Proc. Indian Acad. Sci. (Anim. Sci.), Vol. 97, No. 6, November 1988, pp. 505–517.

Bioenergetics and reproductive efficiency of *Atractomorpha crenulata* F. (Orthoptera: Insecta) in relation to food quality

M SENTHAMIZHSELVAN and K MURUGAN
Entomology Research Institute, Loyola College, Madras 600 034, India

MS received 14 July 1988; revised 1 September 1988

Abstract. Food consumption and utilization efficiency of *Atractomorpha crenulata* feeding on the leaves of *Ricinus communis*, *Arachis hypogaea* and *Panicum maximum* are discussed. Longevity and fecundity of the insect feeding on *Ricinus communis* were higher as compared to feeding on the other plants. Females tend to consume more food than the males in all the tested food plants. Energy allocated by the female to egg production varied between 7 and 15% of the assimilated energy during the adult phase.

Keywords. Food quality; food utilization; reproductive efficiency; *Atractomorpha crenulata*.

1. Introduction

Information on the quantitative food consumption and utilization of insects has been reviewed by Slansky and Scriber (1985) and Muthukrishnan and Pandian (1987a). Most of the relevant publications on the bioenergetics of insects relate to lepidopteran larvae. While basic information on the bioenergetics of acridids is provided by Delvi and Pandian (1971, 1972), the present work attempts to correlate the effect of food quality on food consumption and utilization of *Atractomorpha crenulata*, a phytophagous acridid weighing 0·4 g. As the reproductive efficiency of insects depends upon their life style and feeding pattern (Muthukrishnan and Pandian 1987b), different strategies are adopted by different insects to maximise their investment on reproduction (Calow 1973; Thompson 1975). In insects, the energy allocated to reproduction varies from 2–81% of their consumed energy (Llewllyn and Qureshi 1978; Slansky 1980). While Ananthakrishnan *et al* (1985) have considered the effect of food quality (*Ricinus communis*, *Arachis hypogaea* and *Panicum maximum*) on food consumption, longevity and fecundity of *A. crenulata* on dry weight basis for 24 h period with special reference to sensory morphology, the present paper reports the reproductive efficiency and food utilization efficiencies of *A. crenulata*.

2. Materials and methods

Eggs of *A. crenulata* reared in the laboratory were obtained from the soil before hatching. The newly emerged nymphs were weighed individually and reared in plastic terraria (375 ml capacity). The nymphs were fed *ad libitum* on weighed quantities of the leaves of the food plant (*R. communis*, *A. hypogaea* and *P. maximum*), twice a day. To serve as control, a sample leaf of identical age was dried at 60°C to constant weight in order to estimate the water content (Waldbauer 1968). Every day before feeding, unfed remains and the faeces egested by the insect were removed and dried for each instar and the adult. The nymphs were weighed after moulting into the successive instar as well as the adult female during the oviposition period which was determined by the development of oocyte in the ovary (Murugan and Jacob 1988), whereas food consumption by the male was estimated once in 30 days. Eggs were collected from the wet soil provided in the terraria in specimen tubes (5 × 5 cm). Following the gravimetric method of Waldbauer (1968) food consumption (C), egestion (FU) and growth (P) were estimated. Energy contents of the food, faeces and insect were estimated in a Parr 1421 semi-micro bomb calorimeter following the standard procedure described in the instruction manual. The increase in temperature due to the burning of the sample was recorded in a Omniscribe[R] recorder. Once in five estimations, the bomb was standardised by using benzoic acid. Using these energy values the mass budget involving C, FU and P was converted into energy budget expressed in Joules. Growth was estimated as the difference between the energy content at the commencement of an instar or the adult stage and at the end of that particular stage.

Bioenergetics parameters were estimated following the IBP formula of Petrusewicz and Macfadyen (1970)

$$C = FU + P + R. \tag{1}$$

Assimilation was calculated as the difference between food consumed and that of faeces;

$$A = C - FU, \tag{2}$$

metabolism was calculated as the difference between assimilated energy and that of growth

$$M = A - P. \tag{3}$$

Rates of feeding (Cr), assimilation (Ar), production (Pr) and metabolism (Mr) were calculated by dividing the respective quantitative values expressed on per insect basis by the mid body weight of the live insect (g) and duration of the instar/adult stage expressed in J/g live insect/day (Waldbauer 1968). The following formulae were used to compute the rates and efficiencies:

$$Cr = \frac{\text{Consumption (J/insect)}}{\text{Mid body weight (g)} \times \text{duration of the instar/stage}} \tag{4}$$

$$Ar = \frac{\text{Assimilation (J/insect)}}{\text{Mid body weight (g)} \times \text{duration of the instar/stage}} \tag{5}$$

$$Pr = \frac{\text{Production (J/insect)}}{\text{Mid body weight (g)} \times \text{duration of the instar/stage}} \tag{6}$$

$$Mr = \frac{\text{Metabolism (J/insect)}}{\text{Mid body weight (g)} \times \text{duration of the instar/stage}}. \tag{7}$$

Assimilation efficiency (Ase) was calculated in percentage relating energy assimilated (A) to that of ingested (C). Production efficiencies (Pe_1 and Pe_2) were calculated in percentage relating production (P) to ingestion (C) and assimilation (A).

