Ecological energetics of the grasshopper *Poecilocerus pictus* in Bangalore fields*

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Abstract. The structure and biomass of *Poecilocerus pictus* population in four fields in Bangalore were estimated by direct observation method. Results on the density of *P. pictus*, the survivorship curve of the grasshopper and the growth of the population are reported.

The data on feeding rates, assimilation and conversion obtained in the laboratory were applied to the size and structure of the *P. pictus* populations in the different fields to estimate the rate and efficiency of energy flow through the population. The results indicate the defensive mechanism developed by the plant against predation. Efficiencies of exploitation, assimilation and production by the populations averaged 3·4, 34 and 15% respectively. Factors like predation, food and space do not appear to regulate the size of the population. Probably it is controlled by intrinsic population factors.

1. Introduction

Ever since Lindemann (1942) published the classical paper on trophic dynamics, studies on productivity have mostly been made with estimations on rate and efficiency of energy flow through different trophic levels (e.g., Odum 1957; Golley 1960). However, the complexity of an ecosystem, the fluctuating environmental factors and the diversity of fauna and flora have been forcing ecologists either to choose a simple ecosystem for estimation of quantum of energy transferred from one trophic level to the other (see Engelmann 1961), or to study the productivity of the key species in a complex ecosystem (e.g. Saito 1965). Thus efforts were made to choose a simple ecosystem or to simplify the complexity in the food chain by choosing only the key species from one or more trophic levels.

Calotropis gigantea (Asclepidacea), a producer, contains considerable amount of glycoside poison (Brower 1969); no vertebrate feeds on it; however, inverte-

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brates like the grasshopper *Poecilocerus pictus* (Acridiodea; Orthoptera) and the monarch butterfly *Danaus chrysippus* (Danidae; Lepidoptera) are the only major primary consumers of the plant; *P. pictus*, in turn, is predated by an invertebrate secondary consumer, the praying mantis *Mantis religiosa*. The presence of glycoside poison in *C. gigantea* has enforced a natural simplification of the food chain and the food chain is almost isolated from the rest of the food web in any chosen ecosystem. Thus, *C. gigantea* → *P. pictus* → *M. religiosa* food chain in an ecosystem offers an excellent opportunity for estimations of rate and efficiency of energy transfer from producer to consumer populations. The present paper reports on structure, biomass and energy transfer through the grasshopper *Poecilocerus pictus* population in chosen Bangalore fields.

2. Meterials and Methods

2.1. *The fields covered*

(i) Sarrakki, a small field of 5,000 m² situated 15 km south of Bangalore, (ii) Hindustan Aeronautics Limited (HAL), a field of 5,600 m² situated in Bangalore Airport, (iii) Eblur field of 30,000 m² area, a site for military exercising and (iv) Hindustan Machine Tool (HMT) field, situated in Jalahalli, a field of 5,000 m² bound by a railway track on one side and factory and residential areas on other sides. The HAL, HMT and Sarrakki fields are either protected by natural and man-made boundaries, and the Eblur field was free from human and other animal intervention on *C. gigantea* → *P. pictus* → *M. religiosa* food chain due to firing exercises for six days in a week. Population study was made in Sarrakki during 1970 and 1971, while in the other three fields, it was restricted to 1971 only.

2.2. *The producer*

In addition to the chemical defence developed in it, *C. gigantea*, a perennial shrub is almost of no economic importance and hence least disturbed by man, cattle etc.

2.3. *Consumer*

For the following five reasons *P. pictus* was chosen as the consumer species :

    (i) *P. pictus* ejects a stinking fluid, when disturbed and hence even in residential areas like Sarrakki, it is least disturbed.

    (ii) It feeds mainly on *C. gigantea* and hence prefers to remain mostly on one host plant throughout its life; the just hatched hoppers wander from their hatching burrows in search of the host plant. As hatching occurs in mass, the plant nearest to the burrow is the first attacked; if the plant is completely destroyed, the hoppers migrate to nearby plants during the first two instar periods, covering a maximum distance of 200 m. Mature females move about in search of oviposition site in the vicinity of the same plant. For these reasons, *P. pictus* may be regarded as almost sedentary, occupying more or less one and the same plant throughout its life.

    (iii) There is only one generation of *P. pictus* in a year and so hatching, maturation, breeding and mortality are more or less synchronised.

(iv) *P. pictus* is a large (grows to 4 to 7 g) colourful grasshopper, which seldom escapes the sight of an observer.

(v) *P. pictus* on *C. gigantea* can be closely observed and without disturbance. Further it is possible to assign each individual to its sex and life stage noting the key features (table 1).

2.4. *Estimation of biomass*

Regular fortnightly visits were made to the chosen fields. Each *C. gigantea* plant in the field was closely examined; the number of *P. pictus* on it was counted and every individual was assigned to its sex and life stage. As successive observations with a lapse of 15 days in between were made, it is likely that during the interval, a few individuals hatched or died and a few others moulted. To account approximately these dynamic changes in density and age (= life stage) structure of *P. pictus* population, the actual number of individuals belonging to the same sex and life stage recorded in two successive observations were averaged. The mean of two such census collected during successive fortnights of a calendar month is the mean density of the grasshopper for the respective life stage and sex.

In the laboratory, mid body weight and the corresponding energy content for each life stage and sex of *P. pictus* (reared at 26° C, which is approximately equivalent to the temperature of the chosen fields) were previously estimated (table 2). Corresponding values from table 2 were used to convert the number of individuals belonging to a particular life stage and sex into biomass values.

