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THE SIGNIFICANCE OF THE MIGRATION RATE OF INDIVIDUALS IN THE REGULATION OF INTENSIVITY OF PENETRATION OF THE HABITAT BY POPULATIONS OF TWO SPECIES OF *CARABIDAE: CARABUS ARCENSIS* HRBST. AND *PTEROSTICHUS NIGER* SCHALL.*

Analysis was made of the significance of the migration rate of individuals in the regulation of intensivity of penetration of a given section of the population's area. Study areas were marked out in a pine wood and the imagines of *Carabus arcensis* Hrbst. and *Pterostichus niger* Schall. caught in traps in these areas were marked with individual numbers. Observations were next made of the rate at which they left the study area. It proved that with increasing intensivity of penetration of the habitat by part of the individuals — expressed by a decrease in the rate of their disappearance — the percentage of individuals not penetrating that habitat increased.

Publications have appeared of recent years containing descriptions of the migrations of *Carabidae* from one habitat to another. K a b a c i k (1957) in studying the seasonal variations in the number of individuals of *Carabus arcensis* Hrbst. caught in a pine wood and in the clearing adjacent to it reached the conclusion that this species periodically migrates between the two habitats referred to above. T h i e l e (1960) writes that many small field *Carabidae* migrate from fields to shelter belts. Some species migrate there for the winter and others — such as *Nebria brevicollis* F. — to lay eggs. This same author (T h i e l e 1960) observed during studies of the distribution of *Carabidae* in

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cultivated fields that marked individuals of *Pterostichus vulgaris* L. migrated between the field and fringe of shelter belts. According to my investigations (Grüm 1962) the areas of occurrence of imagines and larvae of several species of the genus *Carabus* L. and *Pterostichus* Bon. living in the mosaic of forest habitats in the Kampinos Forest, do not completly coincide, which causes yearly migrations of adult insects. The above authors searched for the sources of migrations of *Carabidae*, finding them in the differences in the habitat and the degree of attraction, varying periodically, of its elements.

The present study, in which the question of the effect exerted by habitat structure on the migrations of *Carabidae* has been omitted, is concerned with the significance of the migration rate of individuals in the regulation of intensivity of penetration of the investigated section of the population's collected for the regulation processes taking place within the area. The answer to this question was supplied by analysis of the rate at which marked individuals of *Carabus arcensis* Hrbst. and *Pterostichus niger* Schall. left the study area.

AREA AND METHODS

The investigations were made in the east part of the Kampinos Forest near the field station of the Institute of Ecology, Polish Academy of Sciences. A total of 80 traps, i.e. jars with tops 6 cm in diameter, were sunk into the ground at intervals of 2.5 m in a pine wood about 40 years old, situated in the middle of varied forest habitats. The area covered by the chequerboard arrangement of the traps was approximately 400 m², while the pine wood in which the study area was several times greater in area. The individuals

Comparison of number of marked and recaptured individuals

Tab. I

Number of individuals	C. arcensis	P. niger
Marked	244	563
Caught once only (not recaptured)	165	401
Caught twice three times four times five times	60 14 4 1	111 44 4 3

of *Carabidae* which fell into the traps were marked with individual numbers (Grüm 1959) and immediately set free near the trap in which they had been caught. Not all the individuals were marked; on account of the possible injury which might be caused, young imagines and which therefore still had very fragile elytra, were not marked. During inspection of the traps new individuals were marked and the numbers recorded of the imagines recaptured

(and previously marked). Inspections were made from May 15th to September 30th, i.e. during the period of abundant occurrance of insects belonging to this family. The traps were inspected every 4 days from 1956 to 1960. A total of 166 inspections was made, during which 244 individuals of *C. arcensis* and 563 of *P. niger* were marked. Some of these marked insects were recaptured (Tab. I). Unmarked young individuals of *C. arcensis* were caught 35 times and similar individuals of *P. niger* 307 times.

