EKOLOGIA POLSKA – SERIA A

Tom X Warszawa 1962 nr 4

LESZEK GRÜM

HORIZONTAL DISTRIBUTION OF LARVAE AND IMAGINES OF SOME SPECIES OF *CARABIDAE*

Institute of Ecology, Polish Academy of Sciences, Warsaw

Our knowledge of the co-occurrence of imagines and larvae of *Carabidae* (*Coleoptera*) is somewhat scanty. The fragmentary data encountered in literature contribute only to what is known about the vertical differences in intensity of occurrence of larvae or imagines. Among the works dealing with this subject that by Arnoldi (1954) discusses the distribution of larvae of *Carabidae* at different depths in different types of soil, but this author does not identify the species encountered in his investigations. Gilarow (1949) with reference to the problem of locomotory adaptation of the larvae of *Carabidae* to life in the soil states that many of them (chiefly from the genus *Carabus* L.) feed at night on the surface of the soil. Scherney (1955) draws attention to the differences in depth of penetration of the soil by the imagines of several species of *Carabidae*. The investigations made by Kabacik (1957) showed that there are seasonal variations in the penetration of the soil, the litter and its surface by the imagines of *Pterostichus niger* Schall.

The results given in this work are concerned with the question of horizontal distribution of larvae or of adult insects of some species of *Carabidae*. Using a hypothetical diagram of co-occurrence of imagines and larvae of *Pterostichus vulgaris* L. as a basis, an attempt was made at defining the causes of the non-uniform course followed by seasonal variations in numbers of the imagines of this species on four stations. In addition analysis was made of the migrational properties of males and females of seven species of *Carabidae* caught on one of these stations.

STUDY AREA AND METHODS

Investigations were made in the east part of the Kampinos Forest, near the Field Station of the Institute of Ecology of the Polish Academy of Sciences. That part of the Forest consists of a mosaic of forest habitats with varying phytosociological characteristics. The material was collected from six stations marked by consecutive numbers I, II, III, IV, V, VI. The beetles were caught in glass jars sunk in the ground or in plastic jars, the necks of which were about

6 cm. in diameter. Eighty traps were set in a regular chess-board formation, over an area of about 400 sq.m., on station I, which was situated in a pine wood about 40 years old, surrounded by clumps of sedge, marshy ground and other kinds of forest habitats. Station II was situated in a pine and oak forest, with an admixture of young hornbeams, and 32 traps were placed on this station. Station III had 28 traps, and was situated on the border line between a patch of alders and the pine and oak forest referred to above. On the latter two stations the traps were placed in groups of four. The remaining stations had series of 10 traps each, which were placed in a planted pine forest about 36 years old (station IV), among young birches and alder trees on the fringe of the forest and meadow (station V) and on the relatively dry part of a natural meadow (station VI) almost entirely unaffected (contrary to the remaining part of the meadow) by water formed by the abundant rainfall in 1960.

Station I was used during the years 1956–1960, on an average from the end of May to the end of October. The *Carabidae* caught there were marked by a consecutive number (Grüm 1959) and set free again. Intervals between consecutive inspections of this station were different in different years, varying from 4 to 7 days. The remaining stations were used from April 17th to the end of December 1960. The traps on these stations were filled with glycol or a weak solution of formalin. They were inspected every 4 to 6 days.

The following calculations were made separately for each species:

1. The percentage of females in the population of adult insects. Calculation was made of the percentage of females in the population of imagines of the given species caught on each station.

2. The percentage of larvae. Calculation was made of the percentage formed by larvae of the total number of imagines and larvae of the given species caught on each station in 1960.

3. Density of imagines and larvae. The number of imagines and larvae of *P. vulgaris* caught per trap on stations II, III, V and VI was counted.

4. Assessment of the seasonal variations in the number of imagines of *P. vulgaris* caught on four of the stations explored in 1960. This was done by calculating what percentage of imagines, out of the total number of imagines of this species on a given station, was caught in consecutive approximately 20-day trapping periods.

5. Calculation was made of the percentage, in relation to the total number of marked and released individuals of the given sex, of individuals which were not recaptured, the percentage of those individuals which were recaptured over a period of 4–24 days, 25–48 days and 49–96 days from the time of marking, for each of the several most numerously marked species. In addition calculation was made of the percentage of those individuals which were caught for the last time after the expiry of one year or longer as from the time of marking.

Taking into consideration the absolute number of males and females caught in each of the above classes, two sequences of empirical figures were obtained.