Delvi (1972) estimated rates of feeding, assimilation and conversion of *P. pictus* reared from egg to egg stage at 26° C. The data are presented in table 3. Appropriate values from table 3 were applied to estimate the quantum of *C. gigantea* leaf consumed, assimilated and converted by *P. pictus* population in the fields.

Table 1. Key features of different life stages of *Poecilocerus pictus.*

Life stage (instar)	Body length (mm)	Eye band	Antenna Segment (No.)	Antenna Length (mm)	Wing pad	Other features
I	9–12	Absent	8	2	Absent	..
II	10–13	Narrow	8	3	Absent	2 white spots on antenna
III	15–17	Broad	10	4	Sprouting	..
IV	20–24	Broader	12	6	Rudimentary	Ovipositor present in ♀ Ovipositor absent in ♂
V	25–36	Broadest	15	7	Laterally projected	
VI	35–43	Absent	15	12	Turned upwards	
Adult	43–50	Absent	15	13	Fully developed	

Table 2. Mid-body weight and caloric value of the grasshopper *Poecilocerus pictus* fed *ad libitum* on *Calotropis gigantea* at $26 \pm 1°$ C and $70 \pm 10\%$ rh.

Life state (instar)	Sex	Mid-body weight (mg)	Mid calorific value (gcal)
I	♀	36 ± 3·1	53·5 ± 4·61
	♂	33 ± 2·5	49·1 ± 3·7
II	♀	102 ± 14·2	151·7 ± 21·1
	♂	81 ± 6·5	120·4 ± 9·67
III	♀	207 ± 28·5	307·8 ± 42·4
	♂	182 ± 15·6	270·6 ± 23·2
IV	♀	393 ± 43·5	584·4 ± 64·7
	♂	376 ± 48·5	559·1 ± 72·1
V	♀	912 ± 75·6	1356·1 ± 112·4
	♂	798 ± 96·5	1186·6 ± 143·5
VI	♀	2011 ± 160·8	2990·4 ± 239·1
	♂	1484 ± 103·5	2206·7 ± 153·9
Adult	♀	4060 ± 365·5	6050·6 ± 543·5
	♂	2066 ± 185·6	3072·1 ± 276·0

3. Results

3.1. *Population density*

A glance of figures 1 to 4 reveals that during a calendar month hoppers belonging to a minimum of 2 life stages (e.g., March and November) to a maximum of 4 life stages (e.g., July) were present. The possible causative factors responsible for this deviation from synchronised population growth are: (i) Hatching occurred throughout March and April; those hatched during early March matured in July, while those hatched during late April were passing through the IV/V instar, and (ii) Individuals of the same brood and those hatched simultaneously did not moult to next instar on the same day even under controlled laboratory conditions; the magnitude of such individual variations in moulting is magnified as a hopper grew older (see Delvi 1972). Maximum density of *P. pictus* (in terms of number) occurred in the chosen fields during March–April, when hatching takes place.

