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REMARKS ON THE DIFFERENTIATION IN *CARABIDAE* MOBILITY

(Ekol. Pol. 19: 47–56). Within areas of the studied populations of *Carabidae* inhabiting small in acreage forest biotopes the mean mobility of individuals is highest at the periphery of population area and decreases as site conditions improve. Hypothesis is presented according to which the primary cause of the phenomenon are strong site gradients in biotopes with an obviously mosaic pattern.

INTRODUCTION

Earlier studies indicated that in populations of *Carabus arcensis* Hbst. and *C. nemoralis* Müll. inhabiting forest biotopes of a small acreage there occur following changes in the mobility of individuals (Grüm 1971). Under favourable site conditions only few individuals found food; satiated individuals characterized themselves with a low mobility, while hungry ones were quite mobile. These latter emigrated to periphery of the population area where chances of appeasing hunger were by far greater than in the zone favourable in site respect. Satiated individuals being on the periphery of population area distinguished themselves with high mobility and re-emigrated towards regions with favourable site conditions. Hence on the area of favourable site conditions the average mobility of individuals was low and populations of these species consisted of two groups of individuals with unequal mobility (hungry and satiated ones). On the other hand on the periphery of population area – where the average

mobility of individuals was high – no differences in the mobility of hungry and satiated individuals were found.

The present paper deals with the problem of the common occurrence of such changes in mobility of individuals as those described above in *Carabidae* populations and with conditions indispensable for their occurrence.

AREA AND METHODS

The material was collected during two years – in spring and early summer: since May 16 until June 29, 1965 and since June 4 until June 30, 1966. Study areas provided three biotopes of the Kampinos Forest.

1. *Pino-Quercetum* Kozłowska, 1925 with roughly rectangular area of 4 ha with alderwood (*Carici elongatae-Alnetum* Koch, 1926) adjoining the both longer sides. Pine (*Pinus silvestris* L.) in this stand was about 80 years old, while few oaks (*Quercus* sp.) were older. The biotope distinguished itself with a considerably mosaic pattern of site conditions (Grüm 1971). Three habitats, denoted by symbols *Q*, *QA*, and *A*, were identified. First of them (*Q*) was situated in the central part of the biotope, some 40 m distant from *Alnetum*. The second one (*QA*) was located more or less at half the distance between the *Q* site and *Alnetum*. The third one (*A*) was in the ecotone between *Pino-Quercetum* and *Alnetum*.

2. *Vaccinio myrtilli-Pinetum* Kobendza, 1930 included the area of ca 4 ha surrounded by *Caricetum* and alderwood. Pine in this stand was some 45 years old. One site, denoted by symbol *PI*, was identified here.

3. *Vaccinio myrtilli-Pinetum* Kobendza, 1930 (symbol *PII*). This biotope covered a vast area of several hectares distinguished by the least mosaic pattern of site conditions. Pine in this stand was youngest, approximately 35 years old.

Using the previously developed technique (Grüm 1971) of the evaluation of population density and individual mobility, these variables were calculated for several *Carabidae* species, most abundant among those occurring in the above mentioned biotopes.

The procedure of density evaluation is based on checking the number of individuals daily arriving and leaving certain small, arbitrarily selected segment of the population area. The check is ensured by the isolation of the given segment with the aid of a circular plastic fence and digging on its both sides (outer and inner) closely adjoining live-capturing traps, i.e. plastic cylinders with ca 5 cm diameter of entrance.

The mean number of individuals daily present within the fenced segment of terrain, further called plot, was determined with the following equation:

$$\bar{n} = \frac{N_0^2 \bar{t}}{N_1 T}$$

where: N_0 – number of individuals captured in traps of the outer side of fence; N_1 – number of individuals captured in traps of the inner side of fence; \bar{t} – mean time of individual staying within a plot (in days); T – duration of captures (in days) equal to the number of daily captures. The detailed discussion of the above technique of the evaluation of number of individuals present within the plot is given by Grüm (1971).

When the mean number of individuals present within the plot and the area of plot were known, the mean – for the studied period – density of population for the location of plot was determined.

