PATTERNS OF ENERGY UTILIZATION IN THE TROPICAL DRAGONFLY, *DIPLACODES TRIVIALIS* (RAMBUR), AND SOME OTHER AQUATIC INSECTS (ANISOPTERA: *LIBELLULIDAE*)

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The dragonfly larva, *D. trivialis* fed on *Artemia salina* nauplius was reared in the laboratory from hatching until it emerged as an adult. An average individual weighed 46 mg (wet weight) on the 135th day, when it became adult. Total food intake amounted to 61.5 cal. Feeding rate averaged 140 cal/Kcal insect/day. Assimilation efficiency amounted to 91%. Of the total assimilated food, 48.1% was converted into body substance and 51.9% was used on respiration. Rates of intake, assimilation and conversion of other insects are discussed in relation to *D. trivialis*.

INTRODUCTION

Odonates, plecopterans, ephemeropterans and some dipterans are the major aquatic insect consumers. While odonates feed during larval and adult stages, ephemeropterans and dipterans such as chironomids accumulate sufficient food energy during the larval period to tide over the subsequent non-feeding pupal and/or adult stages. Consequently, the food utilization pattern is likely to show considerable adaptive differences between these two insect groups. A number of publications concerning the energy budget of herbivorous insects [e.g. Lepidoptera: *Bombyx mori* (HIRATSUKA, 1920; cf. also WALDBAUER, 1968), Orthoptera: *Oxya velox* (DELVI & PANDIAN, 1971)] and carnivorous insects [e.g. the dragonflies *Pyrrhosoma nymphula* (LAWTON, 1971a), and *Lestes sponsa* (FISCHER, 1966, 1967, 1972)] are available. This paper reports additional information on the pattern of energy utilization in the larva of *Diplacodes trivialis* and compares it with that of other insects.

MATERIALS AND METHODS

Diplacodes trivialis (Rambur) is a common Indian libellulid. The larva usually undergoes 12 instars before ecdysis.

A copulating pair of *D. trivialis* was brought to the laboratory and the last abdominal segment of the female was frequently dipped in water to enable it to oviposit (cf. KUMAR, 1972). The eggs were incubated at 32°C; the freshly hatched larvae were removed to separate glass containers (capacity: 250 ml) with filtered pond water. The experiments were carried out at 32°C with 10 hr photoperiod (10L : 14D). The larvae were fed on *Artemia salina* nauplii (6 to 10 hr old) originally hatched in 17‰ S. The live nauplii (after repeated washing in filtered pond water) were offered individually to the dragonfly larvae once a day between 9 and 10 a.m. The larvae received as many nauplii as they would accept at the time of feeding. There was a distinct change in behaviour of the larvae when the moment of satisfaction was reached.

The number of nauplii predated by *D. trivialis* was counted every day and the total food consumption per instar was calculated by adding the number of nauplii consumed during an instar and multiplying it with the known energy content of the nauplii (1 nauplius = 0.0088 cal; mean of 0 hr and 24 hr; PAFFENHÖFER, 1967).

D. trivialis defecated faeces in the form of pellets. The pellets were collected daily between 8 and 9 a.m. Generally, the pellets were intact and appeared to have incurred no loss. However, a certain amount of dissolvable faecal matter might have been lost, but that was considered to be negligible. The collected faeces were dried, accumulated (separately for each instar) and (pooled faeces of all the instars) bombed to determine the energy content. The quantity of assimilated food was determined, subtracting the calorific equivalents of the faeces from that of consumed food. The assimilation efficiency is expressed as percentage of the consumed energy.

At the commencement of the experiment as many as 50 larvae were fed; of these, 17 died before attaining the third instar. During subsequent instars, there was almost no mortality and 9 individuals survived until emergence. At the termination of each instar 2 to 4 individuals were sacrificed to estimate the water content of the larvae.

The amount of food energy converted for growth was determined from the increase of the energy content of the larvae during each instar. Dry substances of *D. trivialis* belonging to different instars were pooled and the energy content was estimated in a semi-micro bomb calorimeter, following the standard procedure described in the instructions of Parr bomb calorimetry Nos 128 and 130. The mean calorific content of *D. trivialis* is 4925 ± 358.9 Kcal/g dry weight. Since the water content of the larvae at the end of each instar is known, the mean increase in wet weight of all the test larvae of the same instar was converted into dry weight; the dry weight value was converted into energy value using the mean energy content of the larvae. The efficiency of conversion has been calculated as the percentage of food energy assimilated (K_2 or net efficiency; RICHMAN, 1958; PANDIAN, 1967).

