

Interspecific Differences in the Host Plant Utilization of Three Coexisting Lepidopteran Larvae‡

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Bioenergetics of three lepidopteran pests (*Ergolis merione* Walk., *Porthesia scintillans* L. and *Spodoptera exigua* L.), coexisting on castor (*Ricinus communis*), was estimated. Larval duration of these species was 11-13 days. Consumption rate of *P. scintillans* was higher than that of the other two species. Rates and efficiencies of the females were higher than that of the males. Energy allocation to egg production by *P. scintillans* and *S. exigua* was 97 and 175J, respectively. Differences in the rates and efficiencies of food utilization among these pests have been implicated to be an adaptation to survive in the same host plant.

Key Words: Bioenergetics, Food utilization, Lepidopteran pests

Introduction

Striking differences in water, nitrogen, and allelochemical contents of host plants have incited several workers to investigate the effect of food quality on food utilization in insects (Soo Hoo & Fraenkel 1966, Slansky & Feeny 1977). Holometabolus insects, especially several Lepidoptera, a few Coleoptera and Hymenoptera, which pass through non-feeding pupal and/or adult stages display a characteristic pattern of food utilization that is distinctly different from that of Orthoptera and other insects which feed throughout their life (Slansky & Scriber 1985). Closely related species feeding on the same host plant under similar environmental conditions (temperature, photoperiod, humidity, and availability of food), may follow different strategies of growth and reproduction (Muthukrishnan & Pandian 1987). Despite a vast amount of literature on quantitative aspects of nutrition of herbivores being available, little is known on interspecific differences in the rates and efficiencies of food utilization of insects feeding on the same host plant (Scriber & Slansky 1981). The present paper reports bioenergetics of *Ergolis merione*, *Porthesia scintillans* and *Spodoptera exigua*, all feeding on *Ricinus communis*.

Of the three species, *E. merione* is strictly monophagous and colonises the host throughout the year. *P. scintillans* and *S. exigua* are polyphagous and infest the host plant mostly during monsoon. Whereas *E. merione* remains in the lower parts (upto 1m from the soil level) of the plant and feeds during most part of the day, *P. scintillans* and *S. exigua* occur (1m above from the soil level) on the leaves and feed during night times.

Materials and Methods

Newly hatched larvae of *E. merione* were collected from the field, since their eggs remain concealed within the leaf primordia, rendering it difficult to obtain their eggs. Eggs of *P. scintillans* and *S. exigua* were obtained from our laboratory culture and hatched at $29 \pm 1^\circ\text{C}$. The first instar larvae were reared individually in plastic terraria (250ml capacity) on fresh leaves of castor. As soon as the larvae moulted into II instar, they were weighed and recruited to the experiment. A stock culture of larvae of these species was maintained separately. Whenever, the experimental larvae died, larvae of the same age and weight from the stock culture were substituted. The test larvae were reared at

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29 ± 1°C and 75 ± 5% Rh. Sex could not be distinguished during the larval stages of these insects; however, some of the adults of *P. scintillans* and *S. exigua* used for the experiment oviposited in the laboratory. Therefore, it was possible to evaluate the performances of the male and female larvae of these two species and work out separate energy budgets. But the data reported for *E. merione* represent the average performance of both males and females. Food consumption was estimated following the gravimetric method of Waldbauer (1968). Prior to feeding, remanant leaf bits and fecal pellets were collected every day and dried at 60°C. The test insects were weighed at the termination of feeding, pupation, and emergence. Samples of food, initial and terminal stages of the larvae, pupae, and the adults were weighed and dried at 60°C, and the water content was estimated. Energy content of the test materials was estimated in a Parr 1421 semi microbomb calorimeter.

