A C T A T H E R I O L O G I C A

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The Metabolic Energy Requirements of the Redback Vole

[With 7 Tables & 2 Figs.]

Continuing studies on energy cycling through the bog ecosystems of southern Manitoba necessitate information on the energy budget of the redback vole, *Clethrionomys gapperi loringi* (Bailey, 1897). Oxygen consumption, carbon dioxide production and urinary nitrogen excretion were measured for this species in a closed system respirometer over a narrow range of temperatures. At temperatures in the mid 50°'s F oxygen consumption was 6.33 cc/g-hr, in the low 60°'s it was 5.92 cc/g-hr and in the high 60°'s 4.59 cc/g-hr. Over these temperature ranges carbon dioxide production averaged 4.20, 3.60 and 2.90 cc/g-hr respectively and urinary nitrogen 2.475, 1.838 and 1.821 mg per hour respectively. Basal metabolism was approximately 3.97 Kcal/day and active daily metabolism about 6.45 Kcal/day based upon an average 19.1 g vole. The metabolic rates of males were slightly but significantly higher than females.

I. INTRODUCTION

The redback vole, *Clethrionomys gapperi loringi* (Bailey, 1897) is an important component of the mammalian fauna of Manitoba bogs (Buckner, 1958). Recent studies on the bioenergetics of this biotype have placed the major emphasis on the insectivores (Buckner, 1964, 1966; Bergeron & Buckner, 1970): our attention is now begining to focus on the rodent species in the system.

The metabolism of terrestrial vertebrates can be measured directly or extrapolated from laboratory experiments (Golley, 1967). Direct methods such as the D_2O_{18} technique (Lifson *et al.*, 1955), the use of radioactive isotopes (Odum & Golley, 1963), and telemetry have already shown their usefulness. The indirect methods used by Brody (1945) and Swift & French (1954) are now well known and particularly useful in long term studies. The metabolism of small mammals is often determined by measuring the oxygen consumption (Morri-

son, 1947), carbon dioxide production (Brody, 1945) and urinary-nitrogen excretion (Hawk *et al.*, 1949).

It is known that the oxygen consumption can be based on body weight (kg), metabolic size ($kg^{2/3}$ and $kg^{3/4}$), and surface area (m^2) (Chiu & Hsieh, 1960), but it appears that the most useful equation was established by Brody (1945), where the relationship existing between metabolism and body weight is expressed by the formula $Y = a\,W^b$;

where Y = *BMR*
W = body weight in kg
a = specific metabolism = 70.5
and b = a power of transformation = 0.73

On the basis of such information, Buckner (1964) calculated the daily metabolic requirements of four species of shrews (*S. cinereus, S. arcticus, M. hoyi* and *B. brevicauda*) to be 6.1, 6.9, 6.7 and 9.7 Kcal respectively. There were no differences between the sexes (Buckner, 1964, Nelson & Asling, 1962). Similar results had been calculated by Pearson (1947) by assuming a *RQ* (respiratory quotient) of 0.80. The energy requirements of short-tailed shrews found to be a little lower than previously reported (Martinsen, 1969), probably as a result of keeping them on a restricted diet. The metabolism of shrews can also change from season to season as shown by Gębczyński (1965); he found that *ADMR* (average daily metabolic rate) was 8.8 Kcal in summer, 8.5 in autumn and 7.5 in winter.

It is easy to understand that most studies were conducted on voles and mice since they are easier to keep in the laboratory. However, laboratory strains of wild populations showed metabolic differences from wild strains at temperatures of 10 to 20°C (Górecki, 1966). Measures of metabolic rates should be put on a *RMR* (resting metabolic rate) or a *ADMR* basis, although the latter form is more convenient for computing daily energy budgets (Grodziński, 1969). Oxygen uptake was found to be independent of the oxygen supply down to about 80 mm Hg during rest at 27°C, to about 115 mm Hg at 5°C (Segrem & Hart, 1967). The *RMR* of European common voles, *Microtus arvalis* (Pallas, 1779) was found to vary in a straight-line fashion between 5 and 30°C (Trojan & Wojciechowska 1967a, b); at temperatures between 5 and 10°C, the *RMR* of females was higher than that of males. The oxygen consumption is known to increase with a decrease of ambient temperature, as shown by Dawson (1955), McNab & Morrison (1963), and Murie (1961). Fat deposits do not influence the metabolism of animals provided they stay within standard limits of 20 percent of the total body weight (McNab, 1968).

