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BIOMASS PRODUCTION OF CARABID-BEETLES IN A FEW FOREST HABITATS*

ABSTRACT: Biomass production of the zoophagous *Carabidae* was estimated for associations of *Vaccinio myrtilli-Pinetum*, *Pino-Quercetum*, *Tilio-Carpinetum* and *Circaeo-Alnetum*. The production – in terms of dry weight – estimated for an association, changed in the consecutive years of the study. The yearly mean values of the production were the lowest for *Vaccinio myrtilli-Pinetum* ($0.765 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) and the highest for *Circaeo-Alnetum* ($2.010 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), and seemed to be related to the amount of nitrogen in the leaf-fall.

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1. INTRODUCTION

If the range of consumption, as well as the ecological niche and the mechanisms governing rates and directions of chemical element transfer by carabids were known, a relatively good comprehension of their rôle in ecosystems would be acquired.

*Praca wykonana w ramach problemu węzłowego nr 09.1.7 (grupa tematyczna „Produktywność ekosystemów trawiających i leśnych”).

The niche of most carabids inhabiting forests in Europe is determined to some extent by whether they dwell in or on the litter-layer (Gersdorf 1937, Röber and Schmidt 1949), and the prevalence of polyphagous predators amongst them (Lauterbach 1964, Paarmann 1966, Šarova 1970, Obrtel 1971 and others). As far as the changes in rates and directions of matter transfer are concerned, the question of functional and numerical responses to the food availability has been taken into consideration by some investigators. For instance, food shortage may cause a decrease of fertility (Murdoch 1966), as well as a change in the diurnal activity rhythm (Williams 1959, Grüm 1966) or an increase of their mobility (Grüm 1966, 1971a, 1971b). The mobility of the beetles is supposed to be responsible for their mortality (Zimka 1966, Grüm 1975a).

On the other hand, there are no data on the participation of carabids in the energy flow and matter transfer in forest ecosystems, except for comparisons of numbers of species and individuals of carabids and other groups of predatory macrofauna (Kaczmarek 1963, Zimka 1966), or rarely, comparisons of their yearly mean biomasses (Zimka 1973).

This paper is aimed at estimation of biomass production by zoophagous carabids inhabiting litter-layers of a few forest habitats. These estimates are compared with the amount of nitrogen contained in the yearly leaf-fall, i.e., with the basic source of food for the litter-dwelling saprophages.

2. STUDY AREA

The study area consisted of 5 sampling sites located in 4 plant associations: *Vaccinio myrtilli-Pinetum* (2 sampling sites designated with the symbols *VmP* and *P*), *Pino-Quercetum* (1 sampling site - *PQ*), *Tilio-Carpinetum* (1 sampling site - *TC*) and *Circaeo-Alnetum* (1 sampling site - *CA*). All of them were located in the east part of the Kampinos Forest, several kilometers north-west of Warsaw.

The *VmP* sampling site was located almost in the center of a dry area (Grüm 1971a) of several hectares covered by *Vaccinio myrtilli-Pinetum*. The *P* sampling site was located in an area of about 0.2 ha, covered by the same association but surrounded by alder woods and hence, not so dry as the former one. The *PQ* sampling site was located in the central part - relatively dry (Grüm 1971a) - of a rectangular area of about 4 ha. Along the longer sides of the rectangle a relatively wet (Grüm 1971a) *Circaeo-Alnetum* association was present with the *CA* sampling site situated there, next to an alder wood (*Carici elongatae-Alnetum*). The sampling sites *PQ* and *CA* were about 30 meters distant from each other. Within the alder wood, with the water table visible throughout the year, an islet of about 0.15 ha was present. On the islet - covered by a *Tilio-Carpinetum* - the *CA* sampling site was located.

Dr. A. Stachurski and Dr. J. R. Zimka kindly supplied their unpublished data on the organic nitrogen content in the entire leaf-fall of trees, shrubs and herb layer estimated for the following 4 sampling sites: *VmP* ($20.3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), *PQ* ($31.6 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), *TC* ($77.1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) and *CA* ($127.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) for this paper.

3. PRODUCTION IN RELATION TO FERTILITY

3.1. Methods

The methods of estimation of biomass production applied in this paper are based on the following assumptions: (a) The percentage of the egg biomass in the net production of the

generation originating from these eggs is more or less constant. For 4 species studied in this respect, the percentage of the egg biomass in the net production ranged from 8.7% to 10.8% (G r ü m 1975c). (b) The pattern of the individual body weight increase is stable: 14% to 24% of the body weight of the fully grown beetle is gained during the larval development, and the remaining percentage is gained in the first 2–3 weeks of the beetle's life (G r ü m 1973c, 1975b). (c) The distribution of mortality rates over all the stages in the life-cycle follows a stable pattern. Namely, high instantaneous mortality rates are typical for periods of intense body growth or egg production. For instance, on the assumption that the number of individuals lost in the period between egg incubation and teneral beetle appearance is equal to 100, the number of individuals which died during larval development would equal about 98 (G r ü m 1975a). The total loss from the population until the completion of the individual body growth, was found for 6 species to range from 70% to 93% of the egg numbers (G r ü m 1975a).

A relative stability of the above parameters makes it possible to estimate biomass production on the basis of the equation (G r ü m 1975c):

$$P = B_a \left(0.93 + 0.41 \log_e \frac{n_e}{n_a} \right) \quad (1)$$

where: P – biomass production of a generation, B_a – biomass of imagines at the moment of completion of their individual body growth, n_e – number of eggs deposited in the breeding season, n_a – number of imagines originating from these eggs, calculated at the moment of completion of individual body growth.