DESCRIPTION OF THE REPRESENTATIVE CHARACTER OF THE MATERIAL

Bearing in mind the representative character of the information collected for the regulation processes taking place within the area of the population, the area was defined and a description given of way the area in which an individual moves about between its first and last capture is penetrated. Those individuals of insects marked during investigations which were caught at least once after marking (Tab. I) were taken into consideration. In order to describe the homogeneity of the area penetrated by an individual during the above period of its life, the study area was divided into two parts of equal size and uniform shape (*A* and *B*), each containing 40 traps. A more or less uniform number of individuals recorded for the first time on the study area, were caught in each of these parts. Deviations were as much as 3.2% in the case of *C. arcensis* and 1.6% in that of *P. niger*. The probability that the first capture of an individual will take place in part *A* is therefore 0.5. Thus, if the individual is able to move freely over the whole area, then the probability of catching the same individual for a second time in part *A* is equal to 0.25, for the third time 0.125 etc. The probability of its always being caught in part *B* therefore alters similarly with an increase in the number of captures per individual. Thus the probability of catching all the returning individuals always in the same part in which the first capture was made is, in the case of individuals caught twice – 0.5, in those caught three times – 0.25, four times – 0.125 etc. On the basis of the above reasonings calculation was made of the number of individuals caught twice, three times, four times and five times, the next capture of which should take place only in one part of the study area. This is the product of the number of all *n* times caught individuals and the probability of their being caught always in the same part of the study area. The above sequence of figures obtained theoretically was compared using the χ^2 test with the empirical sequence obtained by comparing the number of individuals actually caught in one part only of the area. The results of this comparison indicate that there are no statistical differences between these two sequences (Tab. II). On these grounds the conclusion was drawn that the individual penetrates the area of the study plot at random.

A check was made to see whether the individual leaves the study area

Comparison of the anticipated number of individuals which should be caught exclusively in one part of the study area, with the number of individuals actually caught only in one of the parts

Tab. II

	C. arcensis				P. niger			
Number of captures (n) per individual	2	3	4	5	2	3	4	5
Number of individuals caught a given number (n) of times	60	14	4	1	111	44	4	3
Probability of catching an individual only in one of the two parts of the study area (p)	0.500	0.250	0.125	0.062	0.500	0.250	0.125	0.062
Number of individuals which should be caught exclusively in one part of the study area (a); $a = p \; n$	30.00	3.50	0.50	0.06	55.50	11.00	0.50	0.19
Number of individuals actually caught in one only of the parts of the study area (b)	36	4	1	0	58	9	1	1
$\dfrac{(b - a)^2}{a}$	1.200	0.216			0.113	0.041		
χ^2 with one degree of freedom	1.416				0.154			
$\chi^2 \; \alpha \; 0.05$	3.841				3.841			

Comparison of the anticipated and actual number of those pairs of captures in which the second capture takes place in the external zone of the study area

Tab. III

Zone of the first of pairs of successive captures	Number of days between two consecutive captures	Species	Total number of pairs of consecutive captures	Probability of occurrence of second capture from pair in the external zone of the study area	Number of those pairs of captures in which the second capture takes place in the external zone of the study area	
					anticipated	actual
External	8	C. arcensis	29	0.48	13.9	15
		P. niger	79	0.55	43.4	47
	12	C. arcensis	23	0.48	11.1	15
		P. niger	44	0.55	24.2	24
Internal	8	C. arcensis	29	0.48	13.9	12
		P. niger	67	0.55	36.8	29
	12	C. arcensis	23	0.48	11.1	12
		P. niger	33	0.55	18.1	18

between two successive captures. For this purpose two zones were distinguished in the area – an external zone composed of the 32 extreme traps, and an internal zone, containing 48 traps arranged in the centre of the area. It was found that the number of individuals caught for the first time – i.e. marked individuals (Tab. I) – is not distributed proportionately to the number of traps in the zone, that is, calculated for one trap, the number of individuals caught for the first time is greater in external zone (*C. arcensis* 3.65 and *P. niger* – 9.64) than in the internal zone (*C. arcensis* – 2.64 and *P. niger* – 5.29). This distribution of the number of captures per trap is evidence that individuals caught for the first time migrate beyond the area of the study plot. Among the individuals of *C. arcensis* entering the plot 117 (48%) were caught in the external zone, and 127 (52%) in the internal zone. Corresponding figures for the individuals of *P. niger* entering the plot are 309 (55%) and 254 (45%). Therefore the probability of capture of an individual entering the plot, in the external zone is 0.48 for *C. arcensis* and *P. niger* 0.55.