From the respective maxima, the density decreased—the decrease being the fastest in HAL (figure 2) in comparison to Eblur (figure 3) and Sarrakki (figure 1) —as the calendar month advanced, except in the HMT field (figure 4), in which the decrease became apparent only after August (figure 5). An important biological agent causing hopper mortality is the parasitic sarcophagid *Blaesoxipha kaestneri*; as much as 10·5% of the observed I instar *P. pictus* individuals succumbed to death in the laboratory (Pandian and Delvi 1973). *P. pictus* collected from all the chosen fields barring those from the HMT were found to be infected by *B. kaestneri*. However, hopper mortality due to parasitic infection has not been separately estimated in the fields.
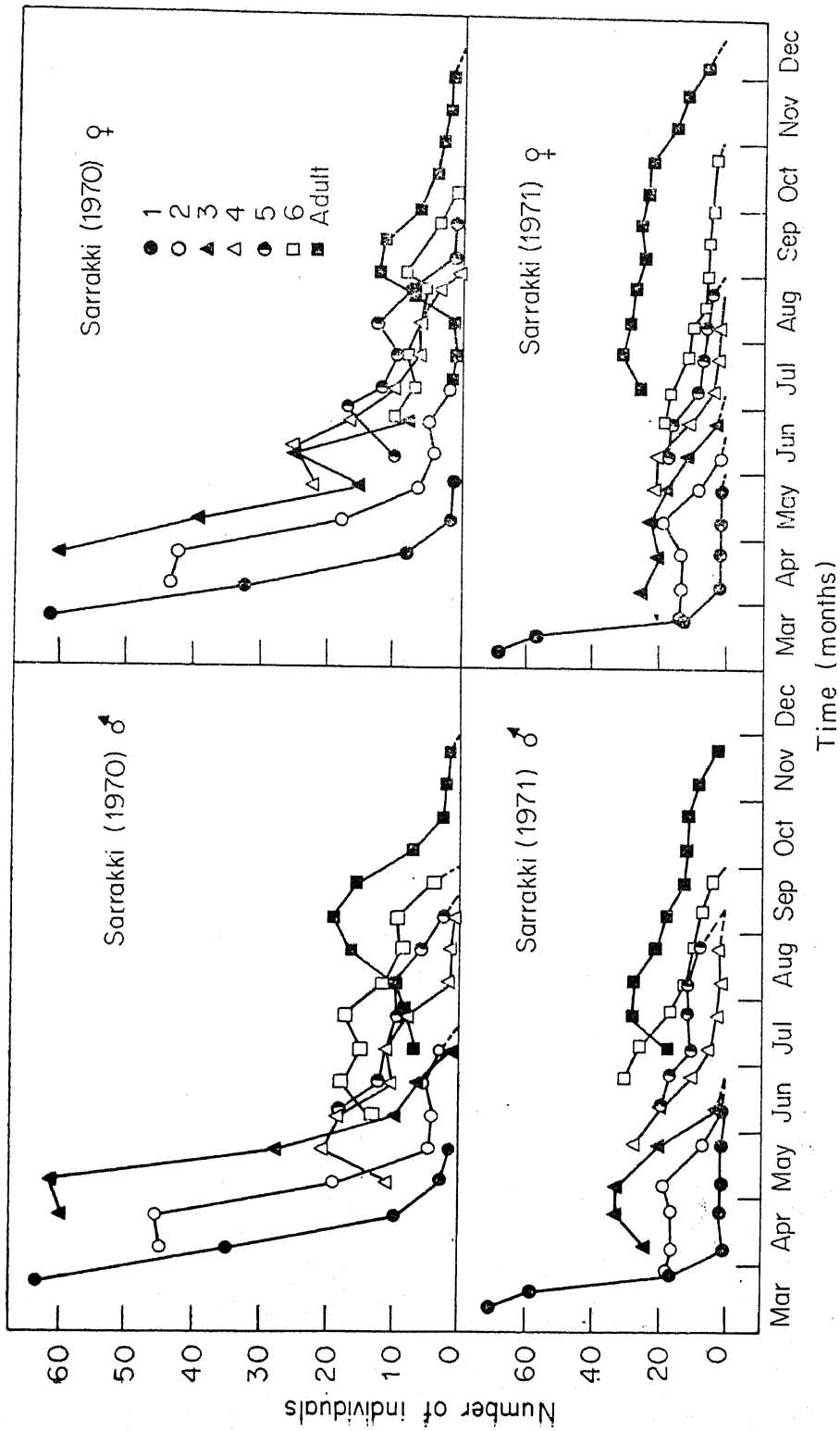
Figure 1. Life stagewise population number as a function of calendar month in the Sarrakki field during 1970 and 1971. 1 to 6 indicate the instar number.
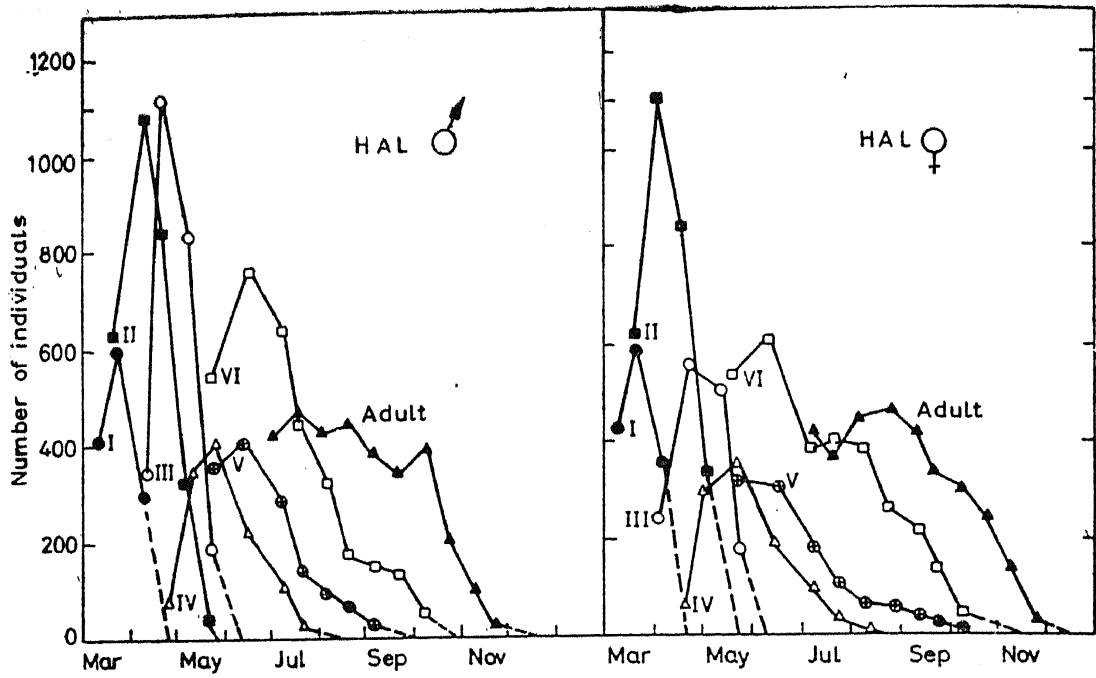
Figure 2. Life stagewise population number as a function of calendar month in the HAL field during 1970 and 1971. I to VI indicate the instar number.
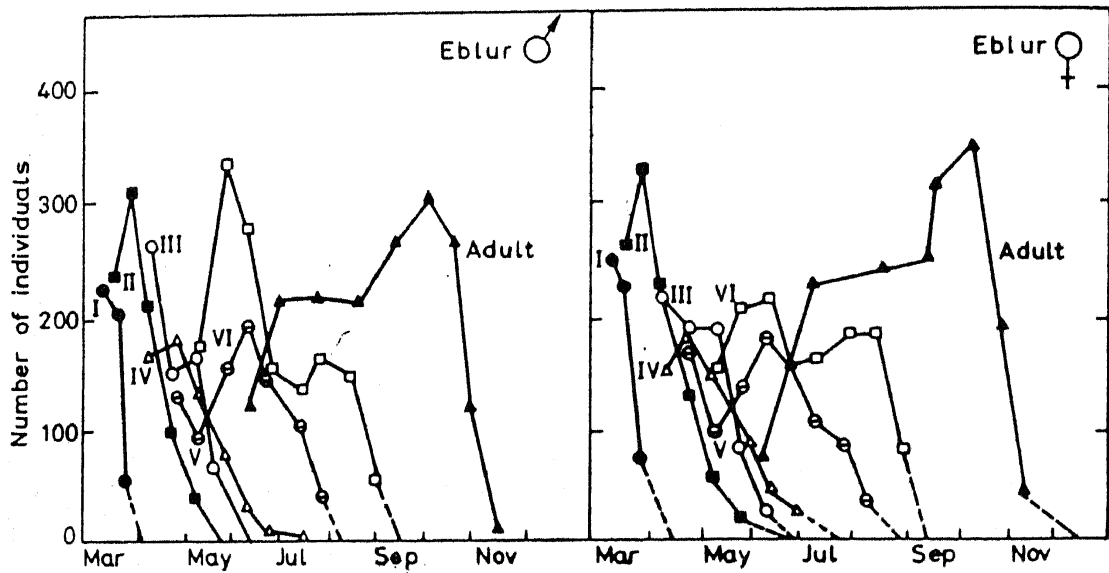