The scheme of energy balance followed in the present study is the IBP formula of Petruszewicz and Macfadyen (1970), represented as

$$C = P + R + FU$$

where, *C* is the energy of food consumed, *P*, the growth, *R*, the energy lost on metabolism, and *FU*, the energy loss through faeces. Assimilation was calculated by subtracting *FU* from *C*. *P* was estimated as the difference in the energy content of the larva at the commencement and termination of each instar, *R* represents the difference between assimilation and production. Rates of feeding (*C_r*), assimilation (*A_r*), production (*P_r*), and metabolism (*M_r*) were calculated by dividing the respective amounts of energy by the product of duration and mid-body weight (g) of the larva; the rates are expressed in kJ/g live insect/day. Efficiencies of assimilation and production were calculated relating to *A* to *C*, and *P* to *C* and *A* in percentage. Energy budget for the non-feeding pupal

and adult stages was prepared following the method of Muthukrishnan and Pandian (1984).

Results

Growth

Newly moulted II instar larvae of the three species weighed 8.5–10.0mg and contained 34–46J. Energy content of the larvae rapidly increased several times with the advancing age. At the commencement of V instar, the energy content increased to 697.5, 551.5 and 4435.6J in *E. merione*, female of *P. scintillans* and *S. exigua*, respectively, while the corresponding values of the terminal larvae were 2157, 1791 and 1903J; the freshly emerged adults contained 1320, 962 and 1002J (figure 1).

Bioenergetics

Corresponding to rapid growth, food energy ingested during each instar increased several times, as the larva moulted from one stage to other. For instance, *C* for *E. merione* increased from 589.5J during II instar to 3840.8J in the VI instar (table 1). Data on food consumption by female and male *P. scintillans* and *S. exigua* are provided in tables 2 and 3. Irrespective of their sex, maximum food was consumed during the final instar of the tested species. With advancing age and the concurrent increase in the body weight, food consumption rate (*C_r*) for the larvae decreased exponentially (figure 2). For instance, in the female *P. scintillans*, *C_r* decreased from 47.5 kJ/g/day (II instar) to 7.51 kJ/g/day (VI instar). Statistically significant negative correlation coefficient (*r*) was obtained for the relation between *C_r* and \log_{10} mid-body weight (g) of the different instars of *E. merione*, *P. scintillans*, and *S. exigua* (table 4). The slope of the regression of *C_r* on $\log W$ of *P. scintillans* larva is significantly higher than that of *E. merione* and *S. exigua*; therefore, it is concluded that *P. scintillans* inflicts maximum damage to *R. communis* compared to the other two species.

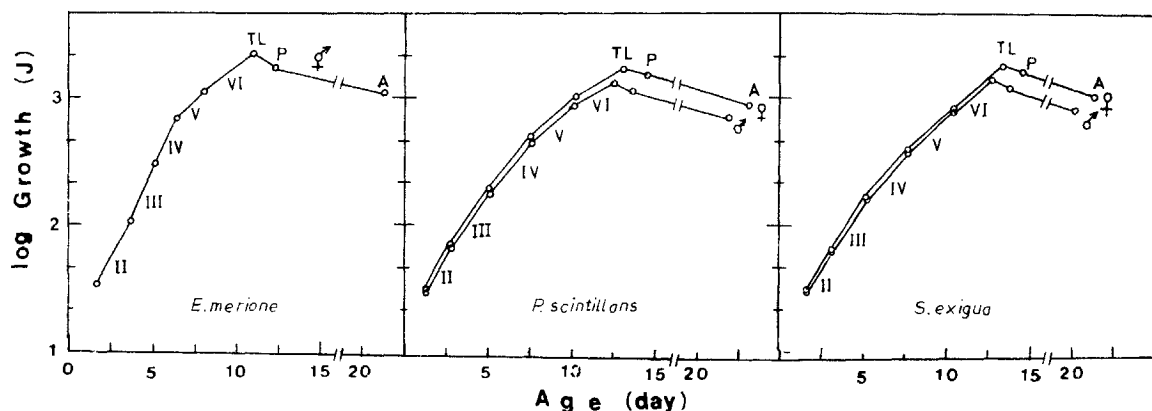


Figure 1 Growth of *Ergolis merione*, female and male of *Porthesia scintillans* and *Spodoptera exigua*. (Roman numerals indicates larval instar. TL, P and A; indicate terminal larva, pupa and adult respectively)

Table 1 Bioenergetics of *Ergolis merione* fed ad libitum on *Ricinus communis* leaf (Each value (J/larva) represents ($\bar{X} \pm SD$) the average performance of 12 larvae)