If the individual migrates beyond the study area between a pair of successive captures, then the second capture from the given pair should take place in the external zone, with a probability of 0.48 for *C. arcensis* and 0.55 for *P. niger*. If the individual did not leave the plot between two successive captures, then the second capture from the given pair should take place primarily in the internal zone, containing 60% of all the traps. In analysing the agreement of the material with the model worked out, comparison was made of the actual number of such pairs of captures, in which the second capture took place in the external zone of the study plot and the anticipated number. This last is the product of probability of capture in the external zone of an individual entering the plot and the total number of pairs of captures. The location of the first of a pair of captures and the time interval between both captures were taken into consideration in the above calculations. The data given in Table III points to the generally slight differences between the expected and actual number of such pairs of captures, in which the second capture took place in the external zone of the plot.

A slightly smaller number of captures than that anticipated was obtained in the case in which the first capture of a pair took place in the inner zone and the time interval between the captures did not exceed 8 days (Tab. III). Therefore marked individuals also penetrate the area lying outside the study plot between consecutive captures.

The analyses made show that the study plot is a homogenous spot situated within the population's area and is representative of the phenomena taking place within the living area.

RATE OF DISAPPEARANCE OF INDIVIDUALS FROM THE STUDY PLOT

The rate of disappearance, defining the rate at which marked individuals leave the study plot, was calculated separately for *C. arcensis* and *P. niger*.

Calculations were made for several years. It was expected that the results would not be uniform during periods of decrease and increase in the number of captures of all individuals (marked and unmarked), since it was assumed that the increase and decrease in the number of captures is determined to a great degree by the migration processes taking place in both species. For this reason the period of occurrence of imagines of *P. niger*, including both increase and decrease in number of captures, was divided into two shorter periods of time. The first of these (from July 1st to August 15th) is characterised by an initial rapid increase in the number of captures and then by stabilisation of this number (Fig. 1). The second (from August 16th to September 30th) covering a continuous decrease in the number of captures.
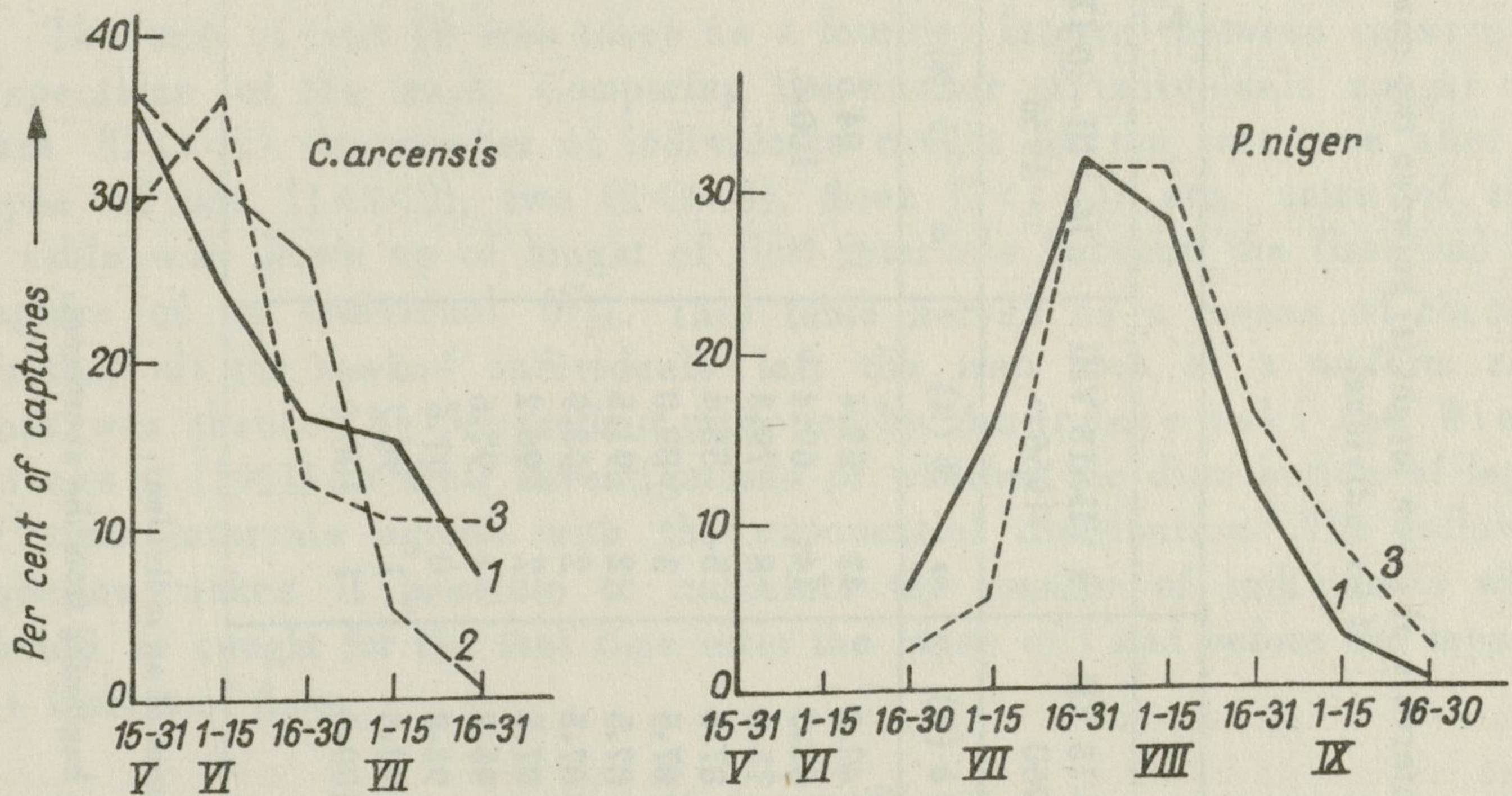

