

Leszek GRÜM

Department of Biocenology, Institute of Ecology, Polish Academy of Sciences,
Dziekanów Leśny (near Warsaw), 05-150 Łomianki, Poland

METHODS OF APPROXIMATE ESTIMATION OF ENERGY FLOW THROUGH CARABID POPULATIONS*

ABSTRACT: Daily energy budgets of teneral and adult beetles of a few species of forest carabids have been used to formulate a set of equations allowing for an approximate daily energy budget estimation of the different life-cycle stages and species. Also, relations between the energy flow through a population and both the adult beetle population density and fertility have been expressed in the form of a regression equation that can be used for a rough estimation of energy flow under field conditions.

KEY WORDS: Carabids, energy budget, energy flow, spatial distribution, working metabolism rate.

Contents

1. Introduction
2. Daily energy budget of the individual in its life-cycle
 - 2.1. Methods
 - 2.2. Results
3. Energy flow through a species generation
4. Some factors affecting the working metabolism rate
5. Discussion
6. Summary
7. Polish summary
8. References

1. INTRODUCTION

Serious problems often arise when estimating population bioenergetics in the field, especially if only one age-class can be quantitatively sampled. This, for example, is usually the case with

*Praca wykonana w ramach problemu międzyresortowego MR II/15 (grupa tematyczna „Zbadanie struktury i zasad funkcjonowania głównych typów fizjocenoz.Polski”).

carabids (Col., Carabidae), where the population density of most stages in the life-cycle — with the exception of adult beetles — cannot be easily estimated. Under such conditions, simplified solutions are desirable, although they only provide rough estimates.

The present paper aims at a description of the general pattern of changes in the daily energy budget of an individual that accompany its weight increase (this allows one to estimate the energy flow through a population from data on the population density of the successive stages of the life-cycle), and elaboration of a method for an approximate calculation of the energy flow through a population, based on a limited amount of field data (this could be a useful approach in the case of extensive studies carried out by using simple sampling methods).

2. DAILY ENERGY BUDGET OF THE INDIVIDUAL IN ITS LIFE-CYCLE

2.1. METHODS

The daily energy budget (DEB) of the individual is the sum total of daily biomass production (P), resting metabolism rate (RMR), and working metabolism rate (WMR), that is the amount of energy expended for mobility.

Daily biomass production includes production due to body weight increase (P_g) and gamete production (P_r). It was assumed, for the sake of simplicity, that 1 mg d. wt of carabid body was the equivalent of 24 Joules. This value is close to the upper limit of calorific coefficients — varying between 24.66 kJ (5889 cal) per 1 g d. wt and 25.28 kJ (6039 cal) per 1 g d. wt — as reported by different authors (Ž y r o m s k a-R u d z k a — in press).

$$P_g = k \frac{W_f - W_i}{T}$$

where: k — calorific coefficient, W_f — final dry body weight, W_i — initial dry body weight, T — study period.

$$P_r = \nu_e W_e k$$

where: ν_e — number of eggs produced by the female in the study period, W_e — dry weight of the ripe egg, k — as above. The ν_e estimation method applied was described by Grüm (1973b).

RMR values were calculated on the basis of the following formula (Grüm 1976b):

$$y = 2.445 - 0.309 x, \quad r = -0.945, \quad p < 0.001$$

where: y — O_2 consumption in $\mu\text{l} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ at $+19^\circ\text{C}$, x — \log_e of dry body weight in mg.

Daily values of WMR were calculated according to the method worked out by Grüm (1978). The method is based on two assumptions: (a) the maximum daily biomass production of individuals of the same developmental stage of different species is proportional to the initial body weight of the individuals (this means that the daily maximum biomass production of the 2nd larval instar of different species, for instance, depends — under constant extrinsic

conditions, such as temperature and food – on the initial body weight of the larvae of different species), and (b) the energy expended for mobility causes a certain decrease in the rate of biomass production. Hence, by plotting the rate of biomass production of the individual against its mobility, it is possible – on the data obtained for the same developmental stage of different species – to draw the appropriate regression line, and calculate the decrease in the biomass production rate per unit of weight and distance.

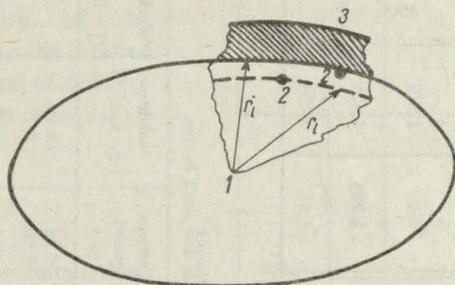


Fig. 1. Diagrammatic representation of a section of the sampling site
1 – releasing centre, 2 – pitfall, 3 – fence

The method of mobility estimation was presented earlier (G r ü m 1971, 1978). It is based on releasing marked individuals in the centre of a round, fenced sampling site, with pitfalls located at two different distances from the centre (Fig. 1). Two variables are estimated: the length of the distance passed by the individual between the centre and the pitfall, and the time-lapse from the release till the capture day.

The probability of capture of the released individual in the pitfalls located on the perimeter of r_l radius (Fig. 1) equals (G r ü m 1978):

$$p_c = \left[(d_l - r_l) \cdot \frac{m_l}{\pi r_l^2} \right] + \frac{m_l}{2 \pi r_l}$$

On the above principle, the distance the individual passed from the centre to the pitfall is calculated according to the formula (both the distance and the other parameters are expressed in l (linear) units, equal to the body length of the individual):

$$D_l = r_l' \frac{\left[\left(p_c - \frac{m_l}{2 \pi r_l} \right) \cdot \left(\frac{\pi r_l^2}{m_l} \right) \right] + r_l}{r_l} + \frac{\pi r_l'}{a}$$

where: r_l' – radius of the fenced sampling site, r_l – radius of the internal perimeter (Fig. 1), p_c – probability of capture in pitfalls located on the internal perimeter, as expressed by the ratio of the number of captured in these pitfalls to the total number of marked individuals captured in the sampling site, m_l – sum of pitfall diameters located on the internal perimeter, a – number of pitfalls located close to the fence, i.e., on the perimeter of r_l radius, p_c – as above.

Table I. Mean daily biomass production of the individual

Species	Beetle	Month	P_g		P_r				$P_g + P_r$ (J · ind. ⁻¹ · day ⁻¹)
			initial body weight (mg d. wt)*	daily increment, (mg d. wt)*	mean number of ripe eggs per female	rate of egg deposition*	mean weight of ripe egg, (mg d. wt)**	daily egg production (mg d. wt)*	
<i>Carabus arcensis</i> Hbst.	teneral	Aug.-Sept.	27.9	2.43	0	0.	0	0	61.05
	adult	June	80.7	0	2.63	0.089	2.49	0.583	14.61
<i>C. glabratus</i> Payk.	teneral	July	88.9	10.62	0.70	0.075	6.59	0.346	275.46
	adult	July	269.2	1.57	5.20	0.075	6.59	2.570	104.00***
<i>C. hortensis</i> L.	teneral	July	71.5	6.15	0	0	0	0	154.50
	adult	July	194.2	0	2.00	0.099	6.41	1.270	31.90
<i>C. nemoralis</i> Müll.	teneral	Aug.-Sept.	45.4	5.41	0	0	0	0	185.95
	adult	June	166.0	0	2.89	0.082	6.04	1.431	35.92
<i>Pterostichus niger</i> (Schall.)	teneral	July	39.1	2.48	5.20	0.141	1.01	0.740	80.89
	adult	July	81.7	0	3.40	0.141	1.01	0.484	12.14

*After Grüm (1978). **After Grüm (1973b). ***Current year adults.

