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Prediction of bioenergetics components of lepidopterous larva

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Abstract. Using the bioenergetics data for the final instar *Achaea janata* larva exposed to a wide range of ration levels and temperatures, a linear regression model to predict the bioenergetics components of lepidopterous larva has been developed. From the dry weight of faeces egested (*F*) it is possible to estimate the consumption (*C*), production (*P*) and metabolism (*R*). Validity of the proposed model has been tested using the data reported in literature.

Keywords. Lepidoptera; bioenergetics components; regression model; *Achaea janata*.

1. Introduction

Reviewing the nutritional ecology of immature insects, Scriber and Slansky (1981) emphasised the significance of quantitative data on food consumption and utilisation in insects for a better understanding of their ecology. Experiments on intake of natural diets usually involve gravimetric measurements (Waldbauer 1968), and are probably among the most tedious in the repertory of experimental entomologists, even with the advent of modern electronic microbalances. Apparently, the complexity of the data collecting process accounts for the relatively scanty work in this area (Klein and Kogan 1974). Literature survey reveals stray attempts to devise indirect methods to collect data on food consumption (Bhattacharya and Waldbauer 1969; Holter 1973; Mathavan and Pandian 1974). However, a comprehensive model that can be followed to determine all the bioenergetics components — consumption (*C*), production (*P*) and metabolism (*R*) is yet to emerge.

2. Material and methods

In lepidoptera, over 80% of the total food consumption for the entire larval period occurs during the final instar (Waldbauer 1968; Muthukrishnan and Pandian 1983a). Therefore, bioenergetics data reported earlier (Muthukrishnan and Pandian 1983b) for the final instar *Achaea janata* L. (Noctuidae; Lepidoptera) reared on a wide range of rations (50 to 500 mg *Ricinus communis* leaf per larva per day) at 22, 27, 32 and 35°C were chosen to develop a linear regression model so as to predict the bioenergetics components of lepidopterous larva. The ease and accuracy with which faeces (*F*) egested by the larvae can be estimated have prompted several workers to choose either components of *F* (sugar: Krishna and Saxena 1962; uric acid: Bhattacharya and Waldbauer 1969, 1970) or whole *F*

(Mukerji and Guppy 1973; Mathavan and Pandian 1974) as an index of *C*. On the same ground, whole *F* has been chosen to predict *C*, *P* and *R* in the present study.

Use of *F* in terms of dry weight for obtaining *C*, *P* and *R* in terms of energy may find wide application in studies on energy flow through consumer populations, as it circumvents the estimation of calorific content. But, before choosing to use mass value of *F*, it is essential that extrinsic factors like temperature and availability of food do not alter the calorific content of *F*. Analysis of variance of calorific values of faeces egested by final instar *A. janata* exposed to different rations and temperatures revealed that neither of them significantly varied the calorific values of *F* (table 1). Therefore, mass values of *F* have been used for predicting *C*, *P* and *R* in terms of energy (Joules).

Data on rates of defaecation (*F*), consumption (*C*), production (*P*) and metabolism (*R*) of final instar *A. janata* as functions of ration and temperature are presented in table 2. Statistical analysis of the data revealed that *F* had significant positive correlations with *C*, *P* as well as *R*. Therefore, separate linear regression equations were calculated for the relation between *F* and *C*, *F* and *P* and *F* and *R*. *P* and *R* of *A. janata* larva receiving lowest rations at the tested temperatures were low and affected the linear relation of *P* and *R* with *F*; hence these values were not considered for the computation of equations to predict *P* and *R*. Using the regression equations, *C*, *P* and *R* in respect of known *F* values were predicted. Goodness of fit of the predicted values with the observed data was tested by chi-square method (Zar 1974).

Table 1. Calorific content (J/mg dry matter) of faeces egested by final instar *Achaea janata* larva fed on different rations of *Ricinus communis* leaf (mg/larva/day) at the tested temperatures.

