Bioenergetics of the western spruce budworm (Lepidoptera: Tortricidae) with comments on endotherm and ectotherm population energetics

NORMAN G. REICHENBACH[1] AND GORDON R. STAIRS

Department of Entomology, Ohio State University, 1735 Neil Ave., Columbus, OH, U.S.A. 43210

Received June 28, 1984

REICHENBACH, N. G., and G. R. STAIRS. 1985. Bioenergetics of the western spruce budworm (Lepidoptera: Tortricidae) with comments on endotherm and ectotherm population energetics. Can. J. Zool. **63**: 1330–1338.

Energetic components (respiration, consumption, frass production, and growth) for larvae of the western spruce budworm (WSB), *Choristoneura occidentalis*, were modeled using multiple regression techniques for a range of temperatures (10–31°C) and body weights (5–200 mg). These functions were used in a simulation of the bioenergetics of the WSB under different variable temperature regimes (average temperatures ranging from 10 to 22°C). Simulation results showed that production increased as temperature increased. Net production efficiencies remained high (maximum ca. 32%) for all temperature regimes save the lowest, in which the maximum net production efficiency (production/assimilation) was 16%. Final assimilation efficiencies ranged from 50 to 52%. Early instar larvae had low total respiration costs, high assimilation efficiencies, low consumption rates, and rapid rates of tissue production. As the larvae increased in size, consumption rates increased, assimilation efficiencies declined, yet the total amount of energy assimilated increased so that production continued. Population energetics of the larvae showed that WSB were similar to other herbivorous ectotherms. Relative to endotherms, ectotherm populations consume similar quantities of energy and exist at higher biomasses per unit area.

REICHENBACH, N. G., et G. R. STAIRS. 1985. Bioenergetics of the western spruce budworm (Lepidoptera: Tortricidae) with comments on endotherm and ectotherm population energetics. Can. J. Zool. **63**: 1330–1338.

Un modèle des composantes énergétiques (respiration, consommation, production de fèces et croissance) des larves de la tordeuse des bourgeons de l'épinette (WSB) *Choristoneura occidentalis* a été mis au point grâce à l'utilisation de régressions multiples dans une gamme de températures (10 à 31°C) et de masses corporelles (5 à 200 mg). Ces fonctions ont servi au cours d'une simulation de la bioénergétique des tordeuses soumises à différents régimes variables de température (températures moyennes variant entre 10 et 22°C). Les résultats de la simulation ont démontré que la production augmente en fonction de la température. L'efficacité de la production nette (production/assimilation) demeure élevée (maximum ca. 32%) à tous les régimes de température, sauf aux températures les plus basses où la valeur production/assimilation maximale est de 16%. L'efficacité de l'assimilation finale va de 50 à 52%. Les larves des premiers stades se caractérisent par un coût respiratoire total faible, une efficacité d'assimilation élevée, un taux de consommation faible et une production rapide de tissus. À mesure que les larves grandissent, les taux de consommation augmentent, l'efficacité de l'assimilation diminue et pourtant la quantité totale d'énergie assimilée augmente, ce qui permet à la production de continuer. Le bilan énergétique de la population de larves est semblable à celui d'autres ectothermes herbivores. Les populations ectothermes consomment des quantités d'énergie semblables à celles que consomment les endothermes, mais leur biomasse par unité de surface est plus élevée.

[Traduit par le journal]

Introduction

Total energy flow (production and respiration) in ectotherm populations may be similar to that of endotherm populations (Bennett and Gorman 1979; Turner et al. 1976), but the allocation of energy to maintenance versus production and the standing crop (biomass) are markedly different in the two groups, reflecting their different functions in ecosystems and mechanisms for ensuring their survival (Golley 1968; McNeill and Lawton 1970; Wieser 1984).

Endotherms use all but 1–3% of the assimilated energy for maintenance owing to both ecological reasons (lower rate of natural increase) and physiological reasons (cost of body temperature maintenance) (Golley 1968; Wieser 1984). Ectotherms, with population structures which favor production and whose total respiration costs are low, allocate 20% or more of the assimilated energy to production (Humphreys 1979; Wieser 1984). Consequently, on a per gram basis, the energy required by ectotherms is low in comparison with endotherms, yet on a population basis, ectotherms, which may have much higher biomasses per unit area than endotherms, consume similar quantities of energy. Therefore, ectotherm populations are not low-energy systems, but rather fixers of large quantities of energy into biomass, and those ectotherms that are abundant

and have short life cycles are important in energy transfer (Turner et al. 1976).

Here we examine the bioenergetics (biomass, consumption, assimilation, respiration, production) and associated efficiency indices of the western spruce budworm (WSB), *Choristoneura occidentalis* Freeman, an abundant and economically important ectotherm herbivore of the coniferous forests (McKnight 1967). A simulation of WSB bioenergetics under different temperature regimes is evaluated with regard to mechanisms which favor production. Population energetics are considered in relation to the functional role of ectotherms in ecosystems.

Methods and materials

WSB were obtained from the Forest Sciences Laboratories, Corvallis, Oregon, and were maintained on McMorran's artificial diet (McMorran 1965). Throughout the experiments a 12 h light : 12 h dark photoperiod was maintained.

Measurements of oxygen consumption (standard metabolic rates; Gordon 1977) were obtained from larvae of both sexes over a range of body weights (3–213 mg fresh weight) at three temperatures (10, 20, 30°C) using standard Warburg manometric techniques (Umbreit et al. 1964). The larvae were placed at the testing temperature 12 h prior to measuring oxygen consumption and were allowed to adjust to the 7-mL flask for ca. 0.5 h. Oxygen consumption was recorded over a 2- to 3-h period and measurements were adjusted to standard temperature and pressure.