Table II. Mean daily working metabolism rate and mobility of teneral and adult beetles

Species	Beetle	Month	Number of individuals captured	Mean time of stay (days)	Probability of capture in internal pitfalls	Distance passed (m)	Mobility (m · day ⁻¹)	Working metabolism rate (J · ind. ⁻¹ · day ⁻¹)
<i>Carabus arcensis</i> *	teneral	Aug.-Sept.	25	1.340	0.2400	18.04	13.46	90.35
	adult	June	147	0.901	0.0680	7.18	7.97	154.79
<i>C. glabratus</i>	teneral	July	31	0.726	0.0317	4.90	6.75	144.45
	adult	July	32	0.849	0.0317	4.90	5.06	347.19
<i>C. hortensis</i>	teneral	July	35	0.614	0.0851	8.19	13.34	229.61
	adult	July	12	0.917	0.0851	8.19	8.93	417.28
<i>C. nemoralis</i> *	teneral	Aug.-Sept.	27	1.772	0.2572	19.29	10.77	117.65
	adult	June	77	1.149	0.0649	7.02	6.11	244.10
<i>Pterostichus niger</i>	teneral	July	109	0.959	0.1376	11.58	12.07	113.55
	adult	July	23	0.674	0.0435	5.61	8.32	163.54

*After Grüm (1978).

The above method makes possible a rough estimation of the horizontal component of the distance passed by the individual, and both the assumptions and detailed considerations on this method of mobility estimation are presented in a paper by G r ü m (1978). Mobility of the individual is expressed by the ratio of the horizontal component of distance to the time it has taken to cover it.

2.2. RESULTS

The data used for the calculations of energy budgets were obtained in the same sampling area and year. Most of them were published in a few previous papers (G r ü m 1973b, 1973c, 1975a, 1975b, 1976b, 1978). Hence, the data quoted in the Tables include references to the original papers.

In Table I the basic data and the results of daily biomass production calculations are shown, and Table II contains the same for the individual mobility and WMR. The latter is the product of the mean body weight of the individual, its mobility, and the value of an index of energy expended per weight unit and distance unit.

The present author (G r ü m 1978) pointed out that the index of energy expended per weight unit per distance unit can be of different values for the individual of the same species, depending on the stage of the life-cycle. Namely, the higher the maximum rate of biomass production by the particular stage, the higher the index value, and when the rate equals zero, the index must be equal to zero even at high mobility. Thus, values of the index lower than the highest of the values found do not reflect the amount of energy expended per

Table III. Daily energy budget of teneral and adult beetles

Species	Beetle	Month	Components of DEB ($J \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$)			DEB ($J \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$)
			P	WMR	RMR	
<i>Carabus arcensis</i>	teneral	Aug.-Sept.	61.05	90.35	47.31	198.71
	adult	June	14.61	154.79		216.71
<i>C. glabratus</i>	teneral	July	275.46	144.45	107.60	527.51
	adult	July	104.00	347.19		558.79
<i>C. hortensis</i>	teneral	July	154.50	229.61	85.83	469.94
	adult	July	31.90	417.28		535.01
<i>C. nemoralis</i>	teneral	Aug.-Sept.	135.95	117.65	77.46	331.06
	adult	June	35.92	244.10		357.48
<i>Pterostichus niger</i>	teneral	July	80.89	113.55	48.15	242.59
	adult	July	12.14	163.54		223.83

weight and distance units alone (this amount should be constant, provided that the locomotory abilities of the animals involved as well as features of the substratum they move on or in are the same), but mainly the dependence on the maximum rate of biomass production of the stage. Consequently, the highest of the index values found should be considered as the closest to the real ones. The mean of the highest values of the index — obtained for teneral beetles, and equal to $9.59 \text{ mg} \cdot \text{g}^{-1} \cdot \text{m}^{-1}$, i.e., $230 \text{ J} \cdot \text{g}^{-1} \cdot \text{m}^{-1}$ — is, therefore, accepted as a measure of the energy expended per weight and distance units.

DEB values of teneral and adult imagines of five carabid species (*Carabus arcensis*, *C. glabratus*, *C. hortensis*, *C. nemoralis*, *Pterostichus niger*) belonging to two developmental types, i.e., spring-breeders and autumn-breeders, are shown in Table III. Thus, for each of the species two estimates of DEB were available for the individuals of different body weight: dry body weight of the teneral beetle ranged from 27% to 48% of the adult beetle dry body weight, depending on the species.

Two assumptions were made: (a) DEB of an individual equals zero when its body weight equals zero, and (b) the curve describing the dependence of DEB on the dry body weight of an individual is of an asymptotic type, i.e., generated by the function $y = a - b(c^x)$.

The function type is indicated by the following: (a) a DEB value of the teneral beetle very close to that of the adult beetle (Table III), and (b) a relatively high RMR per weight unit of the larva (as compared with that of the adult beetle), as well as a relatively high rate of biomass production of the larva.

The rate of biomass production of the larva of *C. nemoralis*, for instance, can be calculated as follows: the dry body weight of the 1st instar and that of the 3rd instar are equal to 3.5 mg and 29.5 mg, respectively, and the development time is about 40 days (all data after Grüm 1975b). Hence, the rate of biomass production is approximately equal to $(29.5 - 3.5) \cdot (3.5 \cdot 40)^{-1}$, that is, $0.737 \text{ mg} \cdot \text{mg}^{-1} \cdot \text{day}^{-1}$, or $737 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. The latter figure is much higher than $119.2 \text{ mg} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ found for the teneral beetle of this species (Grüm 1978). In addition, a high rate of biomass production necessitates a relatively high mobility connected with the searching for food (Grüm 1978), and as a consequence, it causes a relatively high WMR. In general, it seems that DEB value of the larva is not much lower than that of the teneral or adult beetle, and this justifies the above assumption on the function type.

The curves describing DEB changes accompanying the body weight increase of individuals were drawn separately for each of the species listed in Table III. For each curve the correlation coefficient was higher than 0.99 (Fig. 2). The curves relate to active individuals (productive and mobile), and can, therefore, be exclusively used for an approximate estimation of DEB values of the active stages of the life-cycle, i.e., larvae, teneral beetles and adult, reproducing ones.

Apart from that, the relation between the DEB value of adult individuals of different species, and the body weight of these adults — assuming an asymptotic pattern of the relation — has been described (Fig. 3):

$$y = 1130.5 - 1130.5(0.997332^{W_a}) \quad (1)$$

where: y — daily energy budget of the adult individual (DEB_a) in $\text{J} \cdot \text{ind.}^{-1}$, W_a — dry body weight (mg) of the adult beetle.