Practical application of the equation (1), however, may be difficult because of the 2 consecutive years of study, which are necessary to estimate the n_e and n_a values. From the point of view of a student taking into consideration means of shortening the field investigation period, it may be valuable to relate biomass production to one variable – i.e., B_a derived from n_a and the mean individual body weight – and one constant, namely, the mean female fertility (\bar{F}), expressed as the mean number of eggs produced by the female in the breeding season. This, in turn, limits application of this method only to stable populations, in which any long-term trends of increase or decrease in the density are not being observed, i.e., in which a balance between natality and mortality exists.

In the period from the 27th of April 1972 until the end of the breeding season in 1972 female population densities of 8 species (*Carabus arcensis* Hbst., *C. glabratus* Payk., *C. hortensis* L., *C. nemoralis* Müll., *Pterostichus anthracinus* Ill., *P. niger* Schall., *P. oblongopunctatus* F. and *P. vulgaris* L.) were estimated in consecutive fortnights, separately for the PQ, CA and TC sampling sites. At the same time, estimates of fertility of the females were made (i.e., the mean number of eggs produced by the female in each of the fortnightly periods was calculated), which made it possible to calculate the n_e value in 1972. Apart from that, population densities of the imagines originating from the eggs deposited in 1972 were estimated at the moment of completion of individual body growth.

The applied methods of population density estimation were described in separate publications (G r ü m 1971a, 1973a, 1975a), as well as the method of fertility estimation (G r ü m 1973a). The results presented in these publications will now serve to calculate biomass production of one generation for each of the above mentioned species. Then, the relationship between the biomass production and the female fertility can be calculated.

Table I. Number of eggs laid by female in consecutive fortnights of the breeding season
Data recalculated from Grüm (1973a, Table II)

Period	Species							
	<i>C. arcensis</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>C. nemoralis</i>	<i>P. anthracinus</i>	<i>P. niger</i>	<i>P. oblongopunctatus</i>	<i>P. vulgaris</i>
1-15 May	0.8			4.8	11.4		8.0	0.5
16-31 May	4.9			3.5	29.8		17.0	23.2
1-15 June	5.1	0.6		1.5	26.7		11.5	33.3
16-30 June	5.8	5.6		0.7	15.6	4.0	7.2	18.4
1-15 July	5.5	2.9		0.1	8.2	4.7	1.9	10.9
16-31 July	1.4	5.2	0.1		2.2	11.3		3.9
1-15 Aug.		5.9	2.8			24.9		0.9
16-31 Aug.		6.8	8.7			31.6		
1-15 Sept.		2.3	8.3			12.4		
16-30 Sept.		0.7	5.5			1.3		
1-15 Oct.			0.7					
Σ	23.5	30.0	26.1	10.6	93.9	90.2	45.6	91.1

Table II. Number of females per 100 m² in consecutive fortnights of the breeding season

Period	Site	Species							
		<i>C. arcensis</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>C. nemoralis</i>	<i>P. anthracinus</i>	<i>P. niger</i>	<i>P. oblongopunctatus</i>	<i>P. vulgaris</i>
1-15 May	PQ	5.0 ± 0.6			2.9 ± 1.1	2.2 ± 1.5		60.1 ± 25.8	0.4 ± 0.1
	CA	3.0 ± 0.5			2.2 ± 0.6	6.6 ± 4.6		52.2 ± 20.1	5.5 ± 1.8
	TC				0.5 ± 0.2	27.9 ± 13.6		66.3 ± 12.4	2.7 ± 0.7
16-31 May	PQ	4.5 ^a			3.3 ^a	2.4 ^a		87.7 ^a	1.1 ^a
	CA	2.7 ^a			1.3 ^a	11.0 ^a		31.8 ^a	6.6 ^a
	TC				0.5 ^a	25.5 ^a		46.5 ^a	2.6 ^a
1-15 June	PQ	4.1 ± 0.8	0.7 ± 0.1		3.8 ± 0.7	2.6 ± 1.8		115.4 ± 49.9	1.7 ± 0.2
	CA	2.3 ± 1.0	0.5 ± 0.3		0.4 ± 0.3	15.5 ± 5.5		11.5 ± 8.2	7.8 ± 1.7
	TC		0.1 ± 0.1		0.4 ± 0.2	22.9 ± 9.9		26.8 ± 11.9	2.6 ± 0.3
16-30 June	PQ	1.9 ± 0.2	3.0 ± 1.8		0.1 ± 0.1	3.0 ± 2.1	0.2 ± 0.1	6.3 ± 0.5	0.7 ± 0.3
	CA	0.4 ± 0.3	1.1 ± 0.4			37.0 ± 13.1	1.0 ± 0.4	11.8 ± 9.0	5.0 ± 3.1
	TC		0.4 ± 0.1		0.2 ± 0.1	12.5 ± 2.2		27.2 ± 16.0	3.2 ± 1.1
1-15 July	PQ	0.5 ± 0.3	2.1 ± 0.5			3.4 ± 3.2	2.3 ± 0.5	4.3 ± 3.1	0.9 ± 0.5
	CA	0.4 ± 0.2	0.5 ± 0.2			6.8 ± 4.8	2.0 ± 0.7	6.3 ± 9.1	1.2 ± 0.3
	TC		0.7 ± 0.2		0.1 ± 0.1	3.0 ± 2.8	2.7 ± 1.2	3.9 ± 3.0	2.9 ± 1.2
16-31 July	PQ	0.9 ± 0.4	2.3 ± 1.2	2.3 ± 0.2			2.0 ± 0.2		1.1 ± 0.3
	CA	0.4 ± 0.3	2.1 ± 1.2	0.2 ± 0.1			3.6 ± 1.3		1.9 ± 0.9
	TC		1.0 ± 0.4	0.5 ± 0.2		2.0 ± 1.6	2.3 ± 0.5		2.4 ± 0.9
1-15 Aug.	PQ		1.4 ^a	1.6 ^a			1.9 ^a		0.5 ^a
	CA		1.1 ^a	0.5 ^a			2.0 ^a		0.9 ^a
	TC		0.9 ^a	0.7 ^a			1.9 ^a		1.2 ^a
16-31 Aug.	PQ		0.5 ± 0.3	0.9 ± 0.5			1.8 ± 0.6		
	CA			0.8 ± 0.4			0.3 ± 0.2		
	TC		0.7 ± 0.1	0.9 ± 0.3			1.5 ± 0.7		
1-15 Sept.	PQ		0.1 ± 0.1	0.7 ± 0.1			0.3 ± 0.2		
	CA			1.1 ± 0.6			1.5 ± 0.9		
	TC		0.1 ± 0.1	0.2 ± 0.1			0.9 ± 0.5		
16-30 Sept.	PQ			0.4 ± 0.1					
	CA			0.3 ± 0.1					
	TC						0.1 ± 0.1		