Figure 3. Life stagewise population number as a function of calendar month in the Eblur field during 1970 and 1971. I to VI indicate the instar number.
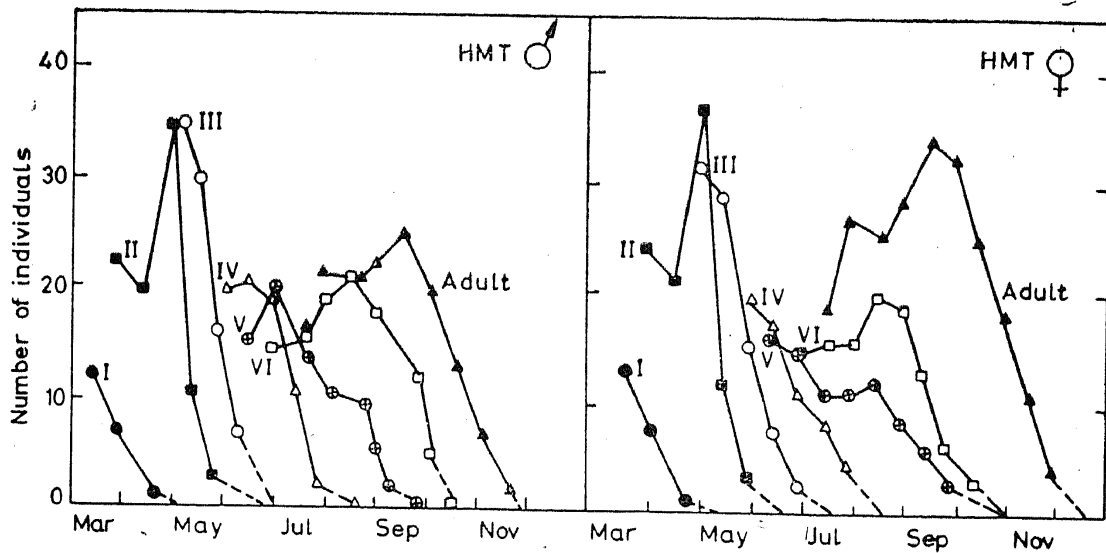
Figure 4. Life stagewise population number as a function of calendar month in the HMT field during 1970 and 1971. I to VI indicate the instar number.
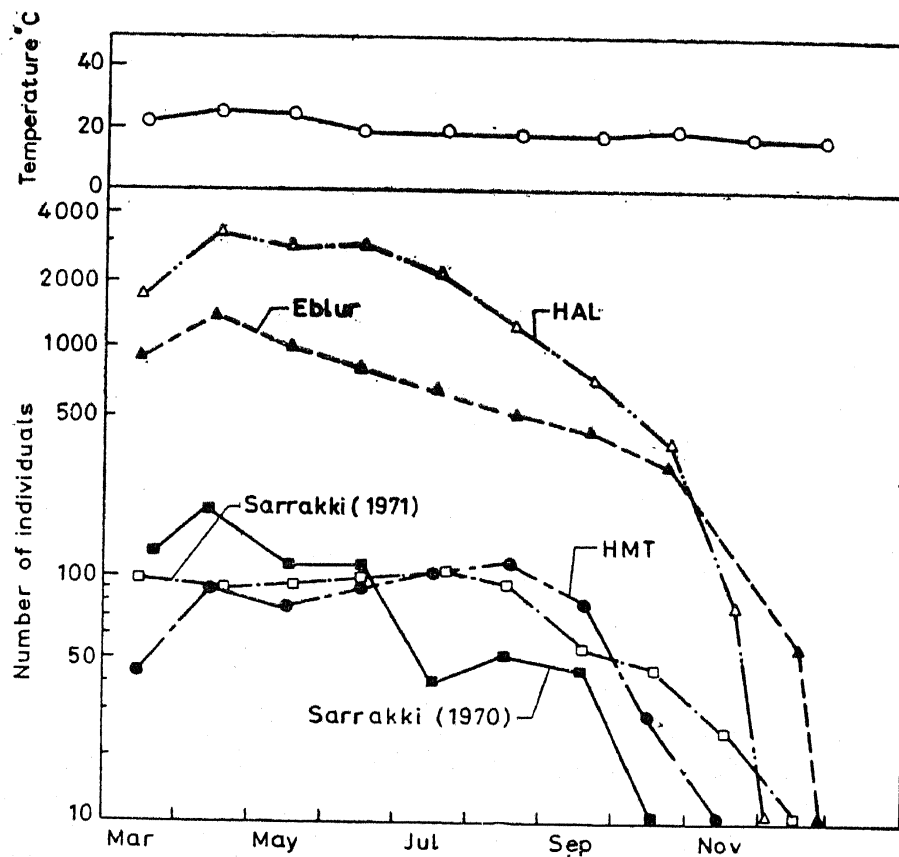