Also, the regression was calculated of the c coefficients in the asymptotic regression equations, expressing DEB changes over the life-cycle, on the body weight of the adult beetles of different species (Fig. 4):

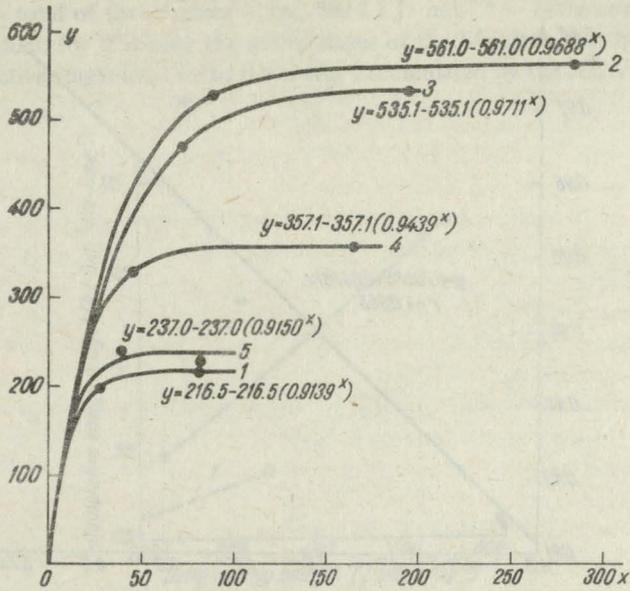


Fig. 2. Regression of DEB on body weight of the individual in its life-cycle
 y – Joules per individual per day, x – mg d. wt
 For explanation of 1–5 see Figure 8

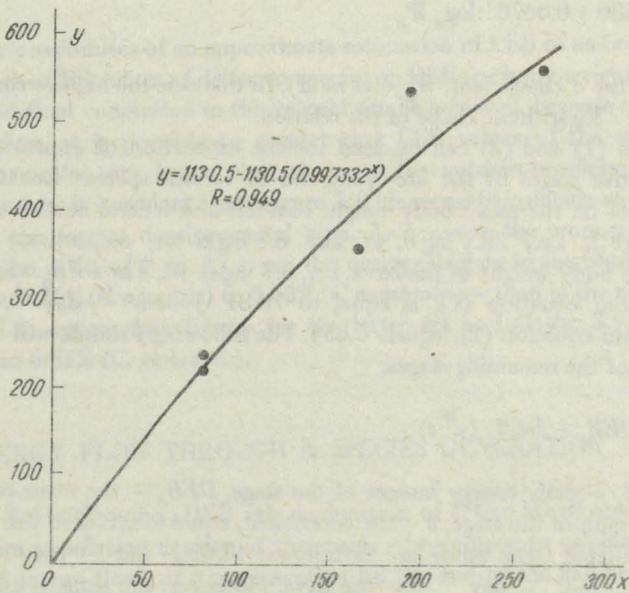


Fig. 3. Regression of DEB on body weight of the adult beetle of different species
 y – Joules per individual per day, x – mg d. wt

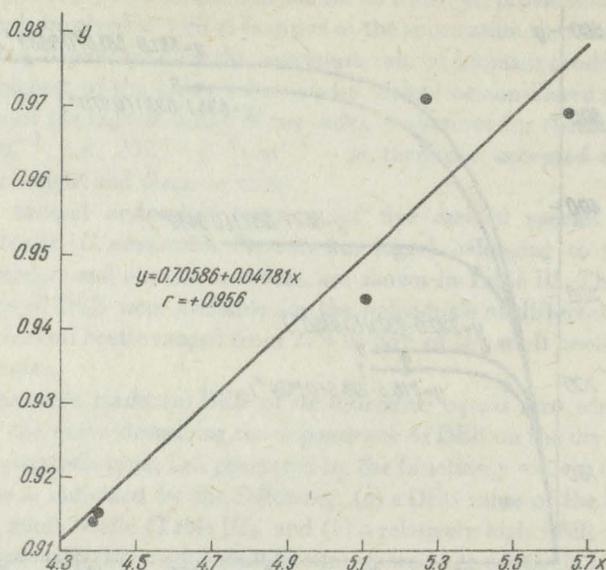


Fig. 4: Regression of the c coefficient on body weight of the adult beetle of different species
 y – value of the coefficient, x – \log_e mg d. wt

$$y = 0.70586 + 0.04781 \log_e W_a \quad (2)$$

where: y – the c coefficient, W_a – as in (1). In this case the highest correlation coefficient was obtained for a logarithmic shape of the relation.

Equations (1) and (2) can be used for the estimation of approximate values of DEB of different active stages of the life-cycle, and of various species. Let us take, for instance, the available data on the mean body weight of adult and teneral beetles of *Pterostichus oblongopunctatus* (F.), i.e., 22.1 mg d. wt and 8.8 mg d. wt, respectively (Grüm 1973c), and approximate body weight of the larva, i.e., 3.7 mg d. wt. The DEB_a , that is, of the adult beetle, obtained from equation (1), is equal to $70.81 \text{ J} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$, and the c coefficient, obtained from equation (2), equals 0.854. The following formula will enable us to estimate the DEB values of the remaining stages:

$$DEB_s = DEB_a - DEB_a (c^W_s)$$

where: DEB_s – daily energy budget of the stage, DEB_a – the same of the adult beetle, W_s – dry body weight of the stage, c – the coefficient, equal to 0.854 in this case.

The calculated DEB values are as follows: $48.65 \text{ J} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$ for the teneral beetle, and $28.68 \text{ J} \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$ for the larva. Moreover, the time of active life of the stages – recalculated from the data given by Grüm (1975a) – approximately equal to 36, 18 and 62 days for the larva, the teneral beetle and the adult beetle in the 1st breeding season, respectively – allows one to calculate the cumulative energy budget (CEB) of these stages:

1032.5 J · ind.⁻¹ for the larva 875.8 J · ind.⁻¹ for the teneral beetle, and 4005.7 J · ind.⁻¹ for the adult beetle. The total of these values — i.e., 5914.1 J · ind.⁻¹ — is the cumulative energy budget of the individual, for it is only the active stages of the life-cycle that assimilate, while the remaining, non-active stages live due to the energy accumulated by the active ones.

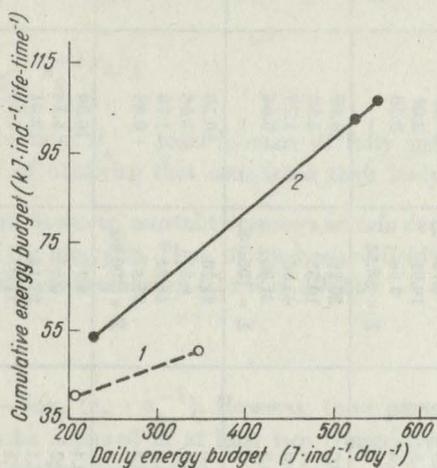


Fig. 5. Relation between cumulative energy budget of the individual and daily energy budget of the adult beetle

1 — spring breeders, 2 — autumn breeders

There are also other possibilities of an approximate estimation of CEB of an individual, namely by the regression of the CEB values of different species on DEB (or body weight) of the adult individual. However, no final conclusion in this respect can be achieved, because of the scarcity of the data. Nevertheless, it is possible to suggest that CEB values of the spring-breeders (*C. arcensis* and *C. nemoralis*) are lower than those of the autumn-breeders (*C. glabratus*, *C. hortensis* and *P. niger*), as it is evident from Figure 5. This seems to coincide with the shorter larval development of the former developmental type. As a result, the proportion of energy used for production (the ratio of P to A) is on the average higher in the representatives of spring-breeders — from 5.26% (*C. arcensis*) to 8.58% (*C. nemoralis*) — than in the representatives of autumn-breeders. The appropriate figures for the latter are as follows: 3.92% (*P. niger*), 4.83% (*C. hortensis*) and 6.81% (*C. glabratus*).

