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Effects of starvation on respiration and major nutrient stores of the prosobranch snail *Bellamya bengalensis* (Lamarck)

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Abstract. The effects of starvation on the metabolic rate and the glucose, glycogen and total lipid contents in the freshwater prosobranch snail *Bellamya bengalensis* (Lamarck) have been investigated. Starvation influenced the metabolic rate of *B. bengalensis*. Although there was an initial increase, the metabolic rate of both the sexes decreased in the later stages of starvation. There was a marked difference in the utilization of nutrient stores between male and female snails starved for 55 days.

Keywords. *Bellamya bengalensis*; metabolic rate; nutrient stores; starvation effects.

1. Introduction

Studies on the effect of starvation on the oxygen consumption of molluscs are sparse. Berg and Ockelmann (1959) studied the effects of starvation on the oxygen consumption of *Ancylus fluviatilis*, starved for 96 hr. Stickle and Duerr (1970) in *Thais lamellosa*, Widdows (1973), Bayne (1973) and Bayne *et al* (1976) in *Mytilus edulis*, Mane (1975) in *Katelysia opima* and Mane and Talikhedker (1976) in *Donax cuneatus* studied respiration in relation to starvation. Heeg (1977) observed the oxygen uptake during starvation and aestivation in the pulmonate snail *Bulinus africanus*.

Not only the metabolic rate but also the nutrient reserves decreased during starvation in a number of molluscs. von Brand (1931) found that in *Helix pomatia* the oxygen uptake and also the carbohydrate reserves decreased during starvation. Emerson (1967) found that the metabolism of the aquatic pulmonate *Planorbis corneus* is carbohydrate oriented because the snail utilized 95% of the original carbohydrate during 58 days of starvation. Emerson and Duerr (1967) found the herbivorous prosobranch *Littorina planaxis* and Stickle and Duerr (1970) found the carnivorous prosobranch *Thais lamellosa* to have lipid oriented metabolism, since these snails utilized lipid during starvation.

It appears that carbohydrate and/or lipid are the main nutrient reserves of molluscs. Many lamellibranchs and pulmonates utilize glycogen (von Brand *et al* 1948; 1957; Martin 1961; Martin and Goddard 1966) whereas, amphineurans utilize lipid (Giese 1966). Some gastropods appear to have carbohydrate oriented metabolism while others have lipid oriented metabolism.

In the present study an attempt has been made to investigate the effects of starvation on metabolic rate and glucose, glycogen and lipid reserves of the herbivorous prosobranch *Bellamya bengalensis* (Lamarck).

2. Material and methods

Animals were collected from a pond at Vengalayapalem village (16°24 N: 80°33′ E). After clearing the encrustations on the shells, the snails were acclimatized in the laboratory at 27 ± 2°C for 96 hr.

2.1 *Respiratory measurements*

Respiratory measurements were made by the method of Ganapati and Prasada Rao (1960) and the dissolved oxygen was estimated by Winkler's method (Golterman 1970). Metabolic rates were measured on individual snails at day 4, 8, 16 and 20 of starvation. Experiments were run for 2 hr and the time of the experiment (1100–1300 hr) was kept constant to avoid the effect of time of day on the respiration of snails. Each snail was used only once and the oxygen consumption for 1 hr was taken into consideration. After the experiment the snails were shelled and the wet weight of the soft parts was determined to the nearest 0·1 mg. The allometric equation $y/x = aX^{(b-1)}$ (Davies 1966; Newell 1970) was used to express the results. All experiments were carried out at constant temperature (27 ± 1°C) and pH ($8{\cdot}9 \pm 0{\cdot}1$). Experiments were performed on 10 males and 10 females at each period of starvation except at day 4 where 40 males and 60 females were used.

2.2 *Statistical procedure*

Regression lines were fitted by the method of least squares. The slopes and intercepts (elevations) of the regression lines are compared separately between males and females at each period of starvation and between successive periods of starvation in males and females using analysis of co-variance (Snedecor and Cochran 1967).

