OXYGEN CONSUMPTION IN THE PROSOBRANCH SNAIL *VIVIPARUS CONTECTOIDES* (MOLLUSCA: GASTROPODA)—I. EFFECTS OF WEIGHT AND ACTIVITY*

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Abstract—1. Metabolic rate (cm^3 O_2/hr and log cm^3 O_2/hr) of *Viviparus contectoides* is dependent on weight and log weight at levels of minimum and intermediate activity in males and minimum activity in females.

2. Weight specific oxygen consumption and log weight specific oxygen consumption of *V. contectoides* is dependent on weight and log weight at levels of intermediate and maximum activity in males and at all activity levels in females.

3. Respiration coefficients are affected by activity level or time of day. They decrease significantly with increasing activity level in males. Respiration coefficients are generally lower than literature values.

4. The relationship of oxygen consumption to weight is similar for males and females at each level of activity.

5. Mean absolute oxygen consumption (cm^3/hr) is greater for females than males at each activity level. Mean weight of females is greater than mean weight of males.

INTRODUCTION

METABOLIC rates of animals are influenced by many factors, including ambient temperature, time of day, time of year, sex, age, level of activity, weight, etc. Additionally, oxygen consumption of aquatic invertebrates may be influenced by pH, osmotic pressure, dissolved oxygen availability, substrate composition, etc. This is the first in a series of papers dealing with the effects or relationships of most of the above parameters to bioenergetics of a prosobranch snail, *Viviparus contectoides*.

The equation $MR = aW^b$, where MR is rate of oxygen consumption or metabolic rate, W is total body weight, a is metabolic rate per unit weight and b is the respiration coefficient, expresses the relationship between oxygen consumption and total body weight. Dividing the above equation by weight gives an expression for weight specific oxygen consumption.

The value of the respiration coefficient has been the subject of great controversy and the value chosen is vital in determining the accuracy of predicting rates of oxygen consumption, or metabolic rate, from total body weight. Reported values for the respiration coefficient are extremely variable, even among closely related species (Barnes & Barnes, 1969), with values ranging from 0·4 to 1·0. Brody (1945) and

Zeuthen (1953) found a value of 0·67 applicable to homeotherms, while Hemmingsen (1960) concluded that a respiration coefficient of $0·75 \pm 0·015$ was the usual value for poikilotherms. While many studies of invertebrates are consistent with Hemmingsen's respiration coefficient (e.g. Roberts, 1957a; Berg & Ockelmann, 1959; Davies, 1966), numerous reports also deviate from this value (e.g. Dehnel, 1960; Newell & Northcroft, 1965; Davies & Walkey, 1966; Åkerlund, 1969; Rising & Armitage, 1969; Huebner, 1973; Åkerlund, 1974).

MATERIALS AND METHODS

Snails used in this study were collected from a small stream in southern Genesee County, Michigan, in September and October, and placed in approximately 30–35 l. of aerated stream water in a 40-l. glass aquarium. An excess of food laden sediment was provided from the collection site. Snails were maintained on a constant cycle of 12 hr of dark and 12 of light, centered at 8.00 local time, at a temperature of $22 \pm 1°C$. They were acclimated for a minimum of 10 days under these conditions at a pH of 8·6–9·2 and an average osmotic pressure of $10·6 \pm 0·3$ mOsm/l. It was determined from another study in this series that snails of both sexes were least active between 9.00 and 11.00 p.m. and were moderately active between 7.00 and 9.00 p.m. Females were most active between 1.00 and 3.00 p.m., while males did not show a period of peak activity. Consequently, all of our tests were performed during these specified time periods.

Snails of each sex were analyzed separately. An abrasive cloth was used to remove symbiotic algae from shells of snails to eliminate any extraneous source of oxygen. Snails were removed from their aerated containers and placed in glass-stoppered 250-ml Erlenmeyer flasks. Exact volumes of each flask were determined by differential weighing of the empty flask and the flask filled with water, with the proper corrections for the density of water.

