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PRODUCTION AND RESPIRATION IN ANIMAL POPULATIONS

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SUMMARY

(1) Analysis is made of 235 energy budgets from the literature to determine the relationship between annual production and respiration in natural populations of animals.

(2) Homoiotherms separate into four groups; insectivores, birds, small mammal communities and other mammals.

(3) Poikilotherms separate into three groups; fish and social insects, non-insect invertebrates and non-social insects.

(4) The invertebrate groups are separable into trophic categories and herbivores have the lowest production efficiency.

(5) There is no relationship between animal weight and production efficiency.

(6) Within the groups derived, species with different habitats (aquatic and terrestrial) do not have different production efficiencies.

(7) There is no firm evidence that production efficiency is dependent upon the magnitude of production.

(8) Distribution of the data indicates that there is no quantum jump in production efficiency between poikilothermic and homoiothermic animals.

(9) Regression equations are given for each of the derived groups relating annual production to respiration (both as $\log_{10}$ cal m^{-2} yr^{-1}) in animal populations.

INTRODUCTION

Engelmann (1966) suggested that there was a linear relationship between annual production and respiration per unit area in animal populations. Additional data have been added to the 'Engelmann line' (Golley 1968; Hughes 1970; McNeill & Lawton 1970; Shorthouse 1971; Lévêque 1973) but the relationship has been analysed seriously only thrice.

McNeill & Lawton (1970) plotted respiration against production (both as $\log_{10}$ kcal m^{-2} yr^{-1}) and were able to separate clearly the homoiotherms from the poikilotherms. They suggested that when sufficient data were available the poikilotherms would be divisible into three groups; short lived with low cost resting (overwintering) stages, short lived with high cost overwintering stages and long lived poikilotherms, and that the production efficiency would decrease in the same order. They showed that the relationship for the short lived poikilotherms had a slope (b in $y = a + bx$) different from 1·0 whether production or respiration was taken as the dependent variable but the slope for the homoiotherm data did not so differ.

Shorthouse (1971) added a few additional data to those considered above and was able to derive predictive equations with narrower confidence intervals by separating the poikilo-

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therms by habitat (aquatic *v.* terrestrial) rather than life cycle duration (for his equations see Humphreys 1978: Table 6).

Grodziński & French in Grodziński & Wunder (1975) analysed the data available for small mammals and separated insectivores from rodents by their different slopes which were respectively greater and less than unity.

Almost every energy budget has been derived from a unique set of assumptions and methods, some of which lead to detectable errors (e.g. Kozlowski's (1968) reinterpretation of Birch's reworking (in Allee *et al.* 1949) of Lindeman's (1942) Cedar Bog budget) while others may lead to undefinable bias (see Humphreys 1978). It has been claimed that these differences in assumptions and methods may introduce sufficient noise into energy budgets to prevent the separation of some of the subdivisions discussed above and particularly the separation of animals by trophic level (Humphreys 1978) as suggested by Kozlovsky (1968). In addition it has been claimed that the resolution obtainable from energy budgets may be insufficient to test hypotheses using energetics methodologies (Humphreys 1978) as attempted by Sutherland (1972).

The number of energy budgets now available should permit the analysis of some of the energy relations of animal populations mentioned above. This has become more important as the original equations derived by McNeill & Lawton (1970) are increasingly being used to complete energy budgets from a knowledge of either production or respiration (Phillipson 1971; Mason 1971, 1977; Hughes 1972; Olah 1976).

MATERIALS AND METHODS

I follow the terminology of Petrusewicz & Macfadyen (1970) to describe the energy budgets where P is net production (that due to growth, Pg, and reproduction, Pr) and R is metabolic heat loss; $A = P + R = C - FU$ all in caloric units. Energy budgets for 235 natural populations were extracted from the literature (Appendix). With one exception (Llewellyn 1975) energy budgets have no variance estimate; differences in methodologies and assumptions used by different workers such as the arbitrary adjustment of R, the inclusion or not of Pr in the estimation of P and the effects of immigration should result in energy budgets that vary widely around the true value (see McNeill & Lawton 1970; Humphreys 1978). No objective method is available to distinguish 'good' from 'bad' energy budgets so I have applied no selection to the data with the following exceptions. The data for *Pogonomyrmex badius* (Golley & Gentry 1964) were excluded as they are widely believed to be aberrant (set Pętal 1978). Budgets partially derived using the equations from McNeill & Lawton (1970) were excluded as were those covering more than one taxonomic category (see below). I have not excluded budgets covering only the larval stages of insects as I did elsewhere (Humphreys 1978).

Where necessary the following conversion factors were used: 1 g carbon = 10·94 kcal. 1 kJ = 0·2388 kcal. Maximum live weight for a species was taken from the original source directly, read from figures, or converted from dry weight assuming 75% water in the living animal (flesh weight only in molluscs) or from caloric value using caloric data for the appropriate group compiled by Cummins & Wuycheck (1971).

The data were initially grouped into 'taxonomic' categories which in some cases were well defined (mice, voles, shrews, fish, social insects, orthoptera, hemiptera, mollusca and crustacea) or, where data were insufficient, into loose taxonomic groups (other mammals, other insects and other non-insect invertebrates). Data for birds were pooled from both

single species studies and community studies and a separate category erected for small mammal community budgets.

Statistical treatment

As discussed by W. Grodziński & N. R. French (personal communication) production cannot occur in the absence of respiration while the converse is not true; theoretically therefore production should be treated as the dependent variable. In practice respiration is calculated from the biomass at different times and ideally as an integral so that the change of biomass plus a constant is tracked. Change in biomass is an index of production which makes respiration the dependent variable in practice. However, as discussed elsewhere (McNeill & Lawton 1970), both R and P are derived from either numbers of individuals or biomass and are thus not strictly independent. I see no alternative to presenting the analyses treating both P and R as dependent variables; this has the added advantage of permitting prediction of the other parameter from either known P or known R.

Least squares regressions were calculated for each of the original fourteen taxonomic groups treating either P or R ($\log_{10}$ cal m^{-2} yr^{-1}) as the dependent variable. Regressions were compared (see below) with each other and pooled if not significantly different until the minimum number of separate groups was found. Within some of the pooled groups the data were analysed in an attempt to separate further taxonomic categories (Diptera from other insects, ants from termites and gastropod from pelecypod molluscs), trophic categories (herbivores from carnivores from detritivores), life cycle duration (short lived, <2 years, from long lived, >2 years), and habitat (aquatic from terrestrial).

Least squares regressions were calculated for each group considered and the lines compared using the analysis of variance procedure of Davies & Goldsmith (1972: Table 7.7). Analyses were conducted to test four relationships within and between the regression lines of the form $\log y = a + b \log x$. Firstly whether x and y were correlated and the slope (b) of the equation differed from zero. Analysis continued to test whether the two (or more) regression lines had a similar slope ($P > 0{\cdot}05$); if the slopes were statistically similar the lines were tested for common intercept (a). If the intercepts were similar the lines were pooled otherwise they were treated as separate groups. In this manner all groups were tested against all adjacent groups before pooling. Finally the individual lines or the common slope for several pooled groups were tested for a slope of 1·00. Where the slope is 1·00, there is no relationship between the magnitude of annual R (or P) per unit area and the production efficiency $P/(P + R) = P/A$.

The estimates for P and R contain unspecified measurement error as well as natural variability. The groups of data are typically non-normal and open ended. In a lengthy discussion of various types of linear regression Ricker (1973) recommends the use of the geometric mean estimate of the functional regression of y on x (the GM regression), especially if it is desirable to avoid decisions about the relative accuracy of measuring x and y. This form of regression gives the best estimate of the slope for predictive purposes and Ricker recommends the use of ordinary symmetrical confidence limits. For this reason I present for the derived groups the functional (GM) regressions and the more familiar least squares predictive equations. Where it is necessary to obtain GM regressions for the common slope of several groups it has been approximated from the weighted mean correlation coefficient for the groups.

Unless specified the equations given are standard predictive regressions. Anyone

interested in the slope of the relationships for specific groups can calculate the slope (v) for the GM regression from the appropriate predictive equations as: $v = b/r$ (Ricker 1973).

The index P/A was also analysed from the individual studies without consideration of the magnitude of P or R. Data were analysed for homogeneity of variances by Bartlett's test (Sokal & Rohlf 1969). Analysis of variance was conducted and the means tested by the Student-Newman-Keuls *a posteriori* test for unequal sample sizes (Sokal & Rohlf 1969).

RESULTS

Variance

Regressions for the original fourteen taxonomic groups have significant heterogeneity in the residual variances ($P < 0{\cdot}005$). This heterogeneity remains after exclusion of several of the more extreme variances and cannot be removed by transformation of the data. I follow McNeill & Lawton (1970) in the belief that the empirical relationship between P and R is of sufficient interest to use standard regression techniques in its analysis. My use of analysis of variance is to obtain objective subdivisions of the data available: while I retain the usual criterion of significance at the 5% probability level, any tests giving probabilities close to the 5% level may be viewed with caution. While moderate heterogeneity of variances is not serious for overall tests of significance, single degree of freedom comparisons may be seriously in error (Sokal & Rohlf 1969).