Overall rates were calculated by dividing the sum of products of the respective rates and the duration for the different life stage by the total number of days of the feeding period as given below:

$$\text{Overall } Cr = \frac{\text{Sum of production of } Cr \text{ and duration for each instar/stage}}{\text{Total feeding period (day)}} \tag{8}$$

$$\text{Overall } Ar = \frac{\text{Sum of production of } Ar \text{ and duration for each instar/stage}}{\text{Total feeding period (day)}} \tag{9}$$

$$\text{Overall } Pr = \frac{\text{Sum of production of } Pr \text{ and duration for each instar/stage}}{\text{Total feeding period (day)}} \tag{10}$$

$$\text{Overall } Mr = \frac{\text{Sum of production of } Mr \text{ and duration for each instar/stage}}{\text{Total feeding period (day)}} \tag{11}$$

Reproductive efficiency (%) was calculated by dividing the energy allocated to egg production to that of energy assimilated during their adult phase (Muthukrishnan and Pandian 1987a)

$$\text{RE (\%)} \frac{\text{Energy allocated to egg production (J/insect)}}{\text{Total energy assimilated during the adult phase}}. \tag{12}$$

3. Results

3.1 *Chemical composition and growth*

Nitrogen and energy contents of *R. communis*, *A. hypogaea* and *P. maximum* were 2·52% and 23·282 J, 1·92% and 19·834 J, and 1·64 and 17·538 J; while water content was 75·2, 68·9 and 66·4%, respectively. Newly moulted I instar nymph of *A. crenulata* weighed 1·7 mg and contained 25·6 J. With progress in development, energy content of the nymph increases exponentially. For instance, energy content of newly emerged adult female and male feeding on *R. communis*, *A. hypogaea* and *P. maximum* was 922·5 and 751·3 J, 851·9 and 714·5 J and 608·3 and 423·7 J, respectively. Developmental period of a female nymph varied from 39·8 days while feeding on *R. communis* to 44·3 days on *P. maximum.* The number of ovipositions decreased from 6 in castor leaf feeding schedule to 4 or 3 in less preferred host plants. Length of life span of *A. crenulata* fed on *R. communis* was 169 days but decreased to 112 days in *P. maximum* feeding regime. Growth of the nymph increased exponentially with advancing age. For instance, I instar nymph feeding on *R. communis* leaf contained 26·5 J grows to 922·5 J during adult stage (figure 1).

3.2 *Bioenergetics*

Food energy ingested by the insect increased with advancing life stage upto I oviposition period and then decreased. For example, food consumption of *A. crenulata* feeding on the leaf of *R. communis* increased from 851 J (I instar) to 9471 J (I oviposition period), and decreased to 6385 J during the last oviposition

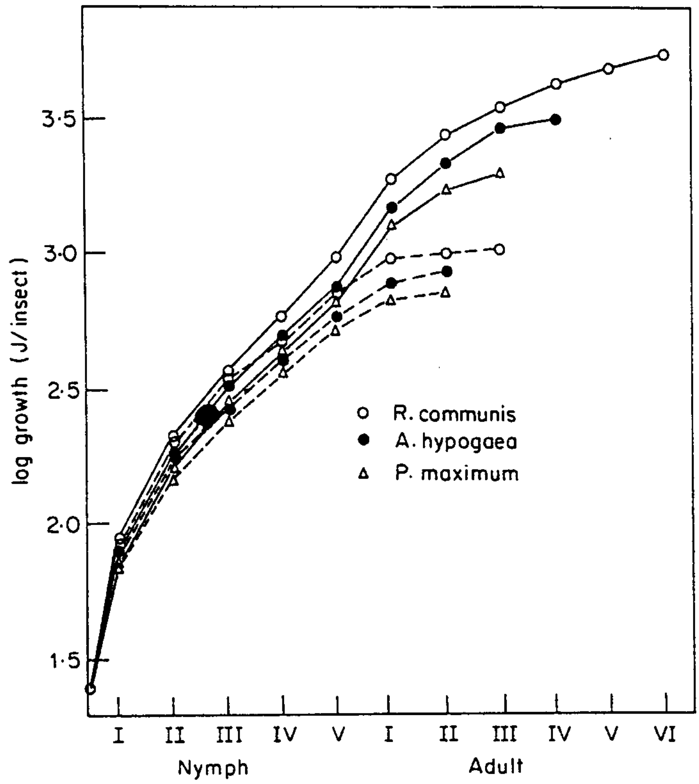

Figure 1. Growth of *A. crenulata* male (broken line) and female (continuous line) fed *ad libitum* on different host plants.

period, including the senescent period as well (table 1). Maximum food consumption by the insect was recorded during the I oviposition period for the females and the first 30 days for the males (tables 1 and 2). For instance, *A. crenulata* feeding on *A. hypogaea* consumed 8813 J during I oviposition period out of the total 36241 J for the entire life span; it constitutes 24% of the total food consumed and the males consumed 7114 J (tables 3 and 4). Females of *A. crenulata* consumed more amount of food than the males in all the tested food plants.

With advancing age and increase in body weight, the consumption rate decreased in all the feeding regimes from the I instar until death of the insect. For instance, the feeding rate of *A. crenulata* while feeding on *A. hypogaea* decreased from 15891 J/g/day during the I instar stage to 710 J/g/day at the time of the final oviposition period (figure 2); whereas feeding rate of the male decreased from 15891–552 J. However, the overall feeding rate of female was less than that of the male. Overall feeding rate of the female feeding on *R. communis* leaf was 2405 J/g/day compared to that of 2551 J/g/day for male (table 7).

Corresponding to the increase in food consumption, faeces egested by the insect also increased. For example, faeces egested by a female insect feeding on *R. communis* was 227 J during the I instar and increased to 4501 J at the time of I oviposition period and then decreased to 3139 J during the final oviposition period (table 1).