^aValues obtained from linear interpolation.

Table III. Number of eggs per 100 m² laid in the 1972 breeding season

Site	Species							
	<i>C. arcensis</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>C. nemoralis</i>	<i>P. anthracinus</i>	<i>P. niger</i>	<i>P. oblongopunctatus</i>	<i>P. vulgaris</i>
PQ	62.6	47.4	20.3	31.5	240.0	144.0	3,353.0	110.0
CA	31.8	25.0	18.8	15.7	1,452.0	134.0	1,188.0	534.0
TC		20.1	11.4	4.8	1,916.0	145.0	1,833.0	249.0

Table IV. Density of the descendant populations of beetles having completed their body growth (number of beetles per 100 m²)

Site	Species and period							
	<i>C. arcensis</i> 3–11 May	<i>C. glabratus</i> 8–16 Aug.	<i>C. hortensis</i> 8–16 Aug.	<i>C. nemoralis</i> 3–11 May	<i>P. anthracinus</i> 3–11 May	<i>P. niger</i> 8–16 Aug.	<i>P. oblongopunctatus</i> 3–11 May	<i>P. vulgaris</i> 26 June–3 July
PQ	9.6 ± 2.9	4.5 ± 1.2	3.9 ± 1.4	9.4 ± 0.6	19.3 ± 9.5	2.2 ± 0.3	285.1 ± 96.5	1.8 ± 0.5
CA	7.5 ± 1.9	6.1 ± 2.6	0.6 ± 0.4	7.5 ± 2.7	23.2 ± 16.3	4.7 ± 1.9	482.7 ± 160.4	9.7 ± 1.6
TC		2.6 ± 1.0	1.2 ± 0.7	2.6 ± 0.9	46.4 ± 41.4	2.4 ± 1.6	103.0 ± 26.6	2.1 ± 0.7

3.2. Results

The female fertility of the species under study – expressed as the mean for the PQ, CA and TC sites – is shown in Table I. It contains the results recalculated from the data published earlier (G r ü m 1973a, Table II¹). The female population densities in the 1972 breeding season are presented in Table II, and the calculated egg production – the product of the female fertility and the female population density – in Table III. Table IV contains the descendant population densities – i.e., originating from the eggs laid in 1972 – of the fully grown imagines, and Table V contains the mean body weight of the fully grown beetles.

Table V. Mean body weight of imagines having completed their body growth

Species	mg dry weight	Number of weighed individuals
<i>C. coriaceus</i>	620.1	10
<i>C. clatratus</i>	307.2	10
<i>C. glabratus</i>	285.2	15
<i>C. violaceus</i>	261.8	10
<i>C. hortensis</i>	194.2	17
<i>C. nemoralis</i>	166.0	10
<i>C. granulatus</i>	93.5	10
<i>P. niger</i>	81.7	18
<i>C. arcensis</i>	80.7	26
<i>C. caraboides</i>	75.3	10
<i>P. vulgaris</i>	53.8	15
<i>P. anthracinus</i>	22.8	15
<i>P. oblongopunctatus</i>	22.1	10
<i>P. nigrata</i>	17.3	10
<i>C. erratus</i>	14.6	10
<i>A. moestum</i>	8.1	11
<i>P. atrorufus</i>	7.0	10
<i>C. micropterus</i>	5.3	10

The population densities of the descendant beetles of the spring breeder species (Larsson 1939) – i.e., *C. arcensis*, *C. nemoralis*, *P. anthracinus* and *P. oblongopunctatus* – were estimated in the 1st decade of May 1973, when all the beetles had completed their body weight increase (G r ü m 1973c, 1975a). The autumn breeders (Larsson 1939) completed their body growth in the 3rd decade of July (*C. glabratus*), or in the 1st decade of August (*C. hortensis* and *P. niger*), or even at the turning point of June and July, as it occurred in the case of *P. vulgaris* (data after G r ü m 1973c, 1975a).

On the basis of the regression equation (1), the biomass production of the generations under study was calculated (Table VI). Then the regression of $\frac{P}{B_a}$ ratio for the female fertility (F) was calculated (Fig. 1):

¹In the Table II of the quoted paper, the rate of egg-laying by *P. niger* should be read 0.141 instead of 0.114.

$$\frac{P}{B_a} = -0.15 + 0.58 \log_e F \quad (2)$$

with $r = +0.93$.