Growth rates, frass production, and consumption rates were measured on larvae of both sexes ranging from 5 to 200 mg fresh weight

---

[1]Present address: Battelle Columbus Laboratories, 505 King Ave., Columbus, OH, U.S.A. 43201.

and at several temperatures (10, 20, 25, 28, 31°C). Individuals were placed in 30-mL plastic cups with cubes of artificial diet and were checked for the above parameters after 1−4 days depending upon the temperature and size of the larvae. The remaining food and the frass produced were then dried at 50°C and weighed. The larvae were weighed (fresh weights) and several were then used to determine dry weights. Measurements were converted to rates on a per day basis save for growth rates where an instantaneous growth rate was calculated using the following equation:

[1] $g = (\ln w_1 - \ln w_0/(t_1 - t_0)$

where g is the daily instantaneous growth rate, w_1 and w_0 are the final and initial fresh weights and $(t_1 - t_0)$ is the time interval (Petrusewicz and Macfadyen 1970).

Dried samples of frass, food, and larvae were processed in a Phillipson microbomb calorimeter to determine the energy content using standard bomb calorimetry methods (Grodzinski et al. 1975). Frass and larval samples were pooled from at least 20 individuals for particular weight and temperature categories. Samples from the range of weights and temperatures were used to see whether weight or temperature had an effect on energy content. Oxygen consumption measurements were converted to energy units (kilojoules) using a respiratory quotient (RQ) of 1.0 which took into consideration that growth was an accumulation of protein, $0.8 < RQ < 1.0$ and fat RQ > 1.0 (Cairns 1982).

The energy budget equation, $C - F = A = R + P$, where C is consumption, F is frass, A is assimilation, R is respiration, and P is production, allows for the calculation of assimilated energy and allows one to check whether the energy budget equation balances (i.e., does $C - F = R + P$). Efficiency indices, assimilation efficiency (A/C), net production efficiency (P/A), and production to respiration ratio $(P/R$ and $P/R')$ were also calculated where $R' = C - F - P$.

Multiple regression models were fit to the data on oxygen consumption, growth rates, frass production, food consumption, and population energetics using the Statistical Analysis System (SAS; Proc GLM and Stepwise) (Anonymous 1979). Following each equation are the sample size, R^2, and the standard errors for the regression coefficients, save the intercept. Variable abbreviations are as follows: wt, fresh weight (milligrams); t, temperature (degrees Celsius); sex was coded 1 for males and 0 for females; R, respiration (microlitres of O_2 per hour); C, consumption (milligrams per day); F, frass production (milligrams per day).

The scaling of the y-axis in Fig. 6 was done for computer plotting purposes and was done as follows: $x = x - \bar{x}/(\text{maximum}(x) - \text{minimum}(x))$.

Simulation methodology

A Fortran program was written to simulate energy flow for male and female larvae from the termination of diapause (second instar) to the beginning of the pupal life stage under different temperature regimes as modeled by a linearized version of a Fourier series equation.

[2] $t(x) = b_0 + b_1 \cos\left(\dfrac{2\pi x}{365}\right) + b_2 \sin\left(\dfrac{2\pi x}{365}\right)$
$+ b_3 \cos(2\pi x)$

The yearly average temperature (b_0) was modified from 2 to 18 to represent different temperature regimes. A b_0 of 2 corresponds to an average temperature of 10°C during the larval life span with a minimum and a maximum temperature of 2.3 and 18.1°C, respectively. For other b_0's, the average, minimum, and maximum temperatures were as follows: $b_0 = 6$, 12.9, 5.1, 20.7; $b_0 = 10$, 15.8, 7.9, 23.6; $b_0 = 14$, 18.9, 11.0, 26.7; $b_0 = 18$, 22.4, 14.5, 30.2. The temperature function was used in the calculation of the time to complete development for each larva as well as the energy components (respiration, growth,
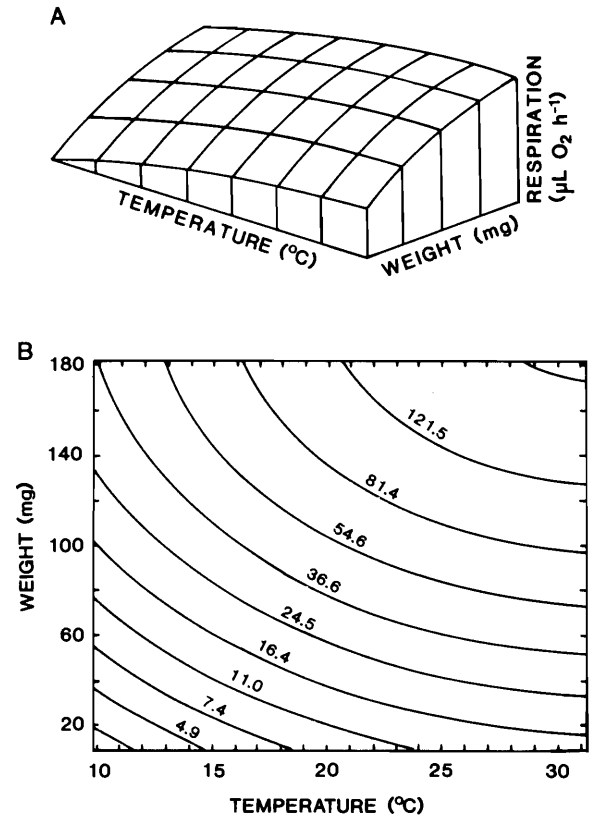

FIG. 1. (A) Response surface of Eq. 3 for the effect of temperature and weight on respiration rates of WSB larvae. (B) Contour plot of Eq. 3. Contours are respiration rates (microlitres of O_2 per hour) in relation to temperature and weight.

consumption, frass production). At 10 intervals (equally spaced in time) the accumulated energy components were calculated (both on a weight and a kilojoule basis), as well as the efficiency indices.

Results and discussion

Respiration rates initially increased rapidly with increased weight and temperature, and then tapered off to a plateau at high temperatures and later instar weights (Fig. 1). There were no significant differences between the sexes, as a main effect, when weight was included in the model.