Fig. 1. Seasonal variations in number of captures
1 — 1956, *2* — 1957, *3* — 1960
Percentage of captures calculated from the total number of captures in a given year

The period of appearance of *C. arcensis* was not divided into shorter sections, since the number of captures of this species — caught from May 15th to July 15th — constantly decreased (Fig. 1). On account of the necessity for corresponding division of the material, only part complied with the conditions for statistical elaboration.

Estimate of the rate of disappearance was made on the basis of a knowledge of the time interval between the first and last captures of an individual. Since individuals caught towards the end of each of the periods previously distinguished had a negligible chance of being recorded during the same period, it was necessary to omit them from the calculations. They would otherwise increase the number of non-returning individuals, which would affect the correctness of the conclusions reached. In order to define the number of final captures in which individuals caught for the first time had less than 0.90 chances of recapture, analysis was made of the length of

Comparison of number of time intervals of given lenght (*t*) between two consecutive captures
of an individual

Tab. IV

t	C. arcensis						P. niger						
	15 V–15 VII 1956		15 V–15 VII 1957		15 V–15 VII 1960		1 VII–15 VIII 1956		16 VIII–30 IX 1956		1 VII–15 VIII 1960		16 VIII–30 IX 1960
	a	*b* (%)	*a*	*b* (%)	*a*	*b* (%)	*a*	*b* (%)	*a*	*b* (%)	*a*	*b* (%)	*a*	*b* (%)
1	6	20.7	6	30.0	7	43.8	43	52.4	11	84.6	29	43.9	7	43.8
2	7	44.8	4	50.0	3	62.5	14	69.4	2	100.0	12	62.0	5	75.0
3	5	62.0	0	50.0	2	75.0	8	79.3			5	69.5	2	87.5
4	3	72.3	3	65.0	2	87.5	5	85.4			1	71.1	1	93.8
5	3	82.7	3	80.0	0	87.5	3	89.0			7	81.7	1	100.0
6	0	82.7	1	85.0	0	87.5	2	91.5			1	83.2		
7	2	89.5	1	90.0	0	87.5	2	93.9			4	89.3		
8	1	93.0	0	90.0	0	87.5	2	96.2			3	94.0		
9	0	93.0	1	95.0	1	93.8	1	97.6			1	95.3		
10	1	96.5	0	95.0	0	93.8	0	97.6			2	97.4		
11	0	96.5	1	100.0	0	93.8	1	98.7			0	97.4		
12	1	100.0			1	100.0	1	100.0			0	97.4		
13											0	97.4		
14											1	100.0		

t — length of time interval between two cousecutive captures of an individual.

a — number of time intervals of given length.

b — percentage formed by all time intervals up to present, beginning from the shorterest.

interval between two consecutive captures of an individual. Calculation was made separately for each period of the total number of intervals and the percentage of intervals of t length of four-day units of time ($t - 1, 2, 3, \ldots n$). Next, beginning with the shortest intervals, the results obtained were summed up to 90% (Tab. IV). The period of time, which included 90% of the intervals after lapse of which a marked individual, if it did not die or emigrate, would be caught with a probability of 0.90, was defined in this way. When calculating disappearance rate only those individuals which had chances of recapture of 0.90, that is, marked during the initial captures, were taken into consideration. The remaining individuals – marked in several of the final captures – with less than 0.90 chances of repeat recording in a given period, were omitted from the calculations.