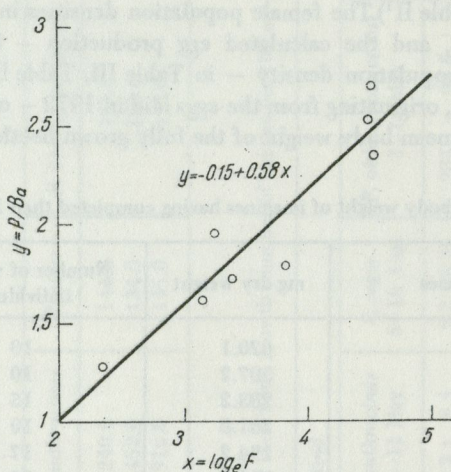


Fig. 1. Relation between the ratio of P/B_a (i.e., biomass production to biomass of adults) and F (i.e., mean number of eggs laid by female)

Hence:

$$P = B_a (-0.15 + 0.58 \log_e F) \quad (3)$$

It should be emphasised, that the $\frac{P}{B}$ ratio is not the value of the biomass turnover, for $B_a \neq \bar{B}$. In the case of carabids – because of difficulties in estimation of numbers of larvae and pupae – the value of B_a is more accessible than that of \bar{B} .

4. YEARLY MEAN BIOMASS PRODUCTION

4.1. Methods

The entire biomass production of carabids in a sampling site is the sum of the biomass productions of separate species inhabiting the site. The species biomass production was calculated on the basis of equation (3).

To estimate population density of the beetles having completed their growth (n_a), the Kudrin's (1965) formula was applied, which made it possible to calculate the density from data on the number of individuals captured in pitfalls.

Table VI. Biomass production (in mg dry weight per 100 m²) by the generations originating from the eggs laid in 1972

Site	Species								Σ
	<i>C. arcensis</i>	<i>C. glabratus</i>	<i>C. hortensis</i>	<i>C. nemoralis</i>	<i>P. anthracinus</i>	<i>P. niger</i>	<i>P. oblongopunctatus</i>	<i>P. vulgaris</i>	
PQ	1,320	2,466	1,216	2,241	869	481	12,288	253	21,134
CA	930	2,651	270	1,551	1,395	884	13,954	1,354	22,989
TC		1,314	431	519	2,588	521	4,828	329	10,530

Table VII. Mean mobility of the investigated species

Species	Mobility in m per day
<i>C. coriaceus</i>	5.45
<i>C. clatratus</i>	5.45
<i>C. glabratus</i>	4.02
<i>C. violaceus</i>	6.05
<i>C. hortensis</i>	6.02
<i>C. nemoralis</i>	4.12
<i>C. granulatus</i>	2.82
<i>P. niger</i>	4.03
<i>C. arcensis</i>	4.73
<i>C. caraboides</i>	3.89
<i>P. vulgaris</i>	2.64
<i>P. anthracinus</i>	0.69
<i>P. oblongopunctatus</i>	0.57
<i>P. nigrita</i>	1.02

$$n_a = \frac{N_i}{D \cdot T \cdot V} \quad (4)$$

where: n_a – number of beetles per 100 m², N_i – number of beetles captured in pitfalls, D – the sum of diameters of the pitfalls (in cm), T – pitfall exposure time (in days), V – mean mobility of the captured beetles (in m per day).

The mean mobility of the beetles – shown in Table VII – was estimated by the method described earlier (Grüm 1971a), and the data on the mobility were taken from the published papers of the present author (Grüm 1971a, 1971b, 1973a, 1975a). Then, the relation between the mobility and the mean dry body weight of the beetle – the latter values shows Table V – was determined (Fig. 2).

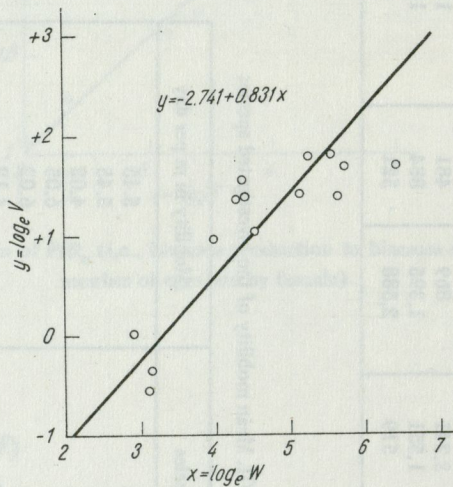


Fig. 2. Relation between V (i.e., mobility) and W (i.e., dry body weight)

$$y = -2.741 + 0.831 x \quad (5)$$

$$r = +0.86$$

where: y – \log_e of mobility, x – \log_e of dry weight (in mg).

The equation (5) was applied to estimate mobility of the species not studied empirically in this respect.

Population densities of the fully grown beetles of the spring breeder species were estimated in the 3rd decade of May, or in the 1st decade of June. This could cause a slight underestimation of density of the beetle populations, and as a consequence, an underestimation of the biomass production. However, the early May estimates of density on the data from pitfalls would cause a serious underestimation of biomass production. The reason is that early in May the temperature falls very often, and this affects the beetle mobility – which may even cease altogether (Grüm 1959) – and thus the population estimate.