[3] $\ln (R) = -1.1469 + 0.0265 \ (wt) - 0.000059 \ (wt^2)$
$+ 0.2207 \ (t) - 0.0034 \ (t^2)$
$+ 0.0031 \ (\text{sex} \times wt)$
(55, 0.97, 0.0028, 0.00002, 0.030, 0.0007, 0.0012)

Growth, measured as an instantaneous rate, increased with temperature and decreased with the weight of the larvae (Fig. 2). Male larvae had slightly higher growth rates for a given temperature than did females.

[4] $g = -0.0933 + 0.0237 \ (t) - 0.0001 \ (t \times wt)$
$+ 0.0029 \ (t \times \text{sex}) - 0.0017 \ (wt \times \text{sex})$
(295, 0.63, 0.0016, 0.000009, 0.0013, 0.0004)

Consumption rates did not vary between the sexes and increased initially with weight and temperature. As tempera-
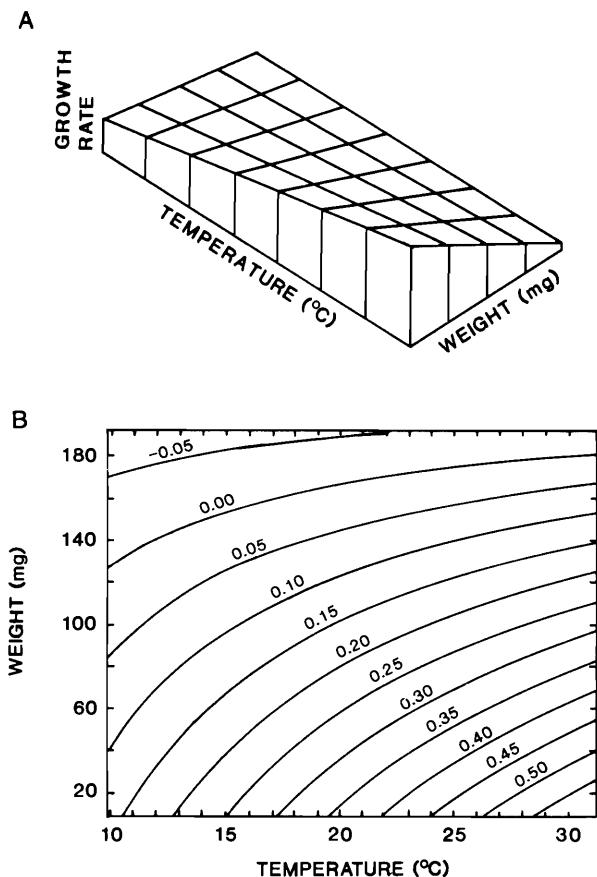
FIG. 2. (A) Response surface of Eq. 4 for the effect of temperature and weight on the instantaneous growth rates (see Eq. 1) of WSB larvae. (B) Contour plot of Eq. 4. Contours are instantaneous growth rates in relation to temperature and weight.

TABLE 1. Energy content and percent water for different materials used to convert weights or volume of oxygen consumed to kilojoules

Material	% water	kJ/g dry weight
WSB larvae (female)[a]	80.7–84.7	22.45
WSB larvae (male)[a]		
<20 mg	84.7	21.10
>20 and <60 mg	84.0	22.60
>60 mg	80.7	24.04
Artificial diet	82.0	19.08
Frass[a]	—	15.62
Respiration (kJ/L)[b]	—	21.10

[a]Samples were pooled from at least 20 animals.
[b]Using a respiratory quotient of 1.0 (Carins 1982).

ture increased beyond 26°C, the consumption rates declined (Fig. 3).

$$[5] \quad \ln (C) = 1.614 + 0.027 \, (wt) - 0.0461 \, (t)$$
$$+ 0.035 \, (t^2) - 0.0006 \, (t^3)$$
$$- 0.0006 \, (wt \times t)$$

(193, 0.75, 0.0037, 0.202, 0.011, 0.0002, 0.0002)

Frass production was similar to, but lower than, the consumption rates (Fig. 4). Sex had a slight effect on frass production, with males producing more frass per day than females
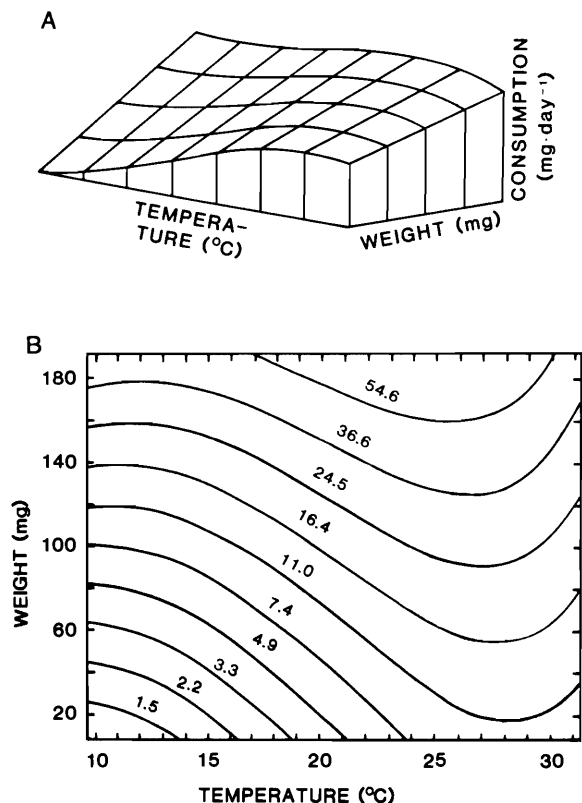