Production as the dependent variable

Regression statistics for the original fourteen 'taxonomic' categories are presented in Table 1. All the relationships are significant ($P < 0{\cdot}003$) and none of the slopes differ significantly from the others; these lines have a common slope of 0·961 ($\pm 0{\cdot}021$ S.E.) which does not differ from a slope of 1·0 ($ts_{233} = 1{\cdot}857$, $0{\cdot}1 > P > 0{\cdot}05$). Sequential comparison of the intercepts permitted pooling of several groups leaving 7 separate regression lines (Table 2); summary analyses of variance for some of the more interesting comparisons are given in Table 3. Within the pooled groups none of the regression lines differs from any other with which it has been pooled and the pooled groups are clearly separated with one exception; the intercepts for the insectivore line differs from that of the birds ($P = 0{\cdot}0001$) but the small mammal community line does not differ from those for the birds or the insectivores. Pooling the insectivore data with those for the small mammal communities results in a regression not significantly different from that for the birds (Table 3). Hence these three lines are kept separate (Fig. 1).

The common slope of the GM regression for the seven derived groups ($v = 1{\cdot}026$) does not differ from 1·0. Re-analysis for common slope, having excluded all budgets for more than one species, gives a common slope not different from 1·0 ($v = 1{\cdot}000$; Table 2). Analysis for common slope between groups for the homoiotherms and poikilotherms separately shows neither differs from unity ($v = 1{\cdot}085$ and 0·984 respectively).

Further taxonomic categories could not be separated from the seven derived groups (Table 3). None of the following could be separated; rodents from non-insectivore mammals, diptera from any non-social insect group, ants from termites nor gastropod from pelecypod mollusca. However splitting the non-social invertebrates into arthropods and non-arthropods gave significant separation but with generally wider confidence

TABLE 1. Regression statistics relating annual production ($\log_{10}$ P cal m^{-2} yr^{-1}) to respiration ($\log_{10}$ R cal m^{-2} yr^{-1}) in animal populations
Community studies for birds and small mammals are included

Group	Regression equation	Correlation coefficient	N	Mean R	Mean P	Standard error intercept	Standard error slope	Significance of slope from 1·0
1. Insectivores	P = 0·608R − 0·684	0·958	6	3·151	1·052	0·127	0·091	< 0·02
2. Mice	P = 0·854R − 0·946	0·920	22	2·893	1·524	0·327	0·081	NS
3. Voles	P = 1·078R − 1·866	0·923	20	3·801	2·233	0·225	0·103	NS
4. Other mammals	P = 0·911R − 1·190	0·963	14	3·724	2·202	0·314	0·074	NS
5. Small mammal communities	P = 1·139R − 2·399	0·840	8	3·859	1·997	0·373	0·304	NS
6. Birds	P = 0·734R − 0·830	0·929	9	4·000	2·105	0·123	0·110	< 0·05
7. Fish	P = 0·834R − 0·249	0·965	9	4·337	3·370	0·196	0·086	NS
8. Social insects	P = 1·002R − 1·048	0·858	13	3·241	2·198	0·437	0·181	NS
9. Orthoptera	P = 0·859R + 0·337	0·919	22	3·432	3·286	0·230	0·081	NS
10. Hemiptera	P = 1·015R − 0·188	0·967	14	2·980	2·838	0·425	0·077	NS
11. All other insects	P = 0·961R − 0·006	0·977	25	3·827	3·673	0·258	0·045	NS
12. Mollusca	P = 1·033R − 0·717	0·860	45	4·832	4·272	0·392	0·094	NS
13. Crustacea	P = 0·946R − 0·231	0·959	9	4·608	4·130	0·254	0·106	NS
14. All other non-insect invertebrates	P = 1·018R − 0·483	0·911	19	3·703	3·286	0·475	0·112	NS
Non-insect invertebrates:								
15. Carnivores	P = 0·979R − 0·407	0·902	11	3·323	2·847	0·531	0·156	NS
16. Detritivores	P = 1·069R − 0·601	0·907	22	4·583	4·298	0·420	0·111	NS
17. Herbivores	P = 0·971R − 0·500	0·943	16	4·617	3·982	0·284	0·092	NS
Arthropods:								
18. Short lived (< 2 yrs)	P = 0·970R − 0·060	0·971	62	3·480	3·316	0·281	0·031	NS
19. Long lived (> 2 yrs)	P = 1·206R − 0·224	0·889	12	3·539	3·120	0·491	0·196	NS

Common slope (± standard error): Groups 1–14 b = 0·961 ± 0·021 N = 235 $ts_{1\cdot0}$ = 1·857 NS v = 1·039
15–17 b = 1·013 ± 0·057 N = 49 $ts_{1\cdot0}$ = 0·228 NS
18–19 b = 0·987 ± 0·035 N = 74 $ts_{1\cdot0}$ = 0·371 NS

TABLE 2. Seven different predictive regression equations relating annual respiration ($\log_{10}$ R cal m^{-2} yr^{-1}) to production ($\log_{10}$ P cal m^{-2} yr^{-1}) in animal populations. The GM regression which better estimates the slope is given below each equation; statistics relate to the predictive regressions

Group	Regression equation	N	Mean R	Mean P	Standard error intercept	Standard error slope	Significance of slope from 1·0
Insectivores	P = 0·608R − 0·864	6	As in Table 1				
	P = 0·636R − 0·952						
Birds	P = 0·734R − 0·830	9	As in Table 1				
	P = 0·790R − 1·055						
Small mammal communities	P = 1·139R − 2·399	8	As in Table 1				
	P = 1·356R − 3·236						
All other mammals	P = 0·885R − 1·084	56	3·447	1·967	0·289	0·0409	< 0·01
	P = 0·938R − 1·259						
Fish and social insects	P = 0·912R − 0·749	22	3·742	2·646	0·470	0·110	NS
	P = 1·042R − 1·234						
Non-insect invertebrates	P = 0·974R − 0·394	73	4·511	3·998	0·397	0·0519	NS
	P = 1·068R − 0·820						
Non-social insects	P = 0·969R − 0·037	61	3·456	3·312	0·288	0·0318	NS
	P = 1·000R − 0·144						

Common slope for above groups: b = 0·942 ± 0·0209 N = 234 $ts_{1·0}$ = 2·758 $P < 0·01$ v = 1·013
Common slope for non-community studies*: b = 0·952 ± 0·0208 N = 210 $ts_{1·0}$ = 2·288 $P < 0.05$ v = 1·014

* Excludes birds, small mammal communities and other budgets pooled for more than one species.

TABLE 3. Synopses of analyses of variance testing for common slopes and intercepts for some of the regressions relating annual respiration ($\log_{10}$ R cal m^{-2} yr^{-1}) to production ($\log_{10}$ P cal m^{-2} yr^{-1}) in animal populations

Group	Test for parallel lines F	d.f.	P	Test for common intercepts F	d.f.	P	Comment
Homoiotherms *v.* poikilotherms	1·5	1,232	0·215	427·7	1,233	$<10^{-5}$	parallel separate
Insectivores *v.* birds	0·8	1,11	0·397	32·1	1,12	0·001	parallel separate
Insectivores *v.* small mammal communities	2·7	1,10	0·131	2·7	1,11	0·129	parallel common
Birds *v.* non-insectivore mammals	0·4	1,64	0·546	12·1	1,65	0·0009	parallel separate
Rodents *v.* other non-insectivore mammals	1·2	1,55	0·288	0·01	1,56	0·928	parallel common
Fish *v.* social insects	0·4	1,17	0·560	0·3	1,18	0·608	parallel common
Diptera *v.* Orthoptera *v.* Hemiptera *v.* all other non-social insects	1·1	3,54	0·361	0·1	3,57	0·977	parallel common
Non-social arthropods *v.* non-arthropod invertebrates	0·01	1,131	0·908	10·7	1,132	0·0014	parallel separate
Non-social insects *v.* non-insect invertebrates	0·0	1,131	0·946	23·5	1,132	$<10^{-5}$	parallel separate
Herbivores *v.* carnivores *v.* detritivores:							
non-insect invertebrates	0·2	2,43	0·799	3·5	2,45	0·038	parallel separate
non-social insects	0·2	2,56	0·823	2·4	2,58	0·102	parallel common
Short *v.* long lived:							
non-insect invertebrates	0·04	1,18	0·842	1·3	1,19	0·273	parallel common
non-social insects	3·2	1,70	0·079	6·1	1,71	0·016	parallel separate
Insect larvae *v.* all stages	0·2	1,58	0·660	0·1	1,59	0·767	parallel common
Aquatic *v.* terrestrial:							
non-social insects	0	1,58	0·984	0·01	1,59	0·924	parallel common
non-insect invertebrates	0	1,44	0·982	0·7	1,45	0·425	parallel common
all invertebrates	0·6	1,130	0·461	2·4	1,131	0·123	parallel common