The unit of time (t) was taken as a four-day interval between consecutive inspections of the traps. Comparing the number of individuals caught only once ($0 < t < 1$), the number of individuals caught for the last time after the lapse of one ($1 < t < 2$), two ($2 < t < 3$), three ($3 < t < 4$) etc. units of time, a table was drawn up of lenght of time intervals between the first and last capture of an individual ($\bar{N}_t$). This table served as a means of checking whether all the marked individuals left the trap area at a uniform rate. This was checked by the method proposed by A n d r z e j e w s k i and W i e r z-b o w s k a (1961) in their investigations of whether the distribution of length of time intervals agrees with the exponential distribution. The following equation makes it possible to calculate the number of individuals which should be caught for the last time after the lapse of t and before the lapse of $t + 1$ units of time:

$$\bar{N}'_t = N_o \left(1 - e^{-P}\right) e^{-Pt},$$

where

N_o – number of marked individuals

$p = \dfrac{1}{\bar{t}_o}$ – coefficient of disappearance rate

$\bar{t}_o = \dfrac{\displaystyle\sum_{t=0}^{m} \bar{N}_t (t + 0.5)}{N_o}$ – mean time interval between

the first and last captures of an individual. The two sequences of figures obtained in this way – one empirical, composed of values $\bar{N}_t$, and the seeond theoretical represented by values $\bar{N}'_t$ – were compared with each other by means of Pearson's test of agreement $\chi^2 =$

$$\sum_{t=0}^{m} \frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$$

On account of the small number of marked individuals verification of the observed values χ^2 were made by comparison with the mean value χ^2, i.e. $E(\chi^2) = r - 1$ and standard deviation

$$D^2(\chi^2) = 2(r - 1) + \frac{1}{N_0}\left(\sum^r_{i=1}\frac{1}{p} - r^2 - 2r + 2\right)$$

Calculations show that the *C. arcensis* population in 1960 and the *P. niger* population during the period from August 16th to September 30th 1956 are composed of individuals characterised by a uniform disappearance rate (Tab. V). In the remaining periods it was not until individuals caught once only ($0 < t < 1$) had been omitted from the empirical sequence that agreement was shown between the distribution of time intervals of the remaining group of individuals and the exponential distribution. For the sequence omitting individuals caught once the number of individuals which ought to be caught for the last time after the lapse of t and before the lapse of $t + 1$ units of time, is defined by the formula:

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

where

N_1 — number of individuals recaptured,

$$p = \frac{1}{\bar{t}_1 - 1},$$

$$\bar{t}_1 = \frac{\sum^m_{t=1}\overline{N}_t(t + 0.5)}{N_1}$$

For comparison of sequences of numbers $\overline{N}_t$ and $\overline{N}_t''$ Pearson's test of agreement χ^2 was used, and verification of the values χ^2 observed was made in the same way.

The results of the above calculations point to the occurrence in the populations examined of two groups of individuals (Tab. VI):

1. group I — with a more rapid disappearance rate, termed in further part of this study "ephemeral", and composed of individuals caught only once.

2. a group of individuals leaving the study plot more slowly — "locals" the penetration of which is concentrated round the study plot. This group includes individuals caught several times over, and part of the individuals caught only once.

The number of individuals included in the "local" group was determined for populations composed of the, above two groups: $N_0'' = N_1 e^p$, coefficient of disappearance rate (p), mean time interval between the first and last capture

Statistical analysis of distribution of intervals of time from first
to last capture of an individual

Tab. V

t	$\bar{N}_t$		$\bar{N}'_t$		$\dfrac{(\bar{N}t - \bar{N}'t)^2}{\bar{N}'_t}$	$\bar{N}_t$	$\bar{N}'_t$	$\dfrac{(\bar{N}t - \bar{N}'t)^2}{\bar{N}'_t}$
0	9	9	6.07	6.07	1.415	45	42.62	0.132
1	3		4.31			9	11.23	0.442
2	2	6	3.07	9.56	1.325	3	3.03	0.001
3	1		2.18					
4	3		1.55					
5	1		1.10					
6	0		0.78	5.10	0.159			
7	0	6	0.56					
8	0		0.39					
9	0		0.28					
10	0		0.20					
11	0		0.14					
12	2		0.10					
$\sum$	21		20.73		2.899	57	56.88	0.575