The mean mobility of individuals was evaluated on the basis of the knowledge of mean time of the stay of individuals within the plot. Individuals captured in traps on the outer side of fence were marked with individual numbers and released in the centre of the fenced plot. They have been captured afterwards in traps of the inner side of fence. Hence the duration of staying within the fence was known for each released individual. It was assumed that individual captured after one day since the moment of release could be trapped at earliest immediately after release, while at latest – just before the next inspection of traps, and thus stayed there half a day. Based on the same assumption an individual captured after two days stayed within fence for 1.5 day, that captured after three days since release – stayed for 2.5 days, etc. Thus the mean duration of individual staying within the fenced plot is determined according to the formula:

$$\bar{t} = \frac{1}{N_1} \sum_{t=1}^m N_t (t - 0.5)$$

Mean mobility is inversely proportional to the mean duration of individuals stay within a plot. For the definite range of plot area size one can compare the mobility using the measure being a ratio between the shortest way which individuals have to cover from the release point (centre of plot) to the nearest trap (those on the inner side of fence) and the mean time for travelling (\bar{t}). The shortest way is the total of plot radius and half the distance between neighbouring traps which are evenly distributed on the inner side of fence. More detailed considerations concerning this method of mobility estimation contains the paper by Grüm (1971).

Apart from the evaluation of mean mobility it was checked if there can be identified groups of individuals differing in mobility, i.e. leaving the area of plot at not uniform rate. The phenomenon of an unequal rate of leaving certain area by marked individuals was found in populations of several carabid species (Grüm 1965, 1971), through the comparison of the conformity between the distribution of intervals of time of certain individuals staying within given area and the exponential distribution.

The following equation produced the number of individuals which ought to be captured after the 1 and before $t + 1$ days since their release in the centre of plot:

$$N'_t = N_1 (1 - e^{-p}) e^{-pt}$$

where: N_1 – number of individuals captured in traps of the inner side of fence; $p = \frac{1}{\bar{t}}$. Two sequences of numbers were obtained: one empirical composed of N_t values and the other theoretical, represented by \bar{N}'_t values. They were compared with each other with the aid of χ^2 -square Pearson's test of goodness of fit.

Due to the small size of the material results were verified by the comparison with mean value X^2 , i.e. $E(X^2)$ and standard deviation $D^2(X^2) = 2(r - 1) + \frac{1}{N_1} \left(\sum_{i=1}^r \frac{1}{p_i} - r^2 - 2r + 2 \right)$. Lack of the statistical goodness of fit for both sequences proves the existence of groups of individuals differing in mobility.

The present studies included populations of *Carabus granulatus* L., *Pterostichus oblongopunctatus* F., and *P. vulgaris* L. For the determination of the density of *C. granulatus* and *P. vulgaris* populations plots with the area of 33 m² (in 1965) and 25 m² (in 1966) with 5 traps on each side of fence were used. Previous analyses (Grüm 1971) indicated the possibility of comparing mobility measures obtained with the aid of 25 and 33 m² plots. Population density and mobility of *P. oblongopunctatus* individuals were determined with the use of smaller plots due to the lower mobility of individuals of this species. In 1965 these were plots of 5 m² area, while in 1966 – of 1 m² area and with four traps on each side of the fence. Mobility measures for *P. oblongopunctatus* obtained with plots 5 and 1 m² in area were not compared with each other.

RESULTS

Population density and mean mobility of *C. granulatus* and *P. vulgaris* individuals in 1965 were calculated only for the *Pino-Quercetum* and *Alnetum* ecotone (plot A 33). In 1966 the both variables were calculated for *C. granulatus* and *P. vulgaris* in the ecotone (plot A 25), while for *P. vulgaris* additionally in the central part of the *Pino-Quercetum* (plot Q 25). The *Pino-Quercetum* and *Alnetum* ecotone was the site preferred by both species (Grüm 1967). *C. granulatus* is probably numerous also in *Alnetum*.

In 1965 population density and mean mobility of *P. oblongopunctatus* individuals were estimated in three different sites: in the central part of *Pino-Quercetum* (plot Q 5) and in both biotopes of *Vaccinio myrtilli-Pinetum* (plots P I 5 and P II 5). In 1966 the evaluation of density and mobility of *P. oblongopunctatus* was carried out only in the biotope of *Pino-Quercetum* with the use of four plots distributed at various distances from *Alnetum*: in *Pino-Quercetum* and *Alnetum* ecotone (plot A 1), in an intermediate site between the ecotone mentioned and the central part of *Pino-Quercetum* (plots Q A 1 and Q A 1'), and

Comparison of the quantity of material collected and results of calculated density and mobility