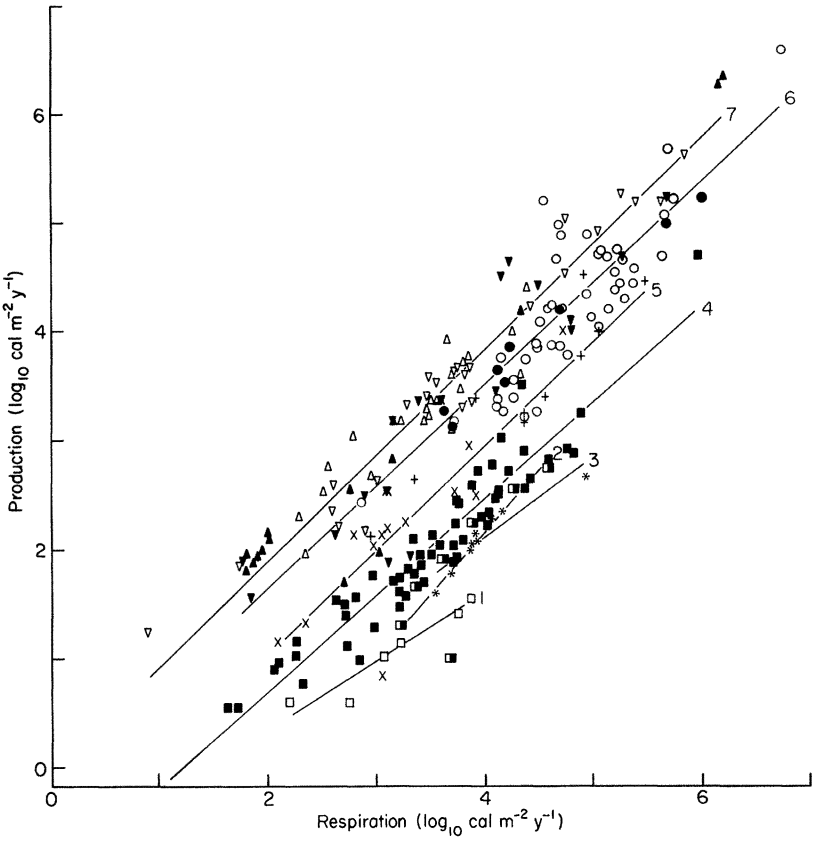

FIG. 1. The relationship between respiration and production (both as $\log_{10}$ cal m^{-2} yr^{-1}) in natural populations of animals. The regression lines, not adjusted for common slope, of the seven derived groups (Table 2) are shown. The points for *Perognathus penicillatis* and *P. baileyi* (Appendix) are not plotted. The lines are numbered 1 = insectivores, 2 = small mammal communities, 3 = birds, 4 = other mammals, 5 = fish and social insects, 6 = non-insect invertebrates and 7 = non-social insects. The symbols denote: □ insectivores, ◨ small mammal communities, ■ other mammals, ✱ birds, + fish, × social insects, ○ molluscs, ● Crustacea, ▼ other non-insect invertebrates, △ Orthoptera, ▲ Hemiptera, ▽ other non-social insects.

intervals than the separation into non-social insects and non-insect invertebrates (95% confidence intervals of P at R = 1 and R = 6 respectively: non-social insects, ±0·596 and ±0·597; non-insect invertebrates, ±0·871 and ±0·806; arthropods, ±0·694 and ±0·693; non-arthropod invertebrates, ±1·073 and ±0·861). The former division is therefore retained.

Habitat

Data for the non-social insects, non-insect invertebrates and both groups pooled could not be separated according to habitat type (aquatic *v.* terrestrial) and all gave common lines (Table 3).

Life stage

Studies conducted on the larval stages only of the non-social insects would be expected to have higher P/A than those studies covering all life stages. Separation of the data by these criteria resulted in common regression lines (Table 3).

Duration of life cycle

Insufficient data are present to separate the non-social insects into long and short lived species. No separation was possible (common intercept; $P = 0{\cdot}273$) between the long lived (> 2 y) and short lived (< 2 y) invertebrates (excluding social insects). However, arthropods are divisible into short and long lived species giving parallel ($P = 0{\cdot}079$) but separate ($P = 0{\cdot}016$) lines (Table 3).

Trophic type

The non-insect invertebrates could be separated into three trophic types; when the intercepts were calculated from the common slope for the three groups ($b = 1{\cdot}013 \pm 0{\cdot}0572$) the efficiency P/A is greatest for detritivores ($a = -0{\cdot}346$), intermediate for carnivores ($a = -0{\cdot}521$) and least for herbivores ($a = -0{\cdot}696$). The non-social insects had common slopes with a marginal level of probability for the intercepts ($P = 0{\cdot}102$); again herbivores had the lowest efficiency P/A but carnivores were intermediate.

Respiration as the dependent variable

Regression statistics for the original fourteen taxonomic groups are presented in Table 4. All the relationships are significant ($P < 0{\cdot}003$) but the slopes are not common ($P = 0{\cdot}012$). Removal of the data for insectivores and molluscs yields parallel lines ($P = 0{\cdot}130$) with a common slope of $v = 0{\cdot}997 \pm 0{\cdot}019$ which does not differ from 1·0.

Analysis of the lines as before yields the same seven groups (Table 5) previously derived but with non-parallel lines ($P = 0{\cdot}044$). Exclusion of the insectivore data yields parallel lines ($P = 0{\cdot}061$) with a common slope ($v = 1{\cdot}012$) not different from unity. Further analysis confirms the taxonomic divisions previously found as well as those for life cycle duration, habitat and trophic type. Non-insect invertebrates again separate into carnivores, detritivores and herbivores with P/A decreasing in that order. Trophic separation

TABLE 4. Regression statistics relating annual respiration ($\log_{10}$ R cal m^{-2} yr^{-1}) to production ($\log_{10}$ P cal m^{-2} yr^{-1}) in animal populations. Community studies for birds and small mammals are included

Group	Regression equation	*N*	Standard error intercept	Standard error slope	Significance of slope from 1·0
1. Insectivores	R = 1·510P + 1.563	6	0·201	0·225	NS
2. Mice	R = 0·992P + 1·392	24	0·348	0.088	NS
3. Voles	R = 0·789P + 2·039	21	0·193	0·076	<0·02
4. Other mammals	R = 1·018P + 1·483	14	0·332	0·083	NS
5. Small mammal communities	R = 0·619P + 2·623	8	0·275	0·163	NS
6. Birds	R = 1·178P + 1·521	9	0·156	0·177	NS
7. Fish	R = 1·117P + 0·574	9	0·227	0·114	NS
8. Social insects	R = 0·694P + 1·816	13	0·534	0·189	NS
9. Orthoptera	R = 0·982P + 0·203	23	0·246	0·092	NS
10. Hemiptera	R = 0·922P + 0·365	14	0·405	0·070	NS
11. All other insects	R = 0·993P + 0·179	24	0·263	0·046	NS
12. Mollusca	R = 0·716P + 1·775	45	0·326	0·065	<0·001
13. Crustacea	R = 0·969P + 0·607	9	0·259	0·110	NS
14. Other non-insect invertebrates	R = 0·812P + 1·041	19	0·414	0·086	<0·05

TABLE 5. Predictive regression equations relating annual production ($\log_{10}$ P cal $m^{-2} yr^{-1}$) to respiration ($\log_{10}$ R cal $m^{-2} yr^{-1}$) in animal populations. GM regressions, which better estimate the slope, are given below each predictive equation; statistics relate to the latter

Group	Regression equation	N	standard error intercept	standard error slope	Significance of slope from 1·0
1. Insectivores	R = 1·510P + 1·572	6	0·200	0·2251	NS
	R = 1·576P + 1·493				
2. Birds	R = 1·176P + 1·524	9	0·156	0·1766	NS
	R = 1·266P + 1·335				
3. Small mammal communities	R = 0·619P + 2·623	8	0·275	0·1635	NS
	R = 0·737P + 2·387				
4. All other mammals	R = 1·007P + 1·466	56	0·308	0·0465	NS
	R = 1·067P + 1·349				
5. Fish and social insects	R = 0·839P + 1·504	22	0·450	0·1015	NS
	R = 0·959P + 1·187				
6. Non-insect invertebrates	R = 0·856P + 1·088	73	0·369	0·0446	$0·01 > P > 0·001$
	R = 0·937P + 0·767				
7. Non-social insects	R = 0·963P + 0·271	61	0·287	0·0322	NS
	R = 0·994P + 0·169				

Common slope for groups 2–7: b = 0·923 ± 0·018, v = 1·007
Common slope for groups 4–7: b = 0·932 ± 0·018, v = 0·999

TABLE 6. Regression equations relating annual population respiration ($\log_{10}$ R cal $m^{-2} yr^{-1}$) to production ($\log_{10}$ P cal $m^{-2} yr^{-1}$) for all significant groups calculated from the common slopes for P (b = 0·942 ± 0·021) and R (b = 0·923 ± 0·018) as dependent variables. The intercepts for a slope of 1·0 are given in parentheses. Slopes (v) for GM regressions, approximated from weighted mean correlation coefficient, are 1·013R and 0·992P

Group	Regression equations	
Insectivores	P = 0·942R − 1·917 (−2·151)	R = 0·923P + 2·180 (2.099)
Birds	P = 0·942R − 1·664 (−1·895)	R = 0·923P + 2·057 (1·895)
Small mammal communities	P = 0·942R − 1·639 (−1·864)	R = 0·923P + 2·016 (1·864)
Other mammals	P = 0·942R − 1·281 (−1·480)	R = 0·923P + 1·632 (1·480)
Fish and social insects	P = 0·942R − 0·863 (−1·078)	R = 0·923P + 1·282 (1·078)
Non-insect invertebrates	P = 0·942R − 0·252 (−0·513)	R = 0·923P + 0·821 (0·513)
Non-social insects	P = 0·942R + 0·056 (−0·435)	R = 0·923P + 0·399 (0·144)
Non-insect invertebrates:		
Herbivores	P = 0·942R − 0·366 (−0·635)	R = 0·923P + 0·941 (0·635)
Carnivores	P = 0·942R − 0·283 (−0·476)	R = 0·923P + 0·695 (0·476)
Detritivores	P = 0·942R − 0·019 (−0·285)	R = 0·923P + 0·626 (0·285)

of the non-social insects is again marginal ($P = 0·058$) with the same rank order of efficiency found previously when the intercept was calculated from the common slope for the three groups.