Flasks containing a snail were filled with water from the aerated containers with care taken to minimally aerate this water during transfer. Flasks were then stoppered, making sure there were no trapped bubbles, and the amount of oxygen consumed was determined after 2 hr. In studies performed during the dark cycle, transfers were done in conditions of minimal light, and snails were kept in the dark during the tests. The amount of dissolved oxygen at the beginning and end of each test was determined by the Winkler method, as presented by Hoar & Hickman (1967), using a Gilmont 2·0 ml Micrometer Buret (Roger Gilmont Industries, Inc., Great Neck, N.Y.). Regression analysis and other statistical analysis were done with Dual IBM 360/67 Processes and statistical significance was defined as $P \leqslant 0.05$.

RESULTS

I have assumed that the rate of oxygen consumption is proportional to the level of activity because of increased metabolic demands at greater levels of activity. Table 1 shows the relationship between metabolic rate and weight in males and females. When comparing oxygen consumption (cm^3/hr) to weight, I found a strong positive relationship under conditions of minimum activity in both sexes, and at intermediate activity levels for females; however, no significant relationship was observed for the intermediate activity level for males or maximum activity levels for either sex.

The relationship between weight specific oxygen consumption (cm^3/g per hr) and weight is not significant for males under conditions of minimum activity. The remainder of the relationships were significant (Table 1).

Table 2 shows the logarithmic relationship between metabolic rate ($cm^3\ O_2/hr$) and weight (g) in males and females at the various levels of activity. A significant relationship exists for males and females at levels of minimum activity, and for males at levels of intermediate activity. However, during periods of intermediate activity in females and maximum activity in both sexes, there was no significant relationship. From this logarithmic comparison of oxygen consumption and weight, I found values for the respiration coefficient that ranged from −0·2324 to 0·6825 in males and 0·0968 to 0·3463 in females.

A logarithmic comparison of the weight specific oxygen consumption and weight in males and females indicated a significant relationship exists for males at levels of intermediate and maximum

Table 1. Equations for the regression lines relating weight (wt) in g to metabolic rate (MR) of *V. contectoides* at different levels of activity

$cm^3\ O_2/hr$	r^2	N
Males		
Minimum activity		
$MR = 0.0917^{***}\ wt + 0.0147$	0.2771	36
(0·0254) (0·0310)		
Intermediate activity		
$MR = 0.0287^*\ wt + 0.0858$	0.1268	32
(0·0137) (0·0177)		
Maximum activity		
$MR = -0.0167\ wt + 0.1419$	0.0358	32
(0·0159) (0·0204)		
Females		
Minimum activity		
$MR = 0.0132^{***}\ wt + 0.0564$	0.7368	65
(0·0009) (0·0029)		
Intermediate activity		
$MR = 0.0034\ wt + 0.1102$	0.0029	30
(0·0114) (0·0235)		
Maximum activity		
$MR = 0.0145\ wt + 0.1254$	0.0824	32
(0·0089) (0·0184)		

$\overset{\circ}{V}O_2$	r^2	N
Males		
Mimimum activity		
$MR = -0.0311\ wt + 0.1461$	0.0461	36
(0·0243) (0·0296)		
Intermediate activity		
$MR = -0.0609^{***}\ wt + 0.1831$	0.3570	32
(0·0149) (0·0192)		
Maximum activity		
$MR = -0.1043^{***}\ wt + 0.2437$	0.6024	32
(0·0155) (0·1990)		
Females		
Minimum activity		
$MR = -0.0128^{***}\ wt + 0.0821$	0.5728	65
(0·0014) (0·0041)		
Intermediate activity		
$MR = -0.0259^{**}\ wt + 0.1254$	0.2092	30
(0·0092) (0·0191)		
Maximum activity		
$MR = -0.0312^{***}\ wt + 0.1579$	0.3672	32
(0·0075) (0·0156)		

$* F \leqslant 0.05 > 0.01$; $** F \leqslant 0.01 > 0.001$; $*** F \leqslant 0.001$; and the numbers in parentheses are the standard errors.

activity and for females at all levels of activity (Table 3).