Figure 5. Total number of individuals observed in different Bangalore fields as a function of calendar month. Upper panel indicates of the mean monthly temperature observed for the fields,

The maximum density of the I and II instar *P. pictus* was observed during March–April. Subsequently, the density decreased, as hoppers passed through III, IV and V instars. Thereafter, the density of the VI instar and adult increased; this increase is mainly due to the fact that the duration of these life stages is extended for a period of over 40 to 130 days. Survivorship curves for either sex are separately shown in figure 5. Typically, these curves are convex and more or less similar to the one established for *Drosophila* (see Odum 1971). This fact may reveal that the decline in population size, especially from October is controlled by endogenous (intrinsic population processes; Price 1975). The growth of the HMT population, which was not subjected to environmental stress of parasitic infection, also followed the typical convex pattern very similar to those of the HAL, Eblur and Sarrakki populations, which suffered considerable mortality due to infection by *B. kaestneri*.

The different patterns of survivorship curves obtained for different insects have been brought under two major categories: Category A representing those for which a concave curve is obtained (e.g., the grasshopper *Parapleurus alliaceus*, Nakamura *et al.* 1971) and Category B representing those with convex curves (Price 1975). From the survivorship curves available for 19 insect species, Price (1975) concluded that those with concave survivorship curves, were subjected to over 70% mortality before they reach mid larval stage and those, with covex survivorship curves, were exposed to less than 40% mortality before reaching mid larval stage. Pandian and Delvi (1973) reported that due to infection by *B. kaestneri*, 22% of the laboratory reared *P. pictus* succumbed to death before reaching the mid-hopper stage.

3.2. *Biomass*

Biomas of *P. pictus* ranged from 1 to 43 and 1 to 347 gcal/m^2 for Sarrakki field during 1970 and 1971, respectively, 0·2 to 96 gcal/m^2 for the HMT field, 1 to 120 gcal/m^2 for Eblur field and 36 to 1,330 gcal/m^2 for the HAL field (figure 6). From the respective initial values in March, increase in the biomass showed a typical log phase of growth during the period from March to May, a steady asymptote level during the period from June to September, when the population was under intensive selection pressure and subsequently declined during October–December. Thus, population growth of *P. pictus*, expressed in terms of biomass, as a function of time, follows a typical sigmoid growth curve.

The year-to-year fluctuation in the biomass of Sarrakki population gives an idea about the annual variations, to which *P. pictus* population in the other fields could be subjected to. Mean biomass for the Sarrakki field averaged 33 and 59 gcal/m^2 for the years 1970 and 1971. The corresponding values for the year 1971 were 63, 70 and 638 g cal/cm^2 for Eblur, the HMT and the HAL fields, respectively. Maximum biomass values available in the literature range from 75 gcal/m^2 for *Orchilimum* in the salt marsh of Georgia (Smalley 1960), to 3,525 gcal/m^2 for *Melanoplus* in the grassland of Tennessee (Van Hook 1971). The values obtained for *P. pictus* in different Bangalore fields fall within the reported range.

3.3. *Energy budget*

To obtain energy budget of *P. pictus* population, data on density, age structure and sex of populations reported for the fields were related to the respective feeding,
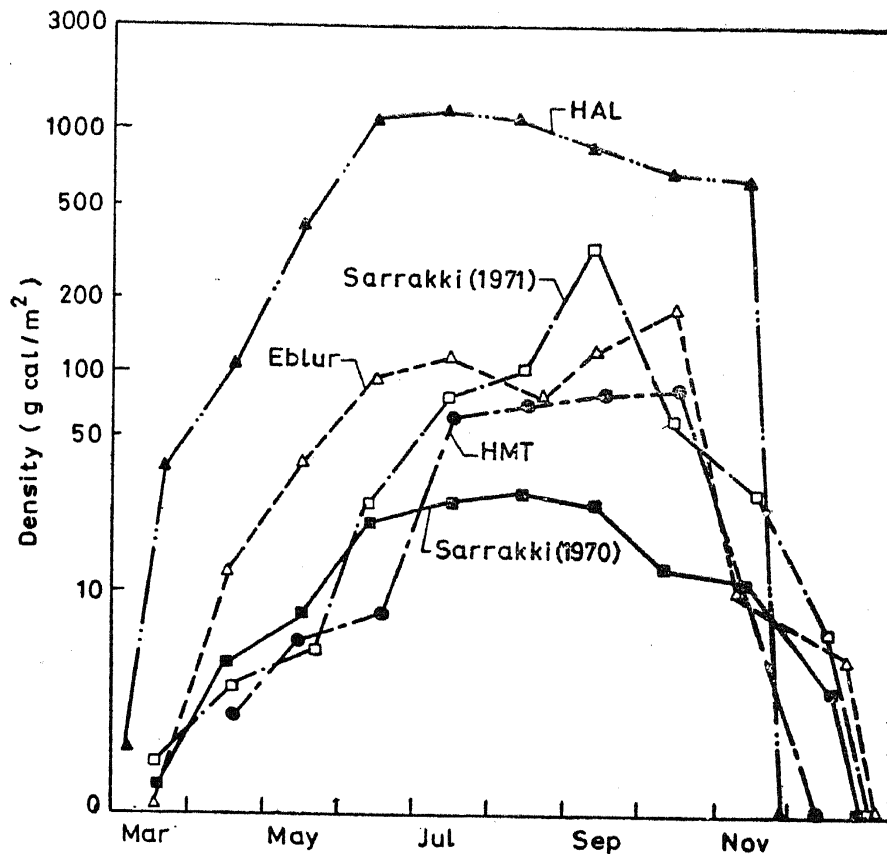
Figure 6. Mean biomass as a function of calendar month in different Bangalore fields.