Instar	D	C	FU	A	P
II	1.5	589.5 ± 33.1	200.4 ± 9.8	389.1 ± 22.6	41.6 ± 2.1
III	2.0	1785.0 ± 95.4	732.9 ± 36.4	1032.1 ± 48.4	200.8 ± 10.4
IV	2.0	2581.7 ± 128.7	1252.9 ± 69.4	1328.8 ± 74.6	418.2 ± 21.8
V	2.5	3135.3 ± 176.2	1581.7 ± 89.4	1533.6 ± 86.2	638.0 ± 32.9
VI	3.0	3840.8 ± 199.4	1951.3 ± 99.8	1889.5 ± 89.9	821.5 ± 44.5
TOTAL	11	11932.3	5719.2	6173.1	2120.1

D, Larval duration; C, Consumption; FU, Faeces; A, Assimilation; P, Production

Corresponding to the increase in C, feces egested by the larvae also increased. On the whole, 5719, 6144 and 7242J of ingested energy was lost as feces in *E. merione*, females of *P. scintillans* and *S. exigua*, respectively (tables 1-3). *E. merione*, female of *P. scintillans* and *S. exigua* assimilated 6193, 5984 and 6206J during the entire larval period at an overall rate of 8.54, 11.71 and 9.79 kJ/g/day, respectively. Statistically significant negative correlation was evident for the A_r as well (table 4). Assimilation efficiency for all the larvae ranged between 42 and 66%. Two-way analysis of variance for the data on the assimilation efficiency revealed that the differences between the instars were more significant ($p < 0.01$) than those between the different species ($p < 0.05$) (table 5). The larvae allocated a major part of the assimilated energy to meta-bolism. With advancing age and increase in biomass, energy allocated to metabolism increased on a proportional scale. For instance, the increase was from 269.2J (II instar) to 1400.7J (final instar) in the females of *S. exigua*. Energy allocated to production of larval tissue by *E. merione*, female *P. scintillans* and *S. exigua* amounted to 2.14, 1.75 and 1.87kJ for the entire larval period. Male *P. scintillans* and *S. exigua* allocated comparatively less energy to production than female. Production rate also decreased with increasing age; however, the decrease was not as much as in the case of c_r or A_r (figure 2).

Net production efficiency (P_{e2}) of the larvae increased with age. For instance, P_{e2} was 6^{1/2}-7% in the II instar larvae and 18-23% in the final instar of the three species. Analysis of variance of the data on net production efficiency (P_{e2}) revealed that the differences in the efficiency between instars ($p < 0.01$) were more the significant than the differences between the species than ($p < 0.05$) (table 5).

Energy accumulated in the terminal larva was allocated to different structures and functions of pupa and

adult. Of the three species studied, *P. scintillans* spun a silky cocoon before pupation, while *S. exigua* made use of extraneous materials like dry leaf-bits and *E. merione* transformed into pupa without spinning a cocoon.

Energy loss on larval exuvia amounted to 23.2, 22.8, and 16.9 J/insect in *E. merione*, females of *P. scintillans* and *S. exigua*, respectively. In addition to this, *P. scintillans* expended 22.7J on the cocoon. Energy loss on pupal case amounted to 36.3, 25.0 and 19.9J in *E. merione*, female *P. scintillans* and *S. exigua* (table 6). Briefly, energy loss on larval exuvia and pupal case depends upon the size of the terminal larva. Energy content of pupa ranged from 1383J (*P. scintillans* male) to 1924J (*E. merione*). Energy content of newly emerged adult *E. merione*, females of *P. scintillans*, and and *S. exigua* was 1320, 962 and 1002J, respectively. Pupal efficiency of *E. merione* was higher than that of other two species. Energy cost of pupal-adult metamorphosis ranged between 653 and 694J in *S. exigua* and between 570 and 636J in *P. scintillans*. Metabolic rate of pharate adult was 671.1, 413.2 and 495.0J/g/day in *E. merione*, females of *P. scintillans* and *S. exigua*, respectively (table 6). *P. scintillans* expended less energy (94.7J) than *S. exigua* (175.1J) or egg production. Egg production efficiency was 9.8 and 17.2% for *P. scintillans* and *S. exigua* respectively.