The *DEB* (daily energy budget) of bank voles was estimated at 10.2 Kcal during winter and 10.6 Kcal during summer; 13.5 and 12.6 Kcal for European common voles; 11.2 and 12.3 Kcal for field mice (Grodziński, 1966). Metabolism and hemoglobin contents of voles were positively correlated except in winter, when high oxygen consumption was observed with the lowest blood hemoglobin content (Shevchenko, 1968). Harvest mice (*Reithrodontomys fulvescens*) showed a reverse energy expenditure pattern; in summer they consumed 5.6 Kcal/day and in winter 8.8 Kcal/day (Gaertner, 1968), an 80 percent increase in energy requirement.

Pregnancy and lactation are periods of intense energetic requirements for European common voles; pregnant females reached a consumption of 18.8 Kcal/day and lactating ones 21.0 Kcal/day (Trojan & Wojciechowska, 1967); this represented increases of 23 and 37 percent energy expenditure compared to non-reproducing females. Kaczmarski (1966) estimated these two functions to require 32 and 122 percent more energy; he also showed that a litter of 4 would require a total of 364 Kcal from the mother. Migula (1969) found that the production and nursing of one young vole required 75.9 Kcal.

Besides reproduction, the *DEB* model is composed of nest life and search for food (Trojan & Wojciechowska, 1969). It was found that mice could spend 2.3 Kcal/day in voluntary activity under different temperatures (10—20—30°C), which made up 12, 16 and 27 percent of their total daily expenditure. The working oxygen consumption of European common voles was 6.5 times the resting value while that of the bank voles was 7 times the resting value (Janský, 1959). The act of swimming in white rats was found to consume 2 or 3 times the basic values (Lustinec, 1958). Similar results were obtained for bank voles (2.0—2.1) and field mice (1.6) (Grodziński & Górecki, 1967).

The influence of nest life on the metabolism of animals was indirectly estimated. Darkness was found to decrease by 27 percent the oxygen consumption of European common voles (Trojan & Wojciechowska, 1968a, b). The effect of huddling with 6 animals or more was also found to decrease the basic requirements of voles by 36 percent (Trojan & Wojciechowska, 1968). Using 4 animals at a time, Grodziński & Górecki (1967) lowered the requirements of bank voles by 13 percent.

II. MATERIALS AND METHODS

The metabolism of redback vole was determined by their oxygen consumption. The apparatus was a modification of the closed-system automatic respirometer used by Buckner (1964). The metabolic cages consisted of battery jars con-

taining a screen mesh floor partly covered underneath by a sheet of polyethylene plastic in order to protect the urinary excretions and soda lime pellets from fecal contamination and permit the latter ones to absorb water and carbon dioxide. The apparatus had also feeding trays and water bottles kept to the side of the jars by suction cups (Fig 1). Food[1] and water were given *ad libidum* at all times. Some nesting materials were also included in the system.

The oxygen consumption was recorded automatically by a manometer-type--respirometer connected to an Esterline Angus Recorder; readings were corrected for each 24-hour period by the introduction of a thermobarometer in the water bath. The manometers were calibrated after each experiment to minimize the possible effect of the room temperature on the water.