Table 1. Bioenergetics of female *A. crenulata* feeding *ad libitum* on *R. communis* leaf at 27 + 1°C, 14:10 L:D, 75% Rh.

Stage	D	*C*	*FU*	*A*	*P*	*R*	*Ae*	Pe_1	Pe_2
Nymph/instar									
I	5·7 ± 0·3	850·91 ± 44·23	227·19 ± 11·92	623·72 ± 33·45	60·67 ± 3·28	563·05 ± 30·36	73·3 ± 3·9	7·62 ± 0·42	9·73 ± 0·54
II	6·2 ± 0·4	1567·85 ± 88·92	465·65 ± 23·39	1102·20 ± 62·27	119·47 ± 6·97	982·73 ± 59·21	70·3 ± 3·9	7·62 ± 0·46	10·84 ± 0·59
III	7·5 ± 0·6	2085·98 ± 123·74	723·84 ± 42·92	1362·14 ± 79·30	165·21 ± 9·86	1196·93 ± 71·24	65·3 ± 3·8	7·92 ± 0·47	12·13 ± 0·68
IV	8·2 ± 0·9	2328·41 ± 144·82	1201·46 ± 78·39	1126·95 ± 79·73	211·42 ± 12·92	915·53 ± 58·88	48·4 ± 3·3	9·08 ± 0·82	18·77 ± 0·92
V	9·0 ± 1·2	2735·48 ± 192·42	1288·41 ± 87·91	1447·07 ± 96·87	339·20 ± 23·06	1107·87 ± 72·97	52·9 ± 3·8	12·14 ± 0·82	23·44 ± 1·28
Adult/oviposition period									
I	19 ± 1·7	9471·00 ± 586·67	4501·58 ± 282·26	4969·42 ± 323·44	927·31 ± 63·57	4042·11 ± 216·26	52·5 ± 3·4	9·79 ± 0·82	18·66 ± 1·31
II	20 ± 2·2	8579·90 ± 584·11	3917·33 ± 280·55	4662·57 ± 329·84	874·11 ± 56·96	3788·46 ± 254·22	54·3 ± 3·7	10·19 ± 0·92	18·74 ± 1·33
III	21 ± 2·6	7262·37 ± 587·95	3380·27 ± 222·13	3882·10 ± 259·95	743·50 ± 50·05	3138·60 ± 203·92	53·5 ± 3·0	10·24 ± 0·84	19·15 ± 1·35
IV	21 ± 3·1	6827·98 ± 513·13	3180·69 ± 208·82	3647·29 ± 225·83	685·73 ± 44·66	2961·56 ± 189·62	53·4 ± 3·7	10·04 ± 0·81	18·80 ± 1·29
V	23 ± 3·6	6621·95 ± 480·84	3170·82 ± 206·16	3451·13 ± 225·83	630·18 ± 43·52	2820·95 ± 171·80	52·1 ± 3·8	9·52 ± 0·79	18·26 ± 1·15
VI	28 ± 6·4	6385·33 ± 464·85	3139·89 ± 198·34	3245·46 ± 212·52	570·56 ± 39·78	2674·90 ± 161·03	50·8 ± 3·8	8·94 ± 0·74	17·58 ± 0·78
Total	168·6	54717·16	25197·13	29520·03	5327·36*	24192·67	53·95	9·74	18·05

*Includes 3490·73 J as egg energy.
Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficients are in percentage.

Table 2. Bioenergetics of male *A. crenulata* feeding *ad libitum* on *R. communis* leaf at 27 ± 1°C, 14:10 L:D, 75% Rh.

Stage	D	C	FU	A	P	R	Ae	Pe_1	Pe_2
Nymph/instar									
I	5·7 ± 0·3	850·91 ± 44·23	227·19 ± 11·92	623·72 ± 33·45	60·67 ± 3·28	563·05 ± 30·36	73·3 ± 3·9	7·62 ± 0·42	9·73 ± 0·54
II	6·2 ± 0·4	1567·85 ± 88·92	465·65 ± 23·39	1102·20 ± 62·27	119·47 ± 6·97	982·73 ± 59·21	70·3 ± 3·9	7·62 ± 0·46	10·84 ± 0·59
III	6·7 ± 0·5	1601·03 ± 82·65	600·07 ± 30·91	1000·96 ± 52·54	124·88 ± 7·15	876·08 ± 46·68	62·52 ± 3·19	7·80 ± 0·40	12·47 ± 0·64
IV	7·2 ± 0·9	1859·76 ± 98·87	1015·35 ± 53·89	844·41 ± 43·84	152·50 ± 8·21	691·91 ± 36·86	45·40 ± 2·54	8·21 ± 0·43	18·06 ± 0·96
V	8·1 ± 1·1	2259·67 ± 124·25	1167·18 ± 64·24	1092·49 ± 60·89	231·39 ± 14·09	861·10 ± 47·46	48·35 ± 2·67	10·24 ± 0·57	21·18 ± 1·17
Adult									
I	30 ± 0	7266·43 ± 422·53	3833·67 ± 221·54	3432·66 ± 203·26	203·46 ± 9·86	3229·20 ± 193·76	47·24 ± 3·82	2·80 ± 0·17	5·93 ± 0·36
II	30 ± 0	5394·37 ± 339·82	2890·30 ± 182·09	2504·07 ± 158·78	114·90 ± 7·99	2389·17 ± 152·54	46·42 ± 2·93	2·13 ± 0·14	4·59 ± 0·28
III	19 ± 0	3674·07 ± 238·84	2127·65 ± 137·54	1546·42 ± 108·52	49·60 ± 3·81	1496·82 ± 98·56	42·09 ± 2·74	1·35 ± 0·09	3·21 ± 0·21
Total	112·9	24474·09	12327·06	12147·03	1056·87	11090·16	49·63	4·32	8·70

Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficiencies are in percentage.