C. arcensis 15 V—15 VII 1960	P. niger 16 VIII—30 IX 1956
$\chi^2 = 2.899$	$\chi^2 = 0.575$
$E(\chi^2) = 2$	$E(\chi^2) = 2$
$D^2(\chi^2) = 3.443$	$D^2(\chi^2) = 3.840$

of the individual $(\bar{t}_1)$ and its variances $S_{(\bar{t}_1)} = \dfrac{1}{\sqrt{N_o''}\; p}$. Calculation was also

made of coefficients of disappearance rate (p) in populations composed of
individuals with uniform disappearance rate from the study plot, mean time
interval between the first and last capture of the individual $(\bar{t}_o)$ and its

variance $S_{(\bar{t}o)} = \dfrac{1}{\sqrt{N_o}\; p}$. Detailed reasonings on the subject of the above means

of mathematical analysis of disappearance are to be found in the study by
Andrzejewski and Wierzbowska (1961), from which all the formulas
were taken.

The influence of mortality on the length of interval between first and last
capture of an individual is obvious, yet this fact would not seem to throw
any doubt on correctness of conclusions as to the division of the populations
into ephemeral and local individuals, correctness based on the reasoning
detailed below: if only disappearance rate is to be decisive in distinguishing
between emphemeral and local groups, then individuals re-emigrating the

Statistical analysis of distribution of intervals
(omitting individuals

| | C. arcensis | | | | | | | |
| | 15 V–15 VII 1956 | | | 15 V–15 VII 1957 | | | | |
t	$\bar{N}_t$	$\bar{N}''_t$	$\dfrac{(\bar{N}_t-\bar{N}''_t)^2}{\bar{N}''_t}$	$\bar{N}_t$	$\bar{N}''_t$	$\dfrac{(\bar{N}_t-\bar{N}''_t)^2}{\bar{N}''_t}$	t	$\bar{N}_t$
1	0 } 6	4.59 } 7.50	0.300	5 5	5.05 5.05	0.001	1	11 11
2	6	2.91		3	3.00		2	7 } 11
3	2	2.32		0 } 6	2.31 } 8.47	0.720	3	4
4	1 } 7	1.85 } 5.64	0.327	1	1.78		4	1
5	4	1.47		2	1.38		5	2 } 9
6	0	1.17		1	1.06		6	4
7	2	0.94		2	0.82		7	2
8	0	0.75 } 4.62	0.031	0 } 6	0.63 } 3.66	1.495	8	4
9	0 } 5	0.60		2	0.49		9	0 } 8
10	2	0.48		0	0.37		10	2
11	0	0.38		1	0.29		11	1
12	1	0.30					12	1
							13	
							14	
							15	
							16	
							17	
$\sum$	18	17.76	0.658	17	17.18	2.216	$\sum$	39

$$\chi^2 = 0.658 \qquad\qquad \chi^2 = 2.216$$
$$E(\chi^2) = 2 \qquad\qquad E(\chi^2) = 2$$
$$D^2(\chi^2) = 3.520 \qquad\qquad D^2(\chi^2) = 3.319$$

following year (Grüm 1962) will be recorded in a number proportionate to the numerousness of these groups. On the other hand if the ephemeral group is to be distinguished on the basis of the high mortality in part of the marked population, then individuals re-emigrating the following year will come mainly from local group. Data given in Table VII, although limited, since they refer only to imagines marked in the period 1956—1957, and that on account of failure to explore the study plot in 1961 — indicate the proportionality of the number of re-emigrating individuals to the numerousness of the groups from which they originate.

of time from first to last capture of an individual
caught only once)

