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EFFECT OF TEMPERATURE ON THE BIO-ENERGETICS OF THE LARVAE OF *BRACHYTHEMIS CONTAMINATA* (FABRICIUS) AND *ORTHETRUM SABINA* (DRURY) (ANISOPTERA: LIBELLULIDAE)

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Freshly emerged larvae of the 2 spp. were reared at 27 and 37 ° C up to emergence. *Artemia salina* nauplii were used as food. Quantity of food consumed, faeces defecated, energy converted and metabolised were estimated for the larval stages. Temperature influenced the number of instars; it varied between 9 and 13. Larval period was 170 days at 27 ° C and 101 days at 37 ° C for *B. contaminata*. *O. sabina* also extended the larval period at the low temperature in comparison to that at the high temperature. Temperature remarkably influenced the energetics parameters. Feeding and assimilation rates were highest at 37 ° C. However, the maximal efficiency of net conversion occurred at 27 ° C.

INTRODUCTION

Bioenergetics deals with the consumption and utilization of food in organisms. Scanning the publications and reviews in this field reveals that such studies have been more abundantly undertaken in herbivore than in carnivore insects (cf. WALDBAUER, 1968; SCHROEDER, 1972; MATHAVAN & PANDIAN, 1975; SCRIBER & SLANSKY, 1981). A rough calculation shows that only about 5-10% of the total published volume on bio-energetics pertain to carnivorous insects (MUTHUKRISHNAN & PANDIAN, 1987), all publications reporting solely on the situation at a constant experimental temperature (FISCHER, 1972; LAWTON, 1971; PANDIAN & MATHAVAN 1974; MUTHUKRISHAN, 1987; JAYAKUMAR, 1989). *Brachythemis contaminata* and *Orthetrum sabina* are tropical and their larvae are exposed to a temperature range of 20-37 ° C during different seasons of the year. No publication is available on the energy budget of tropical odonate larvae, reared at different experimental temperatures. The present paper reports the effect of temperature on growth and bio-energetics under constant temperatures.

MATERIAL AND METHODS

Eggs of *B. contaminata* and *O. sabina* were collected from freshly mated females and incubated at 27 or 37 ± 1° C. The freshly hatched larvae (after passing the pro-larval stage, instar I) were maintained individually at the respective temperatures in containers (capacity 250 ml) with pond water. *Artemia salina* nauplii (6-10 h old) were served as food. The nauplii were originally hatched at 17% salinity; after repeated wash with filtered pond water they were offered as food.

Feeding

Every day the larva was transferred to a feeding container, in which a known number of nauplii were kept; it was allowed to predate and feed on the nauplii for 2 hours and subsequently was transferred to its original container, in which the filtered pond water had been changed in the mean time. Unconsumed nauplii in the feeding container were collected and counted. The number of nauplii consumed by the larva was calculated as the difference between the number of nauplii offered and that collected as unconsumed; the total food consumed per instar was estimated by adding the number of nauplii consumed during an instar and multiplying it with the known energy content (0.0372±0.001 Joules/nauplius; 2.389±0.287 KJ/g dry weight).

The larvae defecated faeces in the form of pellets enclosed in a strong peritrophic membrane, making them convenient to collect. The pellets were collected every day, dried and accumulated separately for each instar; the pooled faeces were bombed to determine the energy content.

The test individuals were weighed at the beginning of the experiment and also after successive moultings. These weights were used to calculate the insect growth at the particular instar. Energy contents were determined using a 1411 Semi-micro bomb calorimeter (Parr Instruments, USA) following standard procedures.

Scheme of energy budget

The scheme of energy balance followed in the present study is that of the IBP formula (PETRUSEWICZ & MacFADYEN, 1970) usually represented as C=P+R+F+U, where C is the food energy consumed, P the growth, R the energy lost as heat due to metabolism, F the faeces and U the nitrogenous excretory products. In the majority of insects the energy content of uric acid (U) in faeces is negligible (about 0.2-0.5% of the faeces energy; HIRATSUKA, 1920; WALDBAUER, 1968; LAWTON, 1969). Therefore, in the present work, F represents the undigested food as well as the excretory nitrogenous wastes.