Discussion

The foregoing results reveal that the moths ingest the host leaf at a rate faster than the butterfly. Field observations on the feeding rhythm and behaviour of these insects showed that the larvae of the moths fed incessantly during night and spent most part of the hot day under the leaf or on the trunk (see Leonard 1957); while *E. merione* larva displayed several feeding bouts during day and night. Such temporal partitioning of the common food resource enables successful coexistence

Table 2 Bioenergetics of male and female *Porthesia scintillans* fed ad libitum on *Ricinus communis* leaf (Each value (J/larvae) represents the average ($\bar{X} \pm SD$) of 9 to 12 larvae)

Instar	Sex	D	C	FU	A	P
II	Female	1.5	715.9±31.2	240.1±12.6	475.8±22.3	40.2±2.8
	Male	1.5	659.3±37.9	235.4±14.9	423.9±25.7	35.6±2.2
III	Female	2.5	1663.6±90.3	727.0±34.8	936.6±42.7	125.4±6.9
	Male	2.0	1241.1±74.2	569.7±34.2	671.4±41.2	96.8±6.2
IV	Female	2.5	2694.2±142.0	1389.7±80.1	1304.5±78.6	352.4±19.1
	Male	2.5	2415.9±126.7	1273.2±67.2	1142.7±60.1	304.4±16.2
V	Female	3.0	3134.3±153.9	1610.0±88.7	1524.3±78.0	529.9±28.6
	Male	3.0	2992.8±164.8	1592.2±89.6	1400.6±77.9	457.9±25.2
VI	Female	3.5	3920.0±171.4	2177.3±106.4	1742.7±85.3	709.4±34.8
	Male	3.0	3601.2±199.8	1977.1±109.5	1624.1±90.2	608.6±34.6
TOTAL	Female	13.0	12128.0	6144.1	5983.9	1757.3
	Male	12.0	10910.3	5647.6	5262.7	1503.3

For abbreviations refer to footnote in table 1

Table 3 Bioenergetics of male and female *Spodoptera exigua* fed ad libitum on *Ricinus communis* leaf (Each value (J/larva) represents ($X \pm SD$) the average performance of 12 larvae)

Instar	Sex	Day	C	FU	A	P
II	Female	1.5	447.9±26.4	144.6±8.5	303.3±16.5	34.1±1.6
	Male	1.5	414.2±28.5	144.6±10.2	269.6±19.2	28.2±1.9
III	Female	2.5	1387.9±98.6	607.8±29.8	780.1±36.5	124.6±6.5
	Male	2.0	1129.4±75.2	529.7±31.4	599.7±40.2	96.0±6.8
IV	Female	2.5	2670.3±163.5	1233.5±85.7	1233.5±85.7	240.9±11.6
	Male	2.5	2257.5±120.3	1232.6±66.2	1024.9±54.3	228.6±12.3
V	Female	3.0	3253.4±212.5	1763.8±106.4	1489.6±98.6	469.2±27.5
	Male	3.0	2923.4±153.5	1604.9±86.7	1318.5±72.3	412.2±22.6
VI	Female	3.5	5686.4±397.6	3289.0±186.4	2399.4±163.5	998.7±39.5
	Male	3.0	5190.2±272.5	2839.0±142.6	2351.2±125.2	846.0±45.2
TOTAL	Female	13.0	13445.9	7038.7	6205.9	1867.5
	Male	12.0	11914.7	6350.8	5563.9	1611.0