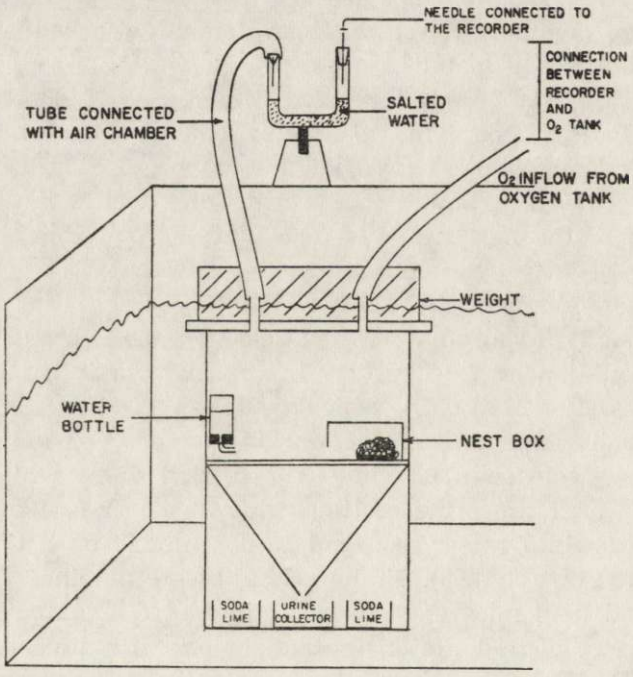

Fig. 1. Typical metabolism cage used to determine the metabolic requirements of redback voles.

The redback voles were captured partly in auxillary trap-lines of a permanent sampling plot of the Vertebrate Ecology Team, and partly from another plot near the Nuclear Research Center of Pinawa, Manitoba. The newly captured voles were brought to the laboratory and acclimatized to their new environment for a minimum of a month. They were then placed under experimental conditions for a one--day period and finally tested for another 24 hours. The metabolic cages were

[1] The pig starter pellets used were composed of: 12.7% free water, 18.1% crude protein, 40.0% crude fat, 3.0% salt.

Table 1

Mean values of oxygen consumption and carbon dioxide production of 20 redback voles tested under 3 different temperatures.

Temperature		Mean weight	HO_2 consumption		CO_2 production	
°F	°C	of animals, g	cc per hr	cc per g-hr	cc per hr	cc per g-hr
69—72	20.6—22.2	19.7	88.6±21.8	4.59±1.02	55.6±10.2	2.88±0.51
62—64	16.7—17.8	19.0	111.9±22.7	5.92±0.95	67.1± 8.8	3.61±0.61
53—57	11.7—13.9	19.1	119.4±24.2	6.33±1.26	78.8±10.9	4.17±0.65

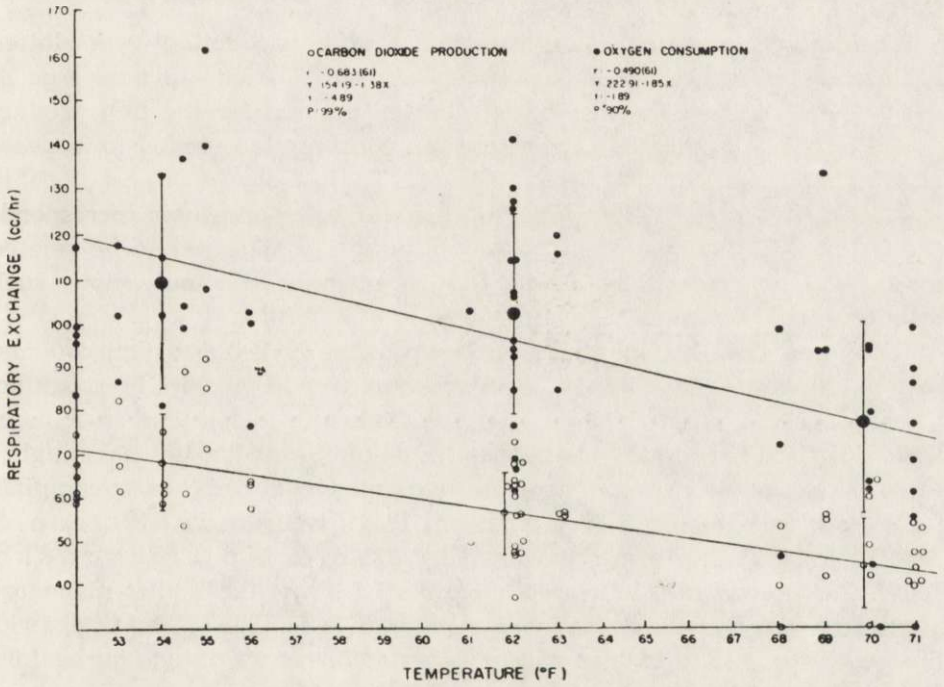

Fig. 2. Oxygen consumption, carbon dioxide production and temperature relationships of 20 redback voles.

immersed in a water bath kept at a constant temperature for the priod of the experiment. The temperatures ranged from 53 to 73° F (11.6 to 22.8° C). The caloric utilization in the metabolic process was calculated after Brody's technique (Brody, 1945).