assimilation and conversion rates estimated for *P. pictus* reared in the laboratory at 26° C (table 3). For this purpose, the following formulae were used:

$$C = \frac{C_r \times MW \times \bar{N} \times t}{1000 \times a} \tag{1}$$

$$A = \frac{A_r \times MW \times \bar{N} \times t}{1000 \times a} \tag{2}$$

$$K = \frac{K_r \times MW \times \bar{N} \times t}{1000 \times a} \tag{3}$$

where C is the consumption, C_r, the feeding rate (gcal/kcal/day), MW, mid-calorific content of the individual, $\bar{N}$, the mean density, t, the time interval between two successive estimates, a, the area of the field (m^2), A, the assimilation, A_r, the assimilation rate, K, the conversion, and K_r, the conversion rate. Since rates are calculated per kilocalorie, the 1000 in the formulae remains constant. The data thus obtained are presented in tables 4 and 5 to show the life stagewise contribution of *P. pictus* to energy transfer in the chosen Bangalore fields. The following generalisations may be made: (i) In all the fields, adult females and VI instar males contributed the largest share to the total energy budget of the population. Despite their largest number and the highest rates of feeding, assimilation and conversion,

Table 3. Rates of feeding, assimilation and conversion in the grasshopper *Poecilocerus pictus* fed *ad libitum* on *Calotropis gigantea* at $26 \pm 1°$ C and $70 \pm 10\%$ rh. Values are expressed in gcal/kcal/day (from Delvi 1972).

Life stage (instar)	Feeding ♀	Feeding ♂	Assimilation ♀	Assimilation ♂	Conversion ♀	Conversion ♂
I	208	199	80	79	48	50
II	368	468	212	231	52	39
III	235	286	112	147	44	64
IV	215	158	87	63	31	29
V	214	166	86	61	31	26
VI	106	142	41	53	20	19
Adult	49	50	16	15	8	4

Table 4. Life stagewise contribution of *Poecilocerus pictus* to total annual energy budget in Sarrakki field during 1970 and 1971. Values are given in gcal/m²/year.

Life stage (instar)	Consumption 1970	Consumption 1971	Assimilation 1970	Assimilation 1971	Production 1970	Production 1971
Male						
I	3·3	2·1	1·3	0·8	0·8	0·5
II	14·5	10·5	7·7	5·6	1·7	1·1
III	45·5	22·2	23·5	11·6	10·1	5·0
IV	19·2	17·9	7·1	6·9	4·2	3·3
V	37·0	41·8	13·2	15·8	5·6	6·6
VI	67·2	89·9	29·9	31·8	11·8	12·1
Adult	48·9	78·7	16·4	26·0	4·1	6·5
Female						
I	3·3	2·1	1·3	0·8	0·8	0·5
II	14·5	10·5	7·7	5·6	1·7	1·1
III	37·5	22·2	17·9	11·6	7·1	5·0
IV	33·6	17·9	13·6	6·9	4·9	3·3
V	51·3	41·8	21·0	15·8	6·6	6·6
VI	42·7	89·9	16·4	31·8	9·0	12·1
Adult	63·2	78·7	20·5	26·0	8·7	6·5

I and II instar contributed, perhaps the least to the total energy budget. (ii) The difference in the quantitative contribution by corresponding instars in different fields reflects the magnitude of difference in the density and biomass. (iii) In comparison to adult males, adult females contributed a far larger share, perhaps due to their reproductive role.

Table 5. Life stagewise contribution of *Poecilocerus pictus* to the total annual energy budget (expressed in gcal/m²) in the chosen Bangalore fields.

Life stage (instar)	Consumption		Assimilation		Production	
	♀	♂	♀	♂	♀	♂
HAL						
I	91	91	36	36	23	23
II	346	346	188	188	39	39
III	312	496	143	255	56	116
IV	471	385	191	148	68	71
V	1500	1534	603	564	217	239
VI	2385	2948	919	1046	450	385
Adult	3339	1608	1076	480	461	121
EBLUR						
I	2	2	1	1	0·5	0·5
II	17	17	9	9	2	2
III	19	23	9	12	2	5
IV	45	34	18	13	6	5
V	403	359	162	133	46	56
VI	698	814	269	289	132	110
Adult	1642	703	533	235	240	59
HMT						
I	0·6	0·6	0·2	0·2	0·1	0·1
II	30·2	30·2	12·8	12·8	6·8	6·8
III	15·4	18·4	7·4	9·5	2·9	4·1
IV	21·3	18·1	8·6	6·9	3·2	3·3
V	89·0	53·3	36·0	19·7	12·9	8·4
VI	85·0	92·0	33·0	32·6	15·9	12·4
Adult	261·0	77·0	85·0	25·8	36·2	6·5

Tables 6 and 7 show energy budget of *P. pictus* populations in different Bangalore fields during the period from March to December. In all the chosen fields, energy transfer from *C. gigantea* to *P. pictus* populations showed a rapid increase from the respective minimum values in March to the highest values in May. This was followed by a period from June to August, when the rates of consumption, assimilation and production by *P. pictus* were steady. Subsequently, these values dwindled almost to zero in December. It may be recalled that the period from March to May represented the log phase of growth, and June to September the steady state of population density. Clearly, the duration from May to September represents the period of active consumption and production of *P. pictus* population; as much as 60 to 70% of annual consumption and production occurred during this period. Faecal matter equivalent to 10,086 and 3,100 g/m² was defecated during the active period of growth in the HAL and Eblur fields. It is during this period that there were frequent monsoon showers, which perhaps facilitated faster decomposition and hence the return of organic matter to the soil.