Quantitative estimations of C were made in Joules. The quantity of assimilated food energy (Ae) was estimated by subtracting F+U from C and that of P by subtracting the initial energy content of the freshly hatched or moulted individuals at the commencement of the experiment, from the final energy content of the individual at the end of the experiment. The term conversion has been used to refer to growth, i.e. P of the IBP terminology. Rates of feeding, assimilation and conversion were calculated to the respective amounts of food enery consumed, assimilated and converted relating to per unit mid live body weight (g) of the insect per unit time (day). Efficiencies of assimilation and conversion (K_2) were calculated in percentage relating Ae and P to the respective amounts of food energy consumed and assimilated.

Standard deviation (SD) and Student's "t" test were calculated following ZAR (1988).

Calculation procedure related to food utilization:

$$\text{Feeding rate} = \frac{\text{Average food consumed (C) (J/day)}}{\text{Mid live body weight of larva (g)}}$$

$$\text{Assimilation rate} = \frac{\text{Average food assimilated (Ae) (J/day)}}{\text{Mid live body weight of larva (g)}}$$

$$\text{Conversion rate} = \frac{\text{Average food converted (P) (J/day)}}{\text{Mid live body weight of larva (g)}}$$

$$\text{Assimilation efficiency} = \frac{\text{Mean food assimilated (Ae)}}{\text{Mean food consumed (C)}} \times 100$$

$$\text{Conversion efficiency} = \frac{\text{Mean food converted (P)}}{\text{Mean food assimilated (Ae)}} \times 100$$

Overall rates (Cr, Ar & Pr) were calculated by dividing the sum of products of the duration of each instar and the rates corresponding to it by the total feeding period.

RESULTS

LARVAL DURATION AND GROWTH

B. contaminata passed through 12 instars in 171±12 days and attained a maximum body weight of 626 J just before emergence at 27° C (Fig. 1; Tab. I); at 37° C, not only the number of instars decreased to 11, but also the life span of the

Table I

Larval duration of *B. contaminata* and *O. sabina* as function of instar and temperature. [± represents SD; — each observation is an average of 10-30 individuals].

Life stage (instar)	*B. contaminata* 27° C Duration (days)	*B. contaminata* 37° C Duration (days)	*O. sabina* 27° C Duration (days)	*O. sabina* 37° C Duration (days)
II	4.3±0.16	4.6±0.16	6.2±0.24	3.0±0.14
III	5.3±0.16	6.3±0.13	4.4±0.28	3.5±0.20
IV	6.7±0.25	4.8±0.23	4.4±0.28	3.0±0.04
V	6.3±0.16	7.1±0.31	6.6±0.17	3.8±0.23
VI	6.4±0.31	9.2±1.59	6.8±0.23	3.8±0.24
VII	8.8±0.14	8.0±1.45	6.2±0.23	4.6±0.20
VIII	12.5±1.14	6.8±0.99	7.2±0.20	5.2±0.31
IX	13.1±1.22	9.8±1.64	11.4±0.28	7.0±0.24
X	34.6±2.93	14.6±2,71	15.8±1.80	10.1±0.28
XI	33.8±3.62	30.0±4.87	20.5±1.45	8.6±1.90
XII	35.8±5.01	(emerged)	17.2±1.95	15.6±0.97
XIII	(emerged)		22.4±2.26	16.2±1.03
XIV			31.2±4.86	20.4±2.15
XV			(emerged)	30.4±4.95
Total	*170.7*	*101.2*	*160.3*	*135.2*