3. ENERGY FLOW THROUGH A SPECIES GENERATION

The data shown in Table IV — i.e., DEB values, duration of active life of separate stages of the life-cycle, and mean population density of the stages — were used to calculate the assimilation (the measure of energy flow) of one generation till the end of the 2nd breeding season. Such a method for calculating the energy flow is based on a troublesome field estimation of population densities of separate stages. Hence, simpler methods of energy flow calculation are worthy of consideration.

Table IV. Calculated assimilation per generation

Species	Stage	Stage duration (days)	Body weight (mg d. wt)	DEB ($J \cdot \text{ind.}^{-1} \cdot \text{day}^{-1}$)	CEB ($\text{kJ} \cdot \text{ind.}^{-1}$)	Mean density* ($\text{ind.} \cdot 100 \text{ m}^{-2}$)	Assimilation of the stage ($\text{kJ} \cdot 100 \text{ m}^{-2}$)
<i>Carabus arcensis</i>	larvae	37	10.5	132.3	4.89	33.41	163.37
	teneral beetles	19	27.9	198.9	3.78	11.13	42.07
	adults, 1st breeding season	92	80.7	216.5	19.91	3.01	59.93
	adults, 2nd breeding season	46	80.7	216.5	9.96	0.20	1.99
	—	—	—	—	$\Sigma = 38.54$	—	$\Sigma = 267.36$
<i>C. glabratus</i>	larvae	105	21.6	278.0	29.19	16.59	484.26
	teneral beetles	20	88.9	527.6	10.55	3.60	37.98
	adults, 1st breeding season	78	285.2	559.0	43.60	1.79	78.04
	adults, 2nd breeding season	39	285.2	559.0	21.80	0.64	13.95
	—	—	—	—	$\Sigma = 105.14$	—	$\Sigma = 614.23$
<i>C. hortensis</i>	larvae	105	16.1	201.0	21.10	10.10	213.11
	teneral beetles	20	71.5	469.4	9.39	3.65	34.27
	adults, 1st breeding season	88	194.2	533.4	46.94	1.78	83.35
	adults, 2nd breeding season	44	194.2	533.4	23.47	0.44	10.33
	—	—	—	—	$\Sigma = 100.90$	—	$\Sigma = 341.26$
<i>C. nemoralis</i>	larvae	40	16.5	219.4	8.77	10.89	95.50
	teneral beetles	20	45.4	331.2	6.62	5.14	34.03
	adults, 1st breeding season	62	166.0	357.1	22.14	2.41	53.36
	adults, 2nd breeding season	31	166.0	357.1	11.07	0.09	1.00
	—	—	—	—	$\Sigma = 48.60$	—	$\Sigma = 183.89$
<i>Pterostichus niger</i>	larvae	105	13.6	166.2	17.45	80.30	1401.23
	teneral beetles	19	39.1	229.4	4.36	8.50	37.06
	adults, 1st breeding season	86	81.7	237.0	20.38	4.00	81.52
	adults, 2nd breeding season	43	81.7	237.0	10.18	1.10	11.20
	—	—	—	—	$\Sigma = 52.37$	—	$\Sigma = 1531.01$

*After Grüm (1975a).

Of such simplified solutions, the methods for estimating the biomass production of carabids (G r ü m 1975b, 1976a) are going to be followed as an example. In an earlier paper (G r ü m 1975b) the basis of calculations was the axiom that when there is no mortality until the completion of body weight increase of an individual, biomass production due to the growth is equal to the sum of body weight of all the fully grown individuals. Thus:

$$P \cdot B_a^{-1} = 1, \text{ when } n_{\mathcal{E}} \cdot n_a^{-1} = 1$$

where: P – biomass production, B_a – total biomass of fully grown beetles, $n_{\mathcal{E}}$ – number of eggs laid, n_a – number of offspring that completed their body growth.

In free-living populations, however, mortality causes a certain decrease in population density of the consecutive stages of the life-cycle. Thus, on the basis of field data a relation between the above-mentioned ratios has been established (G r ü m 1975b):

$$y = 0.93 + 0.41 x$$

where: $y = P \cdot B_a^{-1}$, $x = \log_e (n_{\mathcal{E}} \cdot n_a^{-1})$. However, three parameters have to be estimated in the field, and this can be achieved in at least two consecutive years of study ($n_{\mathcal{E}}$ in the 1st, and both n_a and W_a in the 2nd year).

A further simplification is due to the assumption of balanced natality and mortality in stable populations. Hence, instead of the ratio of $n_{\mathcal{E}}$ to n_a one can apply a measure of fertility (F), that is the number of eggs produced by the female per breeding season. The regression of $P \cdot B_a^{-1}$ on F is expressed by the equation (G r ü m 1976a):

$$y = -0.15 + 0.58 x$$

where: $y = P \cdot B_a^{-1}$, $x = \log_e F$. In this case, the study period can be as short as one breeding season or – when F is assumed constant – it can be even shortened to several days necessary to estimate n_a and W_a .

Similarly:

$$A \cdot (CEB \cdot n_a)^{-1} = 1, \text{ when } n_{\mathcal{E}} \cdot n_a^{-1} = 1$$

where: A – energy flow through population, CEB – cumulative energy budget of the individual, $n_{\mathcal{E}}$ – number of eggs laid, n_a – number of offspring that survived until maximum age.

Because of the troublesome estimation of $n_{\mathcal{E}}$ and CEB , it is often desirable to use the F and DEB_a estimates instead. Therefore, relations between the ratio of A to $DEB_a \cdot n_a$ and F were studied on the basis of the data shown in Table IV, and those on female fertility taken from a paper by G r ü m (1976a).

The appropriate regression is as follows (Fig. 6):

$$y = -4.72 + 17.94 x, r = +0.992$$

where: $y = A \cdot (DEB_a \cdot n_a)^{-1}$, $x = F$, n_a – estimated in the middle of the 1st breeding season.