2.3 *Biochemical methods*

The glucose, glycogen and total lipid contents of snails prestarved and starved for 55 days were also estimated. The glucose and glycogen contents were estimated by the method of Kemp *et al* (1954) and total lipid by the method of Pande *et al* (1963). Immediately prior to chemical analysis, the animals were weighed, removed from the shells and sexed. They were then dissected, foot and visceral mass separated and their wet weight determined to the nearest 0·1 mg. Experiments were performed on 20 animals and the results are expressed as mg per 100 mg of wet weight.

3. Results

Few of the experimental animals died during the beginning weeks of starvation, only 10% mortality was observed on day 20. Most mortality occurred between days 40 and 50. Approximately 40% of the experimental animals were alive on day 55.

Figures 1 and 2 show the relationship of the metabolic rate and weight at different

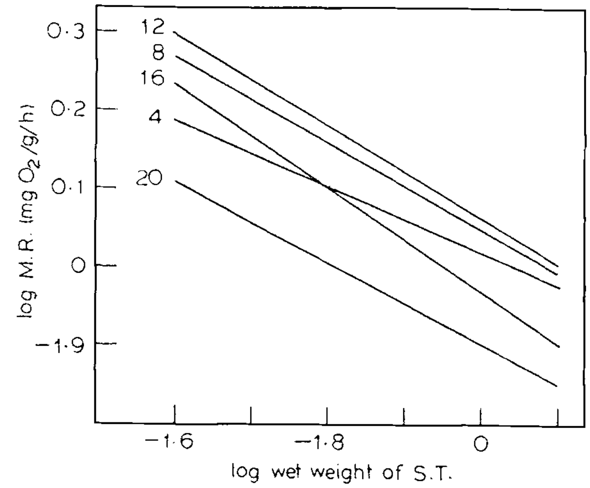

Figure 1. The relationship of log metabolic rate and log wet weight of soft tissues (ST) in males on different days of starvation.

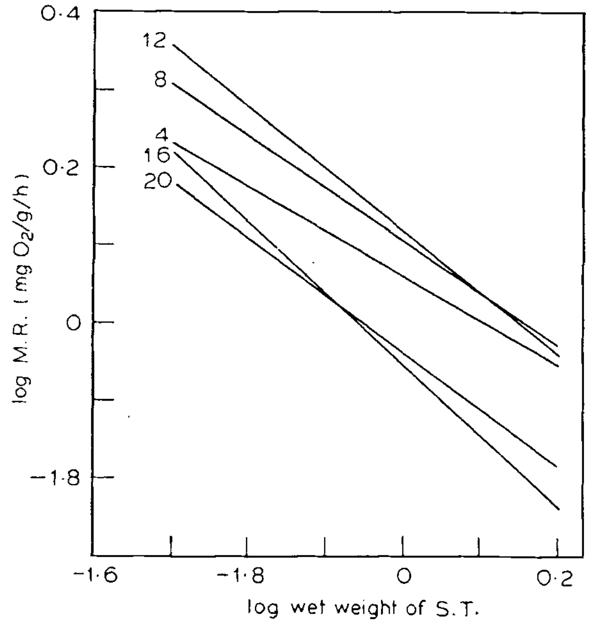

Figure 2. The relationship of log metabolic rate and log wet weight of soft tissues (ST) in females on different days of starvation

periods of starvation in males and females, respectively. The metabolic rate of both the sexes at all periods of starvation is negative linear in relationship with weight when plotted logarithmically. The regression equations are given in table 1. The wet weight of the soft parts and the metabolic rate ranged from 0·33 to 1·24 g and 0·63 to 1·94 mg O_2/g/hr in males and 0·47 to 1·88 g and 0·52 to 2·18 mg O_2/g/hr in females, respectively.

Table 1. Equations of the regression lines: log MR = log $a + (b - 1)$ log W, relating weight (W) in g. to metabolic rate (MR) of *B. bengalensis* at different periods of starvation.