Densities of the beetle populations of the autumn breeders were estimated – in accordance with the previous results (G r ü m 1973c, 1975a) – at the turning point of July and August, or in the 1st decade of August. The exceptions were *Cychnus caraboides* (L.) and *P. vulgaris*. In the case of the former species, the teneral beetles were found as early as in May, and occurred until the mid of June (Table VIII). So, the density was estimated in the second half of June. The teneral beetle appearance of *P. vulgaris* varied in time: in 1973 it ended at the turning point of June and July, but often the end of their appearance occurred in the 1st decade of August (Table VIII). The dates of population density estimates of the fully grown beetles varied accordingly.

Table VIII. Seasonal changes in percentage of teneral beetles in population

Period	Species and numbers of individuals captured				
	<i>C. coriaceus</i> (36)	<i>C. violaceus</i> (70)	<i>C. caraboides</i> (67)	<i>P. vulgaris</i> (449)	<i>P. atrorufus</i> (480)
1–15 June	0	0	100	0	40
16–30 June	0	12	25	2	100
1–15 July	–	50	0	33	87
16–31 July	–	10	0	54	61
1–15 Aug.	33	0	0	33	13
16–31 Aug.	10	0	0	0	3
1–15 Sept.	0	0	0	0	0
16–30 Sept.	–	0	0	–	0

4.2. Results

The entire biomass production was calculated for 4 sampling sites: *VmP*, *P*, *PQ* and *CA*. The material was collected in the *VmP* site during 2 years and in the remaining sites during 4 years.

The numbers of the fully grown beetles (N_i) of separate species captured in pitfalls are shown in Tables IX and X. The first of them contains the species examined for biomass production. In Table X the species, or genera, for some reason neglected in the production calculations are listed. The neglected species were either phytophages, or were supposed to reproduce out of the forest habitats, or supposed to be able to climb the inside of the pitfalls (G r e e n s l a d e 1964, P e t r u š k a 1969), or were found in extremely low numbers. All of them amounted to 162 individuals, i.e., 8.4% of the entire material captured in pitfalls.

The population density of each of the species listed in Table IX was calculated and then multiplied by the appropriate mean dry-body weight of the beetle (Table V). The result of the multiplication – i.e., the biomass of the fully grown beetles (B_a) – is shown in Table XI.

Combining the data contained in Table XI with the estimates of the female fertility (Tables V, XII), the biomass production of separate species was calculated according to formula (3).

The data on the female fertility of the species listed in Table V were taken from an earlier paper (G r ü m 1973a), and those shown in Table XII were either accepted after

Table IX. Number of imagines captured at the moment of their body growth completion

Species	Site and year														Σ
	CA 1960	CA 1961	CA 1963	CA 1964	PQ 1960	PQ 1961	PQ 1963	PQ 1964	P 1956	P 1957	P 1959	P 1960	VmP 1963	VmP 1964	
<i>Carabus clatratus</i> L.	14				3				7			1			25
<i>C. nemoralis</i> Müll.	1	2	2	1	1		2	2			1		1	4	17
<i>C. granulatus</i> L.	23	7	1	6					28	4	8	1			78
<i>C. arcensis</i> Hbst.	1	2	9	11	11	9	53	22	34	34	11	23	189	132	542
<i>Cychrus caraboides</i> (L.)		1							1		1		1		4
<i>Pterostichus anthracinus</i> (Ill.)	1	1	2												4
<i>P. oblongopunctatus</i> (F.)	1	1	14	5	1		37	15	2		1	1	59	55	192
<i>P. nigrita</i> (F.)	5		2	1				3	1	1				1	14
<i>Carabus coriaceus</i> L.						1			2		5				8
<i>C. violaceus</i> L.				1	1	1	2	3						1	9
<i>C. glabratus</i> Payk.	6	10	3	5	3	13	2	15	1	1		8			67
<i>C. hortensis</i> L.	4	7	1	9	3	15	9	2	8	10		10		1	79
<i>Pterostichus niger</i> (Schall.)	1	31	8	25	14	16	23	20	163	50	3	104	9	19	486
<i>P. vulgaris</i> (L.)	5	5		21								1		1	33
<i>Calathus erratus</i> (Sahlbg.)					1	2		1		1			1	1	7
<i>C. micropterus</i> (Dft.)					1	3	6	3				1	8	2	24
<i>Patrobis atrorufus</i> (Strøm.)	89	21	1						16	1		16			144
<i>Agonum moestum</i> (Duft.)	5	26	6	1					2						40

Table X. Species or genera neglected in production calculations

No.	Species (genera)	Number of individuals captured
1	<i>Calosoma inquisitor</i> (L.)	1
2	<i>Carabus nitens</i> L.	1
3	<i>C. cancellatus</i> Ill.	2
4	<i>Leistus ferrugineus</i> (L.)	3
5	<i>Nebria brevicollis</i> (F.)	1
6	<i>Notiophilus</i> sp.	12
7	<i>Blethisa multipunctata</i> (L.)	1
8	<i>Elaphrus cupreus</i> Duft.	2
9	<i>Loricera caerulea</i> (L.)	5
10	<i>Dyschirius globosus</i> (Hbst.)	3
11	<i>Asaphidion flavipes</i> (L.)	1
12	<i>Bembidion</i> sp.	7
13	<i>Epaphius secalis</i> (Payk.)	15
14	<i>Amara</i> sp.	28
15	<i>Stomis pumicatus</i> (Panz.)	1
16	<i>Pterostichus caeruleus</i> (L.)	1
17	<i>P. aterrimus</i> (Hbst.)	2
18	<i>P. angustatus</i> (Duft.)	1
19	<i>P. brunneus</i> (Sturm)	5
20	<i>Agonum obscurum</i> (Hbst.)	17
21	<i>A. gracile</i> Sturm	8
22	<i>Badister peltatus</i> (Panz.)	18
23	<i>B. bipustulatus</i> (F.)	2
24	<i>Chlaenius tristis</i> (Schall.)	1
25	<i>Ch. nigricornis</i> (F.)	1
26	<i>Harpalus</i> sp.	3
27	<i>Bradycellus collaris</i> (Payk.)	1
28	<i>Acupalpus</i> sp.	2
29	<i>Masoreus wetterhalli</i> (Gyll.)	1
30	<i>Metabletus truncatellus</i> (L.)	2
31	<i>Microlestes minutulus</i> (Goeze)	11
32	<i>Cymindis</i> sp.	2