For abbreviations refer to footnote in table 1

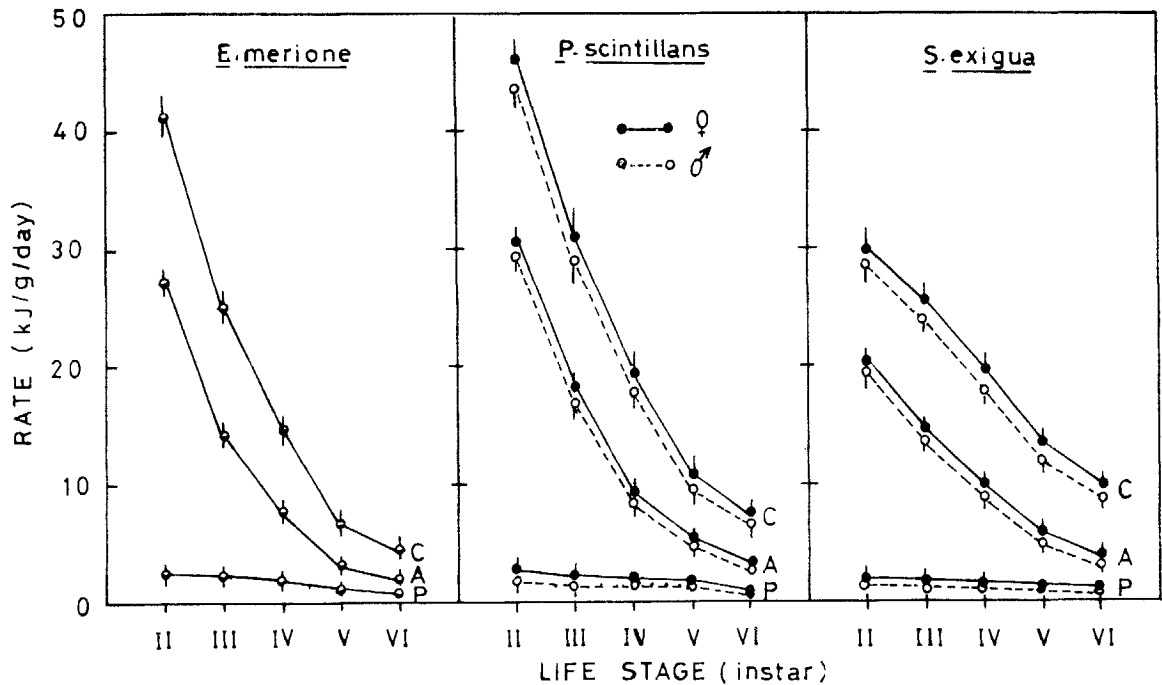


Figure 2 Rates of feeding(C), assimilation(A) and production(P) as a function of instar of *Ergolis merione*, *Porthesia scintillans* and *Spodoptera exigua* at $29 \pm 1^\circ\text{C}$

Table 4 Simple regression analysis of the relation between rates of feeding, assimilation and production and log mid-body weight of the insects

Ergolis merione

$$C_r = 72.25 + (-27.89 \times \log W); r: -0.996 \quad N=5$$

$$A_r = 41.02 + (-10.05 \times \log W); r: -0.985 \quad N=5$$

$$P_r = 4.34 + (-1.34 \times \log W); r: -0.843 \quad N=5$$

Porthesia scintillans

$$C_r = 81.76 + (-31.44 \times \log W); r: -0.968 \quad N=10$$

$$A_r = 41.02 + (-22.77 \times \log W); r: -0.985 \quad N=10$$

$$P_r = 3.91 + (-0.849 \times \log W); r: -0.932 \quad N=10$$

Spodoptera exigua

$$C_r = 53.50 + (-17.93 \times \log W); r: -0.988 \quad N=10$$

$$A_r = 35.86 + (-13.42 \times \log W); r: -0.988 \quad N=10$$

$$P_r = 2.97 + (-0.52 \times \log W); r: -0.932 \quad N=10$$

of the three Lepidopteran pests. A similar time-related resource partitioning has been reported for the phytophagous beetle *Larinus carlinea* and *L. jacea* feeding on *Carduus nutans* (Zwölfer 1975).