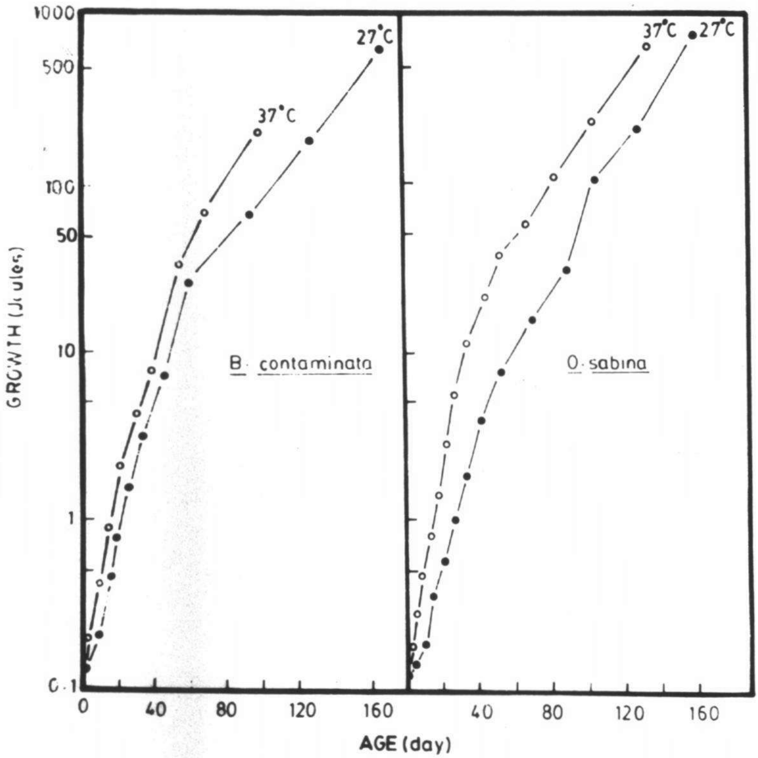

Fig. 1. Growth of *B. contaminata* and *O. sabina* as functions of developmental period and experimental temperature.

larva decreased to 101±9 days; prior to emergence, the insect contained 200 J (Fig. 1).

O. sabina underwent 14 or 15 instars at 27 or 37° C prior to emergence. The larva attained 754 J in 160±10 days just before emergence at 27° C (Fig. 1); the corresponding value for the dragonfly at 37° C was 683 J in 135±8 days (Fig. 1). At higher temperatures, the larval duration as well as the final body weight attained by both species decreased; while *B. contaminata* lost one instar, *O. sabina* added one at 37° C.

The initial energy content of a freshly hatched *B. contaminata* larva averaged 0.126 J at 27 and 37° C; it steadily increased to 25 J at the commencement of the 9th instar and subsequently to 623 J at 27° C (Fig. 1). Though the dragonfly grew to about 33 J at the commencement of the 9th instar at 37° C, it attained only 201 J before emergence (Fig. 1).

O. sabina grew to about 33 or 38 J at 27 or 37° C at the commencement of the 10th or 11th instar and subsequently to 753 or 682 J at these temperatures. The energy content almost doubled during the successive instars. Of the total growth, about 70% occurred during the final instar.

FOOD INTAKE AS A FUNCTION OF LIFE STAGE

B. contaminata consumed nauplii equivalent to 0.17 J during the second instar; the amount of food consumed steadily increased to 983 J in the 12th instar at 27° C (Tab. IV). Of the total food equivalent to 1394 J consumed from the second instar to emergence, 78% was consumed during the 12th instar period. It may be noted that only during the 12th instar period, larvae exhibited more than 70% growth.

Table II

Energy budget of *B. contaminata* fed ad libitum on *Artemia salina* nauplii at 27±1° C — [Each observation is an average of 10-30 individuals; — all values are expressed in Joules/individual].

Instar	Consumed	Faeces	Assimilated	Converted	Metabolized
II	0.172± 0.004	0.013±0.003	0.159	0.038± 0.004	0.121
III	0.423± 0.004	0.046±0.004	0.377	0.046± 0.004	0.331
IV	0.799± 0.008	0.071±0.005	0.728	0.259± 0.004	0.469
V	1.280± 0.004	0.092±0.008	1.188	0.326± 0.008	0.862
VI	2.235± 0.025	0.226±0.004	2.009	0.745± 0.008	1.264
VII	4.627± 0.063	0.448±0.018	4.179	1.489± 0.042	2.690
VIII	15.590± 0.719	1.452±0.036	14.138	4.151± 0.075	9.987
IX	40.935± 4.280	3.397±0.089	37.538	17.815± 0.105	19.723
X	100.977±11.473	11.008±0.457	89.968	39.827± 4.774	50.141
XI	244.132±22.234	29.054±1.401	215.078	110.650± 8.426	104.428
XII	983.002±80.923	123.859±7.714	859.143	450.801±35.275	408.342
Total	*1394.172*	*169.666*	*1224.505*	*626.147*	*598.358*

Table III

Energy budget of *B. contaminata* fed ad libitum on *Artemia salina* nauplii at 37±1° C