FIG. 3. (A) Response surface of Eq. 5 for the effect of temperature and weight on consumption rates (milligrams per day) of WSB larvae. (B) Contour plot of Eq. 5. Contours are consumption rates (milligrams per day) in relation to temperature and weight.
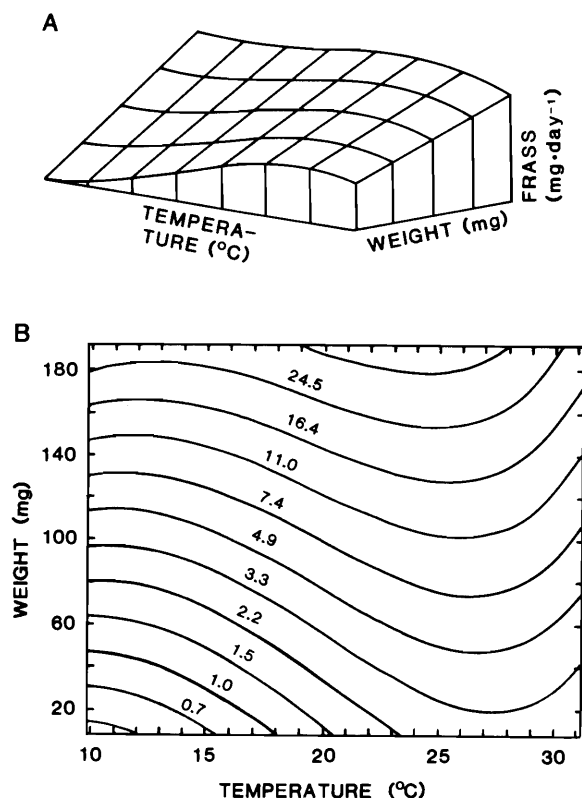

FIG. 4. (A) Response surface of Eq. 6 for the effect of temperature and weight on frass production (milligrams per day) of WSB larvae. (B) Contour plot of Eq. 6. Contours are frass production rates (milligrams per day) in relation to temperature and weight.
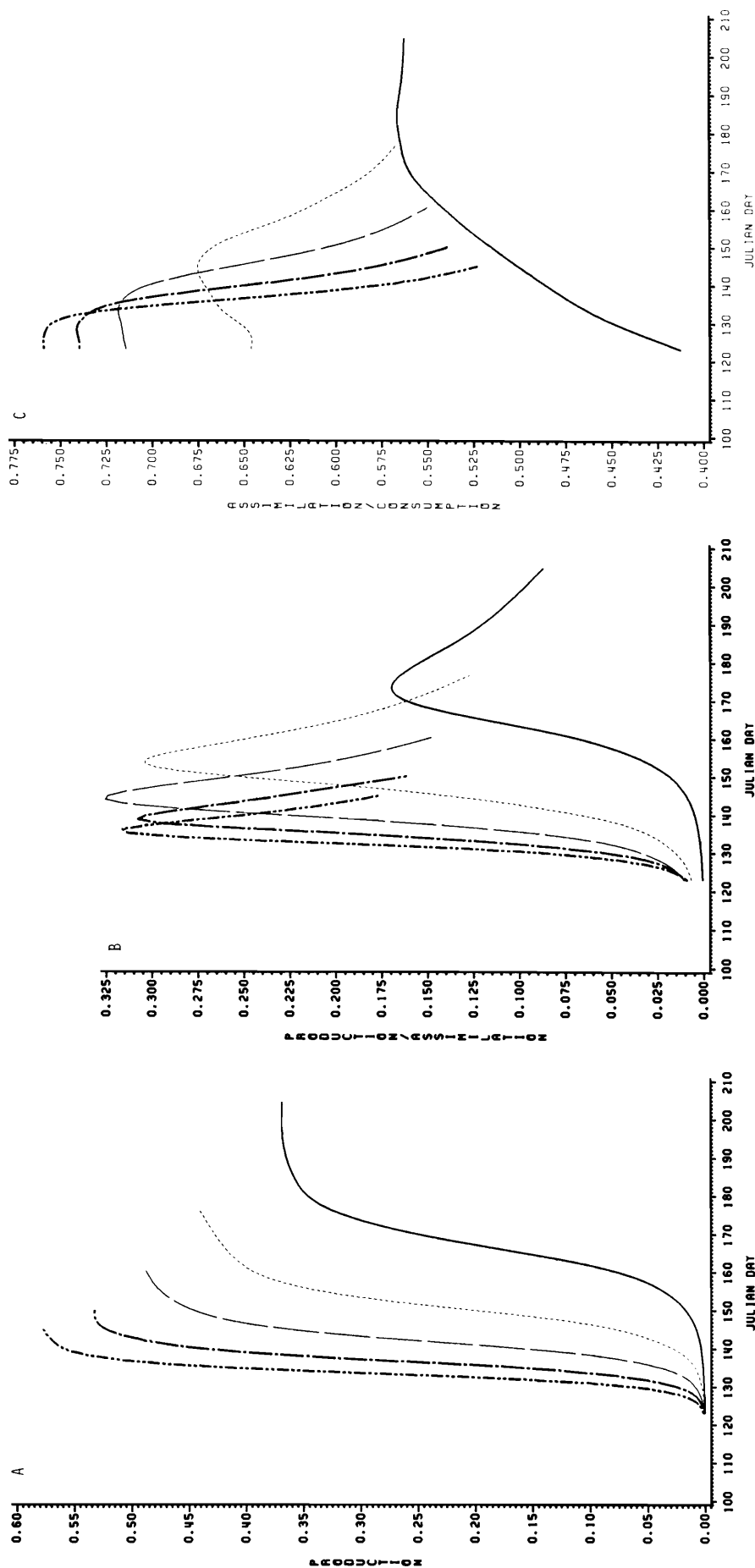
FIG. 5. Simulation results of (A) cumulative secondary production (kilojoules), (B) cumulative production/assimilation, and (C) assimilation/consumption during the entire life-span of male