Period of starvation (days)	Regression equations	
	Male	Female
4	log MR = 0·0224 − 0·4142 log W	log MR = 0·0639 − 0·5718 log W
8	log MR = 0·0506 − 0·5487 log W	log MR = 0·1098 − 0·6718 log W
12	log MR = 0·0657 − 0·5838 log W	log MR = 0·1225 − 0·7842 log W
16	log MR = −0·0292 − 0·6630 log W	log MR = −0·0508 − 0·9271 log W
20	log MR = −0·0953 − 0·5134 log W	log MR = −0·0348 − 0·7245 log W

n = 10 for each sex except at the period 4 days where 40 males and 60 females were used.

Tables 2–4 show the results of ANCOVA comparing the slopes and elevations of the regression lines for various sex-starvation combinations. The results presented in table 2 suggest common slopes and also common elevations for the two sexes for the 4th and 16th day of starvation, thereby indicating no marked differences in the metabolic rate of the male and female snails on these periods of starvation. Further, it is also clear that common slopes or elevations could not be assumed for the two sexes for the remaining periods of starvation (8, 12 and 20 days) suggesting that the metabolic rate of males and females differs significantly on these days.

The position of the regression lines in figures 1 and 2 shows that the metabolic rate in both the sexes is highest on 12th day and lowest on 20th day of starvation. The results of ANCOVA (tables 3 and 4) indicate common slopes amongst different periods of starvation in both the sexes. However, the elevations were significantly different between 4th and 12th day, 12th and 16th day and 16th and 20th day in males (table 3) and between 4th and 12th day and 12th and 16th day in females (table 4). The elevations also were not significantly different between 4th and 8th day and 8th and 16th day in both the sexes and between 16th and 20th day in females.

The above observations suggest that the metabolic rate between days 4 and 8, 8 and 12 in both the sexes and 16 and 20 in female is not significantly different. The difference in the metabolic rate between 4th and 12th day, however, is significantly different in both the sexes.

The effects of starvation on the metabolic rate of different standard weights, calculated from the regression equations presented in table 1, are shown in figures 3 and 4. It is evident from these figures that the general pattern of increase or decrease is same in both the sexes, but the rate at which the metabolic rate increased or decreased is different in different sizes of males and females. The percentage increase from 4th to 12th day in the young (0·5 g) and adult (1·25 g) males was 26 and 6 and in the young (0·5 g) and adult (1·5 g) females was 32 and 6, respectively.

The metabolic rate in both the sexes decreased after 12th day. In males it decreased by 10 to 20% and in females 25 to 43% from 12th to 16th day for different sizes. The metabolic rate showed further decrease of 17 to 25% from 16th to 20th day in males of different sizes while in females it remained more or less constant.

Emerson (1967) while studying the metabolism of *Planorbis corneus* stated that "in order to estimate the weight loss of dry soft parts during starvation, it is necessary to calculate the prestarved weights". Therefore, the wet weight, dry weight and entire

Table 2. Results of analysis of covariance: comparison of the slopes (*b*) and elevations (*a*) of the regression lines of males and females of *B. bengalensis* at different periods of starvation.

Period of starvation (days)	Variable (sex)	d.f.	*Sxx*	*Sxy*	*Syy*	$(b-1)$	Variation from regression S.S.	Variation from regression M.S.	Variance ratio (*F*)		Result
4	Male	39	0·7950	−0·3294	0·5307	−0·4143	0·3939	0·0082	F_{slopes}	0·9208	NS**
	Female	59	0·7081	−0·4048	0·8074	−0·5717	0·5760	0·0099	$F_{elevations}$	2·7030	NS**
8	Male	9	0·1185	−0·0652	0·0391	−0·5502	0·0032	0·0004	F_{slopes}	0·5417	NS*
	Female	9	0·2899	−0·1948	0·1654	−0·6720	0·0345	0·0043	$F_{elevations}$	12·0000	HS*
12	Male	9	0·1402	−0·0819	0·0590	−0·5842	0·0112	0·0014	F_{slopes}	2·2353	NS*
	Female	9	0·3147	−0·2467	0·2089	−0·7839	0·0155	0·0019	$F_{elevations}$	21·0000	HS*
16	Male	9	0·0758	−0·0504	0·0973	−0·6649	0·0638	0·0080	F_{slopes}	0·3750	NS*
	Female	9	0·2343	−0·2171	0·3036	−0·9266	0·1024	0·0128	$F_{elevations}$	0·1700	NS*
20	Male	9	0·0493	−0·0253	0·0343	−0·5132	0·0213	0·0027	F_{slopes}	0·7895	NS*
	Female	9	0·1076	−0·0779	0·0656	−0·7240	0·0092	0·0012	$F_{elevations}$	18·2105	HS*

NS = Not significant; HS = Highly Significant; *d.f. = F_{slopes}: 1,16 and $F_{elevations}$: 1,17; **d.f. = F_{slopes}: 1,96 and $F_{elevations}$: 1,97.