Table 3. Bioenergetics of female *A. crenulata* feeding *ad libitum* on *A. hypogaea* leaf at 27 ± 1°C, 14:10 L:D, 75% Rh.

Stage	D	*C*	*FU*	*A*	*P*	*R*	*Ae*	Pe_1	Pe_2
Nymph/instar									
I	6·1 ± 0·3	775·51 ± 38·21	209·39 ± 10·24	566·12 ± 27·94	57·62 ± 2·82	508·50 ± 24·97	73·0 ± 3·6	7·43 ± 0·38	10·18 ± 0·50
II	7·3 ± 0·4	1158·67 ± 57·52	347·60 ± 17·42	822·07 ± 41·21	86·90 ± 4·35	735·17 ± 36·96	70·0 ± 3·5	7·50 ± 0·38	10·71 ± 0·54
III	8·2 ± 0·5	1938·40 ± 98·89	693·95 ± 35·42	1244·45 ± 63·47	150·42 ± 7·67	1094·03 ± 56·38	64·2 ± 3·3	7·76 ± 0·39	12·09 ± 0·62
IV	9·1 ± 0·7	2094·89 ± 111·23	978·31 ± 51·84	1116·58 ± 60·28	176·39 ± 9·37	940·19 ± 49·83	53·3 ± 2·8	8·42 ± 0·46	15·80 ± 0·84
V	10·0 ± 1·2	2295·94 ± 126·20	1175·52 ± 64·63	1120·42 ± 62·73	254·39 ± 40·27	866·03 ± 22·40	48·8 ± 2·6	11·08 ± 0·67	22·70 ± 1·27
Adult/oviposition period									
I	20 ± 2·3	8813·02 ± 516·13	1355·19 ± 245·50	4457·83 ± 260·22	726·05 ± 43·19	3731·78 ± 217·89	50·6 ± 3·0	8·24 ± 0·44	16·29 ± 0·93
II	21 ± 2·6	7566·78 ± 457·42	3762·84 ± 228·05	3803·94 ± 252·64	649·56 ± 39·33	3154·38 ± 192·56	50·3 ± 3·1	8·58 ± 0·57	17·08 ± 1·07
III	23 ± 3·1	6754·01 ± 428·51	3400·63 ± 215·86	3353·38 ± 212·85	543·17 ± 34·63	2810·21 ± 178·46	49·6 ± 3·0	8·04 ± 0·45	16·20 ± 1·04
IV	26 ± 5·3	4841·80 ± 325·21	2546·48 ± 166·29	2298·32 ± 151·05	336·37 ± 22·16	1961·95 ± 128·24	47·4 ± 3·1	6·94 ± 0·46	14·64 ± 1·15
Total	130·7	36241·98	17469·97	18772·01	2979·38*	15792·63	51·80	8·22	15·87

*Includes 1667·62 J as egg energy.

Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficiencies are in percentage.

Table 4. Bioenergetics of male *A. crenulata* feeding *ad libitum* on *A. hypogaea* leaf at 27 ± 1°C, 14:10 L:D, 75% Rh.

Stage	D	*C*	*FU*	*A*	*P*	*R*	*Ae*	Pe_1	Pe_2
Nymph/instar									
I	6·1 ± 0·3	775·51 ± 38·21	209·39 ± 10·24	566·12 ± 27·94	57·62 ± 2·82	508·50 ± 24·97	73·0 ± 3·6	7·43 ± 0·38	10·18 ± 0·50
II	7·3 ± 0·4	1158·67 ± 57·52	347·60 ± 17·42	822·07 ± 41·21	86·90 ± 4·35	735·17 ± 36·96	70·0 ± 3·5	7·50 ± 0·38	10·71 ± 0·54
III	7·9 ± 0·9	1704·50 ± 91·53	616·69 ± 33·62	1087·81 ± 57·92	128·81 ± 6·99	958·95 ± 51·72	63·8 ± 3·4	7·56 ± 0·42	11·85 ± 0·64
IV	8·7 ± 1·2	2027·02 ± 111·49	921·48 ± 50·71	1105·54 ± 60·79	160·53 ± 8·84	945·60 ± 53·87	54·4 ± 2·62	7·92 ± 0·44	14·52 ± 0·79
V	9·2 ± 1·5	2260·95 ± 129·52	1101·08 ± 62·19	1159·87 ± 65·38	264·79 ± 12·36	945·08 ± 54·69	51·3 ± 2·9	9·50 ± 0·54	18·52 ± 1·04
Adult/month									
I	30 ± 1·0	7113·94 ± 406·88	3941·12 ± 226·48	3172·82 ± 186·58	178·56 ± 10·19	2994·26 ± 171·28	44·6 ± 2·5	2·51 ± 0·15	5·63 ± 0·32
II	29 ± 2·5	4901·52 ± 282·29	2945·81 ± 169·53	1955·71 ± 112·64	64·70 ± 3·75	1891·01 ± 108·98	39·9 ± 2·3	1·32 ± 0·09	3·31 ± 0·21
Total	98·2	19942·11	10083·14	9858·97	941·91	8917·06	49·44	4·72	9·55

Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficiencies are in percentage.