Ration	22°C	27°C	32°C	35°C
50	16.5 ± 0.7	17.4 ± 0.9	*	*
100	17.2 ± 1.1	17.0 ± 0.3	17.7 ± 0.9	16.9 ± 0.7
200	16.8 ± 0.5	17.1 ± 0.6	16.6 ± 0.9	17.5 ± 0.4
300	17.0 ± 0.4	17.8 ± 0.8	17.0 ± 0.9	17.1 ± 0.5
400	17.6 ± 0.7	17.2 ± 0.5	16.9 ± 0.4	17.0 ± 0.7
500	*	*	16.9 ± 0.3	16.9 ± 0.5
Ad libitum	17.9 ± 0.6	17.8 ± 0.9	17.1 ± 0.4	17.4 ± 0.5

Analysis of variance

Source	SS	Df	MS	F-ratio	P**
Total	37.245	76	—	—	—
Between Rations	2.789	4	0.697	1.508	0.1
Between Temperatures	1.514	3	0.505	1.093	0.1
Interaction	6.603	12	0.550	1.190	0.1
Residual	26.339	57	0.462	—	—

Each value ($\bar{X}$±SD) represents the mean of minimum 3 estimations.
*For want of comparable data, values at 50 and 500 mg ration levels were not considered for the analysis of variance. **$P>0.05$ is not statistically significant.

Table 2. Rates of defaecation (*F*) (mg/g larva/day), consumption (*C*), production (*P*) and metabolism (*R*) (kJ/g larva/day) of *A. janata* as functions of ration level (mg leaf/ larva/day) and temperature.

Ration	*F*	*C*	*P*	*R*
		22°C		
50	25.95	1.288 ± 0.121	0.116 ± 0.020	0.745 ± 0.089
100	41.2	1.868 ± 0.203	0.414 ± 0.089	0.744 ± 0.100
200	69.4	2.980 ± 0.473	0.888 ± 0.111	0.924 ± 0.103
300	88.7	3.658 ± 0.473	1.089 ± 0.099	1.061 ± 0.107
400	105.7	4.764 ± 0.731	1.374 ± 0.057	1.528 ± 0.169
Ad libitum	123.8	5.249 ± 0.245	1.477 ± 0.084	1.550 ± 0.298
		27°C		
50	38.3	1.693 ± 0.018	0.069 ± 0.015	0.955 ± 0.022
100	61.4	2.498 ± 0.221	0.419 ± 0.074	1.032 ± 0.082
200	98.9	3.980 ± 0.183	1.011 ± 0.028	1.274 ± 0.132
300	117.1	4.951 ± 0.393	1.354 ± 0.185	1.518 ± 0.105
400	132.8	5.524 ± 0.401	1.448 ± 0.223	1.793 ± 0.257
Ad libitum	170.4	7.176 ± 0.378	1.95 ± 0.120	2.152 ± 0.172
		32°C		
100	64.4	2.639 ± 0.124	0.372 ± 0.021	1.130 ± 0.145
200	92.7	3.939 ± 0.231	0.913 ± 0.062	1.483 ± 0.127
300	116.6	5.042 ± 0.167	1.227 ± 0.068	1.829 ± 0.152
400	129.3	5.946 ± 0.033	1.539 ± 0.044	2.220 ± 0.093
500	147.8	6.767 ± 0.537	1.890 ± 0.181	2.373 ± 0.283
Ad libitum	161.6	7.405 ± 0.791	2.041 ± 0.213	2.593 ± 0.225
		35°C		
100	68.3	2.766 ± 0.108	0.021 ± 0.005	1.588 ± 0.079
200	97.1	4.260 ± 0.358	0.559 ± 0.094	2.005 ± 0.133
300	117.5	5.149 ± 0.436	1.134 ± 0.200	2.037 ± 0.177
400	142.0	6.404 ± 0.578	1.489 ± 0.222	2.502 ± 0.307
500	153.5	7.146 ± 0.388	1.816 ± 0.078	2.736 ± 0.204
Ad libitum	168.7	7.950 ± 0.837	2.021 ± 0.159	2.986 ± 0.362

Each value ($\bar{X}$±SD) represents the average performance of 6 to 9 individuals.