Kurka (1972), or resulted from the author's studies carried out in 1973 and 1974. The subject of these studies were estimates of mean number of ripe eggs in ovaries of females, the duration of the breeding season (i.e., the number of days from 1st until last finding a female containing ripe eggs in her ovaries), and the oviposition rate. The oviposition rate – for the method see Grüm (1973a) – was estimated only for *Patrobus atrofufus* (Ström). In the case of the remaining species listed in Table XII – because of scarcity of the material examined – the appropriate genera characteristics were accepted after the data presented by Grüm (1973a).

The biomass production of separate species was combined for the sampling sites and years. Then the yearly mean biomass production for the site was produced (Table XIII). The entire biomass production for the site is probably slightly underestimated, because – apart from the reasons mentioned in paragraph 4.1. – some small zoophagous species were not taken into consideration. However, it does not seem likely that the calculated production is less than 90% to 95% of the real one.

Table XI. Biomass of individuals having completed their body growth (in mg dry weight per 100 m²)

Species	Site and year														
	CA 1960	CA 1961	CA 1963	CA 1964	PQ 1960	PQ 1961	PQ 1963	PQ 1964	P 1956	P 1957	P 1959	P 1960	V _m P 1963	V _m P 1964	
<i>C. clatratus</i>	1,278				240				212			31			
<i>C. nemoralis</i>	81	438	256	110	71		63	55			28		25	101	
<i>C. granulatus</i>	1,714	1,390	116	596					698	105	208	26			
<i>C. arcensis</i>	73	387	1,017	1,065	699	1,743	1,497	533	827	864	279	585	4,271	2,983	
<i>C. caraboides</i>		191							24		25		23		
<i>P. anthracinus</i>	58	156	182												
<i>P. oblongopunctatus</i>	59	157	1,279	392	51		845	294	39		20	20	1,078	1,004	
<i>P. nigrita</i>	280		174	75				56	19	19				17	
<i>C. coriaceus</i>						273			74		211				
<i>C. violaceus</i>				105	65	236	68	311						26	
<i>C. glabratus</i>	451	2,401	451	525	197	3,120	68	1,574	31	31		251			
<i>C. hortensis</i>	282	1,577	132	887	184	3,379	295	196	247	295		295		25	
<i>P. niger</i>	60	6,030	908	2,127	744	3,112	653	1,702	4,335	1,276	90	2,655	204	427	
<i>P. vulgaris</i>	282	904		1,662								24		21	
<i>C. erratus</i>					40	290		63		19			17	17	
<i>C. micropterus</i>					33	364	106	159				16	113	28	
<i>P. atrorufus</i>	3,621	2,734	76						285	17		273			
<i>A. moestum</i>	204	3,388	456	57					36						

Table XII. Female fertility (approximate values)

Species	Number of dissected females	Mean number of ripe eggs per female	Observed duration of the breeding season (in days)	Rate of egg deposition	Number of eggs deposited in the breeding season
<i>C. coriaceus</i>	5	2.00	45	} 0.086 ^a	7.7
<i>C. clatratus</i>	11	3.64	65		20.3
<i>C. violaceus</i>	11	4.45	60		22.9
<i>C. granulatus</i>	29	3.73	74		23.7
<i>C. caraboides</i>	9	6.00	62		32.0
<i>P. nigrita</i>	38	6.34	75	0.101 ^b	48.0
<i>C. erratus</i>	—	—	—	—	121 ^c
<i>A. moestum</i>	22	6.82	60	0.101 ^b	41.3
<i>P. atrorufus</i>	73	2.79	107	0.118	35.2
<i>C. micropterus</i>	—	—	—	—	125 ^c

^aMean for *Carabus*, after Grüm (1973a). ^bMean for *Pterostichus*, after Grüm (1973a). ^cAccepted after Kurka (1972).

5. NUMERICAL RELATIONS BETWEEN THE BIOMASS PRODUCTION OF THE CARABIDS AND THE AMOUNT OF NITROGEN IN THE LEAF-FALL

For the sampling sites *VmP*, *PQ* and *CA*, the yearly mean biomass production of the carabids (Table XIII) was compared with the amount of nitrogen in the leaf-fall. A similar comparison was made for the entire biomass production of the 8 species listed in Table VI — calculated as a yearly mean value based on the data contained in the Tables VI and XIII — with the amount of nitrogen in the leaf-fall on the sites *VmP*, *PQ*, *TC*, and *CA*.

In both cases a certain tendency to a higher biomass production of carabids accompanied the higher amounts of nitrogen in the leaf-fall (Fig. 3). However, the biomass production of carabids did not increase proportionally to the amount of nitrogen. For instance, the ratio of nitrogen in the leaf-fall on the *CA* site (the richest in this respect) to that on the *VmP* (the poorest) equalled 6.3:1, but the ratio of the biomass production of carabids calculated for the same sites equalled 2.1:1.

