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SPATIAL DIFFERENTIATION OF THE *CARABUS* L.
(*CARABIDAE*, *COLEOPTERA*) MOBILITY

(Ekol. Pol. 19: 1-34). Changes of the mobility of individuals within the area of the ecological population were investigated. The investigations concerned two predatory species of the genus *Carabus* L. In the optimum sites with relatively high population density, where the probability of attack is small, hungry individuals are characterised by a considerable mobility which causes their emigration to the peripheries of the area. On the peripheries of the area, where the population density is low and where is a great probability of attack, the mobility of individuals does not decrease after feeding. In effect the satiated individuals reemigrate to optimum sites, where they show small mobility. The emigration of hungry individuals and the reemigration of satiated individuals seems to be a way of regulating the energy balance of the *Carabus* population in optimum sites with high population density.

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1. INTRODUCTION

One of the basic assumptions of density-dependent reduction of the prey population by the predator population is the dependence of reduction rate on the probability of meetings of predator and prey individuals. It was formulated by Lotka (1923), who expressed the number of attacked prey individuals by the product of the density of prey population, density of predator population and a constant called by him the coefficient of attack. Also the later equations of Thompson (1924), Bailey (1931) and Nicholson and Bailey (1935), who describe a quantitative dependence among the prey population (host) and predator one (parasite), are based on the assumption that the predators move by chance and they attack every met prey individual. Thus the attacked number is a function of the population densities of both components of the relationship, and a constant which characterises the rate of prey searching.

The assumption of the constant rate of searching for prey by predator (or constant coefficient of attack) was criticized by many authors (Thompson 1939, Ulyett 1953, Andrewartha and Birch 1954, Watt 1959), which led to the construction of mathematical models with certain limitation of the mentioned parameter (Gause 1934, Watt 1959).

In the successive publications by Holling (1961, 1964, 1965, 1966) an analysis of the predation process was presented in detail. This author used the Solomon's (1949) division into functional responses determining the number of attacked prey individuals per one predator, and numerical responses causing the changes of numerical proportion between the prey and predator populations. Due to the introduction to this scheme of the concept of basic component, i.e. the component always present in the predator-prey relation, Holling (1961) presented basic components of the functional reaction of predator on its own density and on the density of prey population. They consist of the searching rate of prey by predator, time of the exposure of prey for the predator activity, handling time of consumption and digestion of prey, and the exploitation of prey population as well as the interference among the predators.

Among the basic components of the functional response of the predator on the density of the prey population, Holling mentions the following attributes of predators: the speed with which the individuals move, and the length of their hunting activity. In the instance of *Carabidae* both these attributes change according to the weather conditions (Grüm 1959, Briggs 1961), and also hunger, thus they can have a great influence on the probability of attack.

Williams (1959) while analysing the influence of predator on the diurnal activity rhythm of predator observed that the diurnal activity rhythm of *Feronia madida* (F.) resulted from the adjustment of predators activity to the diurnal activity rhythm of its prey. Šarova (1960) mentions the diurnal activity of nocturnal predatory *Carabidae*, and this she accounts to hunger. The laboratory investigations carried out on the predatory nocturnal *Carabidae* also showed a quick increase of activity of starving individuals and gradual spreading of their activity time to day hours (Grüm 1966).

In the present investigations the mobility of *Carabidae* was expressed by the distance covered by an average individual during a unit of time, which apart from the directions of the individuals movements characterises its displacements. A directional displacement of individuals – mainly emigration – is supposed to be very important in the reduction of population density. Nicholson (1933) states, that the populations' pressure causes the emigration of a part of individuals into the zone of unfavourable environmental conditions, which increases their mortality, thus bringing the population density to the state of equilibrium with the capacity of environment. Similar views on the significance of emigration were expressed by Smith (1935), Errington (1946), Lack (1954) Lidicker (1962) and others. Thorough investigations prove the existence of two groups of individuals – residents and migrants within the population area – in the populations of birds and small mammals (Borowski and Dehnel 1952, Kalela 1954, Naumov 1956, Andrzejewski and Wierzbowska 1961). Pielowski (1962) suggests that small rodents migrating within the population area are more frequently consumed by predator than resident individuals.

Also in populations of *Carabidae* there are present two groups of individuals with different migratory tendencies (Grüm 1965), i.e. more and less mobile individuals. Increased mobility of *Carabidae* – as shown by Zimka (1966) – is a factor of exposure for the attack by frogs. Thus the mobility of individuals probably affecting the reduction of population density would change the quantitative relations among *Carabidae* and their prey, and in this way would influence the probability of attack by individuals.

Taking into account the results of above investigations a hypothesis drawn, that predatory *Carabidae* actively form their probability of attack by adequate changes of their mobility. In order to verify this hypothesis, the relations among the hunger, mobility, the direction of movements of individuals, and the probability of attack were analysed in natural conditions. Numerical values of the above variables, arranged according to the habitats with an increasing population density were investigated within the ecological areas of the populations of predatory *Carabidae*. The investigations concerned the populations of *Carabus arcensis* Hbst. and *Carabus nemoralis* Müll.

2 CHOICE AND CHARACTERISTIC OF THE AREA OF INVESTIGATIONS

The investigations were carried out in the Kampinos Forest near Warsaw, which is characterised by a considerable patchiness of environmental factors: there are two alternate ranges of dunes and marshes, and separate dunes and their groups located among the marshes (Kobendza 1930). This patchiness often causes the occurrence of relatively isolated forest biotopes of the small area, differing considerably as to the humidity and thermal conditions from the neighbouring plant associations. In such environmental conditions a majority of *Carabidae* species probably separates into a number of small but isolated ecological populations at least during the spring and early summer, i.e. in the periods of high water level in the alderwoods and marshes. It makes the investigations of the whole population area easier.

A choice of the season and biotopes, which were investigated, was made from the point of view of the possibility of sampling and quantitative characteristic of the *C. arcensis* population. This species belongs to a spring development type (Larsson 1939): copulation and laying eggs take place in May and June (this is the period of most numerous occurrence of *C. arcensis* imagines), larval development takes place during July and August, and young imagines begin to appear in autumn. *C. arcensis* was classified by Schmidt (1957) to forms with high thermal preference occurring numerously in bright, well insolated forest environments. *C. arcensis* occurs numerously in pine forests in Poland (Borusiewicz and Kapuściński 1950), and as stated by Kabacik (1957) the maximum of its activity takes place at the end of May, in June and July. This was later confirmed by observations in the Kampinos Forest (Grüm 1959, 1965, 1967).

The above informations on the environmental preference of *C. arcensis* decided about carrying out the investigations in spring and early summer, mainly in dry parts of the Kampinos Forest with pine wood. The materials were collected in the following biotopes:

1. *Pino-Quercetum* – the surface area about 4 ha and of a shape close to a rectangle about 80 to 100 m wide, with alderwood along the longer sides. The pine trees in this forest stand were about 80 years old, and the not so numerous oaks were even older. This biotope was characterised by a high patchiness of shrub stratum and herb layer. Three environments were distinguished there, and designated with symbols *Q*, *A* and *QA*. The first of them (*Q*) was located in the central part of the biotope, which was well insolated, and about 40 m far from the neighbouring *Alnetum*. The second (*A*) was situated in the ecotone of associations *Pino-Quercetum* and *Alnetum*, and it formed a long belt some meters wide, shaded by a dense hornbeam shrub stratum. The third of them (*QA*), located between these two was characterised by poor insolation due to the dense hornbeam shrub stratum.

2. *Vaccinio myrtilli-Pinetum* (PI), approximately 45 years old, about 4 ha, surrounded almost completely by *Caricetum* and alderwood. This environment was characterised by a high patchiness of the plant cover, caused by a numerous, however relatively very small, land depressions filled with water during the spring.

3. *Vaccinio myrtilli-Pinetum* (PII), approximately 35 years old, covering a large area above 10 ha, with nearly uniform herb layer and with poor shrub stratum. This biotope neighbored with the fields, mid-forest meadows, alderwood and other plant communities.

The degree of the patchiness of these biotopes can be illustrated by changes of the number of the trapped individuals of *C. arcensis*. These changes are well correlated with the described above variability of plant cover: it is high in *Pino-Quercetum* and *Vaccinio myrtilli-Pinetum* I, but low in *Vaccinio myrtilli-Pinetum* II (Tab. I).

The number variations of caught individuals of *C. arcensis* and *C. nemoralis* in three biotopes of the Kampinos Forest*

Tab. I

		The numbers of trap groups					Variation index
		I	II	III	IV	V	$Y = \frac{1}{x} \sqrt{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2}$
<i>Pino-Quercetum</i>	<i>C. arcensis</i>	47	35	57	44	22	0.287
	<i>C. nemoralis</i>	2	4	7	6	2	—
<i>Vaccinio myrtilli-Pinetum</i> I	<i>C. arcensis</i>	111	172	163	92	66	0.337
	<i>C. nemoralis</i>	2	1	0	4	8	—
<i>Vaccinio myrtilli-Pinetum</i> II	<i>C. arcensis</i>	153	170	157	168	147	0.055
	<i>C. nemoralis</i>	1	0	0	1	0	—

*In each biotope five groups of traps were placed in various places (20 traps in one group), checked from 10 th May to 9 th July 1963.

Apart from that the material was collected on a small island on the lake Bełdany, covered to a large extent by the association *Tilio-Carpinetum* (Traczyk 1965). Some of the investigations previously carried out in the Kampinos Forest were repeated here.

3. METHODS

3.1. Population density

The simplest direct method of determining the density of *Carabidae* population depends on cutting samples of a given surface out from soil and litter layer

and collecting all the animals found in it (Heydemann 1961, Kaczmarek 1963, Greenslade 1964a, Murdoch 1966a, Zimka 1966). It is, however, not very useful in the instance of populations with a low density – thus to the *Carabidae* populations – as it is necessary to collect samples from a large global area, which may lead in consequence to the modification of the environment.

Sometimes the density of *Carabidae* populations is estimated by the number of trapped individuals (Murdoch 1966b, Grüm 1967). This method allows to estimate approximately the population density only in the categories: low density – high density, as the results of trapping depend on the population density and the mobility of individuals (Heydemann 1953, Kaczmarek M. and Kaczmarek W. 1956). The other method of estimation of population density, based on the results of trapping, depends on trapping of individuals, their marking releasing and recapture. Among the others it was used by Skuhravy (1957), Grüm (1959) and Heydemann (1962). From thus obtained data the density is calculated on the basis of Lincoln (1930) equation. However, the application of this method of estimating the density of *Carabidae* is disputable because the number of recaptured individuals is usually small (Skuhravý 1957, Grüm 1959, Heydemann 1962), and the reliable estimation can be only obtained when using large surfaces with a great number of traps.

In the case of populations with relatively low densities, e.g. a population of small mammals, the number of animals living on a given area was estimated by isolation of a part of the field with a known area and by trapping all the individuals there (Gębczyńska 1966). The method of isolating an area and trapping of all individuals there allows for a single estimation of the population density, and the reliability of this method is limited as the degree of isolation of the fenced area from its surroundings is unknown.

1. The method of determining the population density used in this paper (fencing of small plots) is a development of methods of isolation and catching all individuals.