Regression equations for the derived groups are presented in Table 6 for both P and R as the dependent variable; intercepts are given for a slope of 1·0 as well as those calculated from the common slope.

Production efficiency and the magnitude of P or R

We are concerned here with the slope of the regression lines; as both variables are taken as logarithms (simple allometry relationship) then a slope of unity shows that the magnitude of P or R has no effect on production efficiency (P/(P + R) = P/A). By attempting to group the data I am looking for law-like relationships between P and R where both are subject to error and have random variability (functional relationships

sensu Sprent 1969). No independent estimate of the variance of P and R is available in energy budgets so no maximum likelihood estimate of the slope is possible (Sprent 1969). However, the range of the slope for R can be calculated; it lies between the slopes for R as the independent variable and as the dependent variable (in the latter case derived from reciprocal slope P). The range for slope P can be derived in a similar manner.

Taking the specific case of the common slopes in Table 6 the slope ranges between 0·942R–1·083R (i.e. 1/0·923) or 0·923P–1·062P (i.e. 1/0·942) with mean slopes of 1·013 and 0·993 respectively. In general because the slopes are less than 1·0 whether R or P is treated as the dependent variable the range of slope in each case includes 1·0.

The most appropriate estimate of the slope for data of this type is v of the GM regression. In each case v is close to 1·0; while exact confidence intervals are unavailable for v calculated from the common slope, they would have to depart widely from those for b in the predictive equations to show significant departure of the slopes from unity.

In neither of the above treatments is there any evidence that the slope departs from unity; the magnitude of P or R has no effect on production efficiency.

Production efficiency and weight

Regression of maximum live weight ($\log_{10} \mu g$) of the animals against their production efficiency gave the following levels of significance (N): insectivores, $P = 0{\cdot}144(6)$; other mammals, $P = 0{\cdot}462(52)$; fish, $P = 0{\cdot}290(7)$; non-social insects, $P = 0{\cdot}118(52)$; non-insect invertebrates, $P = 0{\cdot}490(31)$. No significant relationship exists between these two variables.

Production efficiency

The mean production efficiency (P/A) is shown for various groups in Table 7 irrespective of the absolute magnitude of P and R. The seven derived groups have significant heterogeneity as do the trophic groups within the non-insect invertebrates. The rank order of production efficiency between the trophic classes for the non-insect invertebrates and the non-social insects is the same as in the previous analyses. However, the between trophic class variances are homogeneous for the non-social insects and the herbivores are clearly separated from the carnivores (SNK: $P < 0{\cdot}05$) but not from the detritivores; herbivores have the lowest production efficiency.

DISCUSSION

This analysis considerably extends previous analyses of the relationship between annual population production and respiration in animal populations (McNeill & Lawton 1970; Shorthouse 1971; Grodziński & French in Grodziński & Wunder 1975). Homoiotherms separate from poikilotherms (McNeill & Lawton 1970) but clear separation is possible within these two groups.

Homoiotherms separate into three (insectivores, birds and other mammals) and possibly four (small mammal communities) groups. Grodzińsky & French in Grodziński & Wunder (1975), taking P as the dependent variable, showed that the slopes for insectivores and rodents were different. I was unable to separate rodents from other non-insectivore mammals; when the latter two groups were pooled the slope did not differ when y = P but did so differ when y = R. Although insectivores were included in the small mammal community budgets, in only 2 (Hansson 1971) of the 8 budgets were

TABLE 7. Mean production efficiency (P/A) ranked in order of increasing efficiency. Statistics were calculated using arcsine $\sqrt{x}$ transformation and have been reconverted for this table. Vertical lines next to the trophic types include statistically common groups using Student-Newman-Keuls *a posteriori* test for unequal sample sizes

Group	P/A %	Standard error	N	Coefficient of variation
1. Insectivores	0·86	0·109	6	35·6
2. Birds	1·29	0·030	9	15·3
3. Small mammal communities	1·51	0·126	8	28·8
4. Other mammals	3·14	0·278	56	29·6
5. Fish and social insects	9·77	0·890	22	29·7
6. Non-insect invertebrates	25·0	3·671	73	36·8
7. Non-social insects	40·7	2·036	61	20·7
Non-insect invertebrates:				
8. Herbivores	20·8	1·38	15	24·9
9. Carnivores	27·6	5·09	11	41·2
10. Detritivores	36·2	4·82	23	34·3
Non-social insects:				
11. Herbivores	38·8	1·93	49	20·7
12. Detritivores	47·0	1·64	6	17·0
13. Carnivores	55·6	0·64	5	9·5

Groups 1–7: Homogeneity $\chi^2 = 127{\cdot}48$ $P < 0{\cdot}005$; ANOVA, $F = 97{\cdot}83$, $P < 0{\cdot}001$. Groups 8–10; Homogeneity $\chi^2 = 6{\cdot}315$, $0{\cdot}05 > P > 0{\cdot}025$; ANOVA, $F = 3{\cdot}541$, $0{\cdot}05 > P > 0{\cdot}025$. Groups 11–13: Homogeneity $\chi^2 = 1{\cdot}608$; $0{\cdot}5 > P > 0{\cdot}1$; ANOVA, $F = 4{\cdot}230$, $0{\cdot}025 > P > 0{\cdot}01$. Groups 1, 3 and 4: Homogeneity $\chi^2 = 1{\cdot}212$, $0{\cdot}9 > P > 0{\cdot}5$. Group $1 = 3$, $1 \neq 4$, $3 \neq 4$ (SNK $P < 0{\cdot}05$).

sufficient insectivores present to affect markedly the community P/A ratio. Comparison of the methodologies used to derive community and single species budgets is beyond the scope of this paper but separation of community from single species budgets in mammals does raise questions as to the validity of the bird line which is based mainly (7 of 9 budgets) on community studies.

Poikilotherms separation clearly into three groups (fish and social insects, non-insect invertebrates and non-social insects). The latter two groups could also be separated into arthropod and non-arthropod species but the resulting regressions had wider confidence intervals so I have retained the former division.

The arthropods but not the invertebrates (both excluding social insects) could be separated into long and short lived species and the latter had the lower production efficiencies. This separation is mainly due to the long lived arthropods belonging to the non-insect invertebrate group which have already been separated from the non-social insects. However, many of the former group are molluscs which probably have long life cycles but have been excluded from the analysis as insufficient information is available in the sources. The separation of the non-insect invertebrates from the non-social insects may be due to the difference in average life cycle within the groups; but this is probably not the case as two other groups (crustacea and general invertebrates), despite both containing mainly short lived species, are not separable from the molluscs. While accepting McNeill & Lawton's (1970) arguments concerning the effects of longevity and cost of overwintering stages on production efficiency it would appear that the resolution of the budgets is insufficient to distinguish the effects. The separation of insects from other invetrebrates appears to be real and not a function of trophic type, longevity or

habitat. Insects are not the 'particularly poor converters' suggested by Calow (1977), at least in natural populations.

Shorthouse (1971) separated aquatic from terrestrial poikilotherms; I was unable to separate any of the invertebrate groupings (excluding social insects) according to habitat. This again indicates the low resolution of energy budgets as terrestrial insects (mainly orthoptera and hemiptera) tend to have low cost resting stages (eggs) while aquatic species tend towards high cost overwintering stages (larvae). In this they contrast with the non-insect invertebrates which mostly fall into one group with high cost overwintering stages (mollusca, crustacea and arachnids) and are longer lived.

I present the groups only as the best available division for predictive purposes; when more data are available some of my groupings may be shown to result from the distribution of data presently available and it may be possible to more clearly describe the effects of habitat, longevity, trophic type and taxa on the relationship between P and R.

With either P or R as the dependent variable the non-insect invertebrates separate into trophic categories (detritivores, herbivores and carnivores: for $y = P$, $P = 0{\cdot}038$; for $y = R$, $P = 0{\cdot}022$) with the main contribution to the separation being between herbivores and detritivores ($P = 0{\cdot}006$). The same comparison for the non-social insects gave marginal significance in each case (for $y = P$, $P = 0{\cdot}102$; for $y = R$, $P = 0{\cdot}058$). When the intercepts were calculated for the common slope within each analysis herbivores had, in each case, the lowest production efficiency (P/A) and carnivores the greatest in three of four analyses. When trophic comparisons were made directly from P/A without regard to the magnitude of P or R (Table 7) rather similar results were obtained; however the analysis was strengthened for the non-social insects which gave significant separation while having homogeneous variances between trophic groups. These results do not support the contention that detritivores have low P/A because of their poor quality food (Macfadyen 1967), that P/A is inversely related to trophic level (Kozlowski 1968) or that high conversion efficiency is associated with herbivory (Calow 1977).

While it has been possible to separate objectively a number of groups with differing production efficiencies there is no longer the clear separation of homoiotherms and poikilotherm data (Fig. 1) seen in McNeill & Lawton (1970: Fig. 1). The production efficiencies of animal populations form a continuum and there has been no quantum jump between poikilotherms and homoiotherms in the evolution of production efficiency.