In order to discover if the differences between them are significant, the sequences were compared by means of the "chi-square".

$$\chi^2 = \frac{\left(x_1 - \frac{\Sigma x P_1}{P xy}\right)^2}{\frac{\Sigma x P_1}{P xy}} + \ldots \frac{\left(x_k - \frac{\Sigma x P_k}{P xy}\right)^2}{\frac{\Sigma x P_k}{P xy}} + \frac{\left(y_1 - \frac{\Sigma y P_1}{P xy}\right)^2}{\frac{\Sigma y P_1}{P xy}} + \ldots \frac{\left(y_k - \frac{\Sigma y P_k}{P xy}\right)^2}{\frac{\Sigma y P_k}{P xy}}$$

with $R = (K - 1) - (S - 1)$,

when: $x_1, x_2, \ldots x_k$ – number of males in each class,

$y_1, y_2, \ldots y_k$ – number of females in each class,

Σx – number of males marked, Σy – number of females marked,

$P_1 = x_1 + y_1$, $P_2 = x_2 + y_2 \ldots$, $P_k = x_k + y_k$,

$P_{xy} = x_1 + x_2 + \ldots x_k + y_1 + y_2 + \ldots y_k$,

K – number of expressions in a sequence, S – number of sequences, R – number of degrees of freedom.

CO-OCCURRENCE OF IMAGINES AND LARVAE

Even a glance at the unprepared data (Tab. I) shows that both imagines and larvae of the given species were caught on certain stations, and on others either imagines or larvae only.

Complete amount of material collected in 1960

Całkowita ilość materiału zebranego w 1960 r.

Tab. I

Species Gatunek	Station Stanowisko	Number of imagines caught Liczba złowionych imagines	Percentage of ♀♀ Procent ♀♀	Number of larvae caught Liczba złowionych larw
Carabus arcensis Hbst.	I	61	48,1	0
	II	39	33,3	0
	III	4	25,0	0
	IV	30	66,6	2
	V	7	42,8	0
Carabus clathratus L.	II	6	83,3	1
	III	17	47,0	0
Carabus glabratus Payk.	I	13	45,5	0
	II	40	47.5	0
	III	10	60.0	0
Carabus granulatus L.	I	6	50,0	1
	III	59	32,2	4
Carabus hortensis L.	I	52	50,0	4
	II	18	66,6	27
	III	29	75,5	17
	V	19	63,1	2
	VI	0	–	1

Tab. I (cont.)

Species Gatunek	Station Stanowisko	Number of imagines caught Liczba złowionych imagines	Percentage of ♀♀ Procent ♀♀	Number of larvae caught Liczba złowionych larw
Carabus nemoralis Müll.	II	4	50,0	2
	III	13	53,8	4
	V	25	60,0	17
Carabus violaceus L.	I	0	–	3
Pterostichus niger Schall.	I	268	51,8	0
	II	33	24,2	0
	III	29	37,9	0
	V	25	32,0	0
Pterostichus vulgaris L.	II	11	36,4	0
	III	65	46,1	1
	V	64	53,0	2
	VI	5	100,0	17

In attempting to establish whether there is any regularity of co-occurrence of larvae and imagines, the percentage of females in a population of imagines of the given species was correlated with the percentage of its larvae. The relatively high coefficient of correlation, +0.63, is evidence of the distinct connec-

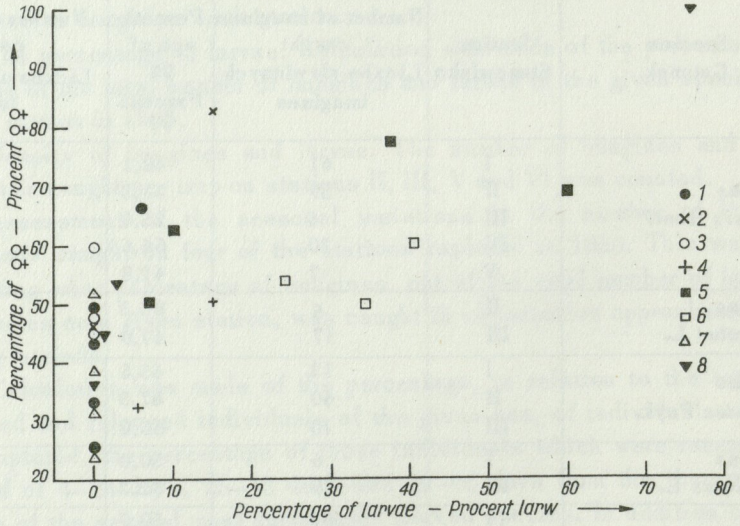

Fig. 1. Connection between occurrence of females and larvae (in %)

Zależność pomiędzy występowaniem samic i larw (w %)

1 – Carabus arcensis Hbst., *2 – C. clathratus* L., *3 – C. glabratus* Payk., *4 – C. granulatus* L., *5 – C. hortensis* L., *6 – C. nemoralis* Müll., *7 – Pterostichus niger* Schall., *8 – P. vulgaris* L.

tion between these values (Fig. 1). It was calculated for the whole of the material collected in 1960. On part of the stations where imagines were present, the larvae of the same species was not caught at all. In such cases the percentage of females among the imagines was generally lower (on an average 42.4%) than the percentage of females on the stations on which both larvae and imagines of the given species were caught (average 60.7%).