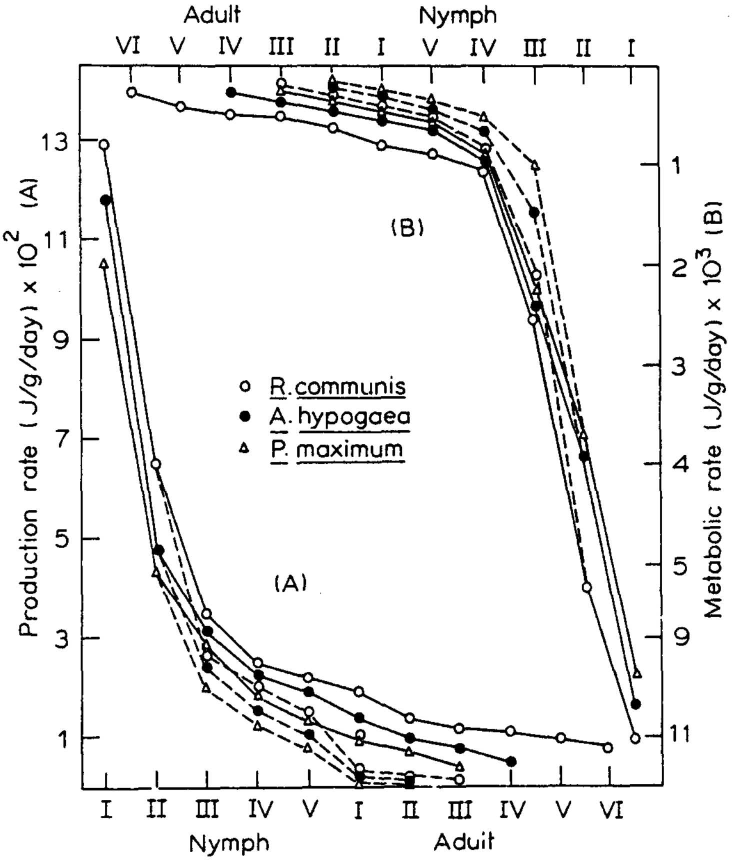

Figure 2. Consumption rate and assimilation rate of *A. crenulata* fed *ad libitum* on different host plants.

Assimilation of energy by the insect was also following a similar trend like that of consumption. For instance, assimilation of a female insect feeding on *P. maximum* was 586 J at the time of I instar and it increased to 4457 J at the time of the I oviposition period. Trends on assimilation rate were also similar to that of the consumption rate (figure 3). For example, the female insect assimilated *P. maximum* at the rate of 10773 J/g/day during the I instar and the rate decreased to 389 J/g/day during final oviposition period. Assimilation efficiency decreased with advancing age. Assimilation efficiency of the insect feeding on *P. maximum* decreased from 72·4% during I instar to 47·4% during the final oviposition period. Major part of the assimilated energy was expended to meet the metabolic requirement of the insect. The female insect feeding on *P. maximum* allocated 24192 J to meet the metabolic requirement from the assimilated energy of 29520 J. Metabolic rate also decreased exponentially with advancing age.

Production of tissue, fat body and egg ultimately increased the energy allocated to production. Females feeding on the tested food plant showed greater increase in production than that of the males (tables 1–6). Production efficiencies increased with advancing age of the nymphal period. However, the adult females feeding on

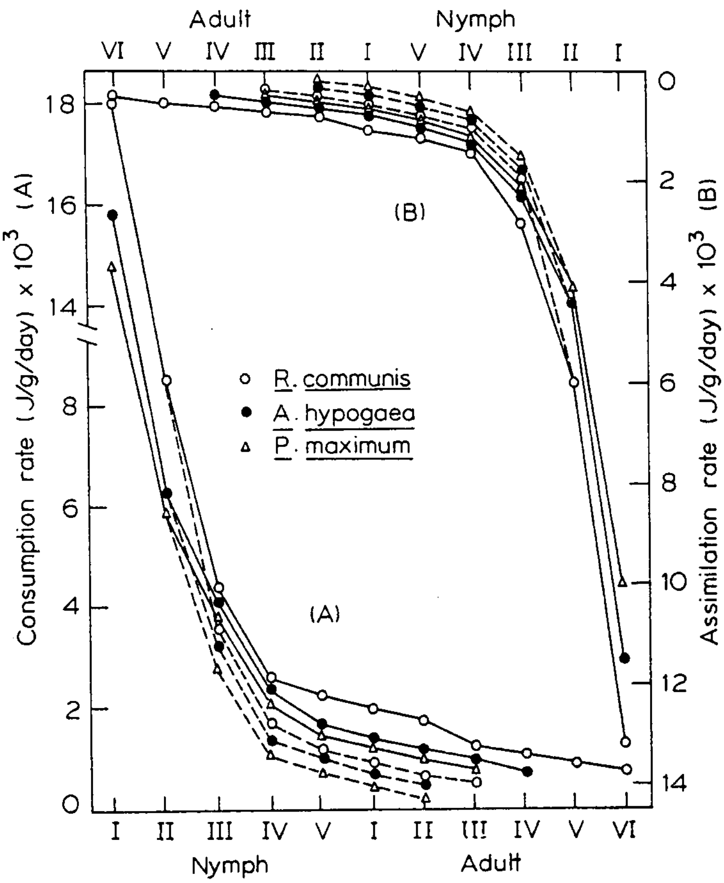

Figure 3. Production and metabolic rate of *A. crenulata* fed *ad libitum* on different host plants.

castor and *A. hypogaea* during the II oviposition period exhibited a moderate increase in the efficiencies of production than during the other periods. For instance, net production efficiency (Pe_2) of females feeding on *R. communis* was 8·7% during I instar and it increased to 23·4% during V instar and subsequently decreased to 16·4 during final oviposition period. *A. crenulata* feeding on castor leaf allocated more amount of assimilated energy to egg production than in the other feeding regimes. Table 8 shows the amount of energy allocated to egg production during the different oviposition period.