The following kinds of round plots were used: plots of a surface area 50 m², fenced by a cardboard 30 cm high, dugged 5 cm into the ground (1964). In 1965 – plots of the area 33 m², fenced in the same way; and in 1966 – plots of the area 25 m² and 125 m² fenced with a corrugated PVC, 25 cm high, also dugged 5 cm into the ground. The living traps, i.e. plastic cylinders with the diameter of the opening 5–6 cm, dugged into the ground in such a way, that their upper edge was on the ground level, were placed directly near outside and inside of the fence. On the 50 m² plots 6 such traps were dugged on both sides of the fence, on 25 m² and 33 m² plots – 5 on both sides of the fence while 11 traps were placed on both sides of the fence on 125 m² plots.

In 1964 three 50 m² plots were in use. One of them was in the *Pino-Quercetum* biotope (symbol Q50), the other in the ecotone of *Pino-Quercetum* and

Alnetum (A50), and the third one in the biotope *Vaccinio-myrtilli-Pinetum* II (PII50). In 1965, four experimental plots were investigated, each 33 m² large: in *Pino-Quercetum* (Q33), in ecotone of *Pino-Quercetum* and *Alnetum* (A33), and in two biotopes of *Vaccinio myrtilli-Pinetum* (PI33 and PII33). In 1965, 10 living traps were installed outside each plot, about 5 m far. In 1966, 6 plots were used, each 25 m² large: in *Pino-Quercetum* (Q25), in the ecotone of *Pino-Quercetum* and *Alnetum* (A25), in both communities *Vaccinio myrtilli-Pinetum* (PI25 and PII25), and on the island on lake Bełdany in biotope of *Tilio-Carpinetum*, where two plots were marked N25 and D25. Apart from that, in the *Vaccinio-myrtilli-Pinetum* biotope I and II, two 125 m² plots (PI125 and PII125) were located, both about 30 m far from the 25 m² plots. The traps were checked daily, about 10 a.m. In 1964 the traps were checked from the 27th of May to mid-June, and in 1965 from the 16th of May to 24th of June. In 1966, in the Kampinos Forest the investigations were carried out from 7th of June to 24th of June, and on the island on lake Bełdany from 19th to 31st of July.

The following procedure was applied for individuals caught in the inside and outside living traps. It was assumed, that the individuals caught outside the fence were migrating to the plot, and these caught inside were emigrating from it. The individuals caught outside (forming the group called N_0) were marked with individual numbers and released in the centre of the plot. These caught inside (forming the group called N_1) were released outside the fence.

Knowing the area of a plot, the population density was determined on the basis of the estimation of mean number of individuals present on the plot during the investigations. For the calculation of the latter the Petruszewicz's (1966) equation was used: $\bar{n} = \frac{N\bar{t}}{T}$, where: N – number of individuals immigrating into the plot during the investigations, T – time of investigations, \bar{t} – mean time of residence of individuals on the plot.

The correctness of the estimations of N and t was discussed.

Since the part of individuals released into the plot after being marked – on the average 19.6% (Tab. II) – were never trapped inside of the fence, it is not known whether the released but not trapped individuals died or escaped outside the fencing, and if so, how many of them? A part of animals not trapped inside (K_0) was trapped (K_1) outside the fencing, i.e. in traps outside of the "maternal" plot, or in traps on plots, or in additional traps (Fig. 1). The possibilities of trapping outside the fencing of individuals which escaped out of the plot can be calculated. These possibilities are determined by a proportion of the number of individuals released outside the plot after trapping them inside of the plot (N_1), to the number of these individuals trapped in consequence outside the fencing (M_1). The number of such individuals not trapped inside, which escaped without control from the plot, can be thus determined approxi-

mat as: $K_0' = \frac{N_1 K_1}{M_1}$.

The comparison of the number of individuals released in the plot (N_0) with the number caught later inside the fencing (N_1)

Tab. II

Year	<i>Pino-Quercetum</i>			Ecotone of <i>Alnetum</i> and <i>Pino-Quercetum</i>			<i>Vaccinio myrtilli-</i> <i>Pinetum I</i>			<i>Vaccinio myrtilli-</i> <i>Pinetum II</i>				Σ
	1964	1965	1966	1964	1965	1966	1965	1966		1964	1965	1966		
Symbol of the plot	Q50	Q33	Q25	A50	A33	A25	PI33	PI25	PI125	PII50	PII33	PII25	PII125	
Surface in m ²	50	33	25	50	33	25	33	25	125	50	33	25	125	
Total number of traps	12	10	10	12	10	10	10	10	22	12	10	10	22	
<i>C. arcensis</i> N_0	32	27	39	23	21	11	91	47	94	66	41	36	62	590
N_1	17	15	36	13	17	11	70	45	88	42	27	34	62	477
<i>C. nemoralis</i> N_0	5	26	1	34	40	5	25	1	11	7	5	1	2	163
N_1	3	22	0	27	37	4	21	1	7	2	3	1	0	128

Because $K'_0 \approx K_0$ (Tab. III), i.e. almost all not trapped individuals left the plot, thus the fencing did not isolate the plot well from its surroundings. Thus, if the fencing is not a good isolation of the plot a certain number of individuals (P) enter the plot from outside without being trapped outside the fence (Fig. 1).

The number of individuals immigrating to the plot (N) is thus higher than the number caught outside the fence (N_0). It was determined from the proportion $\frac{N}{N_0} = \frac{N_0}{N_1}$, out of which $N = \frac{N_0^2}{N_1}$. As the result of this correction the equation determining the mean number of individuals present within the fence is then

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

The mean time of individuals' residence in the plot – assuming it is equal for trapped and not trapped individuals after their release in the centre of the plot – was calculated in the following way. Let's assume the time unit to be one day, i.e. the time between two controls of traps. It was assumed, that the most probable period of residence of individual on a plot (t) was 0.5 of a day. In such instance an individual could be trapped the earliest just after being released, and the latest just before the next control day. Similarly for individuals trapped after two days since their release, the most probable period of their stay on the plot would be 1.5 of a day, and for these trapped after three days – 2.5 days, and so on. Tabulating the number of individuals caught after one day ($0 < t < 1$), two days ($1 < t < 2$), three days ($2 < t < 3$) etc., a distribution of the length of time intervals of the residence of particular individuals on the plot (\bar{N}_t) was made. Then the mean time of individuals' residence in the fenced area was calculated: $\bar{t} = \frac{1}{N_1} \sum_{t=1}^m N_t (t - 0.5)$.

When estimating the mean time of individuals' residence on the plot, two errors can be made. The first of them, leading to an overestimation of the

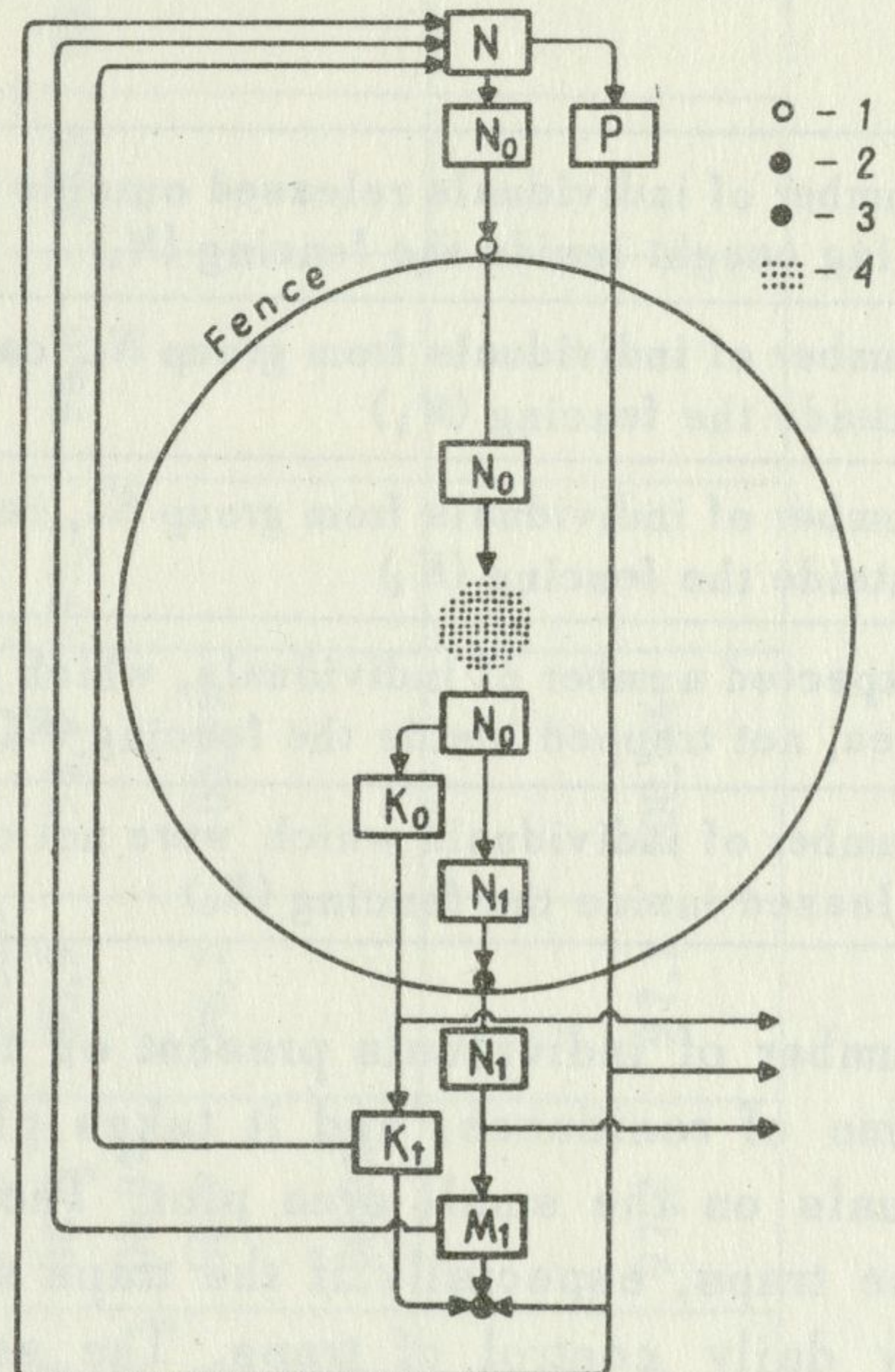


Fig. 1. Diagram of the movements of individuals against the fenced plot, N – individuals immigrating to the plot, N_0 – individuals caught in the outer traps, N_1 – individuals caught in the inner traps and then released outside the fencing, M_1 – individuals from group N_1 caught after their release outside the fence, K_0 – individuals from group N_0 not caught in the inner traps, K_1 – individuals from group K_0 caught in the traps outside the fence, P – not trapped individuals migrating across the plot, 1 – outer traps, 2 – inner traps, 3 – additional traps, 4 – centre of the plot – a place where marked individuals were released

The comparison of the expected and real number of individuals, which escaped from the plot after being released there, and were not trapped inside the fencing

Tab. III

	1964	1965	1966
Number of individuals released outside the plot after being caught inside the fencing (N_1)	104	212	289
Number of individuals from group N_1 , caught in traps outside the fencing (M_1)	9	33	19
Number of individuals from group K_0' , caught in traps outside the fencing (K_1)	5	10	1
Expected number of individuals, which left the plot area, not trapped inside the fencing (K_0')	57.7	64.2	15.2
Number of individuals which were not caught after being released inside the fencing (K_0)	63	64	21

number of individuals present on the plot, relies on the elongation of the mean time of residence, and it takes place in conditions of high mobility of individuals on the small area plot. Then the most mobile individuals stay longer in the traps, especially if the traps are not frequently checked. This was avoided by daily control of traps. The second of the possible errors – shortening of the mean time of residence – leads to an underestimation of individuals present on the plot. This error takes place when the trapping is too short to allow all released individuals to be trapped. This was avoided by additional trapping for some time after releasing in the centre of the plot of the last group of marked individuals. The number of additional trapping days was estimated for each plot separately.