Of the four fields studied, consumption of *C. gigantea* leaf by *P. pictus* population was the highest in the HAL field and it amounted to 16 kcal/m²/year; it was

Table 6. Energy budget of *Poecilocerus pictus* in Sarrakki field during 1970 and 1971. Values are expressed in gcal/m².

Month	Consumption		Assimilation		Production	
	1970	1971	1970	1971	1970	1971
Mar	3·8	9·2	1·5	4·3	0·9	1·5
Apr	51·6	21·4	25·9	10·9	9·1	3·9
May	41·9	46·2	34·2	21·8	13·2	8·1
Jun	85·8	94·7	38·7	36·3	15·9	14·1
Jul	90·3	186·3	33·7	65·4	14·0	26·1
Aug	74·5	170·9	28·9	57·5	10·3	22·4
Sep	78·8	92·2	23·9	30·9	9·2	12·6
Oct	20·0	80·4	6·6	26·5	2·5	10·6
Nov	15·3	50·3	5·1	16·4	1·7	6·7
Dec	··	7·4	··	2·4	··	1·0
Total	462	759	199	272	77	107

Table 7. Energy budget of *Poecilocerus pictus* in the chosen Bangalore fields during 1971. Values are expressed in gcal/m².

Month	Consumption			Assimilation			Production		
	HAL	Belur	HMT	HAL	Eblur	HMT	HAL	Eblur	HMT
Mar	253	20	0·7	123	10	0·3	62	2·7	0·2
Apr	968	102	35	480	45	17	149	17	7·4
May	4367	162	65	1721	63	28	704	26	14·1
Jun	2152	257	89	724	93	35	295	37	14·4
Jul	3736	3765	163	1352	1322	58	522	526	23·3
Aug	2116	127	171	731	45	60	290	18	24·2
Sep	1461	222	186	501	76	66	208	30	25·8
Oct	1028	135	64	337	44	21	127	17	8·2
Nov	31	7	16	10	2·4	5·3	3·6	0·9	2·2
Dec	··	3	1·2	··	1·0	0·4	··	0·4	0·2
Total	16112	4800	791	5979	1701	291	2361	675	119

around 0·7 kcal/m²/year in the Sarrakki or the HMT field. As much as 35 to 40% of the consumed food is assimilated by *P. pictus* populations. Values on energy flow through *P. pictus* population in Sarrakki, HMT, Eblur and HAL fields were 0·2, 0·3, 1·7 and 6·0 kcal/m²/year, respectively (table 8); of these, about 15% is channelled through secondary production by *P. pictus* population.

Table 9 presents exploitation, production and ecological efficiency values of *P. pictus* populations in Bangalore fields. Exploitation efficiency ranged from 0·25 to 11·3% and ecological efficiency from 0·04 to 1·74%; values on production efficiency were around 15%.

Table 8. Energy budget of *Poecilocerus pictus* population in the chosen Bangalore fields. Values are expressed in kcal/m²/year.

Field	Consumption	Assimilation	Production	Respiration
Eblur	4·8	1·7	0·67	1·02
HMT	0·79	0·29	0·12	0·17
Sarrakki	0·61	0·24	0·09	0·15
HAL	16·1	5·98	2·36	3·62

Table 9. Primary productivity (GPP) of *C. gigantea*, exploitation and production efficiencies of *P. pictus* in the chosen Bangalore fields (GPP values from Delvi, 1972).

Field	Number of plants	Biomass of *P. pictus* (gcal/m²)	GPP (Kcal/m²/ year)	Exploitation efficiency (%)	Production efficiency (%)	Ecological efficiency (%)
Eblur	336	63	366	1·31	14·2	0·20
HMT	68	70	294	0·27	15·2	0·04
Sarrakki	56	46	245	0·25	14·5	0·04
HAL	150	638	142	11·34	15·3	1·74

4. Discussion

Maximum biomass values of a number of insects reported by different authors are given in table 10. The HAL field supported the maximum biomass of 1,330 gcal/m² of *P. pictus* population and the Sarrakki the minimum of 43 gcal/m². Of the values available in the literature for grasshopper populations, the highest value of 3,525 gcal/m² is reported by Van Hook (1971) for *Melanoplus* in grassland of Tennessee. Positively, the difference between the biomass of host plants (e.g. *C. gigantea* in Sarrakki: 50 g/m² and *Festuca* and *Andropogon* in grassland Tennessee: 228 g/m²) may be responsible for the difference in the biomass of *P. pictus* and *Melanoplus* in the respective fields. However, mean biomass of *P. pictus* (435 gcal/m²) population in the fields of Bangalore is higher than those of the spittle bug *Neophilaneus lineatus* (340 gcal/m²) in Devon field, England and *Leptopterna dolabrata* (80 gcal/m²) in Berkshire, England.