WSB larvae under different, variable temperature regimes. Average temperature during the larval life stage, 10°C (——), 13°C (—··—), 16°C (— — —), 19°C (——), 22°C (------).
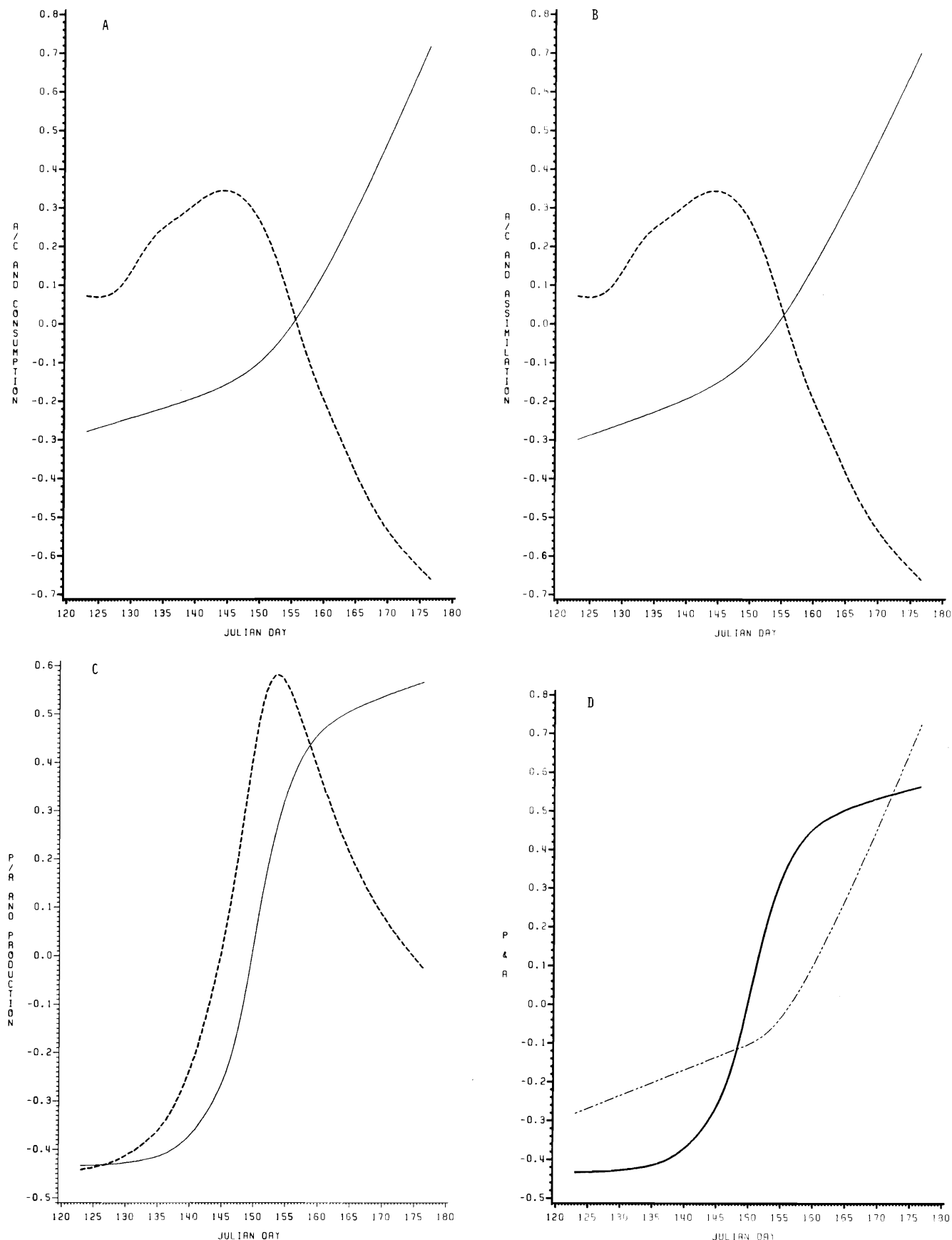
FIG. 6. Simulation results (cumulative) during the entire life-span of male WSB larvae in a variable temperature regime where the average temperature was 13°C. (A) Assimilation/consumption ($---$), consumption (—); (B) A/C ($---$), assimilation (—); (C) production/assimilation ($---$), production (—); (D) production ($---$), respiration (—). Scaling for the y-axis is as follows: $(A/C) = A/C - 0.64/(0.67 - 0.57)$, $C = C - 1.7/(6.1 - 0.06)$, $A = A - 1.0/(3.3 - 0.05)$, $P/A - 0.16/(0.32 - 0.01)$, $P = P - 0.19/(0.44 - 0.0003)$, and $R = R - 0.87/(3.02 - 0.04)$.