4. Discussion

The results presented in this study reveal the following: (i) with advancing age food consumption increases; the other bioenergetics parameters seem to depend on the consumed energy and (ii) energy allocated to egg production increases in the insect fed on the preferred host plant than the one feeding on the alternate hosts. Insects utilize the nutritionally rich host plant more efficiently than the less preferred host

Table 5. Bioenergetics of female *A. crenulata* feeding *ad libitum* on *P. maxicum* leaf at 27 ± 1°C, 14:10 L:D, 75% Rh.

Stage	D	C	FU	A	P	R	Ae	Pe_1	Pe_2
Nymph/instar									
I	6·1 ± 0·5	669·28 ± 36·80	184·72 ± 10·18	484·56 ± 26·68	47·72 ± 2·74	436·84 ± 24·09	72·4 ± 3·9	7·13 ± 0·40	9·85 ± 0·62
II	7·5 ± 0·5	1006·18 ± 59·35	299·84 ± 17·89	706·34 ± 41·72	73·25 ± 4·34	633·01 ± 37·36	70·2 ± 4·2	7·28 ± 0·43	10·37 ± 0·65
III	8·7 ± 1·2	1865·95 ± 113·77	675·47 ± 41·36	1190·48 ± 74·65	138·64 ± 8·67	1051·84 ± 64·27	63·8 ± 3·9	7·43 ± 0·46	11·65 ± 0·71
IV	9·0 ± 1·5	2014·93 ± 128·47	950·03 ± 61·86	1065·90 ± 68·23	160·59 ± 10·39	905·31 ± 60·10	52·9 ± 3·4	7·97 ± 0·51	15·07 ± 0·97
V	9·8 ± 1·9	2113·94 ± 142·39	1097·13 ± 73·58	1016·81 ± 68·14	205·26 ± 14·74	811·55 ± 61·21	48·1 ± 3·3	9·71 ± 0·67	20·19 ± 1·39
Adult/oviposition period									
I	22 ± 4·1	7515·51 ± 524·12	3718·45 ± 260·09	3797·06 ± 272·31	606·88 ± 43·09	3790·18 ± 237·34	50·5 ± 3·5	8·08 ± 0·61	15·98 ± 1·16
II	24 ± 5·7	6719·34 ± 495·07	3371·47 ± 251·32	3347·87 ± 247·78	481·52 ± 36·32	2866·35 ± 214·41	49·8 ± 3·1	7·17 ± 0·62	14·38 ± 1·03
III	25 ± 7·2	3851·58 ± 303·09	2022·93 ± 155·87	1828·65 ± 145·74	215·77 ± 17·76	1612·88 ± 124·31	47·4 ± 3·0	5·60 ± 0·59	11·80 ± 0·98
Total	112·1	25756·71	12320·04	13436·67	1929·63*	11507·04	52·17	7·49	14·36

*Includes 1068·71 J as egg energy.

Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficiencies are in percentage.

Table 6. Bioenergetics of male *A. crenulata* feeding *ad libitum* on *P. maxicum* leaf at 27 ± 1°C, 14:10 L:D, 75% Rh.

Stage	D	C	FU	A	P	R	Ae	Pe_1	Pe_2
Nymph/instar									
I	6·1 ± 0·5	669·28 ± 36·80	184·72 ± 10·18	484·56 ± 26·68	47·72 ± 2·74	436·84 ± 24·09	72·4 ± 3·9	7·13 ± 0·40	9·85 ± 0·62
II	7·5 ± 0·5	1006·18 ± 59·35	299·84 ± 17·89	706·34 ± 41·72	73·25 ± 4·34	633·01 ± 37·36	70·2 ± 4·2	7·28 ± 0·43	10·37 ± 0·65
III	8·0 ± 1·0	1219·08 ± 73·14	430·89 ± 25·91	788·19 ± 43·69	90·09 ± 5·48	698·10 ± 42·69	64·6 ± 3·9	7·39 ± 0·45	11·62 ± 0·67
IV	8·7 ± 1·3	1658·40 ± 111·84	794·37 ± 52·69	864·03 ± 56·65	126·37 ± 8·59	737·66 ± 49·56	52·1 ± 3·6	7·63 ± 0·49	14·63 ± 0·96
V	9·3 ± 1·7	2012·36 ± 144·86	1052·46 ± 75·74	959·90 ± 65·97	180·71 ± 12·09	779·19 ± 57·59	47·7 ± 3·58	8·98 ± 0·62	18·83 ± 1·36
Adult/month									
I	30 ± 1·0	5501·21 ± 412·58	3091·68 ± 236·84	2409·53 ± 189·51	136·43 ± 11·25	2273·10 ± 174·59	43·8 ± 3·4	2·48 ± 0·22	5·66 ± 0·49
II	13 ± 3·5	1685·12 ± 106·38	1036·35 ± 63·25	648·77 ± 43·92	20·39 ± 1·09	628·38 ± 47·28	38·5 ± 2·9	1·21 ± 0·10	3·14 ± 0·25
Total	82·6	13751·63	6890·31	6861·32	674·96	6186·36	49·9	4·91	9·84

Each value (X ± SD) represents the average performance of 5 insects. Values are in J/insect. Efficiencies are in percentage.

