.950	—	T	Hudson (1965)
Perognathus longimembris (Cones) (*Heteromyidae*), pocket mouse	8.2	1.310	6.87	T. G	Chew, Lindberg & Hayden (1967)
	8.0	1.550	—		French et al., (1976)
Reithrodontomys megalotis (Baird) (*Cricetidae*), harvest mouse	9.0	2.500	6.32	T, G	Kenagy & Vleck (1982) Pearson (1960)
Micromys minutus (Pallas) (*Muridae*), harvest mouse	—	6.420 (6.678—7.653) *	—	O	Smirnov (1957)
	8.0	—	7.32		Cross (1967)
	8.7	5.0	7.57		Górecki (1971)
	7.4	2.86	—		This study
Sicista betulina (Pallas) (*Zapodidae*), birch mouse	10.0	3.2	—	H, T, O	Johanssen & Krog (1959)

* in different seasons

found in this study is approximately that expected from the rodent equation (only 11% higher), whereas the values described by Smirnov (1957) and Górecki (1971) exceed the expected value by 157 and 100%, respectively.

The energy metabolism and thermoregulation have thus far been studied in at least five species of very small rodents (with body weights not exceeding 10 g). Other than the European harvest mouse, *Micromys minutus*, these include the 7 g American pigmy mouse, *Baiomys taylori* (Hudson, 1965), an 8 g pocket mouse *Perognathus longimembris* (Chew, Lindberg & Hayden, 1965; Kenagy & Vleck, 1982), the 9 g American harvest mouse, *Reintrodontomys megalotis* (Pearson, 1960), and the 10 g European birch mouse, *Sicista betulina* (Johanssen & Krog, 1959). Their basal metabolic rates (BMR) extend from 1.3—3.2 ml $O_2g^{-1}h^{-1}$, a range into which the determinations for the harvest mouse, made in the present work, fit easily. Only the measurements made by Górcki (1971) and Smirnov (1957), ranging from 5.0—7.65 ml $O_2g^{-1}h^{-1}$ (Table 2) differ markedly. There are, however, no such differences in measurements of daily metabolic rate (ADMR) which were found to vary from 6.32—7.57 ml $O_2g^{-1}h^{-1}$ for these small rodents. The five species of rodents discussed here represent various families (*Muridae, Cricetidae, Heteromyidae* and *Zapodidae*) and feeding types. These very small homeotherms have also apparently developed various energy strategies which can include torpor, hibernation, and behavioural adaptations. The American pigmy, pocket and harvest mice can easily go into torpor for a few hours to several days duration (aestivation). The Europaean birch mouse hibernates for 7 months and can also show daily torpor. The metabolic adaptations of the European harvest mouse, studied in this paper, are not clear. *Micromys minutus* does not hibernate or aestivate (Trout, 1978b), though it does probably have the ability to go torpid. It insulates its nest well, both the above-ground ones during summer, and the underground ones or those inside haystacks during winter. It is more or less omnivorous (Trout, 1978b; Dickman, 1986), and this allows it to remain active all the year round, though each day it must consume a third of its own weight in food (Hawkins & Jewell, 1962; Cross, 1967).

Acknowledgement: The research was supported by the DFG (Sondeforschungsbereich 305: Ökophysiologie) when the senior author (W. G.) was working with Professor Heldmaier's group at the Phillips-University in Marburg. Helpful comments on the manuscript, made by Dr. J. Weiner, were highly appreciated.

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Received 1 September 1987, Accepted 2 November 1987.

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O METABOLIZMIE PODSTAWOWYM I SPOCZYNKOWYM U BADYLARKI *MICROMYS MINUTUS*

Streszczenie

Metabolizm badylarek badano mierząc u nich zużycie tlenu z pomocą skomputerowanego respirometru przepływowego z cyrkonowym analizatorem i częstym zapisem na drukarce. Pomiary wykonywano w szerokim zakresie temperatur otoczenia, od +30°C do −10°C. W okresie wiosny (kwiecień—maj) badylarki adaptowane do temperatury pokojowej wykazywały dobrą termoregulację od strefy termoneutralnej (+29—30°C) do 0°C; przy temperaturze −10°C nie mogły one podnosić już bardziej tempa metabolizmu (Fig. 1). Metabolizm bazalny badylarek (BMR) rejestrowany w temperaturze +30°C osiągał średnio 2,86±0,51 ml $O_2g^{-1}h^{-1}$. Poziom ten jest zbliżony do wartości 2,50 ml $O_2g^{-1}h^{-1}$, którą można przewidywać z allometrycznych funkcji skalujących BMR i ciężar ciała gryzoni (Fig. 2). Zależność metabolizmu spoczynkowego badylarek (RMR, ml $O_2g^{-1}h^{-1}$) od temperatury otoczenia (T_a, °C) w zakresie od 0°C do 30°C dobrze opisuje funkcja regresji prostoliniowej: $RMR=12{,}063-0{,}305\times T_a$ (Tabl. 1, Fig. 2) Wszystkie wartości metabolizmu podstawowego i spoczynkowego (BMR, RMR) podane w tej pracy są drastycznie niższe (1,8—2,2 oraz 1,4—1,8 razy!) od opisywanych w dawniejszych pracach Smirnov'a (1957) i Góreckiego (1971) (por. Tabela 1, Ryc. 2). Różnice te wiążą się głównie z używanymi dawniej respirometrami systemu zamkniętego, które nie dawały możliwości rejestrowania tempa metabolizmu w krótszych okresach czasu.

Zestawiono i porównano tempo metabolizmu podstawowego (BMR) i dobowego (ADMR) u pięciu bardzo małych gatunków gryzoni (*Baiomys tailori, Perognathus longimembris, Reithrodontomys megalotis, Micromys minutus* i *Sicista betulina*). Te najmniejsze w Europie i Ameryce Płn. gatunki gryzoni (o ciężarze ciała 7—10 g) posiadają różne strategie energetyczne. Potrafiły one rozwinąć zdolność do zapadania w torpor lub sen zimowy oraz wiele behawioralnych adaptacji metabolizmu.