TABLE 2. Compiled data on population energetics (kilojoules per square metre per year) for ectotherms and endotherms used in principal component analysis and regression equations used to describe production, respiration, and consumption

Group	Type[a]	Production	Biomass	Respiration	Consumption	Source[b]
Bivalvia	D	73.270	81.220	228.600	—	1
Polychaeta	D	123.930	32.110	126.000	—	1
Isopoda	D	28.050	13.820	118.900	—	1
Isopoda	D	3.770	1.800	25.120	—	1
Gastropoda	D	5.020	2.800	27.630	—	2
Gastropoda	D	2.055	0.270	3.436	—	2
Gastropoda	D	0.226	0.023	0.235	—	2
Gastropoda	D	0.321	0.192	0.359	—	2
Gastropoda	D	0.043	0.001	0.034	—	2
Gastropoda	D	0.036	0.005	0.024	—	2
Gastropoda	D	2.911	0.462	5.620	—	2
Gastropoda	D	0.883	0.491	1.236	—	2
Gastropoda	D	0.483	0.055	0.592	—	2
Gastropoda	D	0.087	0.029	0.074	—	2
Gastropoda	D	1.976	0.192	3.261	—	2
Gastropoda	D	0.041	0.008	0.290	—	2
Gastropoda	D	1.279	0.206	1.918	—	2
Gastropoda	D	0.670	0.258	0.875	—	2
Gastropoda	D	0.155	0.018	0.147	—	2
Gastropoda	D	0.898	0.086	0.482	—	2
Gastropoda	D	1.108	0.462	1.612	—	2
Gastropoda	D	0.068	0.030	0.247	—	2
Gastropoda	D	1.556	1.556	2.438	—	2
Gastropoda	D	0.054	0.005	0.041	—	2
Lepidoptera	EH	94.360	35.286	996.591	1884.58	3
Copepoda	EH	217.710	7.330	397.750	—	1
Copepoda	EH	5.860	1.926	37.680	—	1
Orthoptera	EH	45.220	86.250	77.870	447.99	4
Orthoptera	EH	0.393	0.126	0.938	1.59	5
Hemiptera	EH	0.431	0.113	0.348	—	1
Hemiptera	EH	1.457	0.373	2.500	2.27	6
Diptera	EH	141.930	72.850	294.750	—	1
Diptera	EH	749.440	163.280	891.790	—	1
Echinoidea	EH	208.500	259.580	747.340	1152.20	7
Homoptera	EH	0.330	0.590	3.350	6.32	8
Orthoptera[c]	EH	2.140	0.670	3.600	15.53	8
Orthoptera[c]	EH	16.750	1.670	90.430	321.96	8
Homoptera	EH	293.080	100.900	858.300	2177.14	8
Trichoptera	EH	18.940	3.640	23.030	223.06	9
Diptera	EO	69.920	253.720	163.280	—	1
Diptera	EO	2.850	2.890	4.310	—	1
Diptera	EO	1.000	0.544	1.800	—	1
Diptera	EO	0.754	0.502	1.005	—	1
Diptera	EO	3.260	1.630	5.320	—	1
Isopoda	EC	443.800	184.220	653.140	1256.04	10
Chilopoda	EC	2.550	2.900	9.600	35.50	11
Chilopoda	EC	1.100	0.900	4.000	14.80	11
Araneae	EC	15.755	4.930	14.305	35.58	12
Araneae	EC	1.250	0.732	3.360	4.73	12
Odonata	EC	15.755	4.929	14.315	35.61	13
Araneae	EC	0.548	0.214	1.696	—	14
Serpentes	EC	1.650	2.514	3.968	6.61	15
Serpentes	EC	1.271	1.878	2.965	4.98	15
Sauria[d]	EC	0.560	0.900	0.805	1.61	16
Urodela	EC	2.100	0.840	1.300	4.19	17
Teleostei[c]	EC	36.550	35.800	142.350	178.90	18
Rodentia	H	0.500	0.080	27.630	30.98	8
Rodentia	H	0.460	0.210	15.450	23.45	8
Rodentia	H	2.180	0.790	71.170	—	8
Rodentia	H	0.420	0.140	25.100	—	19
Rodentia	H	1.260	0.475	77.500	157.52	20
Rodentia	H	4.696	5.250	278.235	378.82	21
Rodentia	H	4.689	2.830	60.500	92.95	22
Rodentia[d]	G	1.200	0.265	23.000	26.89	23

TABLE 2. (concluded)

Group	Type[a]	Production	Biomass	Respiration	Consumption	Source[b]
Rodentia	G	0.065	0.014	1.550	1.79	20
Rodentia	G	0.254	0.055	6.428	7.43	20
Passeriformes	O	0.170	0.126	15.070	16.75	8
Passeriformes	O	0.210	0.210	9.590	10.68	8
Rodentia	O	0.040	0.010	2.590	4.40	8
Rodentia[d]	O	0.159	0.020	1.817	2.20	23
Rodentia[d]	O	0.084	0.012	0.779	0.96	23
Rodentia	O	1.221	0.600	62.041	—	24
Rodentia	O	0.239	0.082	10.468	13.38	20
Carnivora	C	0.050	0.050	2.210	—	25
Passeriformes[c]	C	0.170	0.300	16.700	—	26
Insectivora	C	0.130	0.070	27.900	30.14	20
Insectivora	C	0.040	0.004	4.700	5.09	20
Rodentia[d]	C	0.100	0.026	2.700	3.26	23
Insectivora	C	0.017	0.003	0.670	0.75	20
Insectivora	C	0.115	0.224	2.757	3.19	27
Insectivora	C	0.151	0.099	1.652	2.00	27

[a]D, detritivore or deposit feeder; EH, ectotherm herbivore; EO, ectotherm omnivore; EC, ectotherm carnivore; H, endotherm herbivore; O, endotherm omnivore; C, endotherm carnivore.

[b]References: 1, Banse and Mosher 1980 (from Table 1); 2, Mason 1971; 3, this study; 4, Smalley 1960; 5, Duke and Crossley 1975; 6, Hinton 1971; 7, Miller and Mann 1973; 8, Wiegert and Evans 1967; 9, Otto 1975; 10, Johnson 1976; 11, Albert 1983; 12, Edgar 1971; 13, Lawton 1971; 14, Humphreys 1978; 15, Reichenbach 1981; 16, Turner et al. 1976; 17, Burton and Likens 1975; 18, Small 1975; 19, Grodzinski et al. 1966; 20, Hansson 1971; 21, Montgomery et al. 1975; 22, Gorecki 1977; 23, revised figures of Chew and Chew 1970; 24, Baar and Fleharty 1976; 25, Golley 1960; 26, Holmes and Sturges 1973; 27, Pernetta 1976.

[c]Multiple species complexes.

[d]Energy consumed estimated using assimilation efficiencies (Chew and Chew 1970) of the most commonly ingested food items and for the lizard, an 85% assimilation efficiency was assumed since they consume arthropods.

TABLE 3. Comparison of population energetics (for single species only) of endotherms and ectotherms showing the similarity between energy consumed and respired and the differences between biomasses and secondary production

Parameter	S[a]	m[b]	n[b]	Probability[c]	Median (kJ · m^{-2} · year^{-1}) Ectotherm	Median (kJ · m^{-2} · year^{-1}) Endotherm
Consumption	324.0	20	19	0.1189	35.54	10.68
Biomass	630.5	56	25	0.0003	0.87	0.10
Respiration	1078.5	56	25	0.2635	3.52	10.47
Production	586.0	56	25	0.0001	2.07	0.17

[a]Wilcoxon test statistic parameter.

[b]m, sample size for ectotherms; n, sample size for endotherms.