The same rate of escape from the fenced area was assumed for not trapped individuals (K_0) as for those trapped after being marked (N_1). Thus the number of all individuals (N_0), which should be trapped after 1, 2, 3 m days after their release, can be illustrated with the help of the distribution of time intervals of individuals trapped inside the fence (N_1). Thus the number of days during which at least 95% of individuals of N_1 group were trapped determines the period during which at least 95% of all individuals released in the centre of the fenced plot will escape from it (Tab. IV). The traps on each plot were checked for thus determined number of days after the release of the last group of marked individuals, eliminating the possibility of shortening the mean time of the individuals' residence in a plot.

Apart from this method, which determines the population density, based on the knowledge of the number of individuals immigrating into the plot, and of the mean time of their residence, two other methods were also applied.

2. All the individuals present on the plot during fencing were caught. Probably all individuals were trapped, as the trapping lasted much longer than was necessary for catching 95% of the enclosed individuals. This method bears two possible errors. The first is the uncontrolled immigration and emigration of not marked individuals after the fencing, the second – an unrepeatably sample.

3. A method based on the number of individuals found in 100 samples of *Carabidae* hand picked from a surface 0.25 m² (i.e. from a total area of 25 m²). These samples were collected only once in 1965 near to the plots Q33, A33 and P133.

The data on the population densities for two dominant species of *Carabidae* (*C. arcensis* and *C. nemoralis*) in the material from the Kampinos Forest are not based for all the plots on the precise estimations done by the first method. The decisive factor was the number of individuals caught after marking them in traps inside the fence. The population density of *C. arcensis* was determined with the help of the first method on all 13 plots (Tab. V). The same method was applied for determining the population density of *C. nemoralis* on four plots (Tab. V). The population density of both species was determined with the help of the second method, i.e. by catching all the individuals (Tab. V). Apart from that, population densities of both these species were determined, by hand-picking, near to the three plots used in 1965 (Tab. V). The results obtained with the help of the first and second method are significantly coincident (Fig. 2). Therefore, the results obtained with the second method were used further on for the plots, where the estimations of the population density of *C. nemoralis* using the first method were not successful.

3.2. Mobility of individuals

In the investigations of *Carabidae* two methods were used to estimate the individuals mobility.

The first depended on the comparison of the number of trapped individuals with the population density. Mobility index calculated in such way is justified by the proportion of the number of trapped individuals to their mobility and population density (Heydemann 1953, Kaczmarek M. and Kaczmarek W. 1956). The character of mobility expressed by the mean length of way covered by an individual during a unit of time, acc. to Kudrin (1965) is based on the same assumption the way is directly proportional to the number of trapped individuals and inversely proportional to the total surface of traps, time of their exposure, and population density.

The second method is based on marking the individuals, and observations of their movements on the area with traps. Two variants of this method can be distinguished. a) Determining the mobility by comparison of distances and time between two consequent catches of the same individual (Greenblade

The comparison of estimations of population density (number of individuals per 100 m²) obtained with the help of three following methods:

1. Estimation of the number of individuals immigrating to the plot, and of the mean time an individual's residence there; 2. Trapping of individuals, which were on the plot at the time of fencing; 3. Hand-picking of *Carabidae* from the total area of 25 m²

Tab. V

	Method	Plots												
		Q50	Q33	Q25	A50	A33	A25	PI33	PI25	PI125	PII50	PII33	PII25	PII125
<i>C. arcensis</i>	1	4,8	3,2	36,0	2,7	1,2	2,6	12,5	30,2	32,2	15,8	29,9	9,8	11,4
	2	2	3	16	2	3	4	9	32	27,7	14	27	12	12,8
	3	—	0	—	—	0	—	8	—	—	—	—	—	—
<i>C. nemoralis</i>	1	—	1,8	—	4,8	6,5	—	1,4	—	—	—	—	—	—
	2	2	0	0	8	12	0	3	0	0,8	0	0	0	0
	3	—	4	—	—	8	—	0	—	—	—	—	—	—

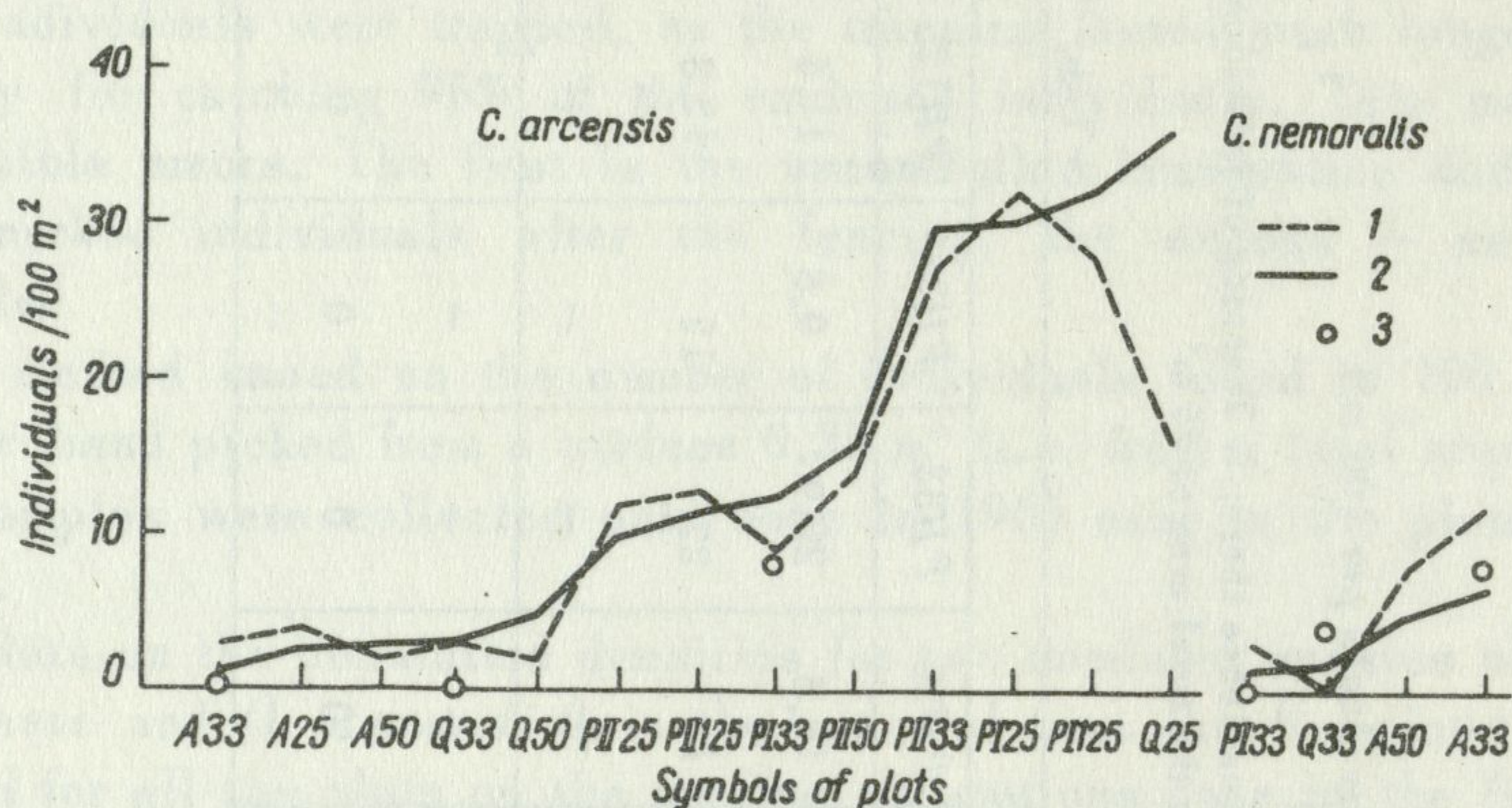


Fig. 2. The comparison of the results of three methods of population density estimation 1 - knowing N, T and \bar{t} (the first method), 2 - by catching out all the individuals (the second method), 3 - from 100 hand-pickings (the third method)

1964a, 1964b). Its basic faults are a relatively small number of trapped marked individuals (as compared with number of marked ones), and the possibility of influencing the results by the distribution of traps. b) Determination of the rate of escape of marked individuals from a certain area with traps (Grüm 1965). It is assumed here that the time between the first and last capture of an individual is inversely proportional to its mobility. This is, however, a rough estimation of mobility, because individuals can leave the area with traps between consequent catches.

In the present paper the applied method of mobility estimation takes into consideration in calculations all individuals caught after being marked in traps inside the fencing, i.e. on the average 80.4% of marked individuals (Tab. II). It was assumed that the time between the release of a marked individual in the centre of a plot and its capture in a trap inside the fence is inversely proportional to its mobility. The mean time of residence of individuals on the plot is thus inversely proportional to the average mobility of tested individuals. The method of its calculation and the way of avoiding the errors were given in chapter 3.1. The mean time of residence on bigger plots is, of course, longer for individuals with similar mobility, than that calculated for smaller plots. In order to compare the data from the plots of various areas a proportion was calculated of the shortest way between the places of release (center of a circular plot) and capture (traps of the inside of fencing) to the mean time of individuals' residence. The shortest way (d) for an individual to the nearest trap is equal to the radius of plot, and to the half of a distance between the neighbouring traps, equally distributed inside of the fencing. It is assumed here, that the individuals after reaching the fence will go along it, which is

consistent with the laboratory observations (Grüm 1966). The mobility of individuals is thus expressed by the length of the shortest way between the places of release and capture made by an individual in a unit of time: $v = \frac{d}{\bar{t}}$

The assumption about the proportion of the mean time of residence on a plot to the shortest way, necessary to compare the mobility on all investigated plots, probably loses its value with the increase of the plots area. On the plots 25 m² and 125 m², situated in biotope *Vaccinio myrtilli-Pinetum I* and *II* it was checked whether there is such a proportion. In both these biotops the plots 25 m² and 125 m² were not far one from another, and the population density of *C. arcensis*, estimated for the given environment on the basis of the data obtained from the plots of different area, was similar (Tab. V). Thus it was assumed that plots 25 m² and 125 m² situated in the same biotope did not substantially differ as to the environmental conditions, which allows to compare the results characterising mobility. As it was found, the proportion of the shortest way to the time during which it is covered did not differ much (2.98 and 3.87 m per day) for the pair of plots *PI25* and *PI125*, but for the pair *PII25* and *PII125* it was nearly the same (7.11 and 7.05 m per day). Thus the model of the shortest way allows for a comparison of mobility on plots of the area from 25 m² to 125 m².

The total length of the way covered by individuals in a unit of time was calculated apart from the mean mobility. It is a product of the population density and mean mobility of individuals, proportional to the number of individuals immigrating to the plot in a unit of time. This ecological parameter was called catchability (Kaczmarek 1963) or the population mobility (Zimka 1966).