Table 4 contains the average values for weight, oxygen consumption and weight specific oxygen consumption for males and females at each level of activity. This shows that females were larger than males ($t = 24.50$, $N = 193$, $P < 0.0001$).

Figure 1 shows the linear relationship between oxygen consumption and weight for females at the minimum activity level. The curvilinear relationship

Table 2. Equations for the regression lines: $\log MR = a + b \log wt$, relating weight (wt) in g to metabolic rate (MR) of *V. contectoides* at different levels of activity

cm³ O₂/hr	r^2	N
Males		
Minimum activity		
$\log MR = 0.0894 + 0.6825^{**} \log wt$	0.1831	36
(0.6898) (0.2427)		
Intermediate activity		
$\log MR = 0.1087 + 0.3728^{*} \log wt$	0.1382	32
(0.0615) (0.1699)		
Maximum activity		
$\log MR = 0.1176 - 0.2324 \log wt$	0.0520	32
(0.0235) (0.1811)		
Females		
Minimum activity		
$\log MR = 0.0678 + 0.3462^{***} \log wt$	0.7708	65
(0.0076) (0.0272)		
Intermediate activity		
$\log MR = 0.0686 + 0.0968 \log wt$	0.0054	30
(0.0318) (0.2482)		
Maximum activity		
$\log MR = 0.1286 + 0.1209 \log wt$	0.1089	32
(0.0498) (0.2105)		

$^{*} F < 0.05 > 0.01$; $^{**} F < 0.01 > 0.001$; $^{***} F < 0.001$; and the numbers in parentheses are the standard errors.

Table 3. Equations for the regression lines: $\log MR = a + (b-1) \log wt$, relating weight (wt) in g to metabolic rate (MR) of *V. contectoides* at different levels of activity

$\overset{\circ}{V}O_2^{\,0}$	r^2	N
Males		
Minimum activity		
$\log MR = 0.0893 - 0.3133 \log wt$	0.0452	36
(0.0229) (0.2469)		
Intermediate activity		
$\log MR = 0.1086 - 0.6287^{***} \log wt$	0.3148	36
(0.0143) (0.1693)		
Maximum activity		
$\log MR = 0.1176 - 1.2320^{***} \log wt$	0.6061	32
(0.0113) (0.1813)		
Females		
Minimum activity		
$\log MR = 0.0676 - 0.6545^{***} \log wt$	0.9000	65
(0.0006) (0.0275)		
Intermediate activity		
$\log MR = 0.0701 - 0.9041^{***} \log wt$	0.3204	30
(0.0119) (0.2488)		
Maximum activity		
$\log MR = 0.1312 - 0.8745^{***} \log wt$	0.3645	32
(0.0188) (0.2108)		

$^{*} F \leqslant 0.05 > 0.01$; $^{**} F \leqslant 0.01 > 0.001$; $^{***} F \leqslant 0.001$; and the numbers in parentheses are the standard errors.

between the weight specific oxygen consumption and weight of females at the minimum level of activity is shown in Fig. 2.
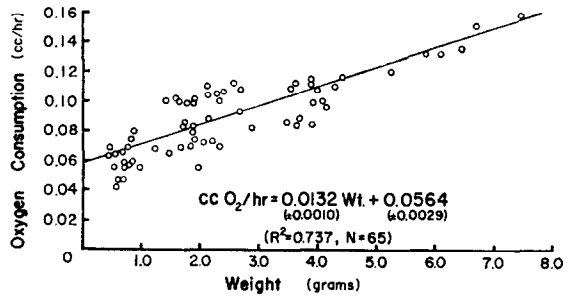

Fig. 1. The linear relationship between oxygen consumption and weight in female *V. contectoides* during periods of minimum activity.
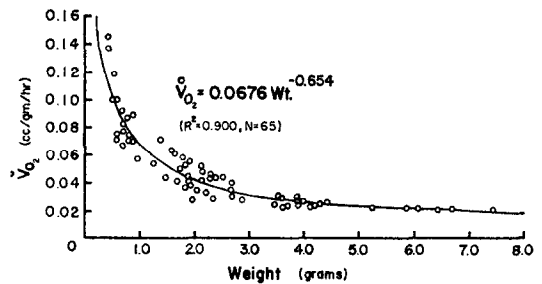