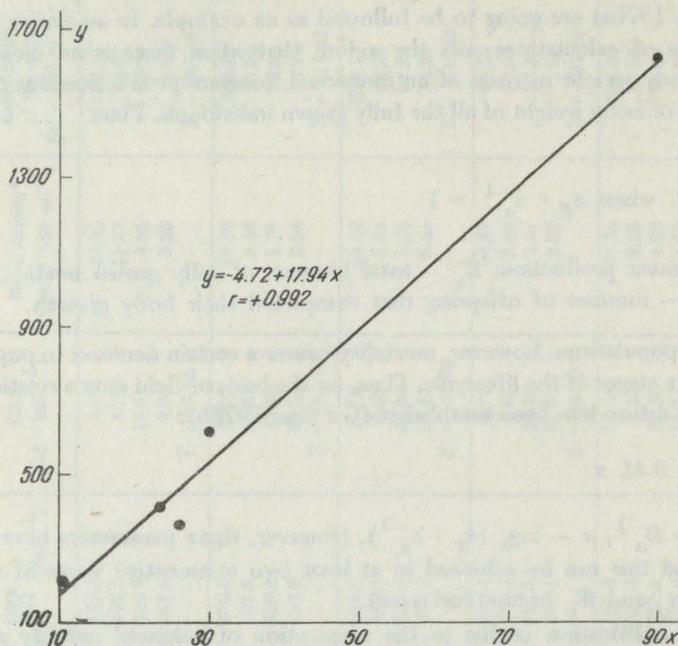


Fig. 6. Regression of the ratio of population assimilation to the product of DEB_a and population density of adult beetles on the fertility of females
 y – ratio of A to $DEB_a \cdot n_a$, x – number of eggs produced by the female in the breeding season

The values of energy flow obtained for the species under study (Table IV) cannot be directly compared with others known from the literature, because different population densities, different species and habitats have to be taken into account. Thus, a critical review of the results obtained is only possible if one compares certain features of energy flow, such as the ratio of P to A . For this purpose, the ratios were calculated for all the *Carabus* species studied. Biomass production of these species, as estimated by Grüm (1975b) in mg per 100 m² per year, was recalculated and expressed in Joules per hectare per year: *C. arcensis* 37.93 kJ · ha⁻¹ · yr⁻¹, *C. glabratus* 39.99 kJ · ha⁻¹ · yr⁻¹, *C. hortensis* 22.96 kJ · ha⁻¹ · yr⁻¹ and *C. nemoralis* 26.23 kJ · ha⁻¹ · yr⁻¹. The respective percentages of biomass production in the assimilation are as follows: *C. arcensis* – 14.2%, *C. glabratus* – 6.5%, *C. hortensis* – 6.7%, *C. nemoralis* – 14.2%.

4. SOME FACTORS AFFECTING THE WORKING METABOLISM RATE

The dependence of the resting metabolism rate on certain properties of an individual (e.g., body weight), or its environment (temperature, for instance) is well evidenced and commonly known. Far less is known about WMR in this respect. The impact of body weight on WMR is undisputable. On the other hand, it seems unlikely that WMR is dependent on the temperature of the environment alone, for there is good evidence that above a certain threshold value, a

correlation between temperature and mobility does not exist in carabids (G r ü m 1959). On the factors stimulating mobility, and thus WMR, hunger seems to play a significant role in carabids (G r ü m 1966, 1971, 1978).

The set of data shown in Table IV makes it possible to draw approximate curves of the WMR changes that accompany the increase in body weight of the individuals. Let us take the following assumptions into account: (a) WMR equals zero when body weight equals zero, and (b) $WMR \leq DEB$. Under such conditions the highest correlation coefficients ($R > 0.99$) between the empiric and theoretical values of WMR were obtained for asymptotic regression curves (Fig. 7). The shape of the curves (Fig. 7) appears different from those describing DEB changes (Fig. 2) — see also the c coefficients. Attention is drawn by the particularly high WMR of *C. hortensis* (Fig. 7). A casual inspection of Figure 7 suggests a necessity of analysing the relations between the WMR and DEB curves. These relations are shown in Figure 8: the lower left parts of the curves concern the fully grown adult beetles, and the lower the body weight of the individual the further to the right hand it is in the curve. These curves illustrate the idea that the lower the body weight of an individual the lower the percentage of energy expended for mobility. However, the lower the body weight the higher the WMR value per weight unit.

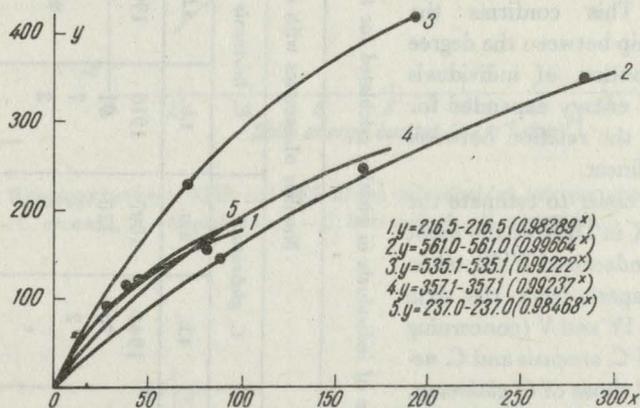


Fig. 7. Regression of WMR on body weight of the individual in its life-cycle

y — Joules per individual per day, x — mg d. wt

For explanation of 1–5 see Figure 8

Special attention should be given to the different “level” of each species curve (Fig. 8): the highest for *C. hortensis*, a little lower for *C. arcensis* and *P. niger*, much lower for *C. nemoralis*, and the lowest for *C. glabratus*. Generally speaking, this coincides with the mean (for teneral and adult beetles) mobility of the species involved: *C. hortensis* $11.13 \text{ m} \cdot \text{day}^{-1}$, *C. arcensis* $10.71 \text{ m} \cdot \text{day}^{-1}$, *P. niger* $10.19 \text{ m} \cdot \text{day}^{-1}$, *C. nemoralis* $8.44 \text{ m} \cdot \text{day}^{-1}$, and *C. glabratus* $5.90 \text{ m} \cdot \text{day}^{-1}$.

According to previous suggestions, carabid mobility is stimulated directly by hunger, but indirectly by difficulties of finding food in a space limited by microclimatic conditions (G r ü m 1971). Carabids — like other litter-dwelling organisms — are distributed in a clumped manner, and especially high values of clumped distribution index can be found for very small sections of their population areas (G r ü m 1973a, 1978). If so, clumped spatial distribution should correlate with mobility and WMR.

For each of the species studied the data on the distribution of individuals in pitfalls were obtained (Table V). The sample unit (core) was one pitfall-day, and the sample size was 2016 such sample units. The measure of spatial distribution was the \dot{m} to m index (Lloyd 1967).

To standardize the WMR values of different species, the WMR values per weight unit were calculated for the individual of 0.001 mg d. wt. The results were plotted against the spatial distribution index obtained for adult beetles (Fig. 9). The relation is expressed by an asymptotic curve equation, with $R = 0.991$ (to simplify the calculations the x axis was rescaled: $x \neq \dot{m} \cdot m^{-1}$, but $x = (\dot{m} \cdot m^{-1}) - 2$). This confirms the suggested relationship between the degree of clumped distribution of individuals and the amount of energy expended for mobility; however, the relation between the variables is not linear.

In practice, it is easier to estimate the proportion of WMR in DEB of the adult beetle, than the standardized WMR value. For this reason, apart from the data presented in Tables IV and V (concerning the adult beetles of *C. arcensis* and *C. nemoralis* in June, and those of *C. glabratus*, *C. hortensis* and *P. niger* in July) additional data on WMR proportion in DEB and spatial distribution of *C. glabratus*, *C. hortensis*, *P. niger* and *Pterostichus vulgaris* (L.) were included (Tables VI, -VII). This way 12 simultaneous estimates of both variables were obtained, and the appropriate regression calculated (Fig. 10):

$$y = 2.8 + 50.95 (0.315^x), R = 0.759$$

where: y is $\dot{m} \cdot m^{-1}$, $x = (85 - \text{WMR}\% \text{ in DEB}) \cdot 5^{-1}$.