III. RESULTS AND DISCUSSION

The mean values of daily oxygen consumption and carbon dioxide production of redback voles are listed in Table 1. Oxygen consumption and carbon dioxide production increased as temperature decreased: the

oxygen consumption increased however, at a greater rate than did carbon dioxide production (Fig. 2), so that the *RQ* values were lower than expected. The redback voles consumed daily 4.59 cc of oxygen per g-hr at 69—72° F, 5.92 cc at 62—64° F and 6.33 cc at 53—57° F. The carbon dioxide production averaged 2.90, 3.60 and 4.20 cc/g-hr for the same gradient of temperatures. The latter figures are surprisingly low when compared to those of Pearson (1962) and Morrison (1948). Assuming *RQ* values of 0.70 and oxygen intakes such as shown above, the CO_2 production should average 3.21, 4.14 and 4.43 cc per g-hr at similar temperatures.

When oxygen consumption and carbon dioxide production were plotted against their respective temperatures, a linear relationship held true at the 90 percent level for the oxygen and 99 percent for the CO_2 production (Fig. 2): as stipulated earlier, oxygen consumption tended to increase at a higher rate than CO_2 production did. Table 2 shows the relationship existing between the respiratory quotients of voles and their corresponding O_2 and CO_2 values. The oxygen consumption appeared to be related directly to the *RQ* values while CO_2 production did not show such relationship.

When analysed by age and sex groups, the oxygen consumption and carbon dioxide production gave interesting trends. Generally speaking, the average consumption of oxygen was higher in males than in females (Table 3). This is contrary to the general opinion that females have higher rates of oxygen consumption; such results have already been compiled for *Peromyscus* (Cook & Hannon, 1954), tree-shrews (Nelson & Asling, 1962), and common voles (Trojan & Wojciechowska, 1967). On the contrary, our results support the hypothesis that males are more sensitive to mild stress when compared to females (Chitty, 1960; Schell, 1967). The oxygen consumption of males was found to be 1.06, 1.08 and 1.08 times those of females for the decreasing order of temperatures. Sub-adult males consumed more oxygen than did females, although the trend was less obvious among adults, where females consumed more at 62—64° F and much less at the two extremes. The carbon dioxide production was a little higher in males at both maximum and minimum temperatures. The production of males amounted to 1.02, 0.96 and 1.04 times those of females for the decreasing order of temperatures.

The carbon dioxide production of redback voles was found to be statistically related to the oxygen consumption at the two extreme temperatures ($P > 99$ percent), while at the middle temperature range tested these two values were related only at the 93 percent level (Table 4). The relationship held true at all temperatures only when voles with *RQ* of 0.73 and over were analysed ($P > 99$ percent). The relationship appeared

Table 2

Relationships between oxygen consumption, carbon dioxide production and the respiratory quotients (*RQ*) of 20 redback voles.

Temperature °F	Temperature °C	O_2 and *RQ* *r*	O_2 and *RQ* *y*	CO_2 and *RQ* *r*	CO_2 and *RQ* *y*
69—72	20.6—22.2	—0.632*	169.20—125.32*x*	0.028	— — —
62—64	16.2—17.8	—0.788*	193.32—131.08*x*	0.223	— — —
3—57	11.7—13.9	—0.663*	257.86—207.28*x*	—0.186	— — —

* Probability > 99% level.

Table 3

Mean values of oxygen consumption and carbon dioxide production of redback voles (analysed by age and sex).