In the present study, direct estimates were made on food intake (C), faeces (F) and growth (P). Using the IBP formula, C = P + R + F (PETRUSEWICZ & MACFADYEN, 1970), food energy assimilated (C – F) and that expended on respiration R = C – (F + P) have been calculated. In his studies on *Pyrrhosoma nymphula*, LAWTON (1971a) has collected data on defecation (F) and growth (P) from the field and respiration (R) in the laboratory. Using these values of F, P and R, he calculated intake of food (C). The feeding rate of *P. nymphula* in the field is 30 to 80% less than the maximum feeding rate in the laboratory; the main reason for this depressed feeding rate is the low food density (LAWTON, 1971b). It is very likely that the density of prey organisms can alter the feeding rate and hence all the other parameters in the energy budget. However, the present preliminary study on the energy budget of *D. trivialis* has been restricted to the feeding schedule described above.

RESULTS

Diplacodes trivialis required 135 days and passed through 12 instars to become adult. The 2nd-8th instars lasted for about 6.6 days each and the 9th, 10th, 11th and 12th instars lasted for 15.8, 21.2, 24.0 and 34.7 days, respectively. The initial weight of freshly hatched larvae averaged 0.01 mg live (wet) weight and they steadily increased their weight to 46.0 mg at the time of emergence (Fig. 1). The larvae steadily increased their weight from 0.01 mg at the beginning of 2nd instar to 3.7 mg at the commencement of 10th instar. However the total growth was rapid during the last 3 instars.

The non-feeding first instar *D. trivialis* lasted for a few hours only; the second instar was very small and as they did not feed on *Artemia* nauplii (but appeared to feed on protozoans), it was not possible to estimate energetics data. Total intake (calories of food/instar) steadily increased from 0.055 cal for the 3rd instar to 32.1 cal for the final instar (Tab. I). On the whole, during the entire larval period, nauplii equivalent to 61.5 cal were consumed by an average larva. The feeding rate of *D. trivialis* (cal/Kcal insect/day; cf. DELVI & PANDIAN, 1972) was 140.3 cal/Kcal/day for the larval period.

Assimilation efficiency did not change appreciably from instar to instar and averaged 91 ± 3.5%.The amount of food material assimilated increased steadily from 0.052 cal during the third instar to 29.225 cal during the final instar (Tab. I). *D. trivialis* assimilated 56.254 cal of food during its entire larval period. Maximum food was assimilated during the last instar. Food energy converted into the dragonfly substance including exuvia was equivalent to 27.051 cal.