Tab. I

Species	Plot symbol	N_0	N_1	\bar{t}	\bar{n}	\bar{v}
<i>Pterostichus oblongopunctatus</i>	Q5	28	24	4.541	329.6	0.73
	PI5	17	15	3.966	169.7	0.83
	PII5	38	33	3.287	319.5	1.00
	A1	30	27	5.278	753.9	0.28
	QA1	16	16	2.937	201.1	0.51
	QA1'	13	12	0.750	45.2	2.00
	Q1	17	14	1.428	126.3	1.05
<i>Pterostichus vulgaris</i>	A33	36	33	4.121	12.1	1.26
	A25	20	16	3.187	35.4	1.44
	Q25	9	9	1.500	6.0	3.07
<i>Carabus granulatus</i>	A33	33	33	2.378	7.0	2.19
	A25	11	10	1.400	7.5	3.28

N_0 — number of individuals released within the plot; N_1 — number of individuals captured following to release; \bar{t} — mean time (in 24 hour cycles) of individual's staying within the plot; \bar{n} — mean density (individuals per 100 m²); \bar{v} — mean mobility (in meters per 24 hours).

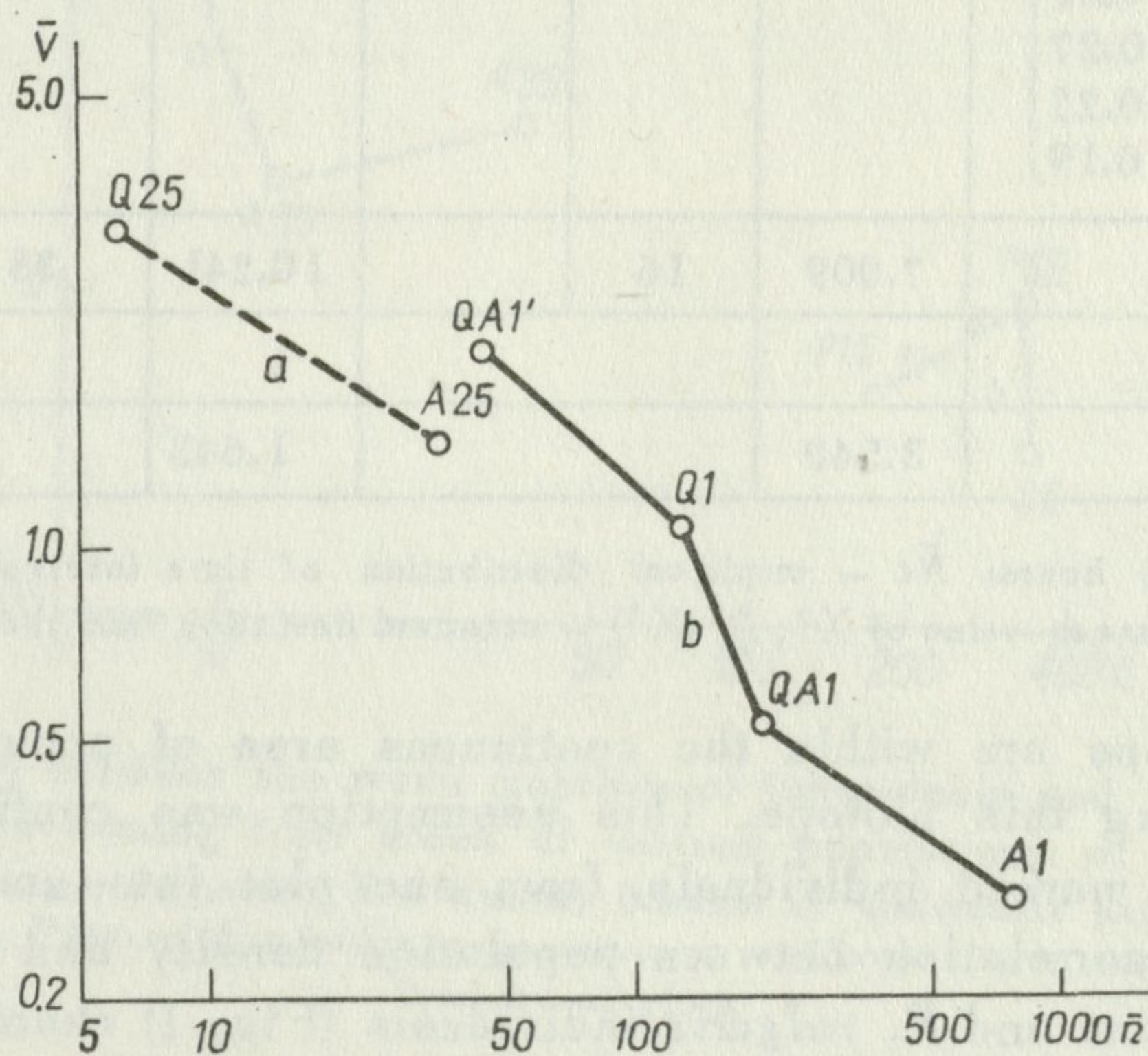


Fig. 1. Relationship between the mean mobility of individuals and the density of population observed within its range