The distinct connection between the percentage of females in the imagines population and the intensity of occurrence of larvae would seem to apply to all the species examined. It is evidence that the varying ratios between larvae and imagines observed are not caused by an unsuitable method of collecting samples, but do in fact exist.

Variations in the ratios of imagines to larvae provide grounds for assuming that they occupy different niches, which do not overlap in the horizontal plane, which may result from the larvae occupying only certain definite enclaves within the living area of the imagines, or in the occurrence of larvae on the fringe of the ecological niche of the imagines. The absence of larvae on part of the stations on which imagines of the same species were caught, or also the non-occurrence of imagines on other stations on which the larvae was present, would seem to

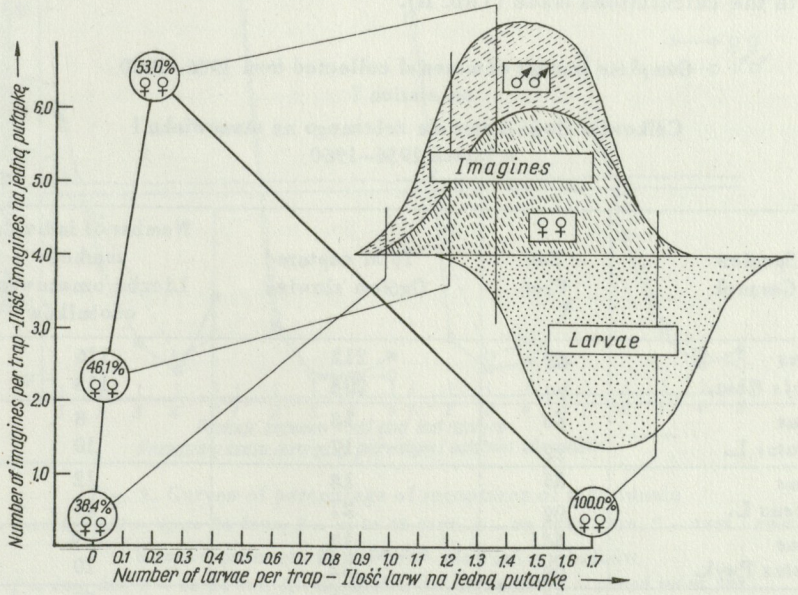

Fig. 2. Hypothetical model of distribution of larvae and imagines of *Pterostichus vulgaris* L. in the light of the mutual dependence of their occurrence

Vertical lines on diagram correspond to assumed localisation of samples

Hipotetyczny model rozmieszczenia larw i imagines *Pterostichus vulgaris* L. na tle wzajemnej zależności ich występowania

Pionowe linie na schemacie odpowiadają przypuszczalnej lokalizacji prób

point to the last of the alternatives referred to above, although it is difficult to say exactly whether this applies to all the species.

As an example – by comparing variations in density of imagines and larvae on different stations an attempt was made to define the mutual localisation of areas of occurrence of larvae and adult insects of *P vulgaris*. As the density of the larvae increases the crowding of the imagines at first increases, then decreases. A model of their mutual distribution in the horizontal plane constructed on this basis shows that the areas of occurrence of imagines and larvae fail to overlap, the females massing in that part of the living area of adult insects in which the larvae live (Fig. 2).

On account of the small amount of material, the above model of distribution of larvae and imagines of *P. vulgaris* is a hypothetical one only, and was used to elucidate the non-uniform course, observed on several stations, followed by the seasonal dynamics of the imagines of this species.

MIGRATION OF MALES AND FEMALES

The migrations show the mechanism by which the numerical preponderance of females over males in the areas of occurrence of larvae is brought about. Information obtained from individual marking of the beetles was taken into consideration in the calculations made (Tab. II).

Complete amount of material collected from 1956–1960 on station I

Całkowita ilość materiału zebranego na stanowisku I w latach 1956–1960

Tab. II

Species Gatunek	Sex Płeć	Total captured Ogółem złowien	Number of individuals marked Liczba oznakowanych osobników
Carabus arcensis Hbst.	♂♂	212	116
	♀♀	204	113
Carabus clathratus L.	♂♂	13	8
	♀♀	17	10
Carabus coriaceus L.	♂♂	18	12
	♀♀	21	11
Carabus glabratus Payk.	♂♂	17	9
	♀♀	22	10
Carabus granulatus L.	♂♂	63	38
	♀♀	103	70
Carabus hortensis L.	♂♂	136	80
	♀♀	172	97
Pterostichus niger Schall.	♂♂	625	287
	♀♀	580	263

Investigations made so far of the migration of *Carabidae* were concerned with other problems. Kabacik (1957), in recording the variations in numbers of *Carabus arcensis* Hbst., in several habitats, reached the conclusion that the population of this species migrates, at the end of the mating season, from damp and shady habitats to dry and sunnier ones. Scherney (1955) found that marked specimens moved distances of from 150–200 m. over a period of seven weeks. Skuhravý (1956) made experiments of a similar character in order to discover what the possibilities are of complete occupation of the habitat by *Carabidae*. These investigations showed the undoubtedly great capacity of these beetles for active locomotion. It must be assumed that the above characteristic of *Carabidae* is a common one and applies to all the species included in this work.