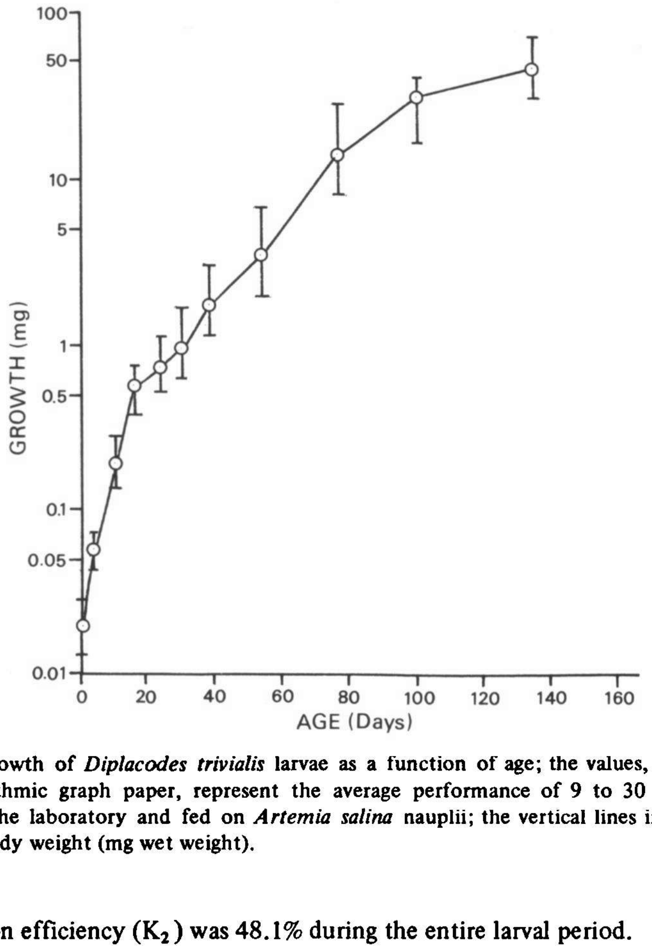

Fig. 1. Growth of *Diplacodes trivialis* larvae as a function of age; the values, plotted on semi-logarithmic graph paper, represent the average performance of 9 to 30 individuals reared in the laboratory and fed on *Artemia salina* nauplii; the vertical lines indicate the range of body weight (mg wet weight).

Conversion efficiency (K_2) was 48.1% during the entire larval period.

DISCUSSION

In the present study *Artemia salina* nauplii were used as food since the nauplius resembles the natural food organisms of *D. trivialis* (such as daphnids) in size, colour and activity. *A. salina* nauplii were preferred over daphnids because of the ease with which *A. salina* could be maintained in the laboratory. Large *D. trivialis* larvae may prefer to feed on relatively large organisms such as chironomids as against the small daphnids; however, left with no choice but to feed on *Artemia* nauplii only, the large dragonfly larvae will expend more energy on predatory activity. Consequently their final body weight may be depressed. In

Table I

Energy balance of the dragonfly larva *Diplacodes trivialis*. (Test individuals were fed from hatching to emergence with an unlimited supply of nauplii of *Artemia salina* at 32°C). All values are given in cal/instar

Instar	Instar period (day)	Consumed	Assimilated	Converted	Oxidized
III	4.5	0.055	0.052	0.020	0.032
IV	6.7	0.176	0.171	0.069	0.102
V	6.1	0.432	0.402	0.197	0.205
VI	7.5	0.607	0.553	0.148	0.405
VII	6.3	0.809	0.737	0.197	0.540
VIII	8.6	1.518	1.358	0.442	0.916
IX	15.8	4.119	3.849	1.083	2.766
X	21.2	7.765	7.205	5.559	1.646
XI	24.0	13.962	12.702	10.873	1.829
XII	34.7	32.105	29.225	8.463	20.762
Total	*135.4*	*61.548*	*56.254*	*27.051*	*29.203*

fact, *Orthetrum sabina* larvae fed on *A. salina* prior to emergence weighed 220 mg, as against the final body weight of 300 mg attained by the same species in the field (Mathavan, unpublished observation).

Basic energetics data for *D. trivialis* are given in Table II. For comparative

Table II

Data on the energy budget of the aquatic carnivore *Diplacodes trivialis* as compared with another carnivore *Pyrrhosoma nymphula* (from LAWTON, 1971a) and the herbivorous dipteran *Hedriodiscus truquii* (from STOCKNER, 1971)

Parameter	*D. trivialis* 32°C	*P. nymphula* 12°C	*H. truquii* 35°C	*H. truquii* 41°C
Instar period (day)	135	688	–	–
Food consumed (cal)	61.5	189.1	32.8	39.65
Food assimilated (cal)	56.3	166.1	19.9	25.4
Converted (cal)	27.1	85.6	11.1	14.2
Respired (cal)	29.2	84.6	8.75	11.25
Feeding rate (cal/Kcal/day)	140.3	45.4	184.2	252.7
Assimilation efficiency (%)	91.4	88.3	60.5	64.2
Conversion efficiency (%) (K_2)	48.1	51	56	56

purposes the basic data of LAWTON (1971a) on *Pyrrhosoma nymphula* and STOCKNER (1971) on the dipteran *Hedriodiscus truquii* are also given. It may, however, be mentioned that the energetics data were collected by these scientists mostly on field populations. The differences in the patterns of energy utilization observed may be due to the combined effects of environmental factors such as habitat temperature (*P. nymphula*: 12°C; *H. truquii*: 41°C) and prey density, and internal factors like genetically moderated physiological strategies.