Temp. °*F*, (°C)	Oxygen				Carbon Dioxide			
	Males		Females		Males		Females	
	Sa	Mean A	Sa	Mean A	Sa	Mean A	Sa	Mean A
69—72	83.6(8)*	104.3(4)	68.4(4)	102.9(4)	51.6(8)	64.6(4)	46.7(4)	63.2(4)
20.6—22.2)		90.5(12)		85.7(8)		56.0(12)		55.8(8)
62—64	109.4(10)	128.2(3)	88.0(5)	136.1(3)	63.6(9)	73.2(3)	67.8(5)	70.9(3)
(16.7—17.8)		114.1(13)		106.0(8)		66.0(12)		69.0(8)
5.3—57	122.5(9)	124.2(4)	100.4(3)	121.4(5)	78,3(9)	83.9(4)	69.5(3)	81.2(5)
(11.7—13.9)		123.0(13)		113.4(8)		80.0(13)		76.8(8)

* The numbers in parentheses refer to the number of animals tested at a given temperature. Sa – subadult, A – adult.

Table 4

Relationships between the oxygen consumption (*X*) and the carbon dioxide production (*Y*) of 20 redback voles.

Tamperature °F	Tamperature °C	cc O_2/hr vs cc CO_2/hr *r*	cc O_2/hr vs cc CO_2/hr *Y*	cc O_2/g-hr vs cc CO_2/g-hr *r*	cc O_2/g-hr vs cc CO_2/g-hr *Y*
9 — 72	20.6 — 22 2	0.725*	2.56+0.34*X*	0.674*	1.47+0.31*X*
2 — 64	16.7 — 17.8	0.421[1]	4.76+0.17*X*	0.285[2]	2.48+0.19*X*
3 — 57	11.7 — 13.9	0.8 2*	2.92+0.42*X*	0.863*	1.38+0.44*X*

* Probability > 99% level. [1] Probability > 93% level. [2] Probability > 78% level.

to be weaker when oxygen and carbon dioxide values were converted to a volume per g-hr basis. This suggests that the weight of animals could have had an influence on either the O_2 consumption or the CO_2 values or on both of them. This contradicts the studies by Pearson (1962) when he mentioned that one need not correct the CO_2 output for weight at various temperatures.

Table 5

The daily urinary-nitrogen excretion of redback voles (mg/g-day).
m – male, f – female.

	Temperature											
°F °C	54 12.2	54 12.2	55 12.8	58 14.4	66 18.9	68 20.0	69 20.5	70 21.1	71 21.6	72 2.22	72 22.2	75 23.8
f	0.874	2.808	9.024	0.849	—	—	—	—	—	—	—	—
f	6.624	3.144	1.392	0.998	3.576	5.256	4.080	2.664	1.838	2.496	3.144	0.838
m	2.832	2.808	0.463	0.749	2.335	2.712	0.802	2.664	0.127	1.435	1.361	0.823
f	2.004	0.559	1.121	0.475	1.013	3 436	1.411	3.168	1.834	1.226	1.073	0.252
f	—	—	—	—	1.802	2.359	3.792	2.592	0.703	1.418	1.632	3.000
Mean	3.084	2.330	3.000	0.768	2.182	3.441	2.521	2.772	1.126	2.627	1.803	1.228
		2.805			2.182				2.802			
Mean weight of voles (g)		21.2			20.2				21.0			
Daily nitrogen excretion (mg/vole)		59.35			44.14				43.70			

The daily urinary-nitrogen measurements were performed on 5 voles using a gradient of temperatures similar to that which was used for their metabolism studies (Table 5). The daily overall production averaged 46.9 mg for animals weighing 20.9 g. The fluctuations of the nitrogen measurements at different temperatures suggested no correlation between the latter values. However, a decrease in nitrogen excretion seemed to have occurred as temperature increased; the average nitrogen excretion at 54, 66 and 72° F indicated a slow decrease from 59.4 to 44.1 mg, to finally reach 43.7 at the higher temperature.

Table 6
The metabolic requirements of redback voles.