\bar{v} — mobility (in metres per 24 hours), \bar{n} — density (number of individuals per 100 m²), a — *Pterostichus vulgaris*, b — *Pterostichus oblongopunctatus*, Q25, A1, ... — symbols of plots

in the centre of the latter biotope (plot Q1). Size of the material collected and results of calculations are given in Table I.

It was assumed that plots situated in not too distant sites of the *Pino-*

Comparison of the distribution of time intervals of individuals' stay within the plot with the exponential distribution

Tab. II

<i>t</i>	<i>Pterostichus oblongopunctatus</i>			<i>Pterostichus vulgaris</i>			<i>Carabus granulatus</i>		
	A1			A25			A33		
	$\bar{N}t$	$\bar{N}t'$	X^2	$\bar{N}t$	$\bar{N}t'$	X^2	$\bar{N}t$	$\bar{N}t'$	X^2
0.5	9	4.65}	4.064	10	4.31}	7.482	18	11.32}	3.935
1.5	3	3.84}		1	3.15}		5	7.44}	
2.5	1	3.19	2.495	1	2.30	2.759	2	4.89}	3.658
3.5		2.64}			1.68		1	3.21}	
4.5	2	2.18			1.23		1	2.11}	
5.5	2	1.81			0.90			1.38	
6.5	1	1.49}			0.65}		2	0.91}	
7.5	2	1.24}		1	0.48}		2	0.60}	0.120
8.5		1.02}			0.35}			0.39}	
9.5	1	0.85			0.25		1	0.26	
10.5	2	0.70			0.19			0.17	
11.5		0.58}	0.450	2	0.14		1	0.11}	
12.5	1	0.48}				0.10}			
13.5	1	0.40		1	0.07}				
14.5		0.33							
15.5	1	0.27							
16.5		0.22							
17.5	1	0.19}							
Σ	27		7.009	16		10.241	33		7.713
$E(X^2)$			2			1			2
$D^2(X^2)$			3.540			1.643			3.613

t – time in 24 hours; $\bar{N}t$ – empirical distribution of time intervals; $\bar{N}t'$ – exponential distribution; $E(X^2)$ – mean value of X^2 ; $D^2(X^2)$ – standard deviation from the mean value.

-*Quercetum* biotope are within the continuous area of population of each of species inhabiting this biotope. This assumption was confirmed by the fact of transition of marked individuals from one plot into another. Hence, the stated negative correlation between population density and mean mobility of *P. oblongopunctatus* and *P. vulgaris* individuals (Fig. 1) characterizes changes in mean mobility of individuals within the population area: the mobility increases along with the impairment of site conditions and is the highest on the periphery of population area. It was found also that on sites optimal for *P. oblongopunctatus* and *P. vulgaris* – these sites characterized themselves with the highest density of population of both mentioned species – there occur two groups of individuals differing in mobility. This conclusion results from the lack of statistical goodness of fit between the exponential distribution and that of intervals of time of individuals staying within plots A1 and A25 (Tab. II).

The results above, characterizing changes in mobility of individuals occurring at the same time within the population area, corroborate with those obtained for the populations of *C. arcensis* and *C. nemoralis* (Grüm 1971).

It was assumed that plots situated in biotopes of *Pino-Quercetum* (plot Q5) and *Vaccinio myrtilli-Pinetum* (plots P15 and P115), due to considerable distances between them and ecological barriers partially dividing them (associations of *Caricetum* or *Alnetum*) are located in areas of different or isolated populations of *P. oblongopunctatus*. It was assumed also that site conditions for *C. granulatus* and *P. vulgaris* in the *Pino-Quercetum* and *Alnetum* ecotone were in 1965 somewhat different than in 1966. Hence characteristics of mobility of these species on plots A33 and A25 (concerning different years) do not reflect changes within the area of one population, but refer to changes in mobility in different populations of the same species.