Instar	Consumed	Faeces	Assimilated	Converted	Metabolized
II	0.256± 0.004	0.013±0.002	0.243	0.100±0.008	0.143
III	0.632± 0.013	0.038±0.005	0.594	0.197±0.013	0.397
IV	1.485± 0.008	0.121±0.009	1.364	0.506±0.029	0.858
V	2.544± 0.092	0.205±0.008	2.339	1.209±0.008	1.130
VI	6.456± 0.276	0.473±0.038	5.983	2.071±0.021	3.912
VII	14.355± 0.314	1.481±0.042	12.874	3.548±0.013	9.326
VIII	26.865± 0.448	2.740±0.089	24.125	7.247±0.029	16.878
IX	48.271± 0.456	4.887±0.252	43.384	18.041±0.148	25.343
X	99.361± 8.372	11.828±0.602	87.533	36.204±1.251	51.329
XI	288.448±23.129	28.849±1.879	259.599	131.352±8.606	128.247
Total	*488.673*	*50.635*	*438.038*	*200.475*	*237.561*

Table IV
Energy budget of *O. sabina* fed ad libitum on *Artemia salina* nauplii at 27±1° C.

Instar	Consumed	Faeces	Assimilated	Converted	Metabolized
II	0.210± 0.004	0.017±0.009	0.193	0.021± 0.004	0.172
III	0.276± 0.004	0.033±0.004	0.243	0.038± 0.001	0.205
IV	0.523± 0.008	0.033±0.001	0.490	0.180± 0.008	0.310
V	1.004± 0.008	0.100±0.001	0.904	0.222± 0.013	0.682
VI	2.485± 0.184	0.314±0.001	2.171	0.444± 0.021	1.727
VII	4.100± 0.163	0.494±0.003	3.606	0.803± 0.038	2.803
VIII	8.564± 0.644	0.858±0.004	7.706	1.999± 0.079	5.707
IX	17.769± 0.644	2.276±0.039	15.493	3.786± 0.079	11.707
X	35.141± 3.925	4.184±0.096	30.957	7.719± 0.159	23.238
XI	51.969± 5.611	5.201±0.186	46.768	15.924± 0.589	30.844
XII	204.534±30.292	20.456±0.056	184.078	77.215± 0.589	106.863
XIII	298.406±41.179	34.915±0.167	263.491	111.143± 8.673	152.348
XIV	1058.723±97.270	120.695±4.327	938.028	534.531±35.459	403.497
Total	*1683.704*	*189.576*	*1494.128*	*754.025*	*740.103*

Therefore, any decrease in the number of instars consequent to changes in environmental factors like temperature, food quantity etc., will have a corresponding effect on the final body weight.

At 37° C, *B. contaminata* increased food consumption from 0.25 J during the second instar to 288 J during the final (11th) instar (Tab. III). Instead of passing on to the 12th instar, the larva emerged as an adult at 37° C. Consequently, total consumption was only 490 J, i.e. the consumption was reduced to about one third of that consumed at 27° C.

O. sabina consumed about 0.21 J during the second instar and the food intake increased to 1059 J during the 14th instar at 27° C; the corresponding values at 37° C were 0.32 J and 943 J. On the whole, *O. sabina* consumed 1683 J or 1650 J at 27 or 37° C (Tabs IV, V), from hatching to emergence.

Assimilation efficiency values obtained ranged from 87.2% in 9th instar *O. sabina* at 27° C to 96.4% for second instar *B. contaminata* at 37° C. The overall efficiency averaged 87.8% and 89.6% for *B. contaminata* at 27 and 37° C, respectively. The values were 88.5 and 89.5% for *O. sabina* (Fig. 2). However, the variations observed between the two temperature series in either species were found statistically not significant ($P > 0.1$).

Conversion efficiency ranged from 10.9% for second instar *O. sabina* at 27° C to 56.9% for the 14th instar of the same species (Fig. 3). Individual variations in the efficiency among the tested instar groups of either species were not marked. No definite trend was apparent when the efficiency values were plotted against life stage (Fig. 3).