A 2

Table 3. Results of analysis of covariance: comparison of the slopes (b) and elevations (a) of the regression lines of males of *B. bengalensis* between successive periods of starvation.

Variable (period of starvation days)	d.f.	Sxx	Sxy	Syy	$(b-1)$	Variation from regression S.S.	Variation from regression M.S.	Level of comparison (days)	Variance ratio (F)		Result
4	39	0·7950	−0·3294	0·5307	−0·4143	0·3939	0·0082	4 and 8	F_{slopes}	0·2209	NS**
									$F_{elevations}$	2·8706	NS**
8	9	0·1185	−0·0652	0·0391	−0·5502	0·0032	0·0004	8 and 12	F_{slopes}	0·1111	NS**
									$F_{elevations}$	2·5555	NS**
									F_{slopes}	0·3864	NS**
									$F_{elevations}$	4·8736	S**
12	9	0·1402	−0·0819	0·0590	−0·5842	0·0112	0·0014	12 and 4	F_{slopes}	0·0638	NS*
								12 and 16	$F_{elevations}$	7·5000	HS*
16	9	0·0758	−0·0504	0·0973	−0·6649	0·0638	0·0080	16 and 20	F_{slopes}	0·1321	NS*
									$F_{elevations}$	7·8400	HS*
20	9	0·0493	−0·0253	0·0343	−0·5132	0·0213	0·0027				

NS = Not significant; S = Significant; HS = Highly Significant; *d.f. = F_{slopes}: 1,16 and $F_{elevation}$: 1, 17; **d.f. = F_{slopes}:1,46 and $F_{elevations}$: 1,47.

Table 4. Results of analysis of co-variance: comparison of slopes and elevations of the regression lines of females of *Bellamya bengalensis* between successive periods of starvation.

Variable (period of starvation days)	d.f.	*Sxx*	*Sxy*	*Syy*	$(b-1)$	Variation from regression S.S.	Variation from regression M.S.	Level of comparison (days)	Variance ratio (F)		Result
4	59	0·7081	−0·4048	0·8074	−0·5717	0·5760	0·0099	4 and 8	F_{slopes}	0·2258	NS**
									$F_{elevations}$	1·9121	NS**
8	9	0·2899	−0·1948	0·1654	−0·6720	0·0345	0·0043	8 and 12	F_{slopes}	0·6129	NS*
									$F_{elevations}$	1.0000	NS*
									F_{slopes}	1·0889	NS**
12	9	0·3147	−0·2467	0·2089	−0·7839	0·0155	0·0019	12 and 4	$F_{elevations}$	3·6800	NS**
								12 and 16	F_{slopes}	0·3784	NS*
									$F_{elevations}$	17·4507	HS*
16	9	0·2343	−0·2171	0·3036	−0·9266	0·1024	0·0128	16 and 20	F_{slopes}	0·4429	NS*
									$F_{elevations}$	0·3582	NS*
20	9	0·1076	−0·0779	0·0656	−0·7240	0·0092	0·0012				

NS = Not significant; HS = Highly Significant; *d.f. = F_{slopes}: 1, 16 and $F_{elevations}$: 1, 17; **d.f. = F_{slopes}: 1, 66 and $F_{elevations}$: 1, 67.