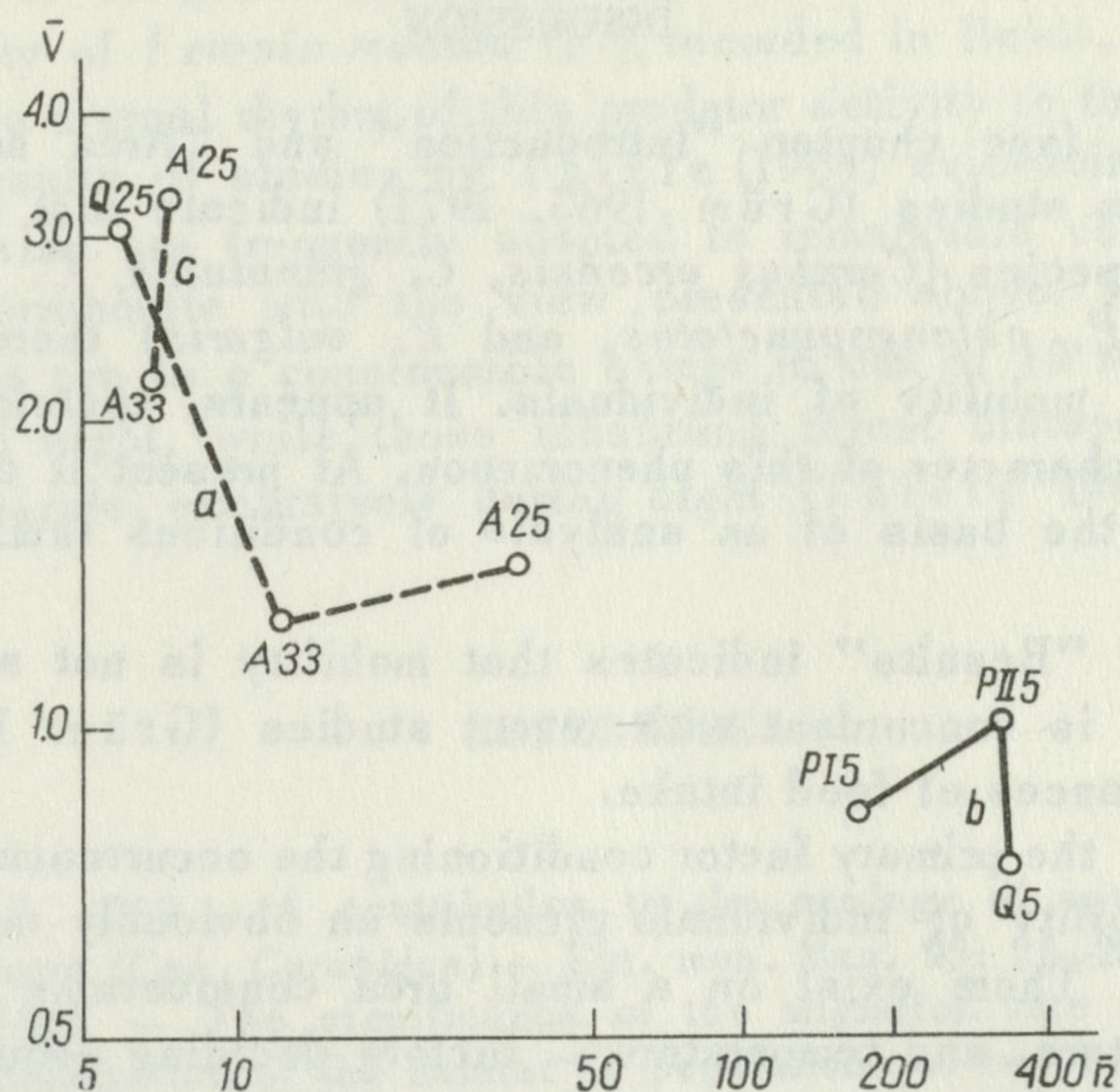


Fig. 2. Relationship between the mean mobility of individuals and population density observed in samples coming from areas of various populations of the same species \bar{v} – mobility (in metres per 24 hours), \bar{n} – density (number of individuals per 100 m²), a – *Pterostichus vulgaris*, b – *Pterostichus oblongopunctatus*, c – *Carabus granulatus*, Q25, A1, ... – symbols of plots

While comparing results obtained for different (in the above discussed aspect) populations, not in all cases the negative correlation between the mean mobility of individuals and population density of definite species was found (Fig. 2). The division of population into two groups of individuals with different mobility was also not so consistently, as within the area of one population, accompanying its high density: e.g. in *C. granulatus* population this division was found (Tab. II) in *Pino-Quercetum* and *Alnetum* ecotone only

in 1966 in spite of the fact that *C. granulatus* population density in 1965 differed only slightly from that calculated for 1966 (Tab. I).