The overall efficiency was 51% at 27° C and 46% at 37° C. Species-dependent variations in the overall efficiency were not statistically significant at the corre-

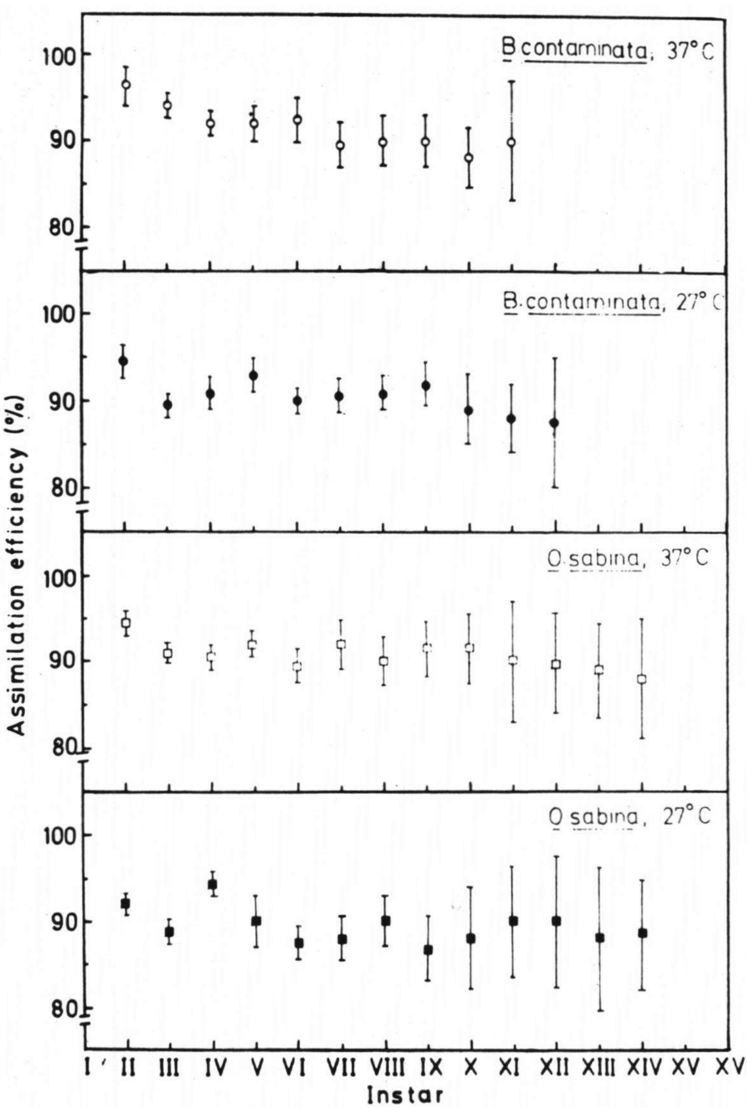

Fig. 2. Instar-wise assimilation efficiency of *B. contaminata* and *O. sabina* at the rearing temperatures.

sponding temperatures ($P > 0.1$). However, the differences in the overall efficiency among the test temperatures series were significant (*B. contaminata* $P < 0.01$; *O, sabina* $P < 0.5$). It may be concluded that the efficiency is temperature-

Table V
Energy budget of *O. sabina* fed ad libitum on *Artemia salina* nauplii at 37±1°C.

Instar	Consumed	Faeces	Assimilated	Converted	Metabolized
II	0.323± 0.008	0.017±0.001	0.306	0.059± 0.001	0.247
III	0.606± 0.008	0.059±0.001	0.547	0.108± 0.001	0.439
IV	0.678± 0.017	0.067±0.001	0.611	0.188± 0.004	0.423
V	1.133± 0.042	0.092±0.004	1.041	0.326± 0.004	0.715
VI	1.786± 0.042	0.188±0.005	1.598	0.611± 0.008	0.987
VII	3.716± 0.005	0.293±0.013	3.423	1.477± 0.013	1.946
VIII	5.974± 0.678	0.602±0.034	5.372	2.707± 0.029	2.665
IX	14.878± 0.803	1.264±0.042	13.615	5.648± 0.109	7.966
X	25.673± 0.854	2.184±0.077	23.489	9.389± 0.310	14.100
XI	49.543± 8.205	4.983±0.181	44.560	16.753± 0.787	27.807
XII	86.960± 8.063	9.138±0.319	77.822	22.330± 3.816	55.492
XIII	154.691±12.025	16.983±0.579	137.708	53.183± 4.469	84.525
XIV	361.497±34.455	41.798±1.521	319.699	123.763±12.314	195.936
XV	942.823±87.587	91.211±7.712	851.612	446.973±39.459	404.639
Total	*1650.281*	*168.879*	*1481.402*	*683.515*	*797.887*