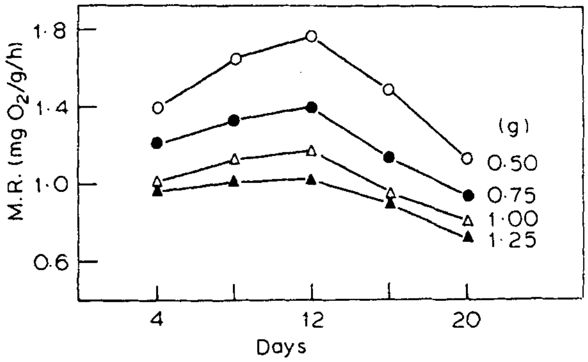

Figure 3. Metabolic rate-starvation curves for male *B. bengalensis* of different body weights.

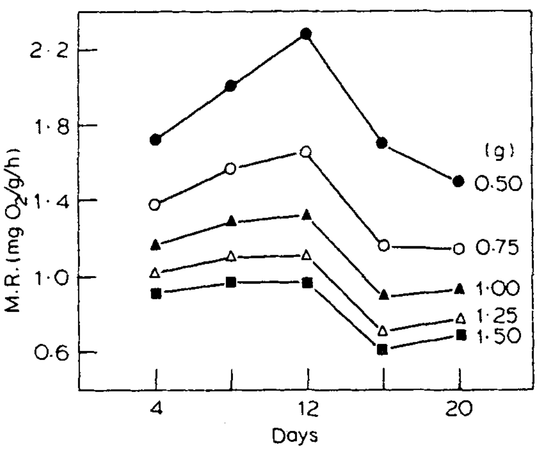

Figure 4. Metabolic rate-starvation curves for female *B. bengalensis* of different body weights.

weight relations are also calculated and a summary of the results is presented in table 5. From this table it is clear that the dry weight of the soft parts of animals starved for 55 days is 87 % of the prestarved weights indicating a loss of 13 %. This is considerably less than the weight loss of 23 % reported for the carnivorous prosobranch *Thais lamellosa* starved for 53 days (Stickle and Duerr 1970).

Few observations were also made on the metabolic rate of snails starved for 55 days. The average metabolic rate ($n = 5$; shell height range 1·8 to 2·5 cm) in males was 0·96 mg O_2/g/hr and in females 0·71 mg O_2/g/hr on 55th day of starvation.

The glucose, glycogen, total lipid contents and their percentage decrease in foot and viscera of male and female snails starved for 55 days are shown in table 6. The glucose, glycogen and total lipid in males and glucose and total lipid in females decreased more in foot than in viscera. Further, the glucose and glycogen contents decreased more in males than in females whereas, the lipid content decreased more in females than in males starved for 55 days.

Table 5. Weight loss of *Bellamya bengalensis* starved for 55 days.

	Control group (average of 20 animals)	Animals starved for 55 days (average of 10 animals)
Wet weight of soft parts of animals expressed as percentage of entire weight	31·00 (±0·7417)	34·36 (±1·8663)
Dry weight of soft parts of animals expressed as percentage of wet weight	18·19 (±0·5764)	13·99 (±1·1706)
Dry weight of soft parts of animals expressed as percentage of entire weight	5·64 (±0·2399)	4·89 (±0·6096)
Dry weight of soft parts of animals after starvation expressed as percentage of original dry weight	—	87·00
Factor		1·15

(Figure in parenthesis indicates standard error).
Factor = Reciprocal of 87%.

Table 6. Glucose, Glycogen and total lipid content of males and females of *Bellamya bengalensis* starved for 55 days.

	Male		Female	
	Foot	Viscera	Foot	Viscera
Glucose (%)				
Control	23·75	29·30	21·50	29·30
Starved	13·13	22·50	13·75	22·76
% Decrease	44·72	23·21	36·05	22·32
Glycogen (%)				
Control	43·75	46·25	23·75	41·25
Starved	16·56	26·25	16·56	21·88
% Decrease	62·14	43·24	30·27	46·96
Total lipid (%)				
Control	0·51	11·19	0·83	17·44
Starved	0·40	9·82	0·55	14·86
% Decrease	20·80	12·20	34·04	14·79