Tab. VI

P. niger								
1 VII–15 VIII 1956			1 VII–15 VIII 1960			16 VIII–30 IX 1960		
$\bar{N}''_t$	$\bar{N}''_t$	$\dfrac{(\bar{N}_t-\bar{N}''_t)^2}{\bar{N}''_t}$	$\bar{N}_t$	$\bar{N}''_t$	$\dfrac{(\bar{N}_t-\bar{N}''_t)^2}{\bar{N}''_t}$	$\bar{N}_t$	$\bar{N}''_t$	$\dfrac{(\bar{N}_t-\bar{N}''_t)^2}{\bar{N}''_t}$
11.18	11.18	0.002	7 } 10	7.45 } 11.95	0.319	0 } 5	2.87 } 5.56	0.056
6.75	12.00	0.083	3	4.50		3	1.55	
5.25			3 } 8	3.49 } 9.96	0.385	2	1.14	
4.08	11.62	0.590	0	2.72		0 } 3	0.82 } 2.22	0.267
3.17			5	2.11		1	0.62	
2.46			0	1.64		1	0.45	
1.91			0 } 8	1.28 } 5.36	1.300	1	0.33	
1.49	4.79	2.150	3	0.99				
1.16			3	0.77				
0.90			0	0.60				
0.70			1	0.47				
0.54			0	0.36				
			0	0.28				
			0	0.21				
			0	0.17				
			0	0.13				
			1	0.10				
39.59		2.825	26	27.27	2.004	8	7.78	0.323

$X^2 = 2.825$ $X^2 = 2.004$ $X^2 = 0.323$
$E(X^2) = 3$ $E(X^2) = 2$ $E(X^2) = 1$
$D^2(X^2) = 5.483$ $D^2(X^2) = 3.574$ $D^2(X^2) = 2.353$

Proportionality of the number of individuals re-emigrating in relation
to the numerousnes of the groups from which they originate

Tab. VII

Species	Group	Numerousness of groups	Percentage of the re-emigrating individuals
C. arcensis	ephemeral	69	13.04
	local	35	14.28
P. niger	ephemeral	54	3.70
	local	39	2.56

SUMMARY AND DISCUSSION OF RESULTS

As can be seen from the literature discussed in the introduction, the sources of migrations of the species of *Carabidae* examined must be sought for in the different suitability of the elements of the mosaic habitat for larvae and imagines. Presumably the differences in the habitat also determine the distance covered by the individuals. Although the distance covered by migrations was not examined in the present investigations, it may be taken that individuals leaving the study plot go beyond the borders of the pine wood in which the traps were set. This is borne out be the slight differences in this wood and its limited area — limited in relation to the area of the plot and to the capacities of *Carabidae* for migration — making it comparatively easy to check whether a given individual is present or not.

Let us consider the reasons for the division observed in the populations of *C. arcensis* and *P. niger* into ephemeral and local individuals. The following relation can be observed between the disappearance rate of local individuals and the percentage of ephemeral individuals in the *C. arcensis* population: the decrease in the disappearance rate of local individuals, i.e. concentration of their migrations round the study plot is concomitant with an increase in the percentage of ephemeral individuals, which only pass through the study plot (Tab. VIII). In cases where there is no division of the population of this species into ephemeral and local individuals, the disappearance rate of the whole population is most rapid. A similar relation is found in the *P. niger* population, comparing data for the period August 16th to September 30th in 1956 and 1960. Thus in 1956 when the population was divided into ephemeral and local individuals, the disappearance rate of all individuals is many times more rapid than the disappearance rate of local individuals in the population of this species divided into emphemeral and local insects in 1960. From July 1st to August 15th in 1956 and 1960 the disappearance rate of local individuals of *P. niger* was indentical, and the percentage of ephemeral individuals differed very slightly (Tab. VIII).

The relation between the percentage of ephemeral individuals and the disappearance rate of local individuals produces the regulating character of the division of the population into two groups of individuals, differing as to disappearance rate. With the increase in concentration of migrations of part of the individuals around the study plot — expressed by decrease in their disappearance rate — there is an increase in the percentage of ephemeral individuals, rapidly leaving the study plot. Thus if intensivity of penetration of a certain part of the population's area increases in part of the individuals, then their number decreases and the number of individuals not penetrating this particular part of the area increases.