[c]Probability of rejecting the null hypothesis that the two groups do not differ from each other.

for a particular temperature and weight.

$$[6] \quad \ln (F) = 1.074 + 0.0298 \, (wt) - 0.534 \, (t)$$
$$+ 0.038 \, (t^2) - 0.0007 \, (t^3)$$
$$- 0.00057 \, (wt \times t)$$
$$+ 0.00016 \, (wt \times t \times sex)$$
$$(199, 0.75, 0.0037, 0.203, 0.0001, 0.00006,$$
$$0.0107, 0.0002)$$

The energy content of the males varied with size, with males of larger size having higher energy values (Table 1). Potentially this was due to increased fat deposition, which could be used by the adult males during flight activity while searching for females. The females did not show a similar trend. Percent water was greater for small larvae than for large larvae (Table

1). Frass energy content did not vary with temperature or sex and the average value was used in all calculations (Table 1).

Assimilation efficiency (A/C; based on laboratory data) rose with increase in temperature and decreased with increase in the weight of the larvae (Spearman's correlation coefficient: $r = 0.196, n = 188, p = 0.007; r = -0.308, n = 188, p = 0.0001$, respectively).

Net production efficiency (P/A; based on laboratory data) decreased with increased weight of the larvae and did not show a significant trend in relation to temperature (Spearman's correlation coefficient $r = -0.363, n = 160, p = 0.0001; r = -0.002, n = 160, p = 0.983$, respectively).

The cumulated bioenergetic components, calculated in the simulation model, showed that the energy budget equation, $C - F = A = P + R$, was not balanced and this was probably due to the R component (Wrightman 1981). The measured respiration rates, on the average, needed to be multiplied by 2.44 to equal the calculated respiration rates. The measured respiration rates were resting rates, where feeding was not taking place and digestive activity was reduced. In the analyses that follow, the calculated R was used.

Weight gain (production) assumed a sigmoidal shape with larvae in the lower temperature regimes weighing less than those in the higher temperature regimes (Fig. 5A). The net production efficiency (Fig. 5B) and assimilation efficiency (Fig. 5C) in relation to time showed a shift in their peak with maxima occurring earlier for higher temperature regimes, indicating that these efficiencies were related to the size of the larvae. The final assimilation efficiencies were slightly higher for larvae in the lower temperature regime (50–52%; Fig. 5C). In contrast, the final net production efficiencies over the entire larval life span were higher for larvae under the higher temperature regimes, ranging from 9 to 18% (Fig. 5B).

The trend in all the temperature regimes (only simulation results at $b_0 = 6$ are shown) was for the assimilation efficiency

to rise to a peak and then decline (Figs. 5C, 6A). This initial rise in assimilation efficiency may be due to the slow rate of ingestion by early instars which might provide sufficient time to extract large amounts of energy from the food. The decline in A/C has been attributed to less selective feeding on foliage by later instar larvae since these larvae consume large quantities of energy (Koller and Leonard 1981). In our experiments, the digestability of the food remained the same from early to late instars and yet a similar trend for A/C was noted. When the assimilation efficiency began to drop, the consumption rates increased (Fig. 6A), yet a net increase in the amount of energy assimilated was noted (Fig. 6B). Hence a "trade off" occurred, as food consumption increased, digestive efficiency declined, yet more energy was assimilated.

The lack of a decline in A/C for larvae in the low temperature regime (Fig. 5C) might be due to their consumption rates never having reached a point where digestive efficiency was sacrificed. The larvae, in the low temperature regimes, did not attain a weight similar to larvae at the higher temperatures. In the higher temperature regimes, large amounts of food were consumed at a lower digestive efficiency, yet at the benefit of a net increase of assimilated energy available for production.

This large amount of assimilated energy allowed for the production efficiency to rise even though the A/C had declined. Eventually the P/A began to decline, ca. several days to 1 week after the peak of the A/C. When the P/A began to decline, weight gain stabilized and the upper portion of the sigmoidal curve for weight versus time was reached (Fig. 6C).

At the point where the P/A began to decline the respiration rates were high, partially because of the activity associated with high consumption rates and the increased size of the larvae. So as more assimilated energy was allocated to respiration, the production of new tissue decreased (Fig. 6D).

Hence the WSB and possibly other lepidoptera have a strategy that involved several "trade offs" which facilitated production (growth and reproduction). Early instar larvae were characterized by low consumption rates, high assimilation efficiency, low total respiration costs, and consequently a high rate of tissue production. As the larvae increased in size, consumption rates increased, assimilation efficiency declined, yet the total amount of energy assimilated increased so that production continued until respiration costs rose exponentially.

Population energetics

Population energy components of the WSB (biomass, production, assimilation, consumption, and respiration) compared well with the trends seen in other ectotherm herbivores (population data was from McKnight (1967) which were used in conjunction with the simulation results ($b_0 = 4$) that produced similar developmental times for WSB as found in McKnight's study).

Data compiled on population energetics of endotherms and ectotherms were categorized as detritivores, ectotherm herbivores, carnivores, omnivores, and endotherm herbivores, carnivores, omnivores, and granivores (Table 2). Initial analysis using principal components (PCA; all the variables being log values) showed that the first component, a measure of tissue (biomass and production) explained 90% of the variance of the data and the second component (a contrast of the tissue component versus respiration and consumption; explained 9% of the variance), allowed for separation of the groups into a maximum of two groups, endotherms and ectotherms.

Comparisons of median values of C, P, B, and R for popu-

lations of ectotherms and endotherms showed no significant differences between R and C, while ectotherms had significantly higher values for P and B (Table 3). Because the biomass of ectotherms exceeded that of endotherms, population respiration rates were similar to endotherms, even though respiration rates on an individual basis were low in ectotherms. Consumption rates followed a similar pattern of being low for ectotherms on an individual basis relative to endotherms, but when compared on a population basis, the two groups consumed similar quantities of energy. Production was higher in ectotherm populations for both ecological and physiological reasons (Golley 1968; Wieser 1984).

ALBERT, A. 1983. Energy budgets for populations of long-lived arthropod predators (Chilopoda: Lithobiidae) in an Old Beech forest. Oecologia, **56**: 292–305.

ANONYMOUS. 1979. Statistical Analysis System (SAS). SAS Institute Inc., Raleigh, NC.