4. Discussion

Decrease in the metabolic rate has been reported in a number of starved molluscs. Lomte and Nagabhushanam (1971) found that the oxygen consumption of the freshwater mussel, *Parreysia corrugata* was reduced to nearly 50% after starving the animals for 10 days. Three-fifths reduction in the initial value of oxygen uptake of the limpet, *Ancylus fluviatilis* was recorded after 96 hr of starvation (Berg and Ockelmann 1959). There was 50 % reduction in the metabolic rate after a period of 8 days starvation in the clams, *Katelysia opima* (Mane 1975) and *Donax cuneatus* (Mane and Talikhedker 1976). In *Bellamya bengalensis* also starvation affected the metabolic rate. In both the sexes the metabolic rate showed an initial increase of about 15 % from 4th to 12th day of starvation. The metabolic rate decreased from 12th day onwards, but the rate of decrease was different in males and females. The metabolic rate of males, from 12th to 16th day, decreased by about 15 % and from 16th to 20th day by another 15 %; whereas the metabolic rate of females, from 12th to 16th day, decreased by about 30 % and from 16th to 20th day it remained more or less constant. Thus ultimately there is only 15 % reduction, from the initial value, in the metabolic rate of both the sexes of *Bellamya bengalensis* indicating that this decrease (15 %) is considerably less than that reported for bivalves, *Parreysia corrugata*, *Katelysia opima* and *Donax cuneatus* (50 %) and *Ancylus* (60 %).

It is of interest to note that, whereas the oxygen consumption of the pulmonates (von Brand *et al* 1948; Duerr 1965) and bivalves (Lomte and Nagabhushanam 1971; Widdows 1973; Bayne 1973, 1976; Mane 1975; Mane and Talikhedker 1976) decreased during starvation, the oxygen consumption of the prosobranch, *Bellamya bengalensis* increased during the initial days of starvation. This is in agreement with the previous work on the carnivorous prosobranch *Thais lamellosa* which also shows an increased oxygen consumption during starvation (Stickle and Duerr 1970).

After 12th day the metabolic rate of both sexes of *B. bengalensis* decreased. Stickle and Duerr (1970) stated that "a decreased oxygen consumption could indicate a lowered metabolic rate or it could indicate a switch in emphasis from a lipid oriented metabolism to a carbohydrate or protein oriented metabolism". von Brand *et al* (1948) found that in pulmonates the lowered oxygen consumption is an adaptation to conserve food stores. The increasing metabolic rate of *B. bengalensis* up to the 12th day of starvation indicates that this snail does not possess this adaptation in the initial stages of starvation. However, decrease in the metabolic rate after 12th day suggests conservation of food reserves or it may indicate a switch in the metabolism as suggested by Stickle and Duerr (1970). Calow (1975) has shown that on starvation, animals may have one of two responses; they may decrease their metabolism immediately as a means of saving energy or they may initially increase their metabolism due to increased activity caused by searching for food. The present study on *Bellamya bengalensis* indicates the possibility of both these responses in starving animals.

Twenty to 40 % of glucose, 30 to 60 % of glycogen and 12 to 34 % of total lipid is lost in snails starved for 55 days. This indicates that the snails utilize more glucose and glycogen than lipid during starvation. The decrease in the lipid content may be due to its direct utilization or it may be converted into carbohydrate during starvation. The results suggest that probably the metabolism of the herbivorous prosobranch, *B. bengalensis* is carbohydrate oriented like the other freshwater snails *Helix pomatia* (von Brand 1931) and *Planorbis corneus* (Emerson 1967). It is possible that some of the protein might have also been utilized during starvation, but no measurements of protein were made in the present study.

It is also interesting to note that, whereas the metabolic rate of males continued to decrease from 16th to 20th day of starvation, the metabolic rate of females remained constant during this period, thereby indicating that the ultimate decrease in the metabolic rate of both the sexes remains the same (15%) at the end of 20 days starvation. Further, when the metabolic rate of males decreased by only about 2%, the metabolic rate of females decreased by about 12% from 20th-55th day of starvation. Furthermore, there was also a marked difference between the male and female snails in the utilization of glucose, glycogen and total lipid stores. These observations suggest that there may be differences in the basic physiological and biochemical processes of the two sexes during starvation and it would be of interest to examine these processes in detail.

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