Table 7. Overall rates of feeding (*Cr*), assimilation (*Ar*), production (*Pr*) and metabolism (*Mr*) of *A. crenulata* feeding on different host plants.

Host plants	Sex	*Cr*	*Ar*	*Pr*	*Mr*
R. communis	Female	2405·29	1270·14	229·22	1040·92
	Male	2551·32	1124·82	97·87	1026·96
A. hypogaea	Female	2405·17	1245·79	199·26	1046·53
	Male	2453·58	1013·00	85·89	927·11
P. maximum	Female	2512·76	1210·85	188·25	1022·60
	Male	2563·38	980·83	77·31	903·52

Table 8. Comparison of food assimilation and egg production of female *A. crenulata* during adult phase.

Food plant	Oviposition–stage	No. of eggs laid	Energy allocated to egg production	Energy assimilated	RE(%)
R. communis	I	58	784·8	4969·02	15·79
	II	52	761·04	4662·57	16·32
	III	43	578·71	3882·10	14·91
	IV	37	494·15	3647·29	13·55
	V	35	459·80	3451·13	13·32
	VI	32	412·23	3245·46	12·70
Total	6	257	3490·73	23857·95	14·63
A. hypogaea	I	42	568·40	4457·83	12·75
	II	38	510·00	3803·94	13·41
	III	32	408·00	3353·38	12·17
	IV	18	182·28	2298·32	7·92
Total	4	110	1668·68	13913·43	11·99
P. maximum	I	37	501·55	3797·06	13·21
	II	30	402·72	3247·87	12·03
	III	12	109·54	1828·65	5·99
Total	3	79	1113·81	8973·58	8·01

plants (Senthamizhselvan 1987). Food consumption of acridids was altered by the presence of both physical and chemical factors (Mulkern 1967; Chapman and Bernays 1977). Orthopterans consume over 60% of their total food consumption during adult phase; it is related to maturation and oviposition, which require a lot of energy (Johannson 1960). *Oryzaephilus surinamensis* is known to consume over 80% of their total food consumption during their adult stage and allocates 42% of its assimilated energy to egg production (White and Sinha 1981). However, *A. crenulata* prefers to feed on nitrogen and water rich leaf with least amount of phenol, when provided with choice of host plant (Sanjayan and Ananthakrishnan 1987). Similar studies were carried out in *Cyrtacanthacris ranaceae* feeding on different host plants by Ananthakrishnan *et al* (1986) who reported a decrease in net production efficiency during III instar and it was due to their estimation of food utilization parameters in 24 h period. This is due to the presence of short-term cellular oscillations and circadian rhythm in feeding activity and different amount of food in gut at different time (Beck 1980; Scriber and Slansky 1981). Assimilation rate of *A. crenulata* depends upon its food consumption rate. Such a positive correlation was also obtained between these two parameters in other phytophagous insects (see Muthukrishnan and Pandian 1987a). Assimilation efficiency decreased with advancing age. This was in accordance with the observations of Muthukrishnan *et al* (1976). Increase in weight, area of the gut and lipid contents of the body with advancing age are the major reasons for the decrease in assimilation efficiency (Gordon 1959). Insects feeding on different food plants exhibit differences in assimilation efficiency which is directly related to the chemistry of the leaf as well as the water content (Pandian and Marian 1985). Somatic growth of the insect is obvious with advancing life stage, ceasing after the commencement of reproductive phase. Further, the growth rate of the insects reflects their reproductive potential.

Virgin females of *A. crenulata* live longer than the reproductive females. Theoretically reproductive investment suggests a conflicting relationship between reproduction and adult survival (Calow 1973; Stearns 1977). If physiological impairment due to failure to reproduce can not act, 'reproductive strain' theory predicts that non-reproducing adults live longer than the reproducing adults (Rockstein and Miquel 1973; Slansky 1980). *A. crenulata* feeding on either *R. communis* or *P. maximum* shows higher energy allocation to egg production during the II oviposition period than the I oviposition period suggest that the energy accumulated during the nymphal period does not seem to make any important contribution to egg production in adults. Insects with larger adult biomass expended most of their available energy on metabolism (Calow 1977). For example, metabolically less active Collembolan *Tomocerus minor* allocate more amount of assimilated energy to egg production than active *Orchesella cincata* (Testerink 1982). *Oxya velox* (0·3 g) feeding on *Digitaria* allocate 24·8% of their assimilated energy to egg production during their adult period (Delvi and Pandian 1971). However, *A. crenulata* (0·4 g) allocate different amount of assimilated energy to egg production in relation to their food ingested (table 8). Species with larger biomass of adult tissue exhibit lesser reproductive efficiency than those with a smaller biomass. For instance, the reproductive efficiency of *Poecilocerus pictus* was 2·8% (weight: 5 g) and of *O. surinamensis* was 41% (weight: 5 mg) (Delvi and Pandian 1972; White and Sinha 1981). However, the reproductive efficiency of *A. crenulata* (0·4 g) varied between 7 and 15%. Statistical analysis of the data on food assimilated during the adult phase with that of the energy allocated to egg production revealed (regression equation: $Y = 299{\cdot}32 + 0{\cdot}215X$; $r = 0{\cdot}982$; $p < 0{\cdot}001$) a significant relation between these two variables and the reproductive efficiency of the insect feeding on preferred host plant (*R. communis*) was greater than that of the other two less preferred host plants.