The results obtained indicate what follows:

1. Within ecological areas of *Pterostichus oblongopunctatus* and *P. vulgaris* populations the mean mobility decreases along with the betterment of site conditions and is highest on the periphery of population area.
2. Within ecological areas of *Carabus granulatus*, *Pterostichus oblongopunctatus*, and *P. vulgaris* populations the division of population into two groups of individuals with different mobility occurs in the zone of favourable site conditions.
3. Both the mean mobility and the division of population into more and less mobile individuals is not a simple function of population density.

DISCUSSION

The present (see chapter "Introduction" and "Area and methods") as well as previous studies (Grüm 1965, 1971) indicate that in populations of six *Carabidae* species (*Carabus arcensis*, *C. granulatus*, *C. nemoralis*, *Pterostichus niger*, *P. oblongopunctatus*, and *P. vulgaris*) there occur identical changes in the mobility of individuals. It appears, therefore, the question of the common character of this phenomenon. At present it can be considered exclusively on the basis of an analysis of conditions indispensable for its realization.

The chapter "Results" indicates that mobility is not a simple function of density what is concordant with recent studies (Grüm 1971) relating the mobility with chances of food intake.

It seems that the primary factor conditioning the occurrence of the described changes in mobility of individuals presents an obviously mosaic pattern of site conditions. There exist on a small area considerable differentiation in insolation, moisture, and temperature – factors deciding about the distribution of epigeic *Carabidae* species according to Thiele (1968) – which cause the aggregation of individuals of given species in definite, optimal for it sites.

In an environment characterized by highly mosaic pattern chances of food acquisition ought to be, in general, lesser under optimum site conditions than under conditions close to pessimum what is indicated by the increase in chances for food gain with the decrease in the density of *Carabus arcensis* population and also that of *C. nemoralis* (Grüm 1971). Such state of affairs seems understandable since predatory *Carabidae* are, in general, polyphagous (Jung 1940, Davies 1959, Skuhřavý 1959, and others). Thus the distribution of the complex of prey species should be more uniform than the distribution of predatory species. Hence quantitative relations between the density of predator population and that of the complex of preys are variable and are least favourable for predator in the site optimal for him.

Good spatial orientation of *Carabidae* which enables them to find way

to optimal sites (Lauterbach 1964) is also essential for the problem discussed.

In homogeneous biotopes where on considerable area occur only slight changes in site conditions, vast cultivated fields providing an example, quantitative relations between density of population of predatory carabid species and the density of the complex of its prey are probably less variable.

Unfortunately, studies on changes in mobility of individuals within areas of predatory *Carabidae* populations inhabiting cultivated fields are lacking. Hence this part of considerations is rather of speculative character. It is probable, however, that changes in the diurnal rhythm of predator activity, and not the periodical emigration of mobile individuals to the periphery of population area present the behaviour enabling the satiation of hunger.

This thesis is confirmed by studies by Williams (1959) who found that the daily activity of *Feronia madida* (F.), recorded in fields, resulted from the adaptation of the diurnal rhythm of this predator activity to the diurnal activity of its prey. Results of studies by Thiele (1964) evidencing that *Carabidae* occurring in fields are frequently adapted to remarkable changes in climatic factors also corroborate with the view presented above. Hence the species inhabiting fields are to a considerable extent (6 out of 10 tested) active both during day and night, while those inhabiting forest biotopes (11 out of 12) are active, as a rule, exclusively during night (Thiele 1964).

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UWAGI O ZRÓŻNICOWANIU RUCHLIWOŚCI *CARABIDAE*

Streszczenie

Przedmiotem badań były zmiany ruchliwości osobników zachodzące w populacjach *Carabidae*, zasiedlających biotopy leśne o niewielkiej powierzchni. Jak stwierdzono, średnia ruchliwość osobników jest najwyższa na peryferiach areału populacji i maleje wraz z poprawą warunków siedliskowych. Jest więc najniższa w strefie korzystnych warunków siedliskowych, przy czym w strefie tej populacja składa się z dwóch grup osobników o niejednakowej ruchliwości.

Przypuszczalnie pierwotną przyczyną opisanych zmian ruchliwości są silne gradienty siedliskowe w mozaikowych biotopach leśnych.

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