Any departure of the slope of the regression equations from unity would imply that the magnitude of P or R affects the production efficiency; if this were the case some cogent theory would be needed to account for the effect. The common slope for the original fourteen taxonomic groups ($y = P$) does not differ from unity nor does that for the twelve parallel lines when $y = R$. In contrast to McNeill and Lawton (1970) who found the slope for the short lived poikilotherms but not the homoiotherms had a slope differing from 1·0, I find the reverse to be the case. Using the more appropriate GM regressions it is clear that the slopes do not differ from unity; when many species are considered the magnitude of P or R does not influence production efficiency. Intraspecific effects are considered later.

McNeill & Lawton (1970) suggested two reasons for the departure of their regression from unity for short lived poikilotherms; animals for some reason limited to low productivity may compensate by having maximum production efficiency, or the slope may reflect the distribution within their analysis of data from species of differing longevity and overwintering costs. Several factors may influence P/A: the energetic cost of competition may increase at high intraspecific productivity levels where species numbers are reduced

and competition tends to be intraspecific and should be most intense; conversely P/A may be reduced in rare species (low density and low productivity) by the energetic requirements of finding resources. Such hypothesis are relative to the species concerned. If productivity influences P/A then different species should be affected over different ranges of P or R depending on their normal values for population density or productivity. The sum effects on the regression lines would not be expected to cause the slope to depart from unity.

The size class structure of a population has an identifiable effect on P/A; young animals tend to have greater P/A than old ones (Calow 1977) so that growing populations with a high proportion of young individuals have greater P/A than stable or declining populations. While this should not cause a departure of the regression from unity, at least within one metabolic class of animals, it may explain the separation of the non-social insects from the non-insect invertebrates. The former tend to have individuals developing rapidly from eggs within one or two seasons and short reproductive life which should give high P/A; most non-insect invertebrates do not have this phenology and would have lower P/A.

The firmest evidence I have shows that the slopes of the regression equations do not depart from unity; until a body of theory is developed and firm empirical evidence obtained to suggest otherwise, I recommend the use of a slope of 1·0 for all the predictive equations in Table 6.

It has been suggested that P/A is greater in high density populations (high production) (Bobek 1969; W. Grodziński & N. R. French personal communication). Examination of the trend in the relationship between P/A and P in species for which there are available more than two energy budgets does not support this contention. Five of seven homoiothermic species show no trend in the relationship while six of eleven poikilothermic species have a direct relationship and three have no trend in the relationship.

None of the five taxa considered showed a significant relationship between adult live weight and production efficiency. The increased efficiency of resource utilization suggested (Cody 1966) for more *K*-selected and hence larger (Southwood 1976) species is not achieved through changes in production efficiency (or P/C; unpublished) within the groups I considered. In addition the field data do not support Fenchel's (1974) view that R/A is directly related to body size.

Despite the larger data base used here the confidence intervals within any regression line do not improve on those of McNeill & Lawton (1970) and in some cases they are wider. Nevertheless the predictive power of the regressions is improved by there being more specific metabolic groups from which to choose. While the failure to improve on the confidence intervals partly reflects my lack of data selection they are a real measure of the innate variability of energy budgets and of the variance introduced by differing methodologies and assumptions. Methodological differences may give at least a twofold variation in the estimate of R (Humphreys 1978); this would give 1·59–1·77 and 1·76–1·84 fold variation in P/A for non-social insects and non-insect invertebrates at production efficiencies in Table 7. This variation compares with 2·7 and 3·2 fold variation in P/A within the 95% confidence intervals in Table 6 for non-social insects and non-insect invertebrates respectively. These methodological differences prevent any true measure of within group plasticity of P/A in animal populations. The contention that the noise introduced into energy budgets by methodological differences may prevent separation of many groups (Humphreys 1978) is clearly incorrect. However, the resolution is low and some subdivisions that would be expected cannot be found.

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APPENDIX

Species or community	Group or common name	Respiration (Kcal m^{-2} yr^{-1})	Production (Kcal m^{-2} yr^{-1})	Authority
Mammalia				
Peromyscus polionotus Osgood	Old field mouse	6·57	0·12	Odum, Connel & Davenport 1962
Peromyscus maniculatus	Deer mouse	0·190	0·014	Chew & Chew 1970
Peromyscus eremicus	Cactus mouse	0·434	0·034	Chew & Chew 1970
Peromyscus leucopus (Rafinesque)	White footed mouse	9·88	0·194	Baar & Fleharty 1976
Perognathus penicillatus	Desert pocket mouse	0·012	0·0001	Chew & Chew 1970
Perognathus baileyi	Bailey's pocket mouse	0·0197	0·0001	Chew & Chew 1970
Perognathus flavus	Silky pocket mouse	0·125	0·009	Chew & Chew 1970
Neotoma albigula	White throated wood mouse	0·112	0·008	Chew & Chew 1970
Sigmodon hispidus Say and Ord.	Cotton rat	8·83	0·53	Golley 1961 in Davis & Golley 1965
Sigmodon hispidus	Cotton rat	13·28	0·302	Fleharty & Choate 1973
Glaucomys sabrinus yukonensis Osgood	Flying squirrel	0·72	0·01	Grodziński 1971
Dipodomys merriami	Merriam's kangaroo rat	5·488	0·300	Chew & Chew 1970
Reithrodontomys megalotis	Western harvest mouse	0·045	0·0035	Chew & Chew 1970
Onychomys torridus	Southern grasshopper mouse	0·653	0·037	Chew & Chew 1970
Proechimys semispinosus (Tomes)	Cavimorpha	11·98	0·602	Gliwicz 1973
Apodemus flavicollis (Melchior)	Yellow necked field mouse	2·643	0·072	Grodziński *et al.* 1970
Apodemus flavicollis	Yellow necked field mouse	3·46	0·136	Grodziński *et al.* 1970
Apodemus flavicollis	Yellow necked field mouse	1·65	0·03	Grodziński *et al.* 1970
Apodemus flavicollis	Yellow necked field mouse	2·518	0·086	Bobek 1971
Apodemus flavicolis	Yellow necked field mouse	1·56	0·054	Bobek 1971
Apodemus flavicollis	Yellow necked field mouse	0·53	0·025	Hansson 1971
Apodemus flavicollis	Yellow necked field mouse	0·21	0·006	Hansson 1971
Apodemus sylvaticus (L.)	Wood mouse	0·95	0·058	Hansson 1971
Apodemus sylvaticus	Wood mouse	2·12	0·063	Hansson 1971
Pitymys subterraneus (De Selys Long.)	Pine vole	5·022	0·08	Grodziński, Janas & Migula 1966
Chlethrionomys glareolus (Schreber)	Bank vole	3·2931	0·0896	Grodziński *et al.* 1970
Chlethrionomys glareolus	Bank vole	5·734	0·166	Grodziński *et al.* 1970
Chlethrionomys glareolus	Bank vole	1·86	0·0377	Grodziński *et al.* 1970
Chlethrionomys glareolus	Bank vole	12·496	0·287	Bobek 1971
Chlethrionomys glareolus	Bank vole	3·892	0·112	Bobek 1971
Chlethrionomys glareolus	Bank vole	2·28	0·063	Hansson 1971
Chlethrionomys glareolus	Bank vole	2·72	0·051	Hansson 1971
Chlethrionomys glareolus	Bank vole	10·804	0·207	Aulak 1973

Chlethrionomys rutilus dawsoni Merriam	Red-backed voles	5·3	0·11	Grodziński 1971
Microtus agrestis (L.)	Field vole	10·72	0·172	Hansson 1971
Microtus agrestis	Field vole	26·31	0·423	Hansson 1971
Microtus agrestis	Field vole	0·98	0·019	Grodziński, Janus & Migula 1966
Microtus arvalis (Pallas)	Common vole	79·74	1·71	Ryszkowski, Goszczynski & Truszkowski 1973
Microtus oeconomus macfarlani Merriam	Tundra vole	1·66	0·04	Grodziński 1971
Microtus oeconomus	Root vole	23·6	0·8	Hagen, Ostbye & Skar 1975
Microtus oeconomus	Root vole	1·5	0·05	Hagen, Ostbye & Skar 1975
Microtus pennsylvanicus p. Ord.	Vole	16·99	0·517	Golley 1960
Arvicola terrestris (L.)	Vole	5·68	0·295	Pelikán 1974
Arvicola terrestris	Vole	7·90	0·39	Pelikán 1974
Tamiasciurus hudsonicus preblei Howell	Red squirrel	5·25	0·08	Grodziński 1971
Spermophilus spilosoma	Spotted ground squirrel	0·051	0·0035	Chew & Chew 1970
Ammospermophilus harrisii	Harriss's antelope squirrel	0·186	0·0105	Chew & Chew 1970
Sciurus carolinensis	Grey squirrel	66·82	0·77	Montgomery, Whelan & Mosby 1975
Lepus californicus	Jack rabbit	2·2	0·121	Chew & Chew 1970
Sylvilagus audubonii	Desert cottontail	0·508	0·031	Chew & Chew 1970
Cricetus cricetus (L.)	Hamster	14·45	1·12	Gorecki 1977
Bos indicus	Indian cattle	971·3	50·8	Odend'hal 1972
Odocoileus virginianus	White-tailed deer	39·5	0·64	Davis and Golley 1965
Adenota kob thomasi (Neumann)	Uganda kob	61·68	0·808	Buechner & Golley 1967
Loxodonta africana	African elephant	23·0	0·34	Petrides & Swank 1965
Mustela rixosua allegheniensis Rhoads	Least weasel	0·543	0·013	Golley 1960
Sorex cinereus hollisteri Jackson	Shrew	1·21	0·01	Grodziński 1971
Sorex minutus (L.)	Shrew	0·57	0·004	Hansson 1971
Sorex minutus	Shrew	1·67	0·014	Hansson 1971
Sorex araneus (L.)	Shrew	5·64	0·026	Hansson 1971
Sorex araneus	Shrew	7·69	0·035	Hansson 1971
Neomys fodiens (Penn)	Water shrew	0·16	0·004	Hansson 1971
Small mammal populations		4·131	0·084	French *et al.* 1976
Small mammal populations		1·714	0·020	French *et al.* 1976
Small mammal populations		8·133	0·182	French *et al.* 1976
Small mammal populations		12·674	0·323	French *et al.* 1976
Small mammal populations		4·904	0·010	French *et al.* 1976
Small mammal populations		2·447	0·046	French *et al.* 1976