Acknowledgements

We express our deep sense of gratitude to Prof. T N Ananthakrishnan for guidance and critically going through the manuscript. Financial assistance through a research project (38(652)/87/EMR–II) sanctioned by the Council of Scientific and Industrial Research, New Delhi, is gratefully acknowledged.

References

Ananthakrishnan T N, Dhileepan K and Padmanaban B 1985 Behavioural responses in terms of feeding and reproduction in some grasshoppers (Orthoptera: Insecta); *Proc. Indian Acad. Sci. (Anim. Sci.)* 94 443–461

Ananthakrishnan T N, Sanjayan K P and Suresh Kumar N 1986 Host plant preferences in *Cyrtacanthacris ranacea* in some malvaceous hosts in terms of food utilization; *Proc. Indian Acad. Sci. (Anim. Sci.)* **51** 351–357

Beck S D 1980 *Insect photoperiodism*: 2nd edition (New York: Academic Press)

Calow P 1973 The relationship between fecundity, phenology and longevity: a system approach; *Am. Nat.* **107** 559–574

Calow P 1977 Ecology, evolution and energetics: a study in metabolic adaptation: *Adv. Ecol. Res.* **10** 1–60

Chapman R F and Bernays E A 1977 The chemical resistance of plants to insect attack; *Pontif. Acad. Sci. Scriptvaria* **41** 603–643

Delvi M R and Pandian T J 1971 Ecophysiological studies on the utilization of food in the paddy field grasshopper *Oxya velox*; *Oecologia (Berl.)* **8** 267–275

Delvi M R and Pandian T J 1972 Rates of feeding and assimilation in the grasshopper *Poecilocerus pictus*; *J. Insect Physiol.* **18** 1829–1843

Gordon H T 1959 Minimal nutritional requirements of the German roach, *Blatella germanica*; *Ann. N. Y. Acad. Sci.* **77** 290–351

Johannson A S 1960 Nutritional-endocrine regulation of insect reproduction; *Proc. Symp. Ontogen. Develop. Insects.* 133–139

Llewllyn M and Qureshi A ZL 1978 The energetics and growth efficiency of *Aphis fabae* reared on different parts of the broad bean plant (*Vicia fabae*); *Entomol. Exp. Appl.* **23** 26–39

Mulkern G B 1967 Food selection by grasshoppers; *Annu. Rev. Entomol.* **12** 509–523

Murugan K and Jacob J P 1988 Haemolymph protein profiles during gonadotrophic period of *Gesonula punctifrons* Stal (Orthoptera: Insecta); *Proc. Indian Acad. Sci. (Anim. Sci.)* **99** 423–427

Muthukrishnan J, Delvi M R and Pandian T J 1976 Assimilation efficiency of *Poecilocerus pictus* and *Mantis religiosa*; *Comp. Physiol. Ecol.* **1** 69–73

Muthukrishnan J and Pandian T J 1987a Insect Energetics; in *Animal energetics* (eds) T J Pandian and F J Vernberg (New York: Academic Press) pp 370–511

Muthukrishnan J and Pandian T J 1987b Relation between feeding and egg production in some insects; *Proc. Indian Acad. Sci. (Anim. Sci.)* **96** 411–416

Pandian T J and Marian M P 1985 Prediction of assimilation efficiency in lepidopterans; *Entomon* **10** 374–382

Petrusewicz K and Macfadyen A 1970 *Productivity of terrestrial animals principles and methods* (Oxford: Blackwell)

Rockstein M and Miquel J 1973 Aging in insects; *Physiol. Insecta* **1** 371–478

Sanjayan K P and Ananthakrishnan T N 1987 Host preferences of some acridids in relation to some biochemical parameters; *Proc. Indian Acad. Sci. (Anim. Sci.)* **96** 15–21

Scriber J M and Slansky F Jr 1981 Nutritional ecology of immature insects; *Annu. Rev. Entomol.* **26** 183–211

Senthamizhselvan M 1987 *Physiological studies on chosen insect pests, predators and parasites*, Ph.D. thesis, Madurai Kamaraj University, Madurai

Slansky F Jr 1980 Quantitative food utilization and reproductive allocation by adult milkweed bug, *Oncopeltus fasciatus*; *Physiol. Entomol.* **5** 73–86

Slansky F Jr and Scriber J M 1985 Food consumption and utilization; in *Comprehensive insect physiology, biochemistry and pharmacology* (eds) G A Kerkuit and L I Gilbert (Oxford: Pergamon Press) pp 87–164

Stearns S C 1977 The evolution of life history traits: a critique of the theory and a review of the data; *Annu. Rev. Ecol. Syst.* **8** 145–171

Testerink G J 1982 Strategies in energy consumption and partitioning in Collembola; *Ecol. Entomol.* **7** 341–351

Thompson J M 1975 Reproductive strategies: a review of concepts with particular reference to the number of offspring per reproductive period; *Biologist* **57** 14–25

Waldbauer G P 1968 The consumption and utilization of food by insects; *Adv. Insect Physiol.* **5** 229–288

White N D C and Sinha R N 1981 Energy budget for *Oryzaephilus surinamensis* (Coleoptera: Cucufidae) feeding on rolled oats; *Environ. Entomol.* **10** 320–326