As it was shown in the previous investigations, two groups could be distinguished among the individuals of *C. arcensis* leaving the area with traps: "resident" ones which stayed in the area of trapping for some time, and "ephemeral" individuals, quickly leaving the controlled area (Grüm 1965). In the present paper it was examined, whether these two groups, with varying mobility, i.e. leaving the plot area with different rate, could be distinguished. For this purpose the method proposed by Andrzejewski and Wierzbowska (1961) was used, which relied on the investigations of the concordance of escaping from the plot (\bar{N}_t) with exponential distribution. A lack of statistical concordance of these distributions testifies the presence of groups of individuals with different mobility.

From the following equation the number of individuals was obtained which should be caught after t , but before $t + 1$ days from their release in the center of the plot, if the distribution agrees with the exponential one: $\bar{N}'_t = N_1 (1 - e^{-p}) e^{-pt}$, where: N_1 - number of all marked and captured individuals, $p = \frac{1}{\bar{t}}$. The two obtained rows of numbers - one empirical made of \bar{N}_t values,

and the other theoretical, represented by values \bar{N}'_t - were compared one to the other with the help of χ^2 test of Pearson: $\chi^2 = \sum_{k=1}^m \frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$.

The results were verified on the level of confidence $\alpha = 0.05$. With regard to the statistical requirements of the verification of results, this analysis was made only for *C. arcensis* on the plots *PI33*, *PI125*, and *PII125*.

3.3. Directions of movements

The directions of movements of marked individuals were investigated by Dobzhansky and Wright (1947). These authors concluded about the not uniform preference of the dispersion directions of *Drosophila pseudoobscura* Fro. individuals, by comparing the empiric distribution of the number of individuals caught at the same distance from the point of their release, (but in different directions) with the curve of normal distribution. Methods proposed by Clark (1962) and Paris (1965) are also only limited to situations, where a group of marked individuals is released in the centre of the given area and then caught in points uniformly distant from the release place.

An analysis of the direction of movements was made on the basis of materials collected in biotopes of *Pino-Quercetum*, *Vaccinio myrtilli-Pinetum I* and *Vaccinio myrtilli-Pinetum II* in 1963. In each of these biotopes five groups of traps were placed, twenty traps in each. One of these groups was placed in the centre, forming a figure similar to letter T (Fig. 3). Thus the distance

among particular groups of traps varied from 6 to 63 m. The used traps had the opening 6 cm in diameter. In each group of traps certain number of marked individuals was released (N_0), part of which (N_1) was caught in traps of the neighbouring groups (Tab. VI).

The following model of investigations was used to find out whether the individuals of *C. arcensis* move by chance, or whether their movements have a determined direction. It was assumed, that in the conditions of chance movements the possibilities of catching (S) a marked individual in a trap R m far from the place of its

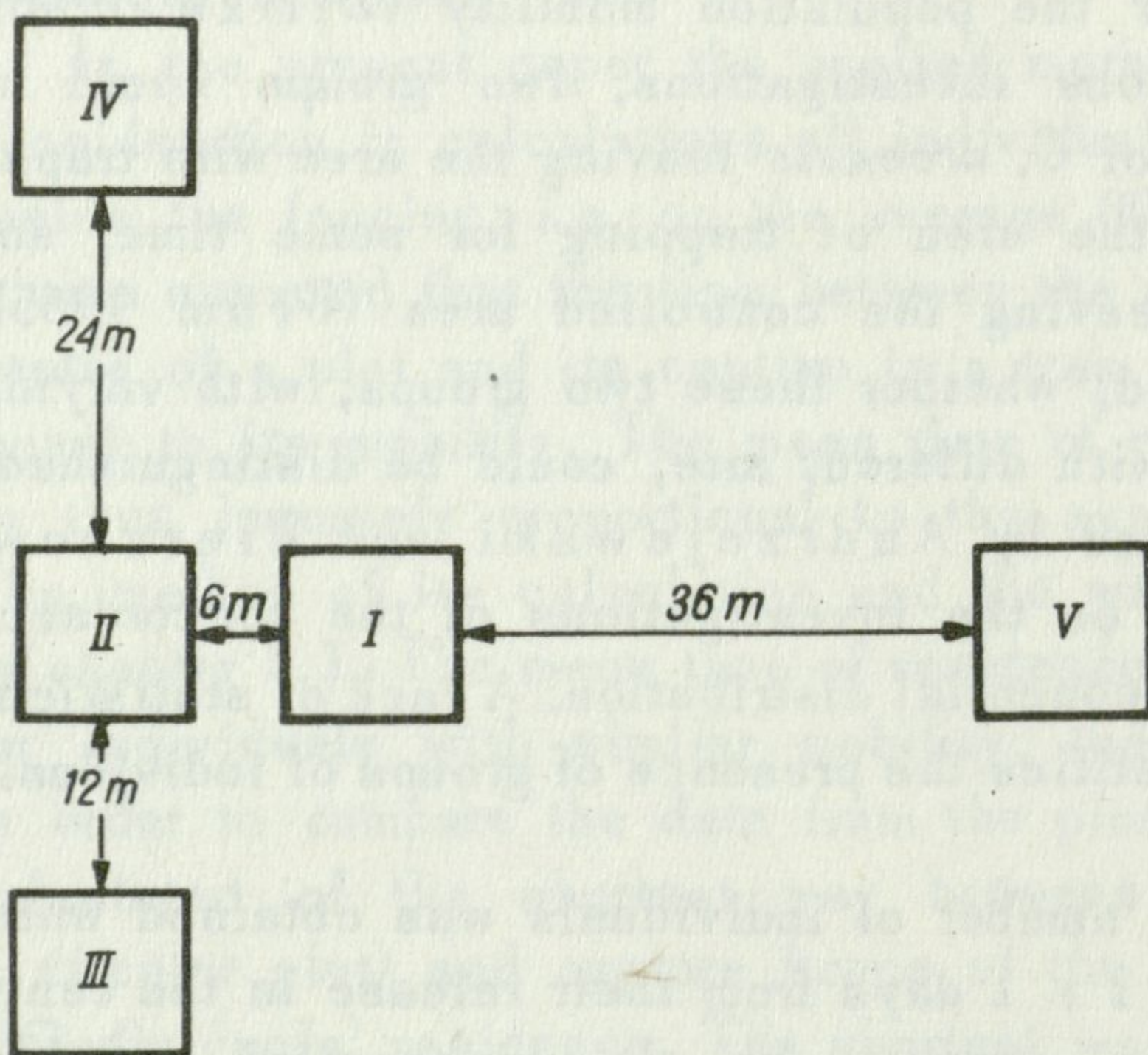


Fig. 3. Diagram of the distribution of traps in biotopes *Pino-Quercetum* and *Vaccinio myrtilli-Pinetum I* and *II*

The comparison of the number of individuals released within a given group of traps, later caught in the neighbouring groups (N_1), with the expected number of individuals which should be caught in the neighbouring groups (n_1)

Tab. VI

<i>a</i>	<i>Vaccinio myrtilli-Pinetum II</i>				<i>Vaccinio myrtilli-Pinetum I</i>				<i>Pino-Quercetum</i>			
	N_0	<i>b</i>	N_1	n_1	N_0	<i>b</i>	N_1	n_1	N_0	<i>b</i>	N_1	n_1
<i>I</i>	110	<i>II</i>	4	3.52	76	<i>II</i>	10	2.43	34	<i>II</i>	2	1.09
		<i>III</i>	3	1.21		<i>III</i>	6	0.84		<i>III</i>	1	0.37
		<i>IV</i>	1	0.77		<i>IV</i>	2	0.53		<i>IV</i>	1	0.24
		<i>V</i>	2	0.55		<i>V</i>	6	0.38		<i>V</i>	2	0.17
<i>II</i>	131	<i>I</i>	6	4.20	105	<i>I</i>	5	3.36	26	<i>I</i>	1	0.83
		<i>III</i>	5	2.10		<i>III</i>	9	1.68		<i>III</i>	3	0.42
		<i>IV</i>	1	1.05		<i>IV</i>	7	0.84		<i>IV</i>	1	0.21
		<i>V</i>	1	0.39		<i>V</i>	4	0.31		<i>V</i>	1	0.08
<i>III</i>	108	<i>I</i>	3	1.19	97	<i>I</i>	4	1.07	39	<i>I</i>	0	0.63
		<i>II</i>	4	1.73		<i>II</i>	10	1.55		<i>II</i>	2	0.91
		<i>IV</i>	3	0.43		<i>IV</i>	4	0.39		<i>IV</i>	1	0.23
		<i>V</i>	1	0.32		<i>V</i>	4	0.29		<i>V</i>	4	0.17
<i>IV</i>	118	<i>I</i>	3	0.83	60	<i>I</i>	2	0.42	33	<i>I</i>	1	0.31
		<i>II</i>	3	0.94		<i>II</i>	7	0.48		<i>II</i>	2	0.35
		<i>III</i>	1	0.47		<i>III</i>	4	0.24		<i>III</i>	1	0.18
		<i>V</i>	0	0.24		<i>V</i>	1	0.12		<i>V</i>	2	0.09
<i>V</i>	99	<i>I</i>	3	0.50	36	<i>I</i>	1	0.18	15	<i>I</i>	1	0.07
		<i>II</i>	3	0.30		<i>II</i>	6	0.11		<i>II</i>	1	0.04
		<i>III</i>	0	0.30		<i>III</i>	3	0.11		<i>III</i>	2	0.04
		<i>IV</i>	1	0.19		<i>IV</i>	1	0.07		<i>IV</i>	0	0.03

- a* — number of the trap groups, where the marked individuals were released,
b — number of the trap groups, where they were caught,
 N_0 — number of the marked and released individuals,
 N_1 — number of the captured individuals,
 n_1 — number of individuals which should be captured.

release, is determined by the ratio of the trap diameter (D) to the length of the circumference of the circle with radius R . Thus if N_0 of marked individuals is released in a certain place, the number of individuals which should be caught in the neighbouring traps (n_1) is determined by the equation $n_1 = N_0 S$. It was checked whether a number of individuals released in their "maternal" group of traps, and then caught in traps from the neighbouring group (N_1), correlated with the number expected (n_1) in the conditions of chance movements. For each group of traps the obtained numbers N_1 and n_1 (Tab. VI) were compared, the correlation coefficient was calculated for respective values N_1 and n_1 , and its significance was verified on the level of confidence $\alpha = 0.01$.

In the case of statistically insignificant correlation coefficient of values N_1 and n_1 , it was concluded, that the movements of individuals are not by chance, but they show certain direction, which is determined by the ratio of N_1 to n_1 . This ratio depends on the number of individuals moving in the direction of a given group of traps, and on their mobility. Directions of movements of individuals were arranged according to the index of population mobility (number of individuals caught in a unit of time), characterising the given group of traps. As only a small number of individuals, released in a maternal group of traps, was captured in the neighbouring groups, the mean index \bar{x} of movements' direction was calculated. This index was calculated for each of the four distinguished classes of population mobility, characterising groups of traps. The following classes of population mobility were distinguished: much lower than population mobility of the maternal group of traps, slightly lower than that, and also slightly higher and much higher than that of the maternal trap group.