Correlation between the disappearance rate and total number of captures of all individuals, both marked and unmarked, was observed in the population of *C. arcensis*. When the total number of captures is small, the population

Disappearance rate and quantitative proportions between groups of individuals with different disappearance rates

Tab. VIII

	C. arcensis			P. niger			
	15 V–15 VII			1 VII–15 VIII		16 VIII–30 IX	
	1956	1957	1960	1956	1960	1956	1960
Coefficient of disappearance rate (p)	0.227	0.260	0.341	0.252	0.252	1.310	0.307
Mean time between first and final captures of an individual ($\bar{t}$)	4.39	3.85	2.93	3.96	3.96	0.76	3.25
Variance of mean time ($S_{\bar{t}}$)	0.926	0.820	0.641	0.558	0.684	0.101	0.990
Number of marked individuals	66	38	21	93	47	57	43
Number of individuals included in local group (N_o''')	22.59	22.05	absence of division into groups with different disappearance rates	50.18	33.45	absences of division into groups with different disappearance rates	10.87
Percentage of local individuals	34.2%	58.0%		53.9%	71.1%		25.3%
Percentage of ephemeral individuals	65.8%	42.0%		46.1%	28.9%		74.7%
Total number of captures of marked and unmarked individuals	126	86	41	411	190	75	99

is not divided into ephemeral and local individuals, and its disappearance rate is most rapid. With an increase in the total number of captures the percentage of ephemeral individuals rises and the disappearance rate of local individuals decreases (Tab. VIII). The total number of captures — depending on population density and the mobility of individuals (Heydemann 1953, M. Kaczmarek and W. Kaczmarek 1956) provides a good description of the microclimatic suitability of the habitat for *Carabidae* (Thiele and Kolbe 1962, Thiele 1964). It may therefore be concluded that the population of *C. arcensis* divides into ephemeral and local individuals under favourable habitat conditions.

REFERENCES

1. Andrzejewski, R., Wierzbowska, T. 1961 — An attempt at assessing the duration of residence of small rodents in a defined forest area and the rate of interchange between individuals — Acta Ther. 5: 153—172.
2. Grüm, L. 1959 — Sezonowe zmiany aktywności biegaczowatych (*Carabidae*) — Ekol. Pol. A, 7: 255—268.
3. Grüm, L. 1962 — Horizontal distribution of larvae and imagines of some species of *Carabidae* — Ekol. Pol. A, 10: 73—84.
4. Heydemann, B. 1953 — Agrarökologische Problematik, dargetan an Untersuchungen über die Tierwelt der Bodenoberfläche der Kulturfelder — Diss. Kiel.
5. Kabacik, D. 1957 — Z badań nad biegaczowatymi (*Carabidae*) lasu sosnowego — Ekol. Pol. B, 3: 239—242.
6. Kaczmarek, M., Kaczmarek, W. 1956 — O metodyce badań zoocenotycznych w zakresie zbiorów ilościowych naziemnej fauny bezkręgowców — Ekol. Pol. B, 2: 131—136.
7. Thiele, H—U. 1960 — Gibt es Beziehungen zwischen der Tierwelt von Hecken und angrenzenden Kulturfeldern? — Z. angew. Entomol. 47: 122—127.
8. Thiele, H—U. 1964 — Experimentelle Untersuchungen über die Ursachen der Biotopbindung bei Carabiden — Z. Morph. Ökol. Tiere 53: 387—452.
9. Thiele, H—U., Kolbe, W. 1962 — Beziehungen zwischen bodenbewohnenden Käfern und Pflanzengesellschaften in Wäldern — Pedobiologia 1: 157—173.

ZNACZENIE TEMPA PRZEMIESZCZEŃ OSOBNIKÓW W REGULACJI INTENSYWNOŚCI PENETROWANIA ŚRODOWISKA PRZEZ POPULACJE DWU GATUNKÓW
CARABIDAE: CARABUS ARCENSIS HRBST.
I *PTEROSTICHUS NIGER* SCHALL.

Streszczenie

Analizowano znaczenie tempa przemieszczeń osobników w regulacji intensywności penetrowania badanego wycinka areału populacji. W lesie sosnowym założono poletko badawcze, na którym znakowano indywidualnymi numerami łowione w pułapki imagines *Carabus arcensis* Hrbst. i *Pterostichus niger* Schall. Następnie śledzono, w jakim tem-

pie opuszczają one poletko. Metodę oceny tempa opuszczania poletka badawczego (tempa ubywania) przyjęto za Andrzejewskim i Wierzbowską (1961). Jak się okazało, w miarę wzrostu intensywności penetrowania środowiska przez część osobników — wyrażonego spadkiem tempa ich ubywania — w populacji rośnie procent osobników nie penetrujących tegoż środowiska.

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