Type of analysis	Temperature, °F (°C) 53—57 (11.7—13.9)	62—64 (16.7—17.8)	69—72 (20.6—22.2)
Mean daily urinary-nitrogen excretion (mg/vole)	59.35	44.14	43.70
Daily energy for protein catabolism (Kcal)	1.57	1.17	1.16
Daily metabolic requirements (Kcal)	13.25 13.50	12.53 12.77	9.91 10.15
SDA for proteins; 40% of calories derived from protein catabolism (Kcal)	0.629	0.468	0.463

Table 7

The metabolic requirements of redback voles using the calorific conversion of oxygen and *RQ* values.

Temperature °F	Temperature °C	Maximum *RQ*	Daily O_2 consumtion (liter)	Calorific conv. (Kcal)
69—72	20.6—22.2	.78	2.126	10.15
62—64	16.7—17.8	.76	2.688	12.77
53—57	11.7—13.9	.74	2.856	13.50

Based on oxygen consumption, carbon dioxide production and urinary--nitrogen excretion, the metabolic requirements of redback voles are listed in Table 6. In order to sustain their needs at a fairly low temperature, the voles need to increase their energy intake by 34 percent. At a temperature of 53—57° F, which is thought to be about the yearly average temperature of the Manitoba bogs (Buckner, 1964), the voles had to burn up to 12 percent of their daily energy budget (*DEB*) to

sustain their protein metabolism. The *DEB* of redback voles fell within the limits set by several workers (Kaczmarski, 1966, Trojan & Wojciechowska, 1967). However, the increase of their daily budget from 69—72° F to 53—57° F contradicted the results of Górecki (1968).

The requirements were also calculated using the calorific conversion of oxygen and maximum values of *RQ*. Although such estimations are of maximum values, they fall very close to those produced earlier (Table 7), that is within 2 percent of the former values. By substituting these values in Brody's (1945) equation, one can calculate the expected *BMR*. For redback voles weighing 19.1 g, the basal requirements should amount to 3.97 Kcal/day. Their calculated *ADMR* at 70—72° F amounted to 6.45 ± 2.48 Kcal/day and the *ADMR* corrected for *SDA* (Specific dynamic action) of proteins averaged 5.98 ± 2.48 Kcal/day. The wide discrepancy between the observed and calculated values suggests that the measurements were not made in the thermoneutral zone, which is known to be above 72° F for voles. A simple χ^2 analysis between the observed and calculated values supports this idea ($\chi^2 = 52.1 > \chi^2$ of tables at 36.2). It is believed however, that a good proportion of the population was in or near the thermoneutral zone. This is supported by the fact that if we do not consider the 3 voles which showed the highest individual χ^2 the newly formed value amounted to 29.2 and proved to be statistically significant at the 99 percent level. This suggested then that 85 percent of the laboratory vole population could have reached a near *BMR* level. The discrepancy between the two values surely would have been reduced had the measurements been taken at a still higher temperature.

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ZAPOTRZEBOWANIE ENERGETYCZNE NORNICY

Streszczenie

Badania przepływu energii w bagiennych ekosystemach południowej Manitoby wymagają informacji o budżecie energetycznym nornicy, *Clethrionomys gapperi loringi* (B a i l e y, 1897). Zmierzono zatem zużycie tlenu, produkcję CO_2 i wydalenie azotu z moczem u tych nornic w respirometrze systemu zamkniętego (Ryc. 1) i w wąskich granicach temperatury otoczenia. Zużycie tlenu w temperaturach ca 12—14°C wynosiło 6,33 cm^3/g-hr, w ca 17—18°C — 5,92 cm^3/g-hr a w temperaturach około 21—22°C — 4,59 cm^3/g-hr (Tabela 1). W tych samych zakresach temperatur produkcja dwutlenku węgla wynosiła odpowiednio 4,20, 3,60 i 2,90 cm^3/g-hr (Tabela 2) a azotu w moczu odpowiednio 2,475, 1,838 i 1,821 mg/hr (Tabela 5). Dla przeciętnej nornicy o ciężarze ciała 19,1 g metabolizm podstawowy (*BMR*) wynosił 3,97 Kcal/dzień a średni metabolizm dobowy (*ADMR*) — 6,45 Kcal/dzień (Tabele 6, 7). Tempo metabolizmu samców było istotnie wyższe niż samic (Tabela 3).