The biomass of herbivorous orthopterans outweigh the biomass of other herbivorous insects in any particular ecosystem. For instance, Qasrawi (1966) and Hinton (1971) reported the maximum biomass for the grasshopper *Chorthippus paralellus* and the spittle bug *Neophilaneus lineatus*, respectively; the work was carried out in the adjacent sites of the Devon field in England during 1965. Hinton reported that these two insects co-exist and feed on the same host plant and hence both these insects are given equal opportunity to grow in that field. Under these

Table 10. Data on maximum biomass (gcal/m²) of some insects (values reported in dry or wet weight were converted into energy considering 5000 gcal/g dry weight (Golley 1961).

Species and habitat	Biomass	Reference
Poecilocerus		
(a) HAL Field	1330	Present paper
(b) (i) Sarrakki (1970)	43	Present paper
(ii) Sarrakki (1971)	347	Present paper
(c) Eblur Field	120	Present paper
(d) HMT Field	96	Present paper
Melanoplus		
(a) Old Field, Michigan	300	Weigert (1965)
(b) Old Field, Georgia		
Oecanthus sp.	1750	Odum *et al* (1962)
(c) Grassland, Tennessee	3525	Van Hook (1971)
Orchilimum		
Salt marsh, Georgia	75	Smalley (1960)
Chorthippus		
Devon, England	1130	Qasrawi (1966)
Hedriodiscus		
Thermal spring, Canada	172	Stockner (1971)
Neophilaneus		
Devon, England	340	Hinton (1971)
Leptopterna		
Berkshire, England	80	McNeill (1971)
Pyrrhosoma		
Durham, Scotland	2	Lawton (1971)

situations, the orthoptera *C. paralellus* grew to a maximum biomass of 1,130 gcal/m², while *N. lineatus* only to 340 gcal/m². Furthermore, the mean maximum biomass of orthopterans given in table 10 under items 1 to 4 amounts to 871 gcal/m², while the corresponding value for the bugs (items 6 and 7) is only 210 gcal/m². Van Hook 1971) also concluded that the orthopterans were the most important herbivorous species in terms of both number and biomass. As may be expected, the carnivorous insects like *Pyrrhosoma nymphula* could hardly afford to maintain the maximum biomass of only 2 gcal/m² (Lawton 1971).

Of the four fields studied, ingestion, assimilation and secondary production by *P. pictus* populations were the highest in the HAL field; these values were 16, 6 and 2·5 kcal/m²/year. Corresponding values available in the literature are 77, 26 and 4 kcal/m²/year for multispecies orthopteran populations in South Carolina (Weigert and Evans 1967). Ingestion rate of the grasshopper *Orchilimum fidicinum* reported by Odum and Smalley (1959) is about 108 kcal/m²/year. Low rate of ingestion exhibited by *P. pictus* population reflects the effectiveness of the chemical defence mechanism developed by *C. gigantea* to reduce herbivory. Efficiency values for assimilation (34%) and production (15%) estimated for *P. pictus* population are very close to those reported for grasshopper populations by Odum and

Smalley (1960) and Weigert and Evans (1967). However, *P. pictus* spends about 60% of the assimilated energy on metabolism whereas the orthopteran populations expended as much as 84% of the assimilated energy on metabolism. One reason for the difference may be that *P. pictus* is almost sedentary; but the other orthopterans are very good walkers and runners, if not fliers. It is known that the cost of transport for locomotory activity is very heavy, especially for such small insects in comparison to larger mammals (see Price 1975).

Another important result of this work is the theory of endogenous regulation. The available theories on population regulation process have been classified into two categories by Price (1975): (i) Exogenous population process, in which density-dependent factors like predation, food and space predominantly regulate the population size. (ii) Endogenous population process, in which factors like pathological effects in response to crowding, process with the genetic component, social interaction and dispersal regulate the population size.

As *P. pictus* accumulates the poison gained from *C. gigantea*, only a few predators feed on it. However, it is infected by *B. kaestneri*. Though mortality due to the parasitoid infection has not been separately estimated in the fields, it has been clearly noted that *P. pictus* was not infected by *B. kaestneri* in the HMT field. The survivorship curve obtained for *P. pictus* populations in all the fields showed an uniform trend, indicating that the parasitoid *B. kaestneri* was not a very important exogenous agent in the regulation of *P. pictus* population.

Secondly, the exploitation efficiency of *C. gigantea* leaf by *P. pictus* population ranged between 0·25 to 11·3% and averaged 3·4%, which is comparable to the efficiency values available in the literature for leaf feeders (see Price 1975). In the HMT and Sarrakki, the productivity of *C. gigantea* ranged from 245 to 294 kcal/m²/year, but the exploitation efficiency by *P. pictus* was less than 0·27%. On the other hand, the efficiency was as high as 11·3% in the HAL field, in which *C. gigantea* productivity was the least (142 kcal/m²/year). Hence the availability of food is not a limiting factor for herbivores (Ricklefs 1973), especially for the leaf feeders like *P. pictus*.

Thirdly, *C. gigantea* appears not to limit *P. pictus* even as habitat. For instance, tin Eblur field, there were as many as 336 *C. gigantea* plants, where the mean biomass of *P. pictus* was only 63 gcal/m², whereas as few as 150 *C. gigantea* in HAL field supported the largest biomass of *P. pictus* (638 gcal/m²). Clearly, the extrinsic factors like predation, food and space appear not to contribute one way or the other to the regulation of *P. pictus* population. Therefore, it is concluded that intrinsic population factors may control the population size of *P. pictus*.

Acknowledgements

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