The relations shown in Figures 9 and 10 are in accordance: the higher the degree of clumped distribution, the

Table V. Index of spatial distribution of individuals in pitfalls, calculated for teneral (t.b.) and adult (a.b.) beetles

Number of individuals in sample (i)	Number of samples with i individuals											
	<i>Carabus arcensis</i>		<i>C. glabratus</i>		<i>C. hortensis</i>		<i>C. nemoralis</i>		<i>Pterostichus niger</i>			
	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.
0	1969	1813	1944	1897	1916	1998	1986	1919	1746	1925		
1	46	168	70	110	91	16	30	88	231	81		
2	1	26	2	7	7	2		8	35	7		
3		4		2	2			1	4	3		
4		3										
5		1										
6		1										
$\dot{m} \cdot m^{-1}$	1.75	5.02	1.47	3.10	4.26	20.20	-	3.87	1.73	5.97		

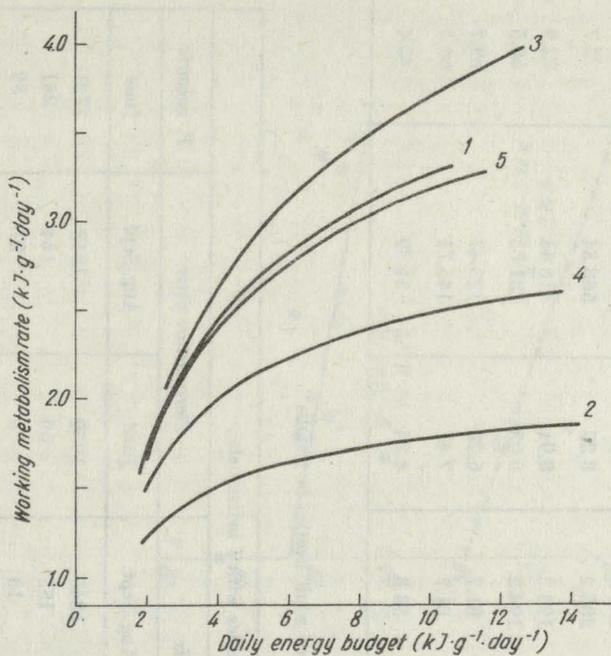


Fig. 8. Relations between WMR and DEB of the individual (cf. interpretation in the text)
 1 - *C. arcensis*, 2 - *C. glabratus*, 3 - *C. hortensis*, 4 - *C. nemoralis*, 5 - *P. niger*

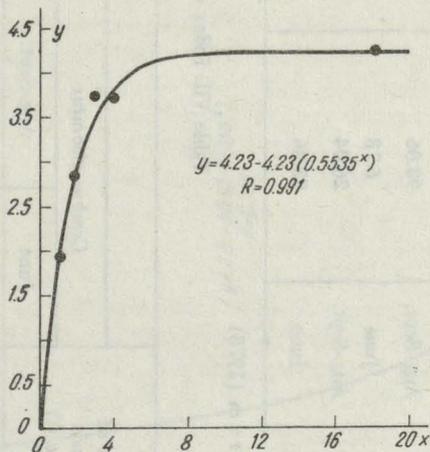


Fig. 9. Regression of the standardized WMR value on the spatial distribution index of adult beetles
 y - kJoules per g d. wt per day, x - ($\dot{m} \cdot m^{-1}$) - 2

Table VI. WMR percentage in DEB of an adult beetle in different months

Species	Month	P^* (J · ind. ⁻¹ · day ⁻¹)	RMR* (J · ind. ⁻¹ · day ⁻¹)	Weight* (mg d. wt)	Mobility* (m · day ⁻¹)	WMR (J · ind. ⁻¹ · day ⁻¹)	Per cent of WMR in DEB
<i>Carabus glabratus</i>	June	42.29	107.60	285.2	5.15	353.47	70.2
	Aug.-Sept.	106.01	107.60	285.2	8.28	568.34	72.7
<i>C. hortensis</i>	June	0.00	85.83	194.2	8.91	416.44	82.9
	Aug.-Sept.	98.06	85.83	194.2	6.03	281.83	60.5
<i>Pterostichus niger</i>	June	6.78	48.15	81.7	6.28	123.47	69.2
	Aug.-Sept.	26.04	48.15	81.7	7.41	145.71	66.3
<i>P. vulgaris</i>	June	23.36	35.17	53.8	4.24	54.89	48.4

*After Grüm (1978).

Table VII. Index of spatial distribution of adult beetles in pitfalls

Number of individuals in sample (<i>i</i>)	Number of samples with <i>i</i> individuals						
	<i>Carabus glabratus</i>		<i>C. hortensis</i>		<i>Pterostichus niger</i>		<i>P. vulgaris</i>
	June	Aug.-Sept.	June	Aug.-Sept.	June	Aug.-Sept.	June
0	1965	1990	1999	1845	1950	1843	1721
1	48	24	15	155	60	144	241
2	3	2	2	13	6	27	39
3				3		1	9
4						1	5
5							
6							1
$\bar{m} \cdot m^{-1}$	4.14	10.73	22.39	2.46	4.67	3.46	3.23

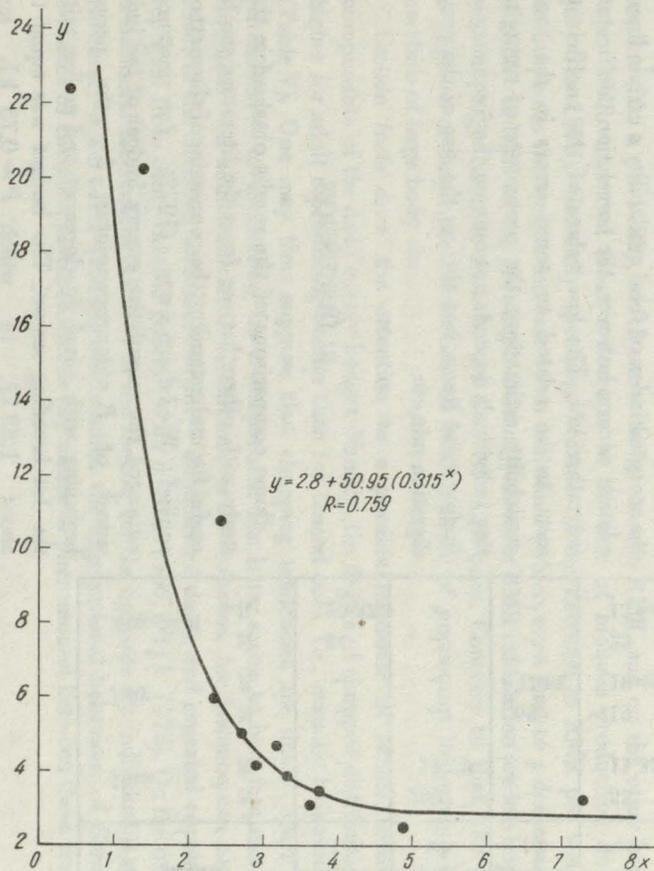


Fig. 10. Regression of spatial distribution index on a derivative of WMR proportion in DEB of the adult beetle
 $y - \dot{m} \cdot m^{-1}$, $x - (85 - \text{WMR}\% \text{ in DEB}) \cdot 5^{-1}$