(continued)

APPENDIX (*continued*)

Species or community	Group or common name	Respiration (Kcal m^{-2} yr^{-1})	Production (Kcal m^{-2} yr^{-1})	Authority
Small mammal populations		20·69	0·348	Hansson 1971
Small mammal populations		40·88	0·596	Hansson 1971
Aves				
Passerculus sandwichensis (Gmelin)	Savannah sparrow	3·55	0·04	Odum, Connel & Davenport 1962
Telmatodytes palustris (Brewster)	Long-billed marsh wren	87·5	0·457	Kale 1965
Avifauna		7·49	0·11	Wiens & Nussbaum 1975
Avifauna		7·28	0·10	Wiens & Nussbaum 1975
Avifauna		11·54	0·19	Wiens & Nussbaum 1975
Avifauna		14·39	0·23	Wiens & Nussbaum 1975
Avifauna		8·49	0·14	Wiens & Nussbaum 1975
Avifauna		8·43	0·12	Wiens & Nussbaum 1975
Avifauna		5·0	0·06	Holmes & Sturges 1973
Actinopterygii				
Rutilus rutilus (L.)	Roach	118·4	10·7	Mann 1965
Alburnus alburnus (L.)	Bleak	314·2	30·5	Mann 1965
Leuciscus leuciscus (L.)	Dace	23·7	1·5	Mann 1965
Perca fluviatilis (L.)	Perch	23·2	1·8	Mann 1965
Gobio gobio (L.)	Gudgeon	37·0	2·6	Mann 1965
Notothenia neglecta Nybelin		80·63	6·12	Everson 1970
Aspius aspius L.		0·905	0·135	Backiel 1970
Hippoglossoides platessoides (Fabr.)	Plaice	8·556	2·5	MacKinnon 1973
Fish population		2·299	0·453	Backiel 1971
Insecta				
Hedriodiscus truquii (Bellardi)	Diptera: Stratiomyidae	6·387	2·091	Stockner 1971
Hedriodiscus truquii	Diptera: Stratiomyidae	7·778	2·308	Stockner 1971
Hedriodiscus truquii	Diptera: Stratiomyidae	6·95	4·091	Stockner 1971
Hedriodiscus truquii	Diptera: Stratiomyidae	7·387	5·099	Stockner 1971
Pentaneura sp.	Diptera	116·5	86·4	Tilly 1968
Cardiocladius sp.	Diptera	57·2	114·5	Tilly 1968

Glyptotendipes barbipes (Staeger)	Diptera: Chironomidae	263·0	165·0	Kimerle & Anderson 1971
Glyptotendipes barbipes	Diptera: Chironomidae	27·0	18·0	Kimerle & Anderson 1971
Glyptotendipes barpipes	Diptera: Chironomidae	730·0	459·0	Kimerle & Anderson 1971
Glyptotendipes barbipes	Diptera: Chironomidae	58·0	37·0	Kimerle & Anderson 1971
Tipula excisa Schum.	Diptera: Tipulidae	5·816	4·765	Hofsvang 1973
Leptoterna dolobrata (L.)	Heteroptera: Miridae	0·103	0·1269	McNeill 1971
Leptoterna dolobrata	Heteroptera: Miridae	0·101	0·140	McNeill 1971
Leptoterna dolobrata	Heteroptera: Miridae	0·062	0·0638	McNeill 1971
Leptoterna dolobrata	Heteroptera: Miridae	0·088	0·0956	McNeill 1971
Leptoterna dolobrata	Heteroptera: Miridae	0·064	0·0898	McNeill 1971
Philaneus spumarius L.	Homoptera: Cercopidae	22·60	15·963	Wiegert 1964
Philaneus spumarius	Homoptera: Cercopidae	1·07	0·096	Wiegert 1964
Philaneus spumarius	Homoptera: Cercopidae	0·53	0·048	Wiegert 1964
Neophilaenus lineatus	Homoptera: Cercopidae	0·597	0·359	Hinton 1971
Strophingia ericae (Curt.)	Homoptera: Psylloidea	1·452	0·687	Hodkinson 1973
Strophingia ericae	Homoptera: Psylloidea	0·073	0·077	Hodkinson 1973
Strophingia ericae	Homoptera: Psylloidea	0·079	0·086	Hodkinson 1973
Eucallipterus tiliae	Homoptera: Aphididae	1436·1	1982·1	Llewellyn 1975
Eucallipterus tiliae	Homoptera: Aphididae	1589·8	2327·7	Llewellyn 1975
Melanoplus sanguinipes G. and B.	Orthoptera: Acrididae	25·42	26·18	Van Hook 1971
Melanoplus bivittatus (Say)	Orthoptera: Acrididae	3·38	2·28	Bailey & Mukerji 1977
Melanoplus bivittatus	Orthoptera: Acrididae	3·09	1·77	Bailey & Mukerji 1977
Melanoplus femurrubrum (De Geer)	Orthoptera: Acrididae	3·01	1·92	Bailey & Mukerji 1977
Melanoplus femurrubrum	Orthoptera: Acrididae	2.84	1.54	Bailey & Mukerji 1977
Melanoplus spp.	Orthoptera: Acrididae	1·120	0·638	Wiegert 1965
Melanoplus spp.	Orthoptera: Acrididae	0·596	0·373	Wiegert 1965
Melanoplus spp.	Orthoptera: Acrididae	8·690	4·573	Wiegert 1965
Conocephalus fasciatus (De Geer)	Orthoptera: Acrididae	3·66	2·34	Van Hook 1971
Orchelimum fidicinium Rehn and Hebard	Orthoptera: Acrididae	18·6	10·8	Smalley 1960
Orchelimum vulgare Harris	Orthoptera: Acrididae	5·088	1·237	Hackworth, Ake & Matta 1973
Encoptolophus sordidus costalis (Scudder)	Orthoptera: Acrididae	1·72	1·567	Bailey & Reigert 1973
Encoptolophus sordidus costalis	Orthoptera: Acrididae	1·577	1·554	Bailey & Reigert 1973

(*continued*)

APPENDIX (*continued*)

Species or community	Group or common name	Respiration (Kcal m^{-2} yr^{-1})	Production (Kcal m^{-2} yr^{-1})	Authority
Trimerotropis saxatilis McNeill	Orthoptera: Acrididae	0·22	0·094	Duke & Crossley 1975
Chorthippus parallelus Zett.	Orthoptera: Acrididae	8·71	6·1	Gyllenberg 1969
Chorthippus parallelus	Orthoptera: Acrididae	7·2	5·9	Gyllenberg 1969
Chorthippus parallelus	Orthoptera: Acrididae	6·4	5·1	Gyllenberg 1969
Chorthippus parallelus	Orthoptera: Acrididae	5·1	4·0	Gyllenberg 1969
Chorthippus parallelus	Orthoptera: Acrididae	0·338	0·345	Qasrawi 1966
Chorthippus parallelus	Orthoptera: Acrididae	0·192	0·207	Qasrawi 1966
3 spp. Orthoptera	Orthoptera:	21·6	4·0	Odum, Connel & Davenport 1962
Orthoptera population	Orthoptera:	0·924	0·477	Menhinick 1967
Onychiurus procampatus Gisin	Collembola	3·04	2·61	Healey 1967
Pyrrhosoma nymphula (Sulz.)	Odonata: Zygoptera	3·17	3·94	Lawton 1971
Pyrrhosoma nymphula	Odonata: Zygoptera	3·67	3·59	Lawton 1971
Frenesia missa	Trichoptera	440·7	170·6	Tilly 1968
Potamophylax cingulatus Steph.	Trichoptera	5·501	4·53	Otto 1975
Trichoptera		67.5	20.9	Teal 1957
Chimabacche fagella Schiff.	Lepidoptera	1·06	0·43	Winter 1971
Chimabacche fagella	Lepidoptera	0·46	0·16	Winter 1971
Nebria brevicollis (F.)	Coleoptera: Carabidae	0·415	0·389	Manga 1972
Pterostichus oblongopunctatus F.	Coleoptera: Carabidae	0·802	0·146	Weidemann 1971
Rhynchaenus fagi L.	Coleoptera: Curculionidae	2·009	2·199	Grimm 1973
Aphodius rufipes (L.)	Coleoptera: Scarabaeidae	189·67	200·3	Holter 1975
Pteromalus puparum (L.)	Hymenoptera: Ichneumonidae	0·056	0·073	Chlodny 1968
Pimpla instigator (Fabr.)	Hymenoptera: Ichneumonidae	0·008	0·017	Chlodny 1968
Lasius alienus (Först)	Hymenoptera: Formicoidea	54·79	10·23	Nielsen 1972
Pogonomyrmex occidentalis (Cresson)	Hymenoptera: Formicoidea	0·962	0·108	Rogers, Lavigne & Miller 1972
Pogonomyrmex occidentalis	Hymenoptera: Formicoidea	1·172	0·138	Rogers, Lavigne & Miller 1972
Pogonomyrmex occidentalis	Hymenoptera: Formicoidea	1·297	0·153	Rogers, Lavigne & Miller 1972
Pogonomyrmex occidentalis	Hymenoptera: Formicoidea	0·126	0·014	Rogers, Lavigne & Miller 1972
Psammotermes hybostoma	Termitidae	1·149	0·0069	Lepage cited in Wood & Sands 1978
Ancistrotermes cavithorax	Termitidae	1·899	0·1779	Josens cited in Wood & Sands 1978
Macrotermes subhyalinus	Termitidae	7·378	0·9176	Lepage cited in Wood & Sands 1978
Odontotermes smeathmani	Termitidae	1·259	0·3478	Lepage cited in Wood & Sands 1978
Nasutitermes costalis (Holm.)	Termitidae	5·388	0·3339	Wiegert 1970