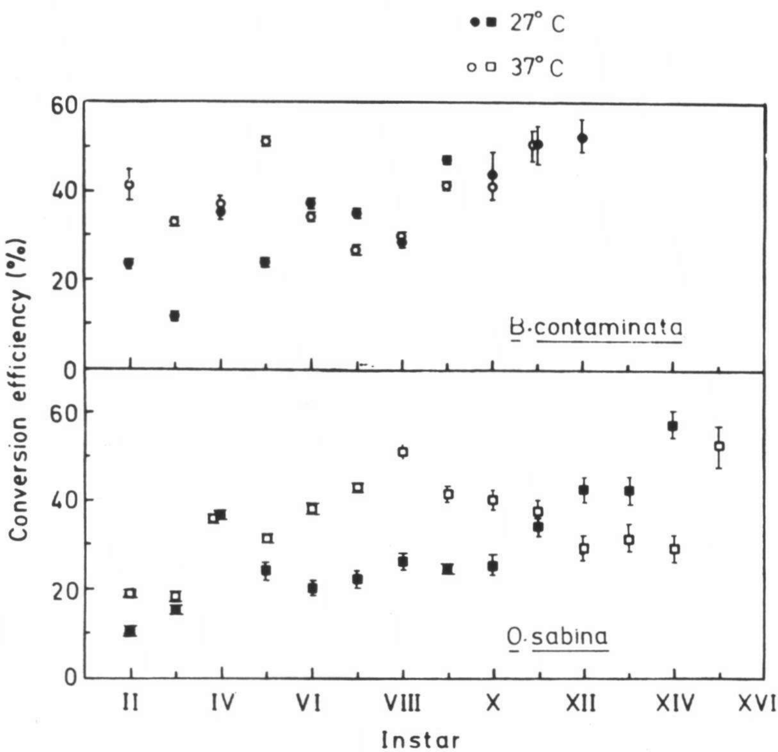

Fig. 3. Instar-wise conversion efficiency of *B. contaminata* and *O. sabina* at the rearing temperatures.

-dependent rather than species-dependent.

The exuviae of each instar were separately collected, dried, and their respective energy contents calculated. Calorific contents of exuviae of either species (different instar and temperatures) averaged 1843.5±493.3 J/g dry weight and this value was comparable with that (18.9 KJ, range: 18.4-19-4 KJ/g dry weight) reported for exuviae of *Pyrrhosoma nymphula* (LAWTON, 1971). Total exuviae production amounted to 59 J at 27° C and to 17 J at 37° C in *B. contaminata*, which corresponds to 9 and 8% of the total conversion at the respective temperatures. In *O. sabina*, the corresponding values were 9% and 8% of the total conversion at 27 and 37° C, respectively.