Among the carabids dwelling on the sites studied the species active as imagines mainly on the surface of the litter-layer, and those active more often inside the litter-layer were distinguished (Fig. 4). To the latter group *Agonum moestum* Duft., *Pterostichus nigrita* F., *P. niger* and *Patrobis atrorufus* were included, for the percentage of these beetles captured inside the litter-layer was higher than the mean percentage calculated for the entire set of the 18 species.

The entire production of these 4 litter-active species was well correlated with the amount of nitrogen in the leaf-fall (Fig. 5). Contrary to that, the production of the remaining surface-active species seemed to be independent of that factor (Fig. 5).

On the assumption that the nitrogen content in the body of each stage in the life-cycle of carabids is approximately equal to 10% of dry body weight (Grüm 1973b), the amount of nitrogen in the biomass production of the carabids — later transferred to higher predators like frogs, birds and small mammals — was compared with the amount of nitrogen in the leaf-fall, i.e., the nitrogen transferred to saprophages. The ratio of the nitrogen built in the net

Table XIII. Biomass production (in mg dry weight per 100 m² per year)

Species	Site and year													
	CA 1960	CA 1961	CA 1963	CA 1964	PQ 1960	PQ 1961	PQ 1963	PQ 1964	P 1956	P 1957	P 1959	P 1960	VmP 1963	VmP 1964
<i>C. clatratus</i>	1,674				314				278			41		
<i>C. nemoralis</i>	99	534	312	134	87		77	67			34		30	123
<i>C. granulatus</i>	2,245	1,821	152	781					914	137	272	34		
<i>C. arcensis</i>	123	650	1,708	1,789	1,174	2,928	2,515	895	1,389	1,451	469	983	7,175	5,011
<i>C. caraboides</i>		372							47		49		45	
<i>P. anthracinus</i>	144	387	451											
<i>P. oblongopunctatus</i>	121	323	2,635	807	105		1,741	606	80		41	41	2,221	2,068
<i>P. nigrita</i>	546		339	146				109	37	37				33
<i>C. coriaceus</i>						358			97		276			
<i>C. violaceus</i>				137	85	309	89	407						34
<i>C. glabratus</i>	821	4,370	821	955	358	5,678	124	2,865	56	56		457		
<i>C. hortensis</i>	491	2,744	230	1,543	320	5,879	513	341	430	513		513		43
<i>P. niger</i>	148	14,834	2,234	5,232	1,830	7,655	1,606	4,187	10,664	3,139	221	6,531	502	1,050
<i>P. vulgaris</i>	694	2,224		4,088									59	52
<i>C. erratus</i>					104	751		163		49			44	44
<i>C. micropterus</i>					85	943	274	412				41	293	72
<i>P. atrorufus</i>	7,061	5,331	148						556	33		532		
<i>A. moestum</i>	398	6,607	889	111					70					
∑	14,565	40,197	9,919	15,723	4,462	24,501	6,939	10,052	14,618	5,415	1,362	9,232	10,310	8,530
Yearly mean for site	20,101				11,488				7,657				9,420	
Standard deviation	± 11,805				± 7,769				± 4,889				± 889	

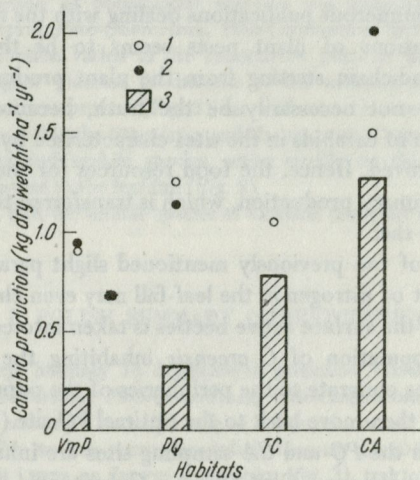


Fig. 3. Biomass production of carabids versus amount of nitrogen in leaf-fall
 1 – mean for 8 species, 2 – mean for 18 species, 3 – 10 kg·ha⁻¹·yr⁻¹ of nitrogen

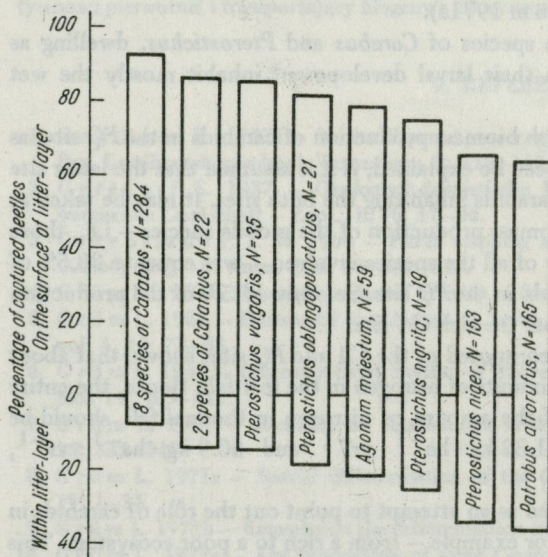


Fig. 4. Vertical distribution of carabids

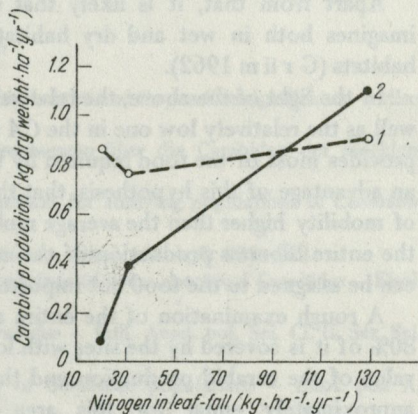


Fig. 5. Biomass production of surface active and litter active species versus amount of nitrogen in leaf-fall
 1 – surface active species, 2 – litter active species

production of carabids to that contained in the leaf-fall was equal to 0.0046, 0.0036 and 0.0016 for the VmP, PQ and CA sites, respectively.