3.4. Probability of attack

The following method of estimation of this variable was used, based on distinguishing the satiated individuals. It was found in the laboratory conditions that satiated individuals usually vomit their crop contents during their handling. Percentage of vomiting individuals when taking them out of traps is a good indicator of their satiation in field conditions. Marked individuals after their release in the centre of the fenced plot were additionally fed, with dead frogs, placed around the place of their release. Then the percentage of vomiting individuals, i.e. of the satiated ones was estimated out of the individuals caught outside the fencing (where no additional food was given) and out of these trapped inside the fencing. The latter had a great chance to find the food before trapping. In such way individuals of *C. arcensis* were tested on the plot P1125 (after the period of investigations for estimating their mobility and population density), and also individuals of *Pterostichus niger* Schall. caught in fencings established in July 1966 on the island on lake Bełdany.

The percentage of satiated individuals of *C. arcensis* among these caught inside and outside the fencing is almost equal (13.8% and 15.9%) before the period of additional feeding. During the feeding of *C. arcensis* the percentage of satiated individuals among those caught outside the fencing is similar as that before additional feeding (13.5%) but the percentage of satiated individuals among these caught inside is much higher (76.5%). *P. niger* individuals were additionally fed only on one (D25) of two investigated plots at the same time. On the plot with no additional food, the percentage of satiated individuals among those caught outside the fencing was twice lower than among these caught inside (5.7% and 12.0%, relatively). Percentage of satiated individuals

on the plot with additional food was, however more than 10 times higher among those caught inside than among those caught outside the fencing (70.9% and 5.7%, relatively).

Number of individuals trapped inside the fencing in a unit of time is a function of the population density and mobility of individuals, it represents thus the total length of way covered by the individuals in a unit of time. Thus, the percentage of satiated individuals among those caught outside the fencing expresses the probability of attack after covering a unit of distance by an individual.

4. RESULTS

4.1. Distribution of investigated species

The distribution of *C. arcensis* and *C. nemoralis* in some biotopes of the Kampinos Forest was investigated. Two methods were used: 1. Determination of the number of individuals caught in a unit of time in one trap. This method, frequently used (Heydemann 1961, 1964, Thiele and Kolbe 1962, Thiele 1964, Lauterbach 1964), allowed to analyse the occurrence of both species in many habitats. 2. Estimation of the population density of these species in several habitats.

The following results of trapping were at disposal: 1. Catches from 10th May to 9th of July, 1963, when 5 groups of traps checked were placed in biotopes of *Vaccinio myrtilli-Pinetum* I (PI) and II (PII) and *Pino-Quercetum* (Tab. I). Out of the five groups of traps in *Pino-Quercetum*, one was placed in its ecotone with *Alnetum* (A), two in dry and sunny part of this biotope (Q) and two in a part of *Pino-Quercetum* (AQ) several meters far from the ecotone with *Alnetum*. 2. Catches from traps with a weak dilution of formalin (25th of May-25th of September 1963, and 15th of May-4th of September 1964). Formalin traps were arranged in 5 rows, four of which were equivalent in their distribution to the four previously distinguished habitats denoted with symbols Q, QA, A and PII. One of these rows was situated in a habitat of a similar character to QA habitat. It was located on a small island within the neighbouring *Alnetum* (W). A total of 880 individuals of *C. arcensis* and 194 individuals of *C. nemoralis* were caught in formalin traps in 1963 and 1964.

On the basis of the results of trapping the following characteristic of *C. arcensis* and *C. nemoralis* distribution was given: *C. arcensis* was trapped most numerously in both biotopes of *Vaccinio myrtilli-Pinetum* (PI and PII), and the least numerously in the ecotone of *Pino-Quercetum* and *Alnetum* (A) and on the island (W) in *Alnetum*. *C. nemoralis* was trapped mainly on this island (W) and in a transitory habitat between *Pino-Quercetum* and its ecotone with *Alnetum* (QA). The lowest number of this species was caught in both biotopes *Vaccinio myrtilli-Pinetum* (Fig. 4).

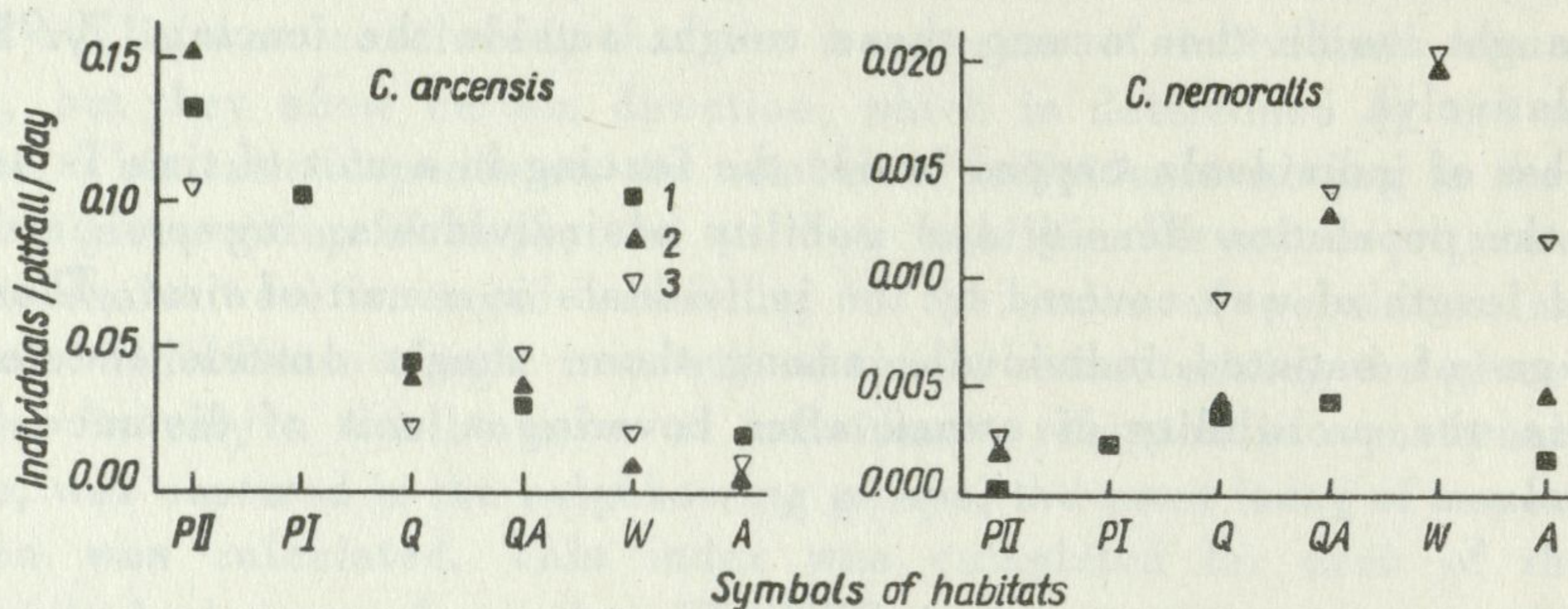


Fig. 4. Distribution of *C. arcensis* and *C. nemoralis* in the studied habitats of Kampinos Forest

1 — living traps (1963), 2 — formalin traps (1963), 3 — formalin traps (1964)

Quantitative distribution of both species was compared with the water content in the soil of three habitats — *Vaccinio myrtilli-Pinetum II*, *Pino-Quercetum* and ecotone of the latter with *Alnetum*. The water content in soil was determined by drying the soil samples to constant weight at 105°C in June 1964. The lowest percentage of water was found in the soil of biotope *Vaccinio myrtilli-Pinetum II* (5.6%), where *C. arcensis* was trapped very numerously, opposite to *C. nemoralis* (Fig. 4). In *Pino-Quercetum* (8.4% water in soil) *C. arcensis* was caught less numerously, but the number of trapped individuals of *C. nemoralis* was greater. In the ecotone of *Pino-Quercetum* and *Alnetum* (24.2% water in soil) *C. arcensis* was caught in low numbers, while *C. nemoralis* in relatively high.

Changes of distribution of *C. arcensis* and *C. nemoralis* were investigated in habitats, in which the population density and percentage of water content in soil were known. The known amount of precipitations in May and June 1964, 1965 and 1966 (in mm), was correlated with the changes in population density in biotopes *Vaccinio myrtilli-Pinetum II* and in two habitats of biotope *Pino-Quercetum*: Q and A. It was found, that the population density of *C. arcensis* in the habitat with the highest water content in soil did not change significantly with the increase of the amount of precipitations, but maintained the low level (Fig. 5). However, the population density, which was high in a habitat with average water content in soil, decreased decidedly with the increase of the amount of precipitations. Simultaneously the opposite direction of the changes of the density of *C. arcensis* was observed in a relatively dry biotope *Vaccinio myrtilli-Pinetum II* (Fig. 5). Thus with the increase of the amount of precipitations, the zone of high population density of *C. arcensis* moved towards the relatively dry biotope. Population density of *C. nemoralis* has a tendency to increase together with the increase of the amount of precipitations, both in habitats with the highest and average percentage of water in soil (Fig. 5).

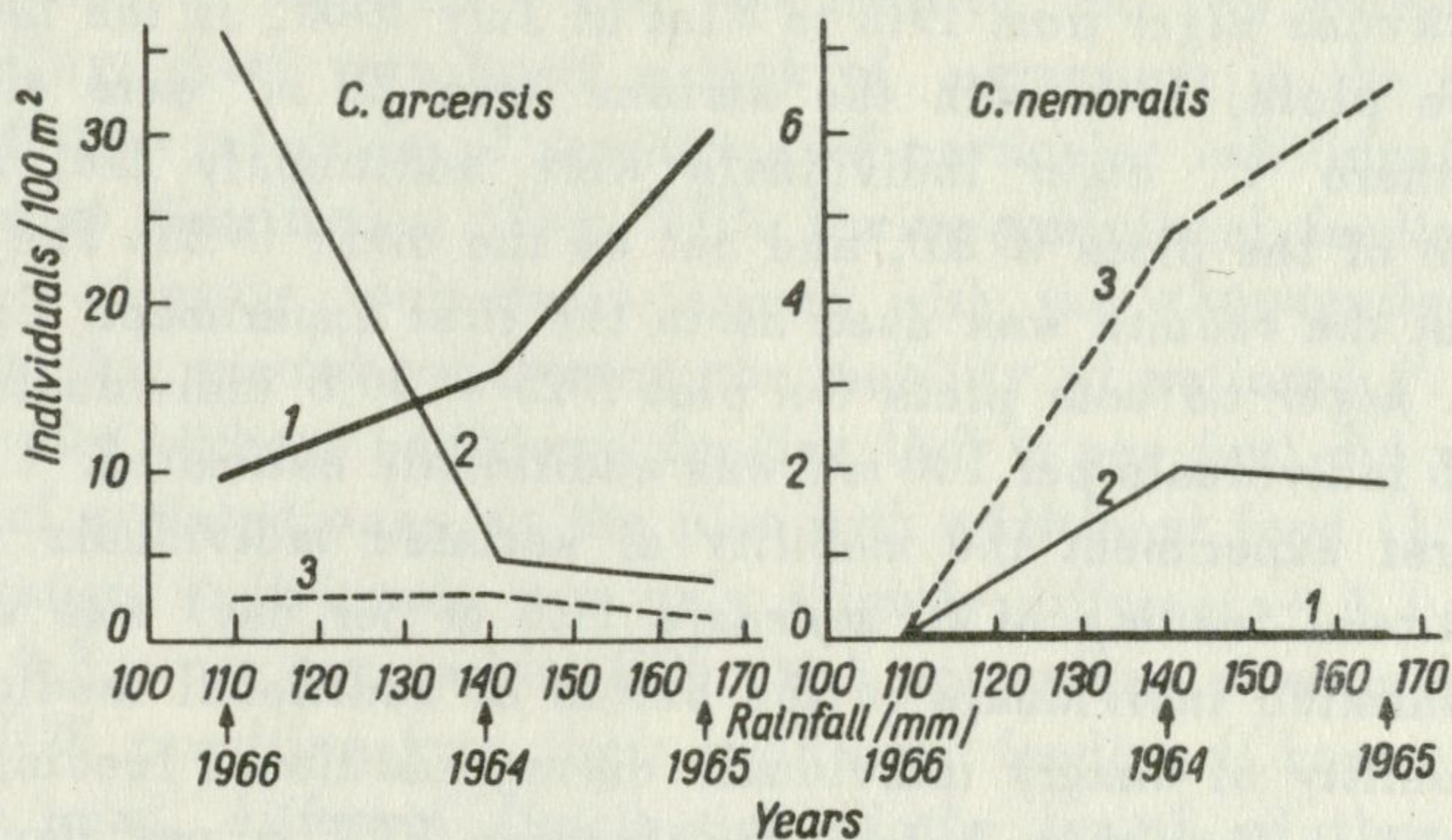


Fig. 5. The relation between the sum of falls in May and June and the changes of population density of *C. arcensis* and *C. nemoralis* in three habitats