Fig. 2. The curvilinear relationship between weight specific oxygen consumption and weight in female *V. contectoides* during periods of minimum activity.
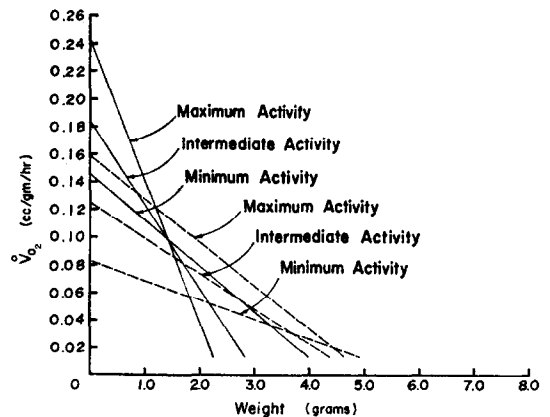

Fig. 3. A comparison of the linear relationship between weight specific oxygen consumption and weight in males (——) and females (- - - -) during various periods of activity.

Figure 3 shows the linear relationships between the weight specific oxygen consumption and weight for both males and females at each level of activity. This shows a successive increase in the slope of weight specific oxygen consumption on weight, with increasing levels of activity, in both males and females.

Table 4. The average values for weight and metabolic rate of *V. contectoides* at different levels of activity

	Wet wt (g)	Dry wt (g)	Oxygen consumption (cm³ O₂/g)	$\overset{\circ}{V}O_2$ (cm³ O₂/g per hr) (wet w)	$\overset{\circ}{V}O_2$ (cm³ O₂/g per hr) (dry w)	N
Male						
Minimum activity	1·14	0·32	0·117	0·102	0·366	36
Intermediate activity	1·21	0·33	0·120	0·099	0·364	32
Maximum activity	1·21	0·33	0·122	0·101	0·370	32
Female						
Minimum activity	2·45	0·67	0·089	0·036	0·133	65
Intermediate activity	1·82	0·50	0·116	0·064	0·232	30
Maximum activity	1·82	0·50	0·151	0·083	0·302	32

Comparison of results of this study with many previously published papers may require the use of a conversion from wet weight to dry weight of the snails. This relationship has been determined in a previous study (Fenner & Davis, unpublished) to be

$$\text{dry wt} = 0{\cdot}0046 + 0{\cdot}273 \text{ wet wt},$$
$$(0{\cdot}0158) \quad (0{\cdot}0051)$$

$$N = 36 \text{ (17 males, 19 females)}, \quad r^2 = 0{\cdot}988,$$

where weights are in g and the numbers in parentheses are the standard errors for the slope and intercept. Values for dry weight and dry weight specific oxygen consumption for males and females at all levels of activity are included in Table 3.

From an SNK multiple range analysis (Zar, 1974) of the logarithmic relationship between weight specific oxygen consumption and weight, and oxygen consumption and weight at various activity levels in males, I found that changes in activity are associated with significant changes in the slope ($F = 4{\cdot}5015$, d.f. = 2, 94; $P > 0{\cdot}02 < 0{\cdot}05$). Specifically, there was a significant decrease in the slopes from minimum to maximum activity levels ($q = 4{\cdot}3775$, d.f. = 94, 3 slopes, $P > 0{\cdot}005 < 0{\cdot}01$), but neither of these slopes were significantly different from the slope at intermediate activity. Physiologically, as the activity of the male snails increases, the respiration coefficient decreases.

A similar SNK analysis of the logarithmic comparison of weight specific oxygen consumption and weight, and of oxygen consumption and weight in females, indicated that there was no significant change in slope with changes in activity.