3. Results

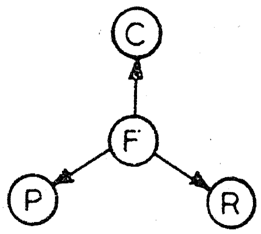
Regression equations used are provided in table 3. Most of the values of *C*, *P* and *R* predicted through simple regression equations (Nos. 1, 3 and 5; table 3) using *F* alone as the independent variable were close to the observed values. The total chi-square values for the differences between the observed values and those obtained through these equations were not statistically significant suggesting that the latter come from the population of observed data. However, comparison of the predicted values provided in table 4 with observed values in table 2 revealed that a few of the predicted values deviated widely from observed values. For instance, *C* value for the larva receiving 50 mg ration at 22°C was (0.974 kJ/g larva/day) 24% less than the observed value (1.288 kJ/g/day). Similarly, the *P* and *R* values in a few

Table 3. Regression equations used for the prediction of bioenergetics components of final instar *Achaea janata*.

Equation Number	Source of data	Regression equation	r	N
1	All temperatures and ration levels	$C = -0.2176 + 0.0459\,F$	0.933	24
2	All temperatures and ration levels	$C = -0.0145 + 0.436\,F + 0.00136\,T$	0.984	24
3	All temperatures and highest 5 ration levels	$P = -0.2673 + 0.0134\,F$	0.945	20
4	—do—	$P = 0.257 + 0.0155\,F + (-0.0263)\,\mathrm{T}$	0.971	20
5	—do—	$M = -0.0636 + 0.0161\,F$	0.901	20
6	—do—	$M = -1.159 + 0.119\,F + 0.0547\,T$	0.945	20

Mean values of F, C, P or R of 6 to 10 observations at the tested temperatures and ration schedules were used for calculating the regression equations. In equations 2, 4 and 7, the numerical value of temperature (T) has been used as the second predictor variable.

ration schedules at 22°C and the 200 mg ration schedule at 35°C included considerable error. To improve the accuracy of estimation the numerical value of temperature (T) was combined with F as a second predictor variable and multiple regression equations were developed (Nos.2, 4 and 6; table 3). These equations used for determining C, P and R values significantly decreased the differences between the two sets of values as well as the total chi-square values. Therefore, it is possible to predict C, P and R in terms of energy from the mass value of F as shown by the schematic pathway given below:



4. Discussion

Bioenergetics data reported for the moth *Platysamia cecropia* fed *ad libitum* at 25, 24, 30 and 27°C (Schroeder 1972) and for the monarch butterfly *Danaus chrysippus* fed on decreased rations or for restricted durations (Mathavan and Muthukrishnan 1976) were chosen to test whether the bioenergetics components can be predicted in line with the model proposed for *A. janata*. Linear regression equations were calculated for the relation between F and C, F and P and F and R using which the bioenergetics data were determined (tables 5 and 6). The error does not exceed 5% for most of the data.

Accuracy of estimation of C from F depends on egestion of a constant fraction of consumed food as faeces. In other words, constancy of approximate digestibility or assimilation efficiency under different experimental conditions determines the accuracy of prediction of C from F. In addition to constant assimilation efficiency, allocation of a definite proportion of digested food for growth (= conversion) and the rest for metabolism would increase the accuracy of prediction of P and R from F. Availability of feed or ration level does not alter the efficiencies of assimilation and conversion of digested food (e.g. *D. chrysippus*: Mathavan and

Table 4. Predicted values of C, P and R (kJ/g larva/day) of the final instar *Achaea janata* at the tested temperatures and ration levels (mg leaf/larva/day).