6. DISCUSSION

The theoretical base for numerous publications dealing with the rôle of predatory carabids as a factor controlling populations of plant pests seems to be the creed, that the carabids participate most in the food-chain starting from the plant production transferred to phytophagous insects. This may not necessarily be the truth, because a slight tendency toward a higher biomass production of carabids in the sites characterised by higher amounts of nitrogen in the leaf-fall has been proved. Hence, the food resources for the carabids seem to originate rather in that part of the primary production, which is transferred to the macrosaprophages like woodlice, earthworms and others.

The superficial picture of the previously mentioned slight parallelism between the carabid production and the amount of nitrogen in the leaf-fall may even change into a closer numerical relation, if high mobility of the surface active beetles is taken into consideration.

For instance, in the population of *C. arcensis* inhabiting the *PQ* site (microclimatically optimal), the hungry beetles emigrate to the peripheries of the population area, i.e., the usually wet *CA* site, feed there and then move back to the optimal *PQ* site (Grüm 1971a).

On the other hand, both the *PQ* and *CA* sampling sites are inhabited also by a few big and mobile species, like *C. coriaceus*, *C. glabratus*, *C. hortensis*, *C. nemoralis* and *P. niger* (Grüm 1967). Spatial distribution of these species partially depends on the amount of rainfall. Namely, the area of high density of a species preferring the dry *PQ* site moves during the dry periods toward the wet *CA* site, and that of another one preferring the *CA* site moves during longer rainy periods toward the *PQ* site (Grüm 1971a).

Apart from that, it is likely that some species of *Carabus* and *Pterostichus*, dwelling as imagines both in wet and dry habitats, in their larval development inhabit mostly the wet habitats (Grüm 1962).

In the light of the above, the relatively high biomass production of carabids in the *PQ* site, as well as the relatively low one in the *CA* site, can be explained, if it is assumed that the latter site provides most of the food required by the carabids inhabiting the both sites. It may be taken as an advantage of this hypothesis, that the biomass production of the mobile species – i.e., those of mobility higher than the average mobility of all the species involved – was equal to 88.5% of the entire biomass production of the carabids in the *PQ* site. So, only 11.5% of the production can be assigned to the food not imported from the rich *CA* site.

A rough examination of the entire area composed of the *CA* and *PQ* sites shows, that about 80% of it is covered by the sites with low amounts of nitrogen in the leaf-fall. Hence, the entire value of the carabid production and that of the amount of nitrogen in the leaf-fall, should be approximately equal for this area to $1.32 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and $50.9 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$, respectively.

The above considerations may be regarded as an attempt to point out the rôle of carabids in the transportation of elements – nitrogen for example – from a rich to a poor ecosystem. This seems to be probable in patchy habitats, providing a singular patch does not exceed 1 ha in area, approximately. Contrary to that, in vast homogeneous areas – like the *VmP* site – the carabids are, perhaps, unable to cover effectively a long distance (Den Boer 1971), and, therefore, can not transport elements from or to the neighbouring habitats.

I am grateful to Mr. R. Kowalski (Commonwealth Forestry Institute) for reading the manuscript and making valuable corrections to the text.

7. SUMMARY

The entire biomass production of zoophagous carabids was estimated separately for the following habitats: *Vaccinio myrtilli-Pinetum*, *Pino-Quercetum*, *Tilio-Carpinetum* and *Circaeo-Alnetum*. In each of the habitats, the carabid production varied in the consecutive years of the study (Table XIII). However, a slight tendency toward a higher biomass production of the carabids in the habitats rich in nitrogen contained in the leaf-fall has been proved (Fig. 3), as well as a clear positive correlation between the production of carabids dwelling inside the litter-layer and the amount of nitrogen in the leaf-fall (Fig. 5). The biomass production of the big and mobile species, active mostly on the surface of the litter-layer, was independent of the nitrogen amount in the leaf-fall (Fig. 5).

A suggestion is put forward, that the mobile species of carabids transport such elements like nitrogen from rich to poor ecosystems.

8. POLISH SUMMARY (STRESZCZENIE)

Oszacowano łączną produkcję biomasy 18 drapieżnych gatunków *Carabidae*, najliczniej występujących w siedliskach *Vaccinio myrtilli-Pinetum*, *Pino-Quercetum*, *Tilio-Carpinetum* i *Circaeo-Alnetum*. W każdym siedlisku produkcja *Carabidae* znacznie zmieniała się w kolejnych latach badań (tab. XIII). Stwierdzono niewielką tylko zbieżność między średnią roczną produkcją biomasy *Carabidae* a ilością azotu organicznego w opadzie liści drzew, podszytu i runa na danym stanowisku (fig. 3), traktowaną jako podstawowy czynnik określający zasobność pokarmową siedliska dla *Carabidae*. Zauważono wyraźną zbieżność między produkcją biomasy ściółkowych gatunków *Carabidae* a dopływem azotu do ściółki leśnej i zupełną niezależność od tego czynnika tych gatunków, które są aktywne na powierzchni ściółki (fig. 5). Wysłunęto przypuszczenie, że ruchliwe gatunki *Carabidae* stanowią element łączący łańcuchy troficzne ekosystemów o różnej produktywności pierwotnej i transportujący biogeny z ekosystemów bogatych do ubogich.

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