DISCUSSION

Viviparus contectoides follows the expected relationship of decreasing weight specific oxygen consumption with increasing weight (Fig. 3; Krogh, 1941; Brody, 1945; Bullock, 1955). The average weight specific oxygen consumption for *Oncomelania nosophora*, a 3-mg snail (estimated assuming a dry weight of 20% of wet body weight), was 1·4 µl O₂/mg per hr (Yanagisawa & Komiya, 1961), while for *Pomacea urceus*, whose dry weight is 2100 mg, the reported value is 0·31 µl O₂/mg per hr (Burky *et al.*, 1972). The range for the dry weight specific oxygen consumption for males in this study was 0·364–0·370 cm³ O₂/g per hr and for females was 0·133–0·302 cm³ O₂/g per hr, as shown in Table 4.

The value for the respiration coefficient depends on time of day, level of activity and average metabolic rate. Part of the variation in literature values may be due to the influences of these parameters. Data summarized in Table 2 indicate a range of respiration coefficients that is generally lower than reported values for many other invertebrates (Zeuthen, 1947, 1953; Hemmingsen, 1950, 1960). Toulmond (1967a, b), however, found that in several species of *Littorina*, the respiration coefficient is much lower in water than in air. He found a range of respiration coefficients in *Littorina* from 0·62 to 0·79 in air and 0·34 to 0·55 in water. As has been pointed out (e.g. Newell & Roy, 1973), this suggests that respiration coefficients for aquatic respiration cannot be meaningfully compared with those for aerial respiration.

Metabolic rate has also been reported to be dependent on temperature (Krogh, 1941; Bullock, 1955) and we have attempted to minimize these effects by maintaining the snails at a constant temperature of $22 \pm 1°C$. Variations in the physiological state of the animals (e.g. reproductive or nutritional state) have also been shown to influence the metabolic rate (e.g. Newell, 1973), and may have caused some of the observed variations.

Physiologically, the relationship between oxygen consumption and weight is the same in males and females; however, these relationships are statistically different because males weigh less than females. This can be seen in Fig. 3 by combining the lines for males and females at each of the activity levels. The resultant line is very similar to the curvilinear relationship presented for females at minimum

activity in Fig. 2. Therefore, the difference in slopes may be attributed to the difference in weight ranges, and not due to the difference in sex. While physiologically there is no difference in the relationship between metabolic rate and weight in males and females, there is an ecological and statistical difference due to the average weight differences.

In this study, I have attempted to determine the relationship between weight and oxygen consumption in *V. contectoides* at differing levels of activity. Phillipson (1963) has indicated the importance of continuous measurements of respiratory rate to account for diurnal rhythms in respiration. At intermediate and maximum activity levels in *V. contectoides*, the effect of activity on rate of oxygen consumption is greater than the effects of weight since the slope does not differ from zero. The relationship between oxygen consumption and body weight has been reported to be dependent on the level of activity during the test period (Newell & Northcroft, 1965; Newell, 1969). It has been observed by Newell (1973) and others that the oxygen consumption of active animals generally exceeds that of quiescent animals. The SNK analysis indicates a decrease in the respiration coefficient with increasing levels of activity in males, but shows no significant change in the respiration coefficient in females with changing activity. However, the slopes for the females lie in the center of the span of change for males and, therefore, it is possible that the females exhibited no significant change in activity in the three levels tested and, consequently, no change in the oxygen consumption was observed. As can be seen in Fig. 3, there was a general increase in the slopes of the lines relating weight specific oxygen consumption to weight, with increasing levels of activity in both males and females indicating that metabolic rate does generally increase with activity. The only feasible way that there can be no significant relationship between oxygen consumption and activity is that small snails are much more active than the larger snails.

While Davies & Walkey (1966) have proposed that the variations in the respiration coefficients should be regarded as deviations from the phylogenetic value of 0·75 reported by Hemmingsen (1960), available data seems to suggest that there is not a phylogenetic, ecological or physiological consistency in the respiration coefficient. There is currently no explanation available for the wide range of *b* values observed in poikilotherms, and it has been suggested (Dehnel & McCaughran, 1964) that a variety of environmental factors and inherent physiological mechanisms are responsible for determining the relationship between weight and oxygen consumption in various species.

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