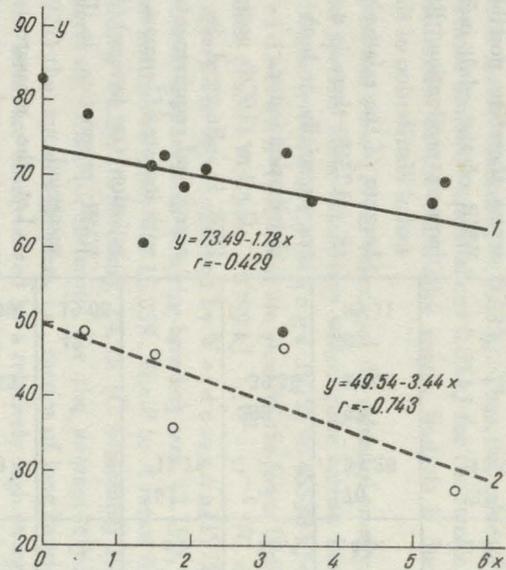


Fig. 11. Regression of WMR percentage in DEB on an index of food availability
 $y - \text{WMR}\%$, $x - \text{availability index}$, 1 - adult beetles, 2 - teneral beetles

Table VIII. Percentage of regurgitating individuals
 N — number of individuals tested, R — percentage of regurgitating individuals, t.b. — teneral beetles, a.b. — adult beetles

Month	<i>Carabus arcensis</i>		<i>C. glabratus</i>		<i>C. hortensis</i>		<i>C. nemoralis</i>		<i>Pterostichus niger</i>		<i>P. vulgaris</i>
	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	t.b.	a.b.	a.b.
June	N	299	—	53	—	18	—	102	—	70	331
	R	11.79	—	11.32	—	0.0	—	11.76	—	34.28	13.90
July	N	—	69	119	106	18	—	—	288	98	—
	R	—	—	37.68	18.49	7.55	5.55	—	39.58	27.55	—
Aug.-Sept.	N	54	—	22	—	183	42	—	—	202	—
	R	20.37	—	13.64	—	8.20	19.05	—	—	39.11	—

higher the WMR proportion in DEB. On the other hand, the variability of such non-standardized values of WMR is rather high, because of the different individual body weight of the species involved. It seems, therefore, possible to improve the estimates of WMR of the adult individual on the basis of daily biomass production, RMR data and the index of spatial distribution of the beetles in pitfalls. However, because of the relatively low correlation coefficient ($R = 0.759$), there is a certain risk of erratic estimates, especially at both low and high values of the distribution index.

Grüm (1978) noticed that WMR proportion in DEB is influenced by the possibility of satisfying energetical requirements of an individual, connected with its rate of biomass production, and expressed by satiation (or hunger). Hence, a certain relation of WMR proportion in DEB to food availability is suspected.

Let the measure of food availability be the percentage of regurgitating (that is, satiated) individuals (Table VIII) divided by mobility: the possibility of satiation depends on — apart from density and mobility of food items — the mobility of the beetle searching for prey. As can be seen from Figure 11, between the WMR proportion in DEB and the accepted index of food availability a certain linear relation occurs; however, the correlation coefficients are rather low. The low values of the coefficients seem to be related to some errors in the food availability estimation: the percentage of regurgitating individuals depends not only on the frequency of finding food items, but also on the size of the prey, digestion rate, etc.

5. DISCUSSION

Some comparisons of the results obtained in this study with others known from the literature can be useful for understanding the properties of the method applied. Weidemann (1972), for instance, estimated the cumulative energy budget of the individual of *P. oblongopunctatus*, for the period beginning with larval development and ending with the 1st breeding season. The budget was equal to about 1.59 kJ, in which $P \approx 0.75$ kJ, and

$P_g \approx 0.59$ kJ. According to the methods presented in this paper, the budget of the individual of the same species and in the same period should amount to over 5.86 kJ. Values of P and P_g — based on the data published earlier (Grüm 1973b, 1973c) — would be as follows: $\beta_r = 45.6$ eggs times 0.293 mg d. wt of the egg biomass times 24 J per 1 mg d. wt ≈ 0.32 kJ. $P_g = 22.1$ mg d. wt of the adult beetle times 24 J ≈ 0.53 kJ. Thus, the value of biomass production of the individual (exuviae omitted) equals about 0.85 kJ for the female. It is evident from the above, that the difference in the cumulative energy budgets is due to different estimates of respiration.

Manga (1972) and Weidemann (1972) calculated the values of energy flow through populations of a few carabid species. Their values vary within quite narrow limits, i.e., from 33651 kJ · ha⁻¹ · yr⁻¹ for *Nebria brevicollis* (F.) (Manga 1972) to 45538 kJ · ha⁻¹ · yr⁻¹ for *P. oblongopunctatus* (Weidemann 1972), and are close to the lower limit of the range found in the present studies (Table IV): from 18389 kJ · ha⁻¹ · yr⁻¹ (*C. nemoralis*) to 153101 kJ · ha⁻¹ · yr⁻¹ (*P. niger*). The figure obtained by Weidemann (1972) for the P to A ratio in his studies on *P. oblongopunctatus* (a spring-breeder) was 43.15%, and that for *Pterostichus metallicus* F. (an autumn-breeder) was 15.25%. The P to A ratios for the species under this study are as follows: 14.2% (*C. arcensis*), 14.2% (*C. nemoralis*) for the spring-breeders, and 6.5% (*C. glabratus*), 6.7% (*C. hortensis*) for the autumn-breeders. A thesis propagated by Thiele (1977) that autumn-breeders, i.e., species of long larval development with winter hibernation of the larva, are characterized by a relatively high energy loss is thus confirmed. The results obtained by Manga (1972) for *N. brevicollis* (an autumn-breeder) seem to be in contradiction to the above, because the P to A ratio was equal to 48.42%. It can be concluded that there still exist different P to A ratios due to different methods of respiration measurement, though certain regularities can be stated.

One may put in doubt the reality of the above-presented results based on various principles of respiration measurement: average daily respiration rate in constant laboratory thermic regime (Manga 1972), which seems to be close to RMR, and on the other hand, RMR and also WMR estimated from a decrease in the rate of biomass production due to mobility (Grüm 1978). Generally speaking, because of the decrease in RMR per weight unit that accompanies the weight increase of an individual (which must lead to a decreasing proportion of RMR in DEB of the growing individual), errors in RMR calculation are less important in the case of large carabids than in the case of small ones. Contrary to that, the errors due to negligence or improper calculation of WMR can be of paramount importance in the case of carabids of large body size.

Certain facts draw the attention to a possible influence of sexual behaviour on the components of the daily energy budget. Namely, the degree of clumped distribution was always higher for adult reproducing beetles than for teneral ones, i.e., sexually immature or maturing (Table V). One may thus suppose that clumping tendencies are due — apart from habitat patchiness — to the seeking for a sex partner. The latter seems to be a frequent behaviour in carabids. An adult individual of *Carabus*, or *Pterostichus*, for instance, can copulate several times in the breeding season (L. Grüm — unpublished data), and repeated copulation was also reported from other carabid genera (Murdock 1966, Dijk 1973). On the other hand, the behavioural mechanism involved in the seeking for the opposite sex individual is still unknown. However, Wautier (1971), who studied the aggregational behaviour of *Brachinus*, found evidence of chemical communication (by means of pheromones) between these beetles.