Trinervitermes geminatus	Termitidae	0·2197	0·0210	Lepage cited in Woods & Sands 1978
Trinervitermes geminatus	Termitidae	8·637	0·3148	Josens cited in Woods & Sands 1978
Trinervitermes trinervius	Termitidae	0·640	0·1330	Lepage cited in Woods & Sands 1978
Arachnida				
Pardosa lugubris (Walckenaer)	Araneae: Lycosidae	0·803	0·298	Edgar 1971
Pardosa palustris (L.)	Araneae: Lycosidae	0·067	0·035	Steigen 1975
Geolycosa godeffroyi (Koch)	Araneae: Lycosidae	0·405	0·131	Humphreys 1978
Lycosa sp. & *Schizocosa* sp.	Araneae: Lycosidae	3·86	2·26	Van Hook 1971
Spiders	Araneae	1·234	0·345	Moulder & Reichle 1972
Oribatid mites	Acarina	1·965	0·430	Engelmann 1961
Urodacus yashenkoi (Birula)	Scorpionida	0·381	0·224	Shorthouse 1971
Crustacea				
Asellus militaris Hay	Amphipoda	486·1	104·5	Teal 1957
Hyalella azteca (Sanssure)	Amphipoda	13·537	4·535	Mathias 1971
Crangonyx richmondensis occidentalis (Hubricht & Harrison)	Amphipoda	5·16	1·363	Mathias 1971
Gammarus pseudolimneus Bousfield	Amphipoda	1039·1	183·0	Tilly 1968
Asellus aquaticus L.	Amphipoda	51·06	16·296	Fitzpatric 1968
Ligidium japonica	Isopoda	16·0	3·50	Saito 1965
Cherax albidus Clark	Decapoda	136·0	158·0	Woodland 1967
Leptodora kindtii Focke	Cladocera	4·379	1·876	Cummins *et al.* 1969
Leptodora kindtii	Cladocera	17·257	7·395	Cummins *et al.* 1969
Other invertebrates				
Japonaria laminata armigera Verhoeff	Diplopoda	30·9	26·9	Saito 1967
Japonaria laminata armigera	Diplopoda	1·51	1·50	Saito 1967
Lithobius forficatus (L.)	Chilopoda	1·998	0·085	Wignarajah 1968
Lithobius crassipes (L. Koch)	Chilopoda	1·268	0·074	Wignarajah 1968
Phagocata velata	Platyhelminthes	13·8	32·5	Tilly 1968
Cognethia sphagnetorum	Enchytraeidae	61·98	12·86	Standen 1973
Cognethia sphagnetorum	Enchytraeidae	63·36	10·39	Standen 1973

(*continued*)

APPENDIX (*continued*)

Species or community	Group or common name	Respiration (Kcal m^{-2} yr^{-1})	Production (Kcal m^{-2} yr^{-1})	Authority
Neanthus virens (Sars.)	Polychaeta	16·7	45·2	Kay & Braefield 1973
Limnodrilus hoffmeisteri Claraparede	Oligochaeta	484·6	173·8	Teal 1957
Allolobophora rosea (Sav.)	Oligochaeta: Lumbricidae	12·727	2·717	Bolton 1969
Sagitta elegans	Chaetognatha	2·45	2·3	Sameoto 1972
Strongylocentrotus droebachiensis	Echinodermata: Echinoidea	178·5	49·8	Miller & Mann 1973
Mollusca				
Scrobicularia plana (da Costa)	Pelecypoda	54·6	17·5	Hughes 1970
Scrobicularia plana	Pelecypoda	476·0	124·0	Hughes 1970
Pisidium virginicum (Gmelin)	Pelecypoda	90·9	81·8	Teal 1957
Modiolus demissus Dillwyn	Pelecypoda	39·0	16·7	Kuenzler 1961
Crassostrea virginica Gmelin	Pelecypoda	5656·0	4132·0	Dame 1976
Crassostera gigas	Pelecypoda	503·0	512·0	Bernard 1974
Tellina tenuis da Costa	Pelecypoda	18·99	3·676	Trevallion 1971
Tellina tenuis	Pelecypoda	13·27	2·079	Trevallion 1971
Tellina tenuis	Pelecypoda	14·57	5·864	Trevallion 1971
Corbicula africana	Pelecypoda	145·1	16·9	Lévêque 1973
Corbicula africana	Pelecypoda	60·0	6·3	Lévêque 1973
Corbicula africana	Pelecypoda	202·3	21·3	Lévêque 1973
Corbicula africana	Pelecypoda	446·7	51·9	Lévêque 1973
Corbicula africana	Pelecypoda	116·4	11·5	Lévêque 1973
Unio tumidus Philipsson	Pelecypoda	23·376	1·684	Tudorancea & Florescu 1968a
Unio pictorum	Pelecypoda	30·4	1·869	Tudorancea & Florescu 1968b
Acmaea scabra (Gould)	Pelecypoda	47·0	49·0	Sutherland 1972
Acmaea scabra	Pelecypoda	50·0	103·0	Sutherland 1972
Acmaea scabra	Pelecypoda	52·0	81·0	Sutherland 1972
Ancylus fluviatilis O.F. Müll.	Gastropoda: Basommatophora	14·81	1·877	Streit 1976
Ancylus fluviatilis	Gastropoda	18·65	2·516	Streit 1976
Littorina irrorata (Say)	Gastropoda: Mesogastropoda	249·4	40·6	Odum & Smalley 1959
Physa integra Haldane	Gastropoda	36·0	169·4	Tilly 1968
Bellamya unicolor	Gastropoda	120·9	58·4	Lévêque 1973
Bellamya unicolor	Gastropoda	116·9	55·0	Lévêque 1973
Cleopatra bulimoides	Gastropoda	183·8	29·2	Lévêque 1973

Cleopatra bulimoides	Gastropoda	163·9	25·6	Lévêque 1973
Cleopatra bulimoides	Gastropoda	164·1	36·8	Lévêque 1973
Cleopatra bulimoides	Gastropoda	187·7	49·3	Lévêque 1973
Cleopatra bulimoides	Gastropoda	13·6	2·5	Lévêque 1973
Cleopatra bulimoides	Gastropoda	90·2	23·0	Lévêque 1973
Cleopatra bulimoides	Gastropoda	43·3	7·8	Lévêque 1973
Cleopatra bulimoides	Gastropoda	24·7	5·8	Lévêque 1973
Melania tuberculata	Gastropoda	172·7	61·8	Lévêque 1973
Melania tuberculata	Gastropoda	30·8	7·9	Lévêque 1973
Melania tuberculata	Gastropoda	43·4	18·4	Lévêque 1973
Melania tuberculata	Gastropoda	34.0	12.8	Lévêque 1973
Tegula funebralis Adams	Gastropoda	578·0	175·0	Paine 1971
Nerita tessellata Gmelin	Gastropoda: Archaeogastropoda	217·3	29·3	Hughes 1971a
Nerita versicolor Gmelin	Gastropoda: Archaeogastropoda	50·9	7·6	Hughes 1971a
Nerita peloronta L.	Gastropoda: Archaeogastropoda	31·4	7·5	Hughes 1971a
Nerita peloronta	Gastropoda: Archaeogastropoda	100·7	14·2	Hughes 1971a
Fissurella barbadensis Gmelin	Gastropoda: Archaeogastropoda	139·3	50·86	Hughes 1971b
Laevapex fuscus (C. B. Adams)	Gastropoda	5·227	1·505	McMahon 1975
Laevapex fuscus	Gastropoda	0·735	0·267	McMahon 1975

CORRIGENDUM

To: Humphreys, W.F., 1979. Production and respiration in animal populations. *Journal of Animal Ecology* 48: 427-453.