1 - *Vaccinio myrtilli-Pinetum* (5.6% of water in soil), 2 - *Pino-Quercetum* (8.4% water in soil), 3 - ecotone of *Pino-Quercetum* and *Alnetum* (24.2% water in soil)

The described relationships show, that *C. arcensis* occurs in habitats with a relatively low humidity, while *C. nemoralis* - in habitats with high humidity. Rains, due to the changes in humidity cause respective movements of the zones of high population density of both species.

The above characteristic of the preference in relation to the physical qualities of habitat of both species are in agreement with the results of laboratory investigations of Schmidt (1957), and Lauterbach (1964). Lauterbach (1964) also studied the humidity and light preference of both discussed species. He found, that *C. arcensis* contrary to *C. nemoralis* prefers lower humidity and stronger light.

4.2. The influence of supplementary food on the mobility

The first experiment was carried out on the plot *PI125*, just after the end of investigations determining the population density and mobility of *C. arcensis* individuals. Large amount of additional food was placed in the centre of the plot, and the *C. arcensis* individuals released on the plot had a great chance of finding it (Chapter 3.4). In order to prevent the changes of the density of *C. arcensis* population, then the preservation of the conditions comparable with these in the period before additional feeding, only such number of individuals was released on the plot, as the number trapped and released outside the fencing. The number of additional days of trapping was determined which allowed for proper estimation of the mean time of individual residence on the plot. Then the mobility of hungry and satiated individuals, and the average

mobility of all individuals were estimated. The second experiment was carried out on *Pterostichus niger* from 19th to 31st of July 1966, on the island on lake Bełdany. Two plots, both with the surface area 25 m² were simultaneously established there. *P. niger* individuals were additionally fed, as described above, on one of the plots (D25), and not on the other (N25). The same method of working out the results was used as in the first experiment. The population density of *P. niger* on both plots (on plot N25 – 30.8 individuals per 100 m², on D25 – 36.5 individuals per 100 m²) was additionally estimated.

In the first experiment the mobility of satiated individuals in the period without additional feeding of *C. arcensis* (1.5 m per day) was similar to the mobility of satiated individuals in the period of additional feeding (1.7 m per day). The mobility of hungry individuals during additional feeding (12.9 m per day) was much higher than before the feeding (7.7 m per day). Additional

Comparison of the exponential distribution with the distribution of the length of time intervals of the residence of individuals on the plot

Tab. VII

<i>C. arcensis</i> , plot P/125						
<i>t</i>	period before additional feeding			time of additional feeding		
	\bar{N}_t	\bar{N}'_t	$\frac{(\bar{N}_t - N_t)^2}{\bar{N}'_t}$	\bar{N}_t	\bar{N}'_t	$\frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$
1	55	34.14	11.80	10	7.99	0.51
2	9	20.89	11.50	5	6.13	0.14
3	5	12.78		4	4.70	
4	4	7.82	0.04	4	3.60	0.00
5	3	4.78		2	2.76	
6	2	2.93		2	2.12	
7	2	1.79		1	1.62	
8	3	1.09		1	1.24	
9	1	0.66		1	0.95	
10	1	0.41		0	0.73	
11	2	0.25	2	0.55		
12	0	0.15	0	0.43		
13	1	0.09	1	0.33		
14			0	0.25		
15			1	0.20		
Σ	88	87.78	23.34	34	33.60	0.65
	Inconsistent with the exponential on the level of confidence $\alpha = 0.05$			Consistent with the exponential on the level of confidence $\alpha = 0.05$		

feeding caused also a significant increase of the percentage of satiated individuals (Chapter 3.4), thus causing a decrease of the mean mobility of all indivi-

duals from 3.9 to 2.2 m per day. Therefore, in the period before feeding, *C. arcensis* population on the plot *P1125* was divided into two groups differing as to their mobility; there was found a lack of agreement in the distribution of the length of time intervals of residence of particular individuals on the plot with exponential distribution (Tab. VII). During additional feeding the rate of escape of *C. arcensis* individuals agreed with the exponential distribution (Tab. VII). In the second experiment the mobility of satiated *P. niger* individuals on the plot without additional feeding (1.8 m per day) did not differ from the mobility of satiated ones on the plot with additional food (1.9 m per day). Mobility of hungry individuals was only slightly different – 4.1 m per day on plot *N25* and 3.3 m per day on plot *D25*. High percentage of satiated individuals on the plot *D25* resulting from their additional feeding (Chapter 3.4) caused, on the other hand, different distribution of the length of time intervals of residence of individuals on the plot than on plot *N25*. Due to the small number of *P. niger* caught after marking, it was impossible to analyse the agreement of escape rate of individuals from the plot with the exponential distribution. The analysis was limited to the comparison of empiric rows of numbers which characterised the escape rate of *P. niger* individuals from plots *N25* and *D25* (Tab. VIII).

Empiric distribution of the length of time intervals of the residence of *P. niger* individuals on the plot

Tab. VIII

<i>t</i>	Plot <i>N25</i> (the food was not given)	Plot <i>D25</i> (the food was given)
	\bar{N}_t	\bar{N}_t
1	31	7
2	7	11
3	7	5
4	3	5
5	1	2
6	1	1
Σ	50	31

Both experiments showed, that hungry individuals are more mobile than the satiated ones, and that additional feeding causes a decrease of the average mobility of individual and prevents the separation of population in to two groups of individuals of unequal mobility, influencing the decrease of percentage of hungry individuals.

4.3. Changes of mobility within the population area

Changes of the mobility of hungry and satiated individuals on the population area were characterised by a comparison of their mobility. This comparison has shown a small increase of mobility of hungry individuals, accompanied by the decrease of population density of both investigated species (Fig. 6). Mobility of satiated individuals shows similar direction of changes to that of the mobility of hungry ones, but differences in the mobility of satiated ones are much greater, for the low population density the mobility of satiated individuals is nearly nine times higher than for the high population density (Fig. 6).

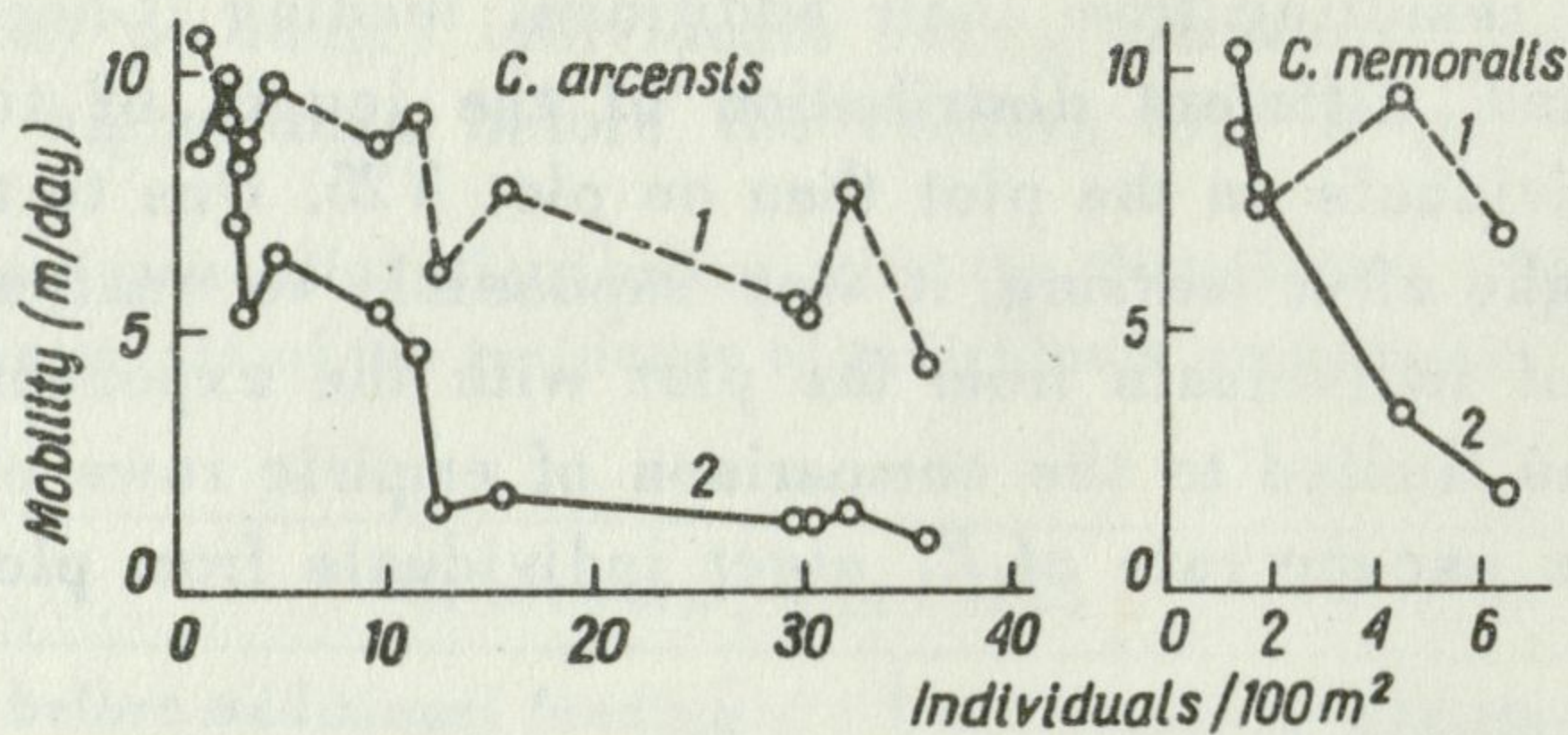


Fig. 6. The comparison of the mobility of hungry and satiated individuals in habitats with different population density
1 - hungry, 2 - satiated

As the particular plots are sometimes located in various plant associations, a question arises whether the observed changes of mobility characterise the processes in one population or in several mutual isolated ones. Good index of distribution of traps on the area of one population is an exchange of marked individuals among the plots. Such an exchange was observed in the population of *C. arcensis* for the following pairs of simultaneously investigated plots: Q50 and A50, Q33 and A33, Q25 and A25, P125 and P1125 and P1125 and P1125. The exchange of marked individuals of *C. nemoralis* between the plots Q33 and A33 was also found. Thus the observed changes of mobility of hungry and satiated individuals are characteristic for the area of one population.