In brief, the mean feeding rate of *D. trivialis* for the entire larval period was 140.3 cal/Kcal/day; of this, 91% was assimilated. Of the total energy assimilated, 48.1% was converted into body substances and 51.9% was used on metabolism. STOCKNER's (1971) elucidation of the energy budget of the herbivorous dipteran *Hedriodiscus truquii* and LAWTON's (1971a) energy budget estimation of the carnivorous zygopteran *Pyrrhosoma nymphula* reveal the following patterns of energy utilization: *H. truquii* ate 218.4 cal of algae/Kcal insect/day (mean values reported for *H. truquii* populations from springs No. 4 and No. 6) during the entire larval stage. About 62% of the consumed food was assimilated by the larva in both springs. About 56% of the assimilated food energy was converted into body substance; the remaining 44% was used on respiration. *P. nymphula* consumed 189 cal during the aquatic larval life span of 688 days; of the total consumed 88% was assimilated. Of the assimilated food, 51% was converted into body substance, and 49% was used on metabolism.

When an insect has to accumulate matter to tide over unfavourable (e.g. low temperature) or non-feeding period(s), it may do so either by increasing the feeding level, the assimilation or conversion efficiency, by reducing metabolic expenses, or by a combination of one or more of these possibilities. The dipterans like *H. truquii* appear to have utilized all these possibilities to accumulate sufficient energy during the feeding larval stage to tide over the non-feeding pupal and adult stages. The recalculated value for the feeding rate reported by DELVI & PANDIAN (1972) for *H. truquii* (STOCKNER, 1971) is 218 cal/Kcal insect/day. This may be compared with low feeding rates of *D. trivialis* (140 cal/Kcal insect/day) and *P. nymphula* (45 cal/Kcal insect/day). Likewise, assimilation (62%) and conversion (56%) efficiencies of *H. truquii* were relatively higher than such values reported for the herbivorous lepidopteran *Bombyx mori* (assimilation efficiency 42% and conversion efficiency 48%; HIRATSUKA, 1920).

Feeding rate values known for the odonates *D. trivialis* (140 cal/Kcal insect/day) and *P. nymphula* (45 cal/Kcal/day) are far lower in comparison with those of herbivorous insects (e.g. *B. mori*: 1159 cal/Kcal/day, *H. truquii*: 218 cal/Kcal insect/day). The feeding rate of a predator is a function of prey density and size, although the ultimate response may involve adjustment of these responses to things like assimilation efficiency. The prey density available to the carnivores in most ecosystems is less than that available to the herbivores. Therefore, herbivorous insects exhibit a high feeding rate but a low assimilation efficiency (e.g. *Oxya velox*, 30%, DELVI & PANDIAN, 1971; *Bombyx mori*, 42%, HIRATSUKA, 1920; *H. truquii* 62%, STOCKNER, 1971). On the other hand, the carnivorous dragonflies *D. trivialis* and *P. nymphula* show a high assimilation efficiency (90%), and hence compensate the low feeding rate at least in part. Thus, in order to assimilate what *D. trivialis* can obtain from 1 cal of food, *H. truquii* requires 1.4 cal of food, *B. mori* 2 cal of food and *O. velox* 3 cal of food.

P. nymphula and *D. trivialis* are exposed to different unfavourable conditions. An extension of the aquatic larval life span over a period of two years by *P. nymphula* is perhaps a consequence of low feeding rate and low field temperatures. Most temperate species usually have one to three years (CORBET, 1962; LAWTON, 1971a, 1971b; SCHALLER, 1973) and at the most and rarely, six years (e.g. *Uropetala carovei*, CORBET, 1962) of aquatic life span. On the other hand, the tropical odonate *D. trivialis*, which is exposed to high field temperatures and whose habitats are temporary seasonal ponds, completes its aquatic larval life span within a short period of 135 days; indeed, several tropical odonates complete the aquatic life span within a short period (e.g. *Orthetrum pruinosum neglectum*, 155 days; KUMAR, 1970) and yet pass through 10 instars. The fast growth rate observed in tropical odonates such as *D. trivialis* (0.2 cal/day, as against 0.11 cal/day in *P. nymphula*) may be ascribed to the high feeding rate exhibited by them. Probably *P. nymphula* may complete development in less than a year, if reared at high temperature with ample food supply. In fact, the temperate dragonfly *Lestes sponsa* is known to complete its larval development in a few months in the field, where there is an ample food supply (FISCHER, 1972).

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