6. SUMMARY

Daily energy budget (DEB) – consisting of P (biomass production), RMR (resting metabolism rate) and WMR (working metabolism rate) – was calculated for teneral and adult beetles of five forest carabid species (*Carabus arcensis*, *C. glabratus*, *C. hortensis*, *C. nemoralis* and *Pterostichus niger*) (Table III).

On the basis of the budgets, a set of 3 regression equations was developed to estimate the approximate value of DEB of an individual. The equations allow one to estimate the approximate value of DEB of different active stages of the life-cycle of different species. The value of the daily energy budget of an adult (DEB_a) expressed in Joules can be calculated from the formula (Fig. 3):

$$DEB_a = 1130.5 - 1130.5 (0.997332 W_a)$$

where: W_a – dry body weight of an adult beetle in mg.

An approximate value of daily energy budget of any other active stage of the life-cycle (DEB_s) can be obtained from the formula:

$$DEB_s = DEB_a - DEB_a \left(c \frac{W_s}{W_a} \right)$$

where: $c = 0.70586 + 0.04781 \log_e W_a$, W_s – individual dry body weight of the given stage in mg.

The estimates of energy flow (A) through the populations of five species (Table IV) were related to the DEB of the adult individual, population density of adult individuals (n_a), and to the number of eggs produced by the female in the breeding season (F) (Fig. 6). The relation expressed by the following regression equation makes possible a rough calculation of energy flow on the basis of three parameters estimated under field conditions:

$$y = -4.72 + 17.94 x, r = +0.992$$

where: $y = A \cdot (DEB_a \cdot n_a)^{-1}$, $x = F$.

A regression of WMR proportion in DEB of the adult beetle on an index of spatial distribution of the beetles (Fig. 10) is suggested as a simplified method for the estimation of WMR in the field.

7. POLISH SUMMARY

Określono dobowy budżet energetyczny (DEB) – na który składała się produkcja biomasy (P), metabolizm spoczynkowy (RMR) oraz energia zużywana na ruchliwość (WMR) – juwenilnego i w pełni wyrośniętego imago 5 leśnych gatunków z rodziny *Carabidae* (*Carabus arcensis*, *C. glabratus*, *C. hortensis*, *C. nemoralis* i *Pterostichus niger*) (tab. III).

Wartości budżetu energetycznego imagines stanowiły empiryczną podstawę do skonstruowania 3 równań regresji, za pomocą których można określić przybliżoną wartość dobowego budżetu energetycznego aktywnych osobników różnych gatunków znajdujących się w różnym stadium cyklu rozwojowego. Przybliżoną wartość dobowego budżetu energetycznego w pełni wyrośniętego imago (DEB_a) – wyrażoną w dżulach – można oszacować z równania (rys. 3):

$$DEB_a = 1130,5 - 1130,5 (0,997332 W_a)$$

gdzie: W_a – ciężar ciała imago podany w mg suchej masy.

Przybliżoną wartość dobowego budżetu energetycznego każdego innego aktywnego stadium rozwojowego (DEB_s) można otrzymać z równania:

$$DEB_s = DEB_a - DEB_a \left(c \frac{W_s}{W_a} \right)$$

gdzie: $c = 0,70586 + 0,04781 \log_e W_a$, W_s – ciężar ciała danego stadium podany w mg suchej masy.

Oceny przepływu energii (A) przez populacje 5 gatunków *Carabidae* (tab. IV) zostały odniesione do dobowego budżetu energetycznego w pełni wyrosniętego imago (DEB_a), gęstości populacji tych imagines (n_a) oraz liczby jaj składanych przez samicę podczas sezonu rozrodczego (F) (rys. 6). Odpowiednie, oparte na powyższych parametrach, równanie regresji pozwala szacunkowo określić przepływ energii przez populację od chwili złożenia jaj aż do zakończenia drugiego sezonu rozrodczego imagines:

$$y = -4,72 + 17,94 x, \quad r = +0,992$$

$$\text{gdzie: } y = A \cdot (DEB_a \cdot n_a)^{-1}, \quad x = F.$$

Przedstawiono także krzywą regresji udziału strat energii na ruchliwość w dobowym budżecie energetycznym osobnika względem wskaźnika rozmieszczenia przestrzennego złowień imagines (rys. 10). Może ona być zastosowana jako możliwie prosta metoda szacowania strat energii związanych z ruchliwością osobnika.

8. REFERENCES

1. Dijk T. S. van, 1973 – The age-composition of populations of *Calathus melanocephalus* L. analysed by studying marked individuals kept within fenced sites – *Oecologia* (Berl.), 12: 213–240.
2. Grüm L. 1959 – Seasonal changes of activity of the Carabidae – *Ekol. pol.* A, 7: 255–268.
3. Grüm L. 1966 – Diurnal activity rhythm of starved Carabidae – *Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol.* 14: 405–411.
4. Grüm L. 1971 – Spatial differentiation of the *Carabus* L. (Carabidae, Coleoptera) mobility – *Ekol. pol.* 19: 1–34.
5. Grüm L. 1973a – Patterns of *Carabus arcensis* Hbst. distribution within different habitats – *Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol.* 21: 229–233.
6. Grüm L. 1973b – Egg production of some Carabidae species – *Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol.* 21: 261–268.
7. Grüm L. 1973c – Weight increase of newly hatched carabid-beetles – *Bull. Acad. pol. Sci. Cl. II. Sér. Sci. biol.* 21: 499–503.
8. Grüm L. 1975a – Mortality patterns in carabid populations – *Ekol. pol.* 23: 649–665.
9. Grüm L. 1975b – An attempt to estimate production of a few *Carabus* L. species (Col., Carabidae) – *Ekol. pol.* 23: 673–680.
10. Grüm L. 1976a – Biomass production of carabid-beetles in a few forest habitats – *Ekol. pol.* 24: 37–56.
11. Grüm L. 1976b – An attempt to characterize matter transfer by carabid communities inhabiting forests – *Ekol. pol.* 24: 365–375.
12. Grüm L. 1978 – Mechanisms governing rate and direction of energy flow through carabid populations – *Pol. ecol. Stud.* 4(2): 129–175.
13. Lloyd M. 1967 – “Mean crowding” – *J. Anim. Ecol.* 36: 1–30.
14. Manga N. 1972 – Population metabolism of *Nebria brevicollis* (F.) (Coleoptera, Carabidae) – *Oecologia* (Berl.), 10: 223–242.
15. Murdoch W. W. 1966 – Population stability and life history phenomena – *Am. Nat.* 100: 5–12.
16. Thiele H.-U. 1977 – Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behaviour – Springer Verlag, Berlin–Heidelberg–New York, 369 pp.
17. Wautier V. 1971 – Un phénomène social chez les Coléoptères: le gréganisme de *Brachinus* (*Caraboidea*, *Brachinidae*) – *Insectes soc.* 18: 1–84.
18. Weidemann G. 1972 – Die Stellung epigäischer Raubarthropoden im Ökosystem Buchenwald – *Verh. dt. zool. Ges. Helgoland*, 1971: 106–116.
19. Żyromska-Rudzka H. (in press) – Metody oceny biomasy zwierząt glebowych [Methods of biomass estimation in soil animals] [In: *Metody zoologii gleby* (Methods in soil zoology), Eds. M. Górny, L. Grüm] – Państwowe Wydawnictwo Naukowe, Warszawa.