In Figure 4 rates of feeding assimilation and conversion are given as functions

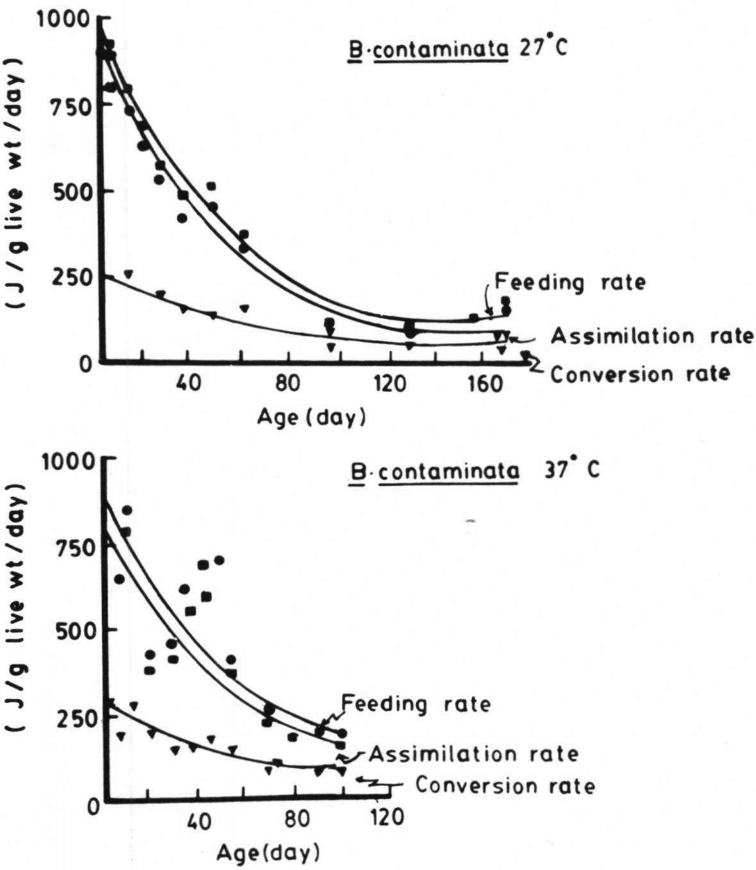

Fig. 4. Rate of feeding, assimilation and conversion of *B. contaminata* at the rearing temperatures of 27 and 37° C.

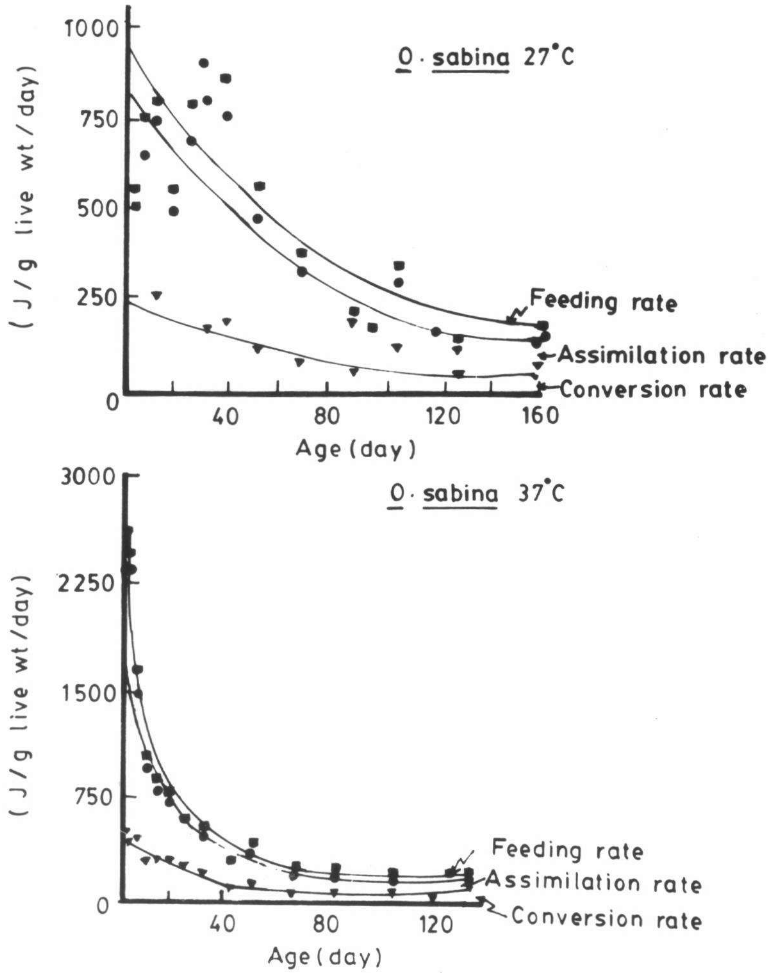

Fig. 5. Rate of feeding, assimilation and conversion of *O. sabina* at the rearing temperatures of 27 and 37° C.

of age in *B. contaminata* larvae. The curvilinear trends obtained for rate functions indicate that with advancing age, less and less food is consumed per unit of time and per unit of weight of the insect; the same is reflected in successive processes, i.e. assimilation and conversion. Similar trends were obtained for the rates of feeding, assimilation and conversion for this species at 37° C. Trends obtained for *O. sabina* at 27 and 37° C are presented in Figure 5. While the trends remained more or less similar in either species at either temperature, the level of function

Table VI
Bioenergetics of *B. contaminata* and *O. sabina* reared in the laboratory on *Artemia salina* nauplii at 27 and 37±1° C.