Ration	C 1	C 2	P 3	P 4	R 5	R 6
			22°C			
50	0.974	1.147	—	—	—	—
100	1.673	1.812	0.287	0.317	0.600	0.535
200	2.968	3.041	0.667	0.754	1.054	0.870
300	3.854	3.883	0.927	1.053	1.364	1.100
400	4.634	4.624	1.155	1.317	1.638	1.302
ad libitum	5.465	5.413	1.399	1.597	1.930	1.518
			27°C			
50	1.540	1.692	—	—	—	—
100	2.601	2.699	0.559	0.499	0.925	1.049
200	4.322	4.334	1.064	1.080	1.529	1.495
300	5.157	5.128	1.309	1.362	1.822	1.711
400	5.878	5.812	1.520	1.605	2.074	1.898
ad libitum	7.604	7.452	2.026	2.188	2.680	2.346
			32°C			
100	2.738	2.837	—	—	—	—
200	4.037	4.071	0.980	0.852	1.429	1.694
300	5.134	5.113	1.302	1.223	1.814	1.979
400	5.717	5.667	1.473	1.420	2.018	2.130
500	6.566	6.473	1.722	1.706	2.316	2.350
ad libitum	7.200	7.075	1.968	1.902	2.538	2.514
			35°C			
100	2.917	3.011	—	—	—	—
200	4.239	4.267	1.039	0.841	1.500	1.911
300	5.176	5.156	1.314	1.158	1.828	2.154
400	6.300	6.224	1.644	1.538	2.223	2.445
500	6.828	6.726	1.800	1.716	2.408	2.582
ad libitum	7.526	7.388	2.003	1.951	2.652	2.763
Total X^2*	0.298	0.272	0.706	0.305	0.765	0.282

* Significance levels of total chi-square values less than 7.01 at degrees of freedom 18, fall at $P > 0.99$.

X^2 values indicate the goodness of fit of the predicted values with the observed values given in table 2. Numerals 1,2,3....6 indicate the number of equation in table 3 used for predicting the values.

Table 5. Observed and predicted values of consumption (C), production (P) and metabolism (R) of *Platysamia cercopia* larva fed on lilac leaves.

Temperature °C	F	Observed C	Predicted C^*	Observed P	Predicted P^{**}	Observed R	Predicted R^{***}
25.0	10.9	293.44	302.2	63.68	61.6	184.13	195.0
24.2	10.8	306.83	300.6	63.21	61.3	198.42	194.2
30.0	9.8	285.07	285.0	57.30	58.3	186.74	185.6
27.0	11.2	309.35	306.9	59.40	62.5	203.07	197.6

$^*C = 131.438 + 15.666F$; $r = 0.832$; $^{**}P = 29.313 + 2.959F$; $r = 0.586$; $^{***}R = 102.043 + 8.529F$; $r = 0.565$.

Values of F(g/larva), C,P and R (kJ/g larva) reported by Schroeder (1972) have been used to test the adequacy of the model proposed for *Achaea janata*. Predicted values were obtained by using the regression equations given below.

Table 6. Observed and predicted values of consumption (C), Production (P) and metabolism (R) of final instar *Danaus chrysippus* larva fed on restricted rations or durations.

Ration Feeding duration	F	Observed C	Predicted C^*	Observed P	Predicted P^{**}	Observed R	Predicted R^{***}
25%	127	216	217.2	35	33.1	54	57.0
50%	166	290	296.2	51	51.8	73	78.3
100%	344	651	656.4	135	137.0	172	175.4
3 hr/day	130	217	223.3	31	34.6	56	58.6
6 hr/day	150	266	263.8	43	44.1	73	69.5
9 hr/day	186	346	336.6	64	61.4	96	89.2
12 hr/day	244	461	454.0	92	89.1	125	120.9

$^*C = -39.82 + 2.024F$; $r = 0.999$; $^{**}P = -27.667 + 0.4786F$; $r = 0.998$; $^{***}R = -12.347 + 0.5459F$; $r = 0.994$.

Values of F,C,P and R (mg(dry)/larva) reported by Mathavan and Muthukrishnan (1976) have been used to test the adequacy of the model proposed for *Achaea janata*. Predicted values were obtained by using the regression equations given above.

Muthukrishnan 1976; *Calocalpe undulata*: Schroeder 1976; *A. janata*: Muthukrishnan 1980). However, variation in habitat temperature brings about significant changes in these efficiencies (see Scriber and Slansky 1981; Schroeder 1981) and is likely to introduce error in the values predicted from F. Inclusion of temperature as an independent variable with F may help to improve the accuracy of prediction. Development of similar linear regression models for larvae of common species of lepidoptera may help to easily assess the damage inflicted by defoliators to agricultural crops as well as in studies on energy flow through consumer species.

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