On page 439 both references to Calow (1977) are incorrect and should be deleted. Calow was referring to individual efficiencies and not population efficiencies as implied by the context.

news and views

Production and respiration in animal communities

from Robert M. May

A WIDELY-quoted generalisation about natural ecosystems is that the efficiency of energy transfer from one trophic level to the next is around 10%; that is, about 10% of the net production of plants ends up as net production of herbivores, about 10% of this makes its way into net production of the first level of carnivores, and so on. The generalisation is largely based on studies of freshwater lakes and of laboratory aquaria, conducted in the 1950s. One early articulation of this notion is in Slobodkin's elegant and influential *Growth and Regulation of Animal Populations* (Holt, Rinehart and Winston; 1961), where his speculative list of candidates for valid ecological generalities leads off with "Food-chain efficiencies and ecological efficiencies in nature are approximately constant for all species".

Unfortunately, subsequent research on terrestrial and on other kinds of aquatic communities has overthrown this appealing generalisation, showing that the efficiency of energy transfer from one trophic level to the next can vary very widely. This is a pity, for valid 'ecological laws' are thin on the ground, and we can ill afford to lose any of the few we thought we had.

To determine overall efficiencies of energy transfer, two questions must be answered. First, what fraction of the net production at one trophic level is actually assimilated by creatures at the next level? Second, how do these creatures apportion the assimilated energy between net production (growth and reproduction) and respiration (maintenance costs)? The second question is amenable to fairly precise answers, but the first question is messier, as it can involve both particularities about the fraction of material that is assimilated rather than excreted by a given species and generalities about the overall fraction of net production at one level that is actually used (consumed) by the next level. Some of these problems and ambiguities can be made more explicit by considering, say, mice and weasels. If we focus on the weasels, it is in principle straightforward to determine the efficiency with which 1 gram or 1 calorie of mouse eaten is transformed into grams or calories of weasel. If we focus on the mouse population, it is hard to determine what fraction of their total biomass appears as net production in the next trophic level. Indeed, the answer ultimately depends on how we keep the books; the very notion of 'trophic level' does not stand up to close examination (where, for example, do the decomposers belong?).

Humphreys (*J. Anim. Ecol.* **48**, 427; 1979) has recently drawn together a large body of literature, to determine the relationship between annual production P and respiration R in natural populations of animals. This synoptic study sheds light on the general issues discussed above. It also has more immediate practical applications. If a relation between P and R can be confidently established for a given group of organisms, then for a species in this group only one of the two quantities need be measured directly, which can be a helpful short-cut in compiling energy budgets for communities; several people have used the earlier study by McNeill and Lawton (*Nature* **225**, 472; 1970) for this purpose. Humphreys analyses a total of 235 energy budgets culled from the literature, and he emphasises that a great variety of different assumptions and possible biases have gone into the individual studies.

Examining regression relations between P and R, Humphreys shows that homeotherms (loosely, warm-blooded animals) can be separated into four significantly different groups: insectivores; birds; small mammal communities; and other mammals. Poikilotherms (cold-blooded animals) separate into three groups: fish and social insects; non-insect invertebrates; and non-social insects. The invertebrate groups further permit significant separation into trophic categories of herbivores, carnivores and detritus feeders. In no case is the relation between P and R significantly different from a simple linear one. The fruits of Humphreys' analysis are summarised in Table 1, which shows the mean 'production efficiency' $P/(P+R)$ or fraction of assimilated energy ($A=P+R$) that is devoted to net production, for the various groupings.

Several interesting patterns emerge. Both for non-insect invertebrates and insects other than social insects, the production efficiency is significantly lower for herbivores than for carnivores and

Table 1 Mean production efficiency, $P/(P+R)$, for various groups of animals.

Group	Mean production efficiency (per cent)	Sample size
Insectivores	0.9	6
Birds	1.3	9
Small mammal communities	1.5	8
Other mammals	3.1	56
Fish and social insects	10	22
Non-insect invertebrates	25	73
Non-social insects	41	61
Non-insect invertebrates		
herbivores	21	15
carnivores	28	11
detritivores	36	23
Non-social insects		
herbivores	39	49
detritivores	47	6
carnivores	56	5

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Table 2. The assimilation efficiencies, or percentage of plant production consumed by feeding-animal species, for various systems.

Plant	Consumers	Percentage of productivity consumed
Beech trees	Invertebrates	8.0
Oak trees	Invertebrates	10.6
Maple–beech trees	Invertebrates	6.6
Maple–beech trees	Invertebrates	5.9
Tulip–poplar trees	Invertebrates	5.6
Grass + forbs	Invertebrates	4-20
Grass + forbs	Invertebrates	<0.5
Alfalfa	Invertebrates	2.5
Sericea lespedeza	Invertebrates	1.0
Grass	Invertebrates	9.6
Aquatic plants	Bivalves	11.0
Aquatic plants	Herbivorous animals	18.9
Algae	Zooplankton	25.0
Phytoplankton	Zooplankton	40.0
Marsh grass	Invertebrates	7.0
Marsh grass	Invertebrates	4.6
Meadow plants	Invertebrates	14.0
Sedge grass	Invertebrates	8.0

detritus feeders. A plausible explanation is that biochemical conversion efficiencies are higher for animals eating other animals than for animals eating plants. Other patterns are shown by Humphreys to be conspicuous by their absence: there is no significant correlation between production efficiency and the magnitude of production (that is, no correlation between P/R and P or R); there is no correlation between production efficiency and animal weight; and, with the groups set out in Table 1, species with different habitats (aquatic and terrestrial) do not have significantly different production efficiencies. Humphreys makes the further point that "there is no quantum jump in production efficiency between poikilothermic and homeothermic animals", but I think Table 1 suggests such a distinction is real (with homeothermic production efficiency typically in the range 1-3%, poikilothermic in the range 10-40%). Admittedly the scatter around the mean values for a given group is such that some social insect species have production efficiencies lower than some mammal species, so that there is no 'quantum jump' between homeotherms and poikilotherms, but the tendency for the typical poikilotherm to have a production efficiency an order of magnitude larger than that of the typical homeotherm remains. Warm-blooded beasts pay a noticeable cost, relative to cold-blooded ones, in order to keep their metabolic machinery ticking over at a constant temperature.

For a community of interacting species, we can get some idea of the overall 'food-chain efficiency' with which energy flows from one trophic level (n) to the next ($n+1$), by combining the mean production efficiencies at level $n+1$ (P_{n+1}/A_{n+1}) with estimates of the fraction of the productivity at level n that actually is consumed (the assimilation efficiency, A_{n+1}/P_n). Pimentel, Levin and Soans (*Ecology* **56**, 381; 1975) have brought together several rough estimates of the percentage of plant production that is consumed by the animal species that feed upon it; their compilation is summarised in Table 2. As mentioned above, any such estimates of assimilation efficiencies suffer, *inter alia*, from the arbitrariness inherent in a crude classification into 'trophic levels'. Convolving Table 1 with Table 2, we see that food-chain efficiencies can vary over two or more orders of magnitude, from less than 0.1% to more than 10%.

In the early 1960s, the tentative '10% rule' engendered enthusiasm for ecological generalisations. The subsequent collapse of the rule, giving way to the complicated variety of patterns shown in Table 1, has, in my opinion, led to an excessive disenchantment with such generalisations. I think the time is ripe to return to these questions, trying to understand the patterns documented by Humphreys and others, both from 'below' (in terms of thermodynamic constraints on production efficiency in different kinds of animals) and from 'above' (in terms, for example, of the possible constraints that energy flow may impose on food web structure). □

Order in amorphous polymers

from Paul Calvert

THE extent of order in the amorphous state of polymers has been debated for many years. Likening the polymer melocules to strands of spaghetti it is difficult to see how they can be packed to high densities unless the strands are largely arranged parallel to their neighbours. After the Chemical Society's recent Faraday Discussion* on Organisation of Macromolecules in the Condensed Phase the situation seems much clearer than two years ago (see *News and Views*, **271**, 507; 1978).

Two types of order have been postulated for amorphous and glassy polymers, the orientational correlations just mentioned and local density fluctuations with regions of tight packing separated by a less dense matrix or by boundary zones. The latter were apparently demonstrated by Yeh and Geil about 10 years ago. They observed 2.5 nm nodular structures in many glassy polymers with electron microscopy in bright and dark field as well as in fracture surface replicas. At the recent meeting D.R. Uhlmann (Massachusetts Institute of Technology) reviewed his small angle X-ray scattering (SAXS) results which show only enough scattering to be consistent with the small thermal fluctuations in density, frozen in at the glass transition temperature in polymethylmethacrylate, polyethylene terephthalate, polycarbonate, polyvinyl chloride and polystyrene (PMMA, PET, PC, PVC, PS). This does not eliminate the possibility of heterogeneities whose density differs significantly from the bulk density but they must be present in very small quantities. Uhlmann also concluded that the bright and dark field electron microscope observations of small nodules were due to electron diffraction effects.

Thus the 'typical' amorphous polymers are essentially homogeneous. Epoxy resins are not but SAXS cannot distinguish between small quantities of voids and larger quantities of low or high density nodules. G.C. Stevens (CEGB, Leatherhead) said that small aggregates could be detected in unreacted liquid epoxy resins by light scattering. P.H. Geil (Case Western Reserve University) pointed out that he had seen annealing of nodular structures in amorphous polyethylene (PE) and in plasticised and unplasticised PVC. It does seem reasonable that crystallisable polymers such as PE should form crystalline nodules at low temperatures. PVC is frequently partly crystalline and its structure is most dependent on the polymerisation conditions, so any strange behaviour is plausible, and important, in this polymer.

Thus there are heterogeneities in some systems and possibly in small amounts in

*Held at the University of Cambridge, 25-27 September, 1979.

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