The castor semilooper, *Achaea janata*, also coexists with these species on *R. communis*. A comparison of the budgets of these four species shows that *A. janata* displays 2-3 times (7.2 kJ/g/day) lesser C_r than these insects (21.9 kJ/g/day). However, *A. janata* displays higher efficiencies of assimilation (52%) and production (35%) (see Muthukrishnan & Pandian 1983) than *P. scintillans* or *S. exigua* (A_e : 47-49%, P_e : ca. 29%) and *E. merione* (A_e : 52% P_e : 35%). Monophagous insects are more efficient converters than the polyphagous ones (Scriber & Slansky 1981). Such adjustments between rates and efficiencies of food utilization are common among lepidopteran insects and this ability suggests an evasion strategy among the coexisting species.

The three species of lepidoptera studied here displayed an inverse relationship between body weight and rates of feeding, assimilation, and production. A similar relationship was also reported in another lepidopteran, *Danaus chrysippus* (Mathavan &

Table 5 Two way analysis of variance (ANOVA) of the data on assimilation efficiency and production efficiency (P_{e_2}) of the chosen pests

Source of variance	SS	DF	MS	F-ratio	P
Assimilation efficiency					
Total	997.77	14	—	—	—
Between species	18.26	2	9.13	6.09	< 0.05
Between instars	967.70	2	241.93	161.29	< 0.01
Error	11.81	8	1.5		
Production efficiency (P_{e_2})					
TOTAL	1132.52	14	—	—	
Between species	52.98	2	26.49	7.18	< 0.05
Between instars	1050.05	4	262.05	71.14	< 0.01
Error	29.49	8	369		

Table 6 Energy budget of non-feeding pharate pupa and pharate adult *Ergolis merione*, *porthesia scintillans* and *Spodoptera exigua*. (Each value (J/insect) represents the average performance of 9 to 15 insects)

Parameter	<i>Ergolis merione</i>	<i>Porthesia scintillans</i>		<i>Spodoptera exigua</i>	
		Female	Male	Female	Male
Terminal larva	2157.0±36.8	1790.8±83.7	1532.2±78.2	1903.5±102.3	1677.7±91.7
Pharate pupal duration (day)	1.0±0.0	1.0±0.0	1.0±0.0	1.0±0.0	1.0±0.0
Larval exuvia	23.2±1.3	22.8±1.3	18.0±1.2	16.9±1.7	14.8±0.6
Silk	—	22.7±1.4	18.6±1.3	—	—
Pupa	1924.1±81.6	1626.0±76.9	1382.7±78.1	1715.8±86.0	1507.3±79.7
Pupal duration (day)	7.5±0.3	9.0±0.4	9.0±0.5	8.0±0.3	8.0±0.3
Pupal case	36.3±1.8	25.0±1.7	22.7±1.2	19.9±1.4	15.5±1.3
Adult	1320.1±16.3	961.7±46.5	790.9±47.3	1002.0±51.8	838.5±46.5
Pupal efficiency (%)	68.6±2.6	59.1±2.2	57.2±2.1	58.4±2.4	55.6±2.8
Egg production	Not available	94.7±5.5	—	175.1±18.9	—
" " efficiency %	—	9.8±0.5	—	17.5±1.2	—
Adult at death	422.5±23.7	212.1±8.7	328.7±13.8	196.3±9.4	366.5±21.4
Adult duration (day)	3.0±0.4	3.5±0.4	3.0±0.0	3.9±0.5	3.2±0.2
Mr-pharate pupa*	671.1±42.8	413.2±19.3	391.4±18.9	495.0±23.7	482.5±28.4
Mr-pharate adult*	321.8±16.5	318.5±12.6	292.9±12.5	334.4±26.3	342.2±24.7
Metamorphic metabolic rate*	359.4±20.5	325.2±18.3	290.4±18.2	347.8±24.1	360.6±23.8

* J/g live insect/day

Bhaskaran 1975). Rapid growth and accumulation of metabolically less active lipids by the larvae, are obviously responsible for the decrease in rates with the increasing body weight or advancing age (Slansky & Scriber 1985). Of the two species for which fecundity was estimated, *S. exigua* allocates a greater fraction of the energy accumulated to egg production; it produces 204 eggs at the expense of 175J compared to 144 eggs at the cost of 95J by *P.scintillans*. It is likely that in the 'r' and 'k'-continuum (Pianka 1970), *S. exigua* may find a place ahead of *P.scintillans* towards the 'r' end.

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