While analysing the influence of physical environment on the mobility of individuals the attention was drawn to the following findings. First, the mobility of satiated individuals is much higher in the zone of low population density than in the zone of high density. Second, the mobility of satiated individuals of *C. arcensis* reaches the highest values in the habitat with a relatively high water content in soil (A), but the mobility of satiated individuals of *C. nemoralis* is the highest in the habitat with relatively low humidity of soil (Q). Thus it was concluded, that unsuitable environment conditions cause high mobility of the satiated individuals.

Comparison of the exponential distribution with the distribution of the length of time intervals of the residence of individuals on the plot

Tab. IX

t	<i>C. arcensis</i>					
	plot PI33			plot PII125		
	\bar{N}_t	\bar{N}'_t	$\frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$	\bar{N}_t	\bar{N}'_t	$\frac{(\bar{N}_t - \bar{N}'_t)^2}{\bar{N}'_t}$
1	49	38.67	2.74	40	36.11	0.42
2	10	17.30	3.08	12	15.08	0.64
3	4	7.74	} 0.63	5	6.30	} 0.02
4	3	3.46		3	2.63	
5	1	1.55		1	1.10	
6	0	0.69		1	0.46	
7	2	0.31				
8	0	0.14				
9	0	0.06				
10	1	0.03				
Σ	70	69.95	6.45	62	61.67	1.08
	Inconsistent with the exponential on the level of confidence $\alpha = 0.05$			Consistent with the exponential on the level of confidence $\alpha = 0.05$		

As it was shown in chapter 4.2., the escape rate from the plot PII125 by marked individuals of *C. arcensis* was not consistent with the exponential distribution (Tab. VI), what can be explained by the same number and considerable difference of the mobility of hungry and satiated individuals. A similar situation was observed in the population of this species on plot PI33 (Tab. IX). However, the rate of escape of *C. arcensis* individuals from plot PII125 was consistent with the exponential distribution (Tab. IX), as the mobility of hungry and satiated individuals did not differ much here (hungry 9.0, satiated 4.5 m per day). Both plots, where the rate of escape from the fenced area did not agree with the exponential distribution were characterised by a significant population density (Tab. V). On the plot PII125, where the rate of escape was consistent with the exponential distribution, the population density of *C. arcensis* was nearly twice lower than on the plots PI33 and PII125.

Taking into consideration the results of the above analysis, and also the influence of additional feeding on the mean individuals' mobility, discussed in chapter 4.2, it can be concluded that the following decide about the high mobility: hunger in the area with suitable habitat conditions, and unsuitable habitat conditions on the peripheries of the population area.

4.4. Preferred directions of movements

It was found, that the calculated correlation coefficients between values N_1 (number of individuals, released in one group of traps, and caught later in one of the neighbouring groups) and n_1 (expected number of these individuals in the conditions of chance movements) in all three biotopes have positive values: *Pino-Quercetum* $r = +0.122$; *Vaccinio myrtilli-Pinetum* $r = +0.558$, *Vaccinio myrtilli-Pinetum II*, $r = +0.775$. However, only in the last of these biotopes the coefficient is significantly different from zero. Therefore, in this biotope characterised by the lowest degree of patchiness of its habitat the movements of marked *C. arcensis* individuals were very close to the assumed model of chance movements. However, in two other biotopes with much higher degree of patchiness of their habitats, individuals of *C. arcensis* did not move by chance, but with a preference of certain direction.

The calculations show that in homogenous *Vaccinio myrtilli-Pinetum II* the ratio of values N_1 to n_1 was relatively constant. This ratio in two much more heterogenous biotopes was very changeable, and it reached the highest values in groups of traps belonging to classes of much lower and much higher population mobility, than the mobility characterising the area of maternal group of traps (Tab. X). Thus, movements of marked individuals of *C. arcensis* took place mainly among the habitats characterised by great differences in the population mobility from habitats with high population mobility to these with low one, and inversely.

Index of the direction of movements calculated for four distinguished classes of population mobility of *C. arcensis*

Tab. X

Classes of population mobility expressed by the ratio of this mobility in the place of catch to the population mobility on the maternal area	<i>Pino-Quercetum</i>	<i>Vaccinio myrtilli-Pinetum I</i>	<i>Vaccinio myrtilli-Pinetum II</i>
Much higher mobility	11.30	22.85	1.99
Slightly higher mobility	3.05	5.93	2.89
Slightly lower mobility	3.32	3.18	2.45
Much lower mobility	6.40	10.41	1.45

Closer characteristic of migrants (i.e. these released in maternal group of traps but caught in one of the neighbouring ones) show, that only 6.3% of them is trapped in the maternal group of traps before they are caught in other traps. On the other hand, 12.5% of individuals never caught in other groups of traps, is recaptured in maternal traps. Thus it can be concluded, that the migrating part of *C. arcensis* population is formed mainly of individuals not associated with the maternal group of traps, i.e. probably more mobile.

Further explanations concerning the preferred direction of movements were obtained by correlation of population mobility with the probability of attack of individual. A positive correlation of population density and population mobility (Fig. 7) shows, that the directional movements of individuals connect the area

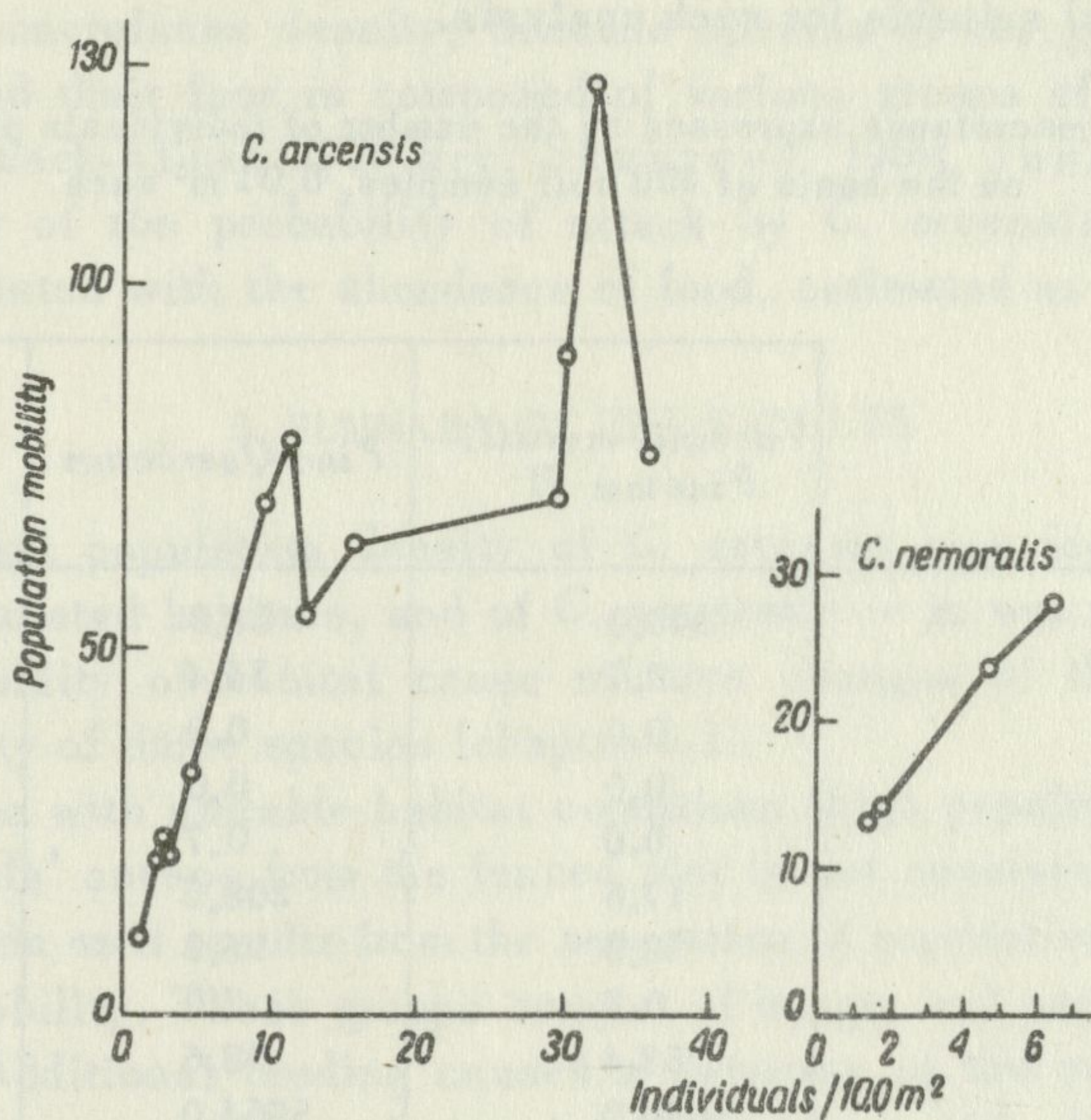


Fig. 7. Dependence between the population mobility (product of population density and individual mobility) and the population density