BAAR, S. L., and E. D. FLEHARTY. 1976. A model of the daily energy budget and energy flow through a population of the white-footed mouse. Acta Theriol. **21**: 179–193.

BANSE, K., and S. MOSHER. 1980. Adult body mass and annual production/biomass relationship of field populations. Ecol. Monogr. **50**: 355–379.

BENNETT, A., and G. GORMAN. 1979. Population density and energetics of lizards on a tropical island. Oecologia, **42**: 339–358.

BURTON, T., and G. LIKENS. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology, **56**: 1068–1080.

CAIRNS, S. 1982. Growth energetics in relation to temperature of the larvae of *Rhopaea verreauxi* (Coleoptera: Scarabaeidae). Oecologia, **54**: 32–40.

CHEW, R., and A. CHEW. 1970. Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. Ecol. Monogr. **40**: 1–21.

DUKE, K., and D. CROSSLEY, JR. 1975. Population energetics and ecology of the rock grasshopper, *Trimerotropis saxatilis*. Ecology, **56**: 1106–1117.

EDGAR, W. 1971. Aspects of the ecological energetics of the wolf spider *Pardosa* (*Lycosa*) *lugubris* (Walckenaer). Oecologia, **7**: 136–154.

GOLLEY, F. B. 1960. Energy dynamics of a food chain of an old-field community. Ecol. Monogr. **30**: 187–206.

―――― 1968. Secondary productivity in terrestrial communities. Am. Zool. **8**: 53–59.

GORDON, M. 1977. Animal physiology: principles and adaptations. Macmillan Publishing Co., New York.

GORECKI, A. 1977. Energy flow through the common hamster population. Acta Theriol. **22**: 25–66.

GRODZINSKI, W., A. GORECKI, K. JANAS, and P. MIGULA. 1966. Effect of rodents on the primary productivity of alpine meadows in Bieszczady Mountains. Acta. Theriol. **11**: 419–431.

GRODZINSKI, W., R. KLEKOWSKI, and A. DUNCAN (*Editors*). 1975. Methods for ecological bioenergetics. IBP Handbook No. 24. Blackwell Scientific Publications, Oxford.

HANSSON, L. 1971. Estimates of the productivity of small mammals in a south Swedish spruce plantation. Ann. Zool. Fenn. **8**: 118–126.

HINTON, J. M. 1971. Energy flow in a natural population of *Neophilaenus lineatus* (Homoptera). Oikos, **22**: 155–171.

HOLMES, R., and F. STURGES. 1973. Annual energy expenditure

by the avifauna of a northern hardwoods ecosystem. Oikos, **24**: 24–29.

HUMPHREYS, W. F. 1978. Ecological energetics of *Geolycosa godef-froyi* (Araneae:Lycosidae) with an appraisal of production efficiency in ectothermic animals. J. Anim. Ecol. **47**: 627–652.

——— 1979. Production and respiration in animal populations. J. Anim. Ecol. **48**: 427–453.

JOHNSON, W. S. 1976. Population energetics of the intertidal isopod, *Cirolana harfordi*. Mar. Biol. **36**: 351–357.

KOLLER, C. N., and D. E. LEONARD. 1981. Comparison of energy budgets for spruce budworm *Choristoneura fumiferana* (Clemens) on Balsam fir and White spruce. Oecologia, **49**: 14–20.

LAWTON, J. H. 1971. Ecological energetics studies on larvae of the damselfly, *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. **40**: 385–419.

MASON, C. F. 1971. Respiration rates and population metabolism of woodland snails. Oecologia, **7**: 80–94.

MCKNIGHT, M. 1967. Ecology of the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) in Colorado. Ph.D. dissertation, Colorado State University, Fort Collins.

MCMORRAN, A. 1965. A synthetic diet for the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). Can. Entomol. **97**: 58–62.

MCNEILL, S., and J. LAWTON. 1970. Annual production and respiration in animal populations. Nature (London), **225**: 472–474.

MILLER, R., and K. MANN. 1973. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. III. Energy transformations by sea urchins. Mar. Biol. **18**: 99–114.

MONTGOMERY, S., J. WHELAN, and H. MOSBY. 1975. Bioenergetics

of a woodlot gray squirrel population. J. Wildl. Manage. **39**: 709–717.

OTTO, C. 1975. Energetic relationships of the larval population of *Potamophylax cingulatus* (Trichoptera) in a south Swedish stream. Oikos, **26**: 159–169.

PERNETTA, J. 1976. Bioenergetics of British shrews in grassland. Acta Theriol. **21**: 481–497.

PETRUSEWICZ, K., and A. MACFADYEN. 1970. Productivity of terrestrial animals: principles and methods. International Biological Programme. F. A. Davis Co., Philadelphia.

REICHENBACH, N. 1981. Energy use and the life histories of syntopic species of garter snakes in Ohio. M.S. thesis, Ohio State University, Columbus.

SMALL, J. W. 1975. Energy dynamics of benthic fishes in a small Kentucky stream. Ecology, **56**: 827–840.

SMALLEY, A. E. 1960. Energy flow of a salt marsh grasshopper population. Ecology, **41**: 672–677.

TURNER, F. B., P. A. MEDICA, and B. W. KAWALEWSKY. 1976. Energy utilization by a desert lizard (*Uta stansburiana*). US/IBP Desert Biome Monograph No. 1. pp. 1–57.

UMBREIT, W., R. BURNS, and J. STAUFFER. 1964. Manometric techniques. 4th ed. Burgess, Minneapolis.

WEIGERT, R. G., and F. EVANS. 1967. Investigations of secondary productivity in grasslands. *In* Secondary productivity of terrestrial ecosystems. *Edited by* K. Pertrusewicz. PWN, Warzawa and Krakow. pp. 499–518.

WIESER, W. 1984. Low production "efficiency" of homeotherm populations: a misunderstanding. Oecologia, **61**: 53–54.

WRIGHTMAN, J. A. 1981. Why insect energy budgets do not balance. Oecologia, **50**: 166–169.