Parameter	*B. contaminata*		*O. sabina*	
	27° C	37° C	27° C	37° C
Larval duration (days)	171	101	160	135
Number of instars	12	11	14	15
Food intake (J)	1394.173	488.673	1683.704	1650.281
Food assimilated (J)	1224.507	438.038	1494.128	1481.402
Converted (J)	626.149	200.475	754.025	683.515
Exuviae (J)	58.576	16.736	69.036	54.392
Feeding rate*	294.554	418.818	395.806	411.287
Assimilation rate*	258.989	376.978	350.200	367.773
Conversion rate*	131.796	173.217	174.891	169.033
Assimilation efficiency (%)	87.8	89.6	88.7	89.8
Conversion efficiency (%)	51.1	45.7	50.4	46.1

* Joules/g live nymph/day

changed according to the species and temperature.

Feeding rate of *O. sabina* from hatching to emergence averaged 402 J/g live larva/day at either temperature. About 85% of the ingested food was assimilated, 48% of the assimilated food was converted; of the latter, 12% was lost through exuviae. At either temperature, 52% of the assimilated food was used for respiration (Tab. VI).

In *B. contaminata* feeding rate averaged 294 and 418 J/g live larva/day at 27 and 37° C, respectively. Of this, 11% was lost via faeces. Of the assimilated food energy, 48.5% was converted and the rest lost on respiration at either temperature; 8.5% of the total conversion was lost as exuviae (Tab. VI).

DISCUSSION

Analysis of data on the assimilation efficiency of the larvae showed that irrespective of temperature, instar or species it is around 89% with a standard deviation of about 5%. However, an in-depth analysis showed that assimilation efficiency is directly proportional to temperature and indirectly proportional to instar. This confirms the high assimilation efficiency value reported by LAWTON (1971) for the zygopteran *Pyrrhosoma nymphula* (88%) and by PANDIAN & MATHAVAN (1974) for the anisopteran *Diplacodes trivialis* (91%). Comparable high efficiency values (86%) have also been reported for the terrestrial carnivorous dyctiopteran *Mantis religiosa* (MUTHUKRISHNAN, 1987).

Working on the effect of temperature on the energy balance of carnivorous *Mantis religiosa*, MUTHUKRISHNAN (1987) showed that the assimilation efficiency was maximal in the initial nymphal instars and decreased with advancing age. Temperature also influenced the assimilation efficiency in *M. religiosa* irrespective of life stage or sex, and it is directly proportional to temperature. This evidence is similar to the one obtained in the present study.

However, FISCHER (1972) reported an assimilation efficiency of 50% for larval *Lestes sponsa.* The low efficiency in this zygopteran may be due to (1) the nature of food, (2) the methodology of calculation and (3) some experimental error. Consumption of *B. contaminata* at 37° C was reduced to about one third of the consumption at 27° C. Correspondingly, the final body weight attained by the larva was also only a third of that at 27° C. Therefore, food intake is an important factor that determines growth rate as well as final body weight.

At 27° C, both *B. contaminata* and *O. sabina* consumed food equivalent to over 1.045 KJ/g life weight/day (5 day old nymph). Feeding rate decreased to less than 209 J/g/day in the 160 day old larvae. The trend obtained for the rates of assimilation and conversion as a function of age, was more or less parallel to the one obtained for feeding rate-age relationship in either species. At 37° C, the feeding rate in the 3 day old *O. sabina* was as high as about 2.34 KJ/g/day. Such high feeding rate exhibited during the young age compensated for the reduction of life span from 160 days to 135 days, as well as for the final body weight obtained. However, *B. contaminata* failed to compensate by a high feeding rate and also showed a great reduction in the larval duration. The result is the smaller final body weight at emergence.

The larval feeding rates of either species at either temperature are relatively lower than the ones reported for lepidopterans. However, the larvae compensated the low feeding rate through high assimilation efficiency and assimilation rate. Further, there was no need for the larvae to accumulate the reserve energy, as dragonflies feed during the adult stage also, while some lepidopterans do not feed during the adult stage and have to accumulate energy for the non--feeding pupal and adult periods.

Overall production efficiency of *B. contaminata* and *O. sabina* ranges from 46-51%. This value is comparable to the one obtained in other odonates (*P. nymphula:* 51%, LAWTON, 1970; *D. trivialis:* 48%, PANDIAN & MATHAVAN, 1974). However, other carnivores like *Speliphoron violaceum* show a conversion efficiency of about 80% and *M. religiosa* displays a conversion efficiency of only about 25-45%. These values are exceptionally high or low. It may be concluded that dragonflies have an overall production efficiency of 50%, which is common in many of the carnivorous insects (MUTHUKRISHNAN & PANDIAN, 1987).

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