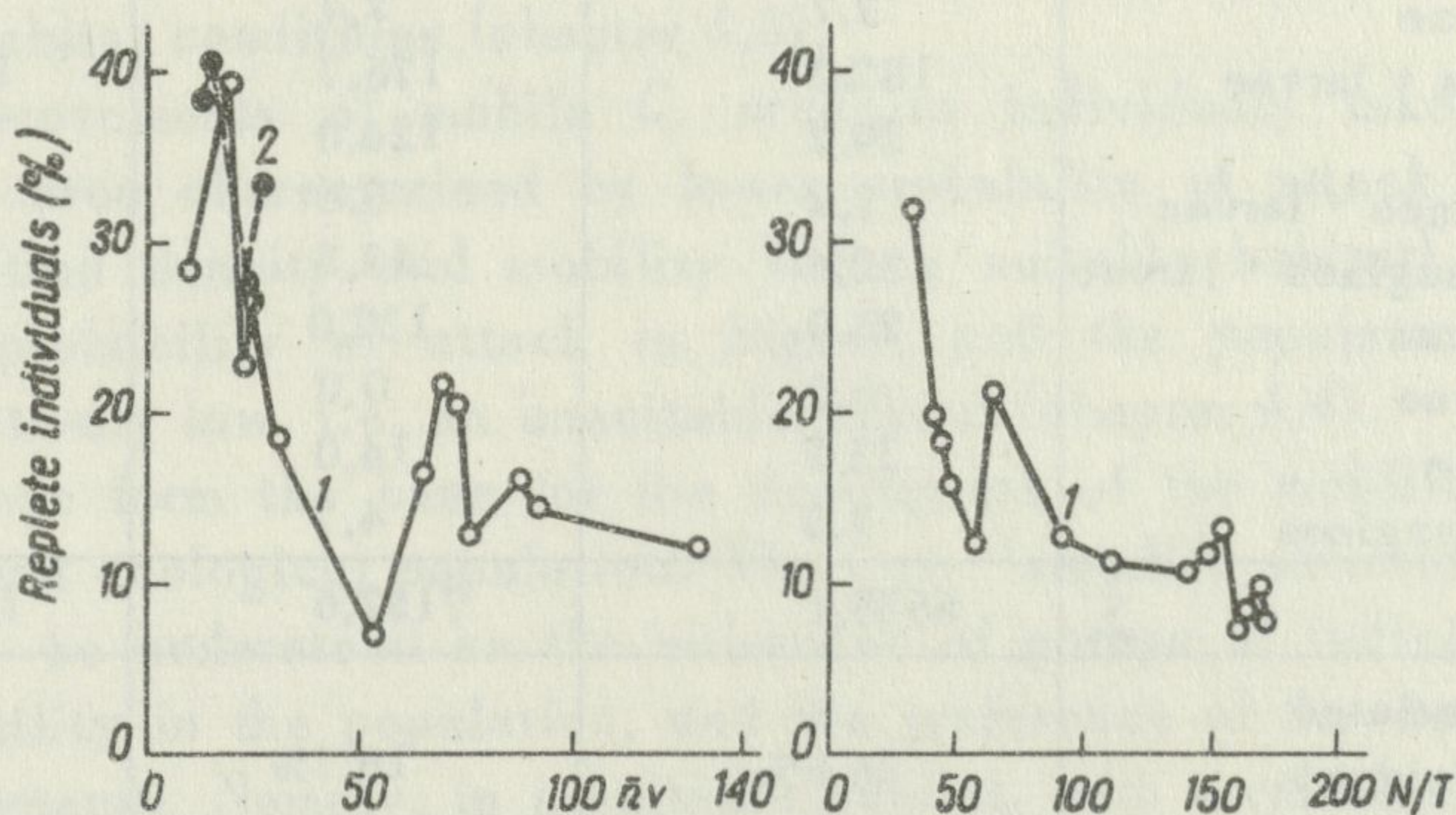


Fig. 8. Dependence between the population mobility ($\bar{n}v$ or $N:T$) and the probability of attack

1 - *C. arcensis*, 2 - *C. nemoralis*

of suitable habitat conditions and high population density with the peripheries of the population area having much poorer habitat conditions. But the comparison of the probability of attack with the values of population mobility show inverse proportion of these variables (Fig. 8). This dependence was not found in the population of *C. nemoralis*, which was probably the result of small number of plots (only four) suitable for such analysis.

Density of epigeal macrofauna expressed by the number of individuals per 1 m², estimated on the basis of 300 soil samples, 0.01 m² each

Tab. XI

	<i>Vaccinio-myrtilli- Pinetum II</i>	<i>Pino-Quercetum</i>	Ecotone <i>Alnetum</i> and <i>Pino-Quercetum</i>
<i>Enchytraeidae</i>	340.0	68.0	910.0
<i>Lumbricidae</i>	9.7	34.4	52.5
<i>Arionidae</i>	0.0	0.0	6.1
<i>Isopoda</i>	0.0	0.0	46.7
<i>Diplopoda</i>	0.0	0.7	10.0
<i>Chilopoda</i>	17.6	208.5	6.0
<i>Pseudoscorpiones</i>	18.0	15.3	8.0
<i>Opiliones</i>	0.7	2.0	16.7
<i>Araneida</i>	53.4	38.6	84.0
<i>Collembola</i>	5640.0	5964.0	6740.0
<i>Protura</i>	0.0	68.0	25.0
<i>Thysanoptera</i>	230.0	104.0	15.8
<i>Dermaptera</i>	0.0	4.0	0.7
<i>Homoptera</i>	10.0	120.0	430.0
<i>Heteroptera</i>	3.3	7.3	4.0
<i>Lepidoptera</i> larvae	2.7	2.7	4.1
<i>Diptera</i> imagines + larvae	182.0	176.7	1881.7
<i>Formicidae</i>	29.2	124.0	3.0
<i>Carabidae</i> imagines + larvae	7.4	5.6	8.7
<i>Staphylinidae</i> imagines + larvae	52.6	43.3	113.9
<i>Cantharidae</i> larvae	25.0	132.0	15.0
<i>Lampyridae</i> larvae	0.0	0.0	10.0
<i>Elateridae</i> larvae	25.2	14.0	15.3
<i>Curculionidae</i> imagines	9.3	4.7	19.3
Σ	6658.1	7137.6	10424.6
Percentage of satiated <i>C. arcensis</i> individuals	16.6%	18.7%	26.0%

Changes of the probability of attack by individuals of *C. arcensis* were correlated with the changes of density of epigeal macrofauna treated as an index of abundance of food resources of the habitat. The density of epigeal macrofauna was calculated for three habitats (*PII*, *Q* and *A*) from soil samples.

Closer qualitative analysis of prey of *C. arcensis* is impossible, because of extraintestinal digestion of all species of the genus *Carabus* (Reichenbach-Klinke 1938, acc. Skuhřavý 1959), excluding the possibility of determining the species composition of prey on the basis of the alimentary tract analysis. The abundance of food resources can be estimated approximately on the basis of the epigean macrofauna density, because species of the genus *Carabus* are polyphagous, and their food is composed of various groups of epigean invertebrates (Reichenbach-Klinke 1938 acc. Skuhřavý 1959, Jung 1940, Davies 1959). Changes of the probability of attack by *C. arcensis* individuals are positively correlated with the abundance of food, estimated as above (Tab. XI).

5. SUMMARY OF THE RESULTS

1. The highest population density of *C. arcensis* was found in relatively dry and well insolated habitats, and of *C. nemoralis* – in wet and shaded ones. Changes of humidity of habitat cause relative changes of the areas of high population density of these species (chapter 4.1).

2. On the area with suitable habitat conditions (high population density), the rate of individuals' escape from the fenced plot is not consistent with the exponential distribution as it results from the separation of population into two groups with different mobility. These groups consist of hungry and satiated individuals (chapter 4.3.). Additional feeding causes a decrease of the mean mobility and prevents the separation of population into two groups with different mobility, by decreasing the percentage of hungry individuals (chapter 4.2).

3. The mobility of satiated individuals increases as the habitat conditions become worse on the area of ecological population. The mobility of hungry individuals is however more or less constant and high in suitable and unsuitable habitat conditions (chapter 4.3).

4. The movements of mobile *C. arcensis* individuals take place mainly between an area characterised by lower probability of attack and relatively high population density and mobility (i.e. a suitable habitat) and the area, where the probability of attack is higher, and the population density and mobility relatively low, i.e. an unsuitable habitat (chapter 4.4).

The above form the base for the description of the mobility structure on the area of the ecological population. The term "mobility structure", introduced here, should be understood as the existence of groups of individuals different in their mobility in the population, and the preference of the determined direction of movements. Namely, in a suitable habitat, with a relatively high population density, there are two groups of individuals present mobile (hungry) and not mobile (satiated). On the area with poor habitat conditions, with low population density, mobility of hungry and satiated individuals is similar and high. Mobile individuals of *C. arcensis* move from suitable habitats to the unsuitable areas, and backwards.

The described mobility structure results from changeable probability of attack and reaction of individual to hunger and environmental factors on the area of ecological population of *C. arcensis*. Namely, relatively low probability of attack on the area with high population density causes an increased mobility of a certain number of still hungry individuals. These individuals move towards the peripheries of the population area, where the probability of attack is higher. Satiated individuals, with high mobility in unsuitable environmental conditions on the peripheries of the area, move towards the suitable conditions, where their mobility decreases.

6. DISCUSSION

The directional movements of individuals, described in chapter 5, seem to be of some significance for the compensation of the energy balance of *C. arcensis* population in habitats having high population density and mobility. It is obvious, that the population metabolism, calculated per the unit of surface, will be proportional to its density (resting metabolism of individuals), and also to the population mobility (metabolism connected with individuals movements). It is worth adding, that the metabolism of *Carabidae* moving for several hours a day is, according to the estimation of Grüm (in press) about 100% higher than that of individuals resting for the same unit of time. Because the population mobility and population density of *C. arcensis* are positively correlated, the population metabolism of this species considerably changes on the population area, and is the highest in the optimal habitats. Thus directional movements of individuals connect the areas of significant differences in the population metabolism.

Thus the probability of attack of individuals decreases, with the increase of *C. arcensis* population mobility and density, and is the lowest in the area of the highest metabolism. It may be concluded, that the movements of mobile, satiated individuals, from the peripheries of the population area into the area of high density are a way of restoring the energy losses of population in the area of optimal habitats. As in good environmental conditions only hungry individuals show an increased mobility, it is possible, that such an increase of mobility, however increasing the individuals metabolism, compensates the energy balance of population in suitable habitats with high population densities, by reemigration of satiated individuals.

Also possible are paralelly acting mechanisms of compensation of the population energy balance, relying on the reduction of its density resulting from the increased mobility of individual. Several authors mention the increased mobility of individual as a factor exposing this individual to the attack of predator (Errington 1946, Naumov 1956, Pielowski 1962, and others). The reduction of density of *Carabidae* population, dependent on the population

mobility and the daily rhythm of individuals mobility was shown by Zimka (1966) in his investigations on the food preference of frogs (*Rana arvalis* Nils.), carried out in the same time and in the same biotopes. Also temporary migration of mobile individuals to the areas with poor environmental conditions can cause an increased mortality. However, there is a lack of data confirming the above hypothesis for imagines of *Carabidae*, but many authors mention such possibility as an important one in the reduction of population density of many species of animals (Nicholson 1933, Smith 1935, Lack 1954, Naumov 1956).

It seems, that the mobility structure – and its significance – described for populations of *C. arcensis* is a common one in population of many species of the family *Carabidae*. The separation of population into groups of individuals with different mobility was also found in populations of *C. arcensis* and *P. niger* (Grüm 1965) previously analysed from this point of view. The data of Schjøtz-Christensen (1965) also show the presence of the described separation in populations of several *Carabidae* species.

I am very grateful to Prof. dr. K. Petruszewicz, dr. W. Kaczmarek, A. Stachurski, M. Sc., dr. A. Wasilewski and J. Zimka, M. Sc. for their encouragement and critical remarks during the preparation of this paper.

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PRZESTRZENNE ZRÓŻNICOWANIE RUCHLIWOŚCI BIEGACZOWATYCH Z RODZAJU *CARABUS* L. (*CARABIDAE*, *COLEOPTERA*)

Streszczenie

Zbadano zmiany ruchliwości osobników w obrębie areałów ekologicznych populacji, dwóch gatunków drapieżnych biegaczy: *Carabus arcensis* Hbst., i *Carabus nemoralis* Müll. Jak wykazano, w siedlisku optymalnym – o stosunkowo wysokiej gęstości populacji – w którym szansa zdobycia ofiary jest niewielka, osobniki głodne wykazują znaczną ruchliwość, powodującą ich emigrację na peryferie areału populacji. Na peryferiach areału – gdzie gęstość populacji jest niska, a prawdopodobieństwo zdobycia ofiary stosunkowo duże – ruchliwość osobnika nie maleje po najedzeniu się. W rezultacie najedzone osobniki reemigrują do siedlisk optymalnych, w których cechuje je niewielka ruchliwość. Taka emigracja głodnych i reemigracja najedzonych osobników wydaje się sposobem równoważenia bilansu energetycznego w populacjach gatunków z rodziny *Carabidae* w siedliskach optymalnych, o wysokiej gęstości populacji.

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