The investigations carried out on station I included the tracing of variations in the percentage of individuals recaptured, depending on the lapse of time between the first and last captures. It became clear that females, as compared with males, are characterised by higher values in the "zero days" class and in the "over 1 year" class (Fig. 3).

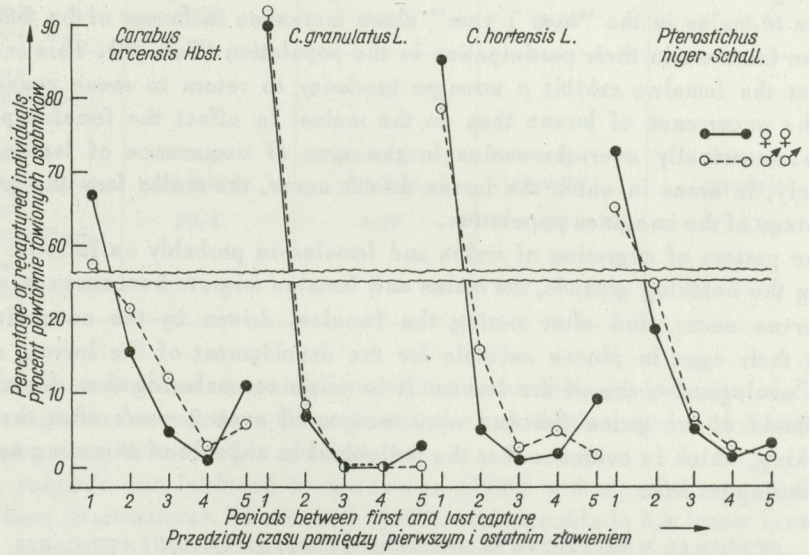

Fig. 3. Curves of percentage of recaptures of individuals
1 – zero days, *2* – up to 24 days, *3* – up to 48 days, *4* – up to 96 days, *5* – over 1 year
Krzywe procentu powtórnych złowień osobników
1 – zero dni, *2* – do 24 dni, *3* – do 48 dni, *4* – do 96 dni, *5* – ponad jeden rok

The "chi-square" method was used to establish whether the differences between curves of the percentage of recaptures of males and females are statistically significant. Calculation made for each of the four species with the largest number of marked specimens, of the probability of lack of differences between the curves referred to gives a figure of 0.10 for *C. arcensis*; 0.99 for *C. granulatus*

(probably it is as large as it is on account of the small amount of material); 0.01 for *C. hortensis* and 0.10 for *P. niger*. Probability calculated for the males and females of all species that the curves of percentage of their recaptures differ from each other significantly is less than 0.001 – and is therefore very small.

The data obtained permit of accepting the significance of the difference between the above curves, which may be attributed to the more strongly defined trends in the locomotion of females. The greater percentage of females in the "over 1 year" class does not in fact result from a greater tendency to settle in one place exhibited by the females, since over a period of from 50–80 days from the time of marking a smaller percentage of them is recaptured than males.

When comparing the data obtained in this work with Skuhravý's material (1956) it will be seen that there is great similarity in the curves of percentage of recaptured individuals; in his experiment, which lasted for one month, a smaller percentage of females then males was recaptured, and the former were caught further away from the site of their previous release.

In classifying the species occurring on station I according to the observed percentage of females, it was seen that the ratio in percentage of recaptured females to males in the "over 1 year" class increases in favour of the females with the increase in their participation in the population (Tab. III). This indicates that the females exhibit a stronger tendency to return to areas connected with the occurrence of larvae than do the males. In effect the females predominate numerically over the males in the area of occurrence of larvae, and reversely, in areas in which the larvae do not occur, the males form the greater percentage of the imagines population.

The pattern of migration of males and females is probably as follows: after leaving the hatching grounds, the males and females migrate from areas in which the larvae occur, and after mating the females, driven by the necessity for laying their eggs in places suitable for the development of the larvae, return to the ecological niche of the larvae. It is worth remembering that the marked individuals of the genus *Carabus* were recaptured even 2 years after the time of marking, which is evidence that the individual is capable of migrating several times during its life.

SEASONAL VARIATIONS IN NUMBERS OF *PTEROSTICHUS VULGARIS*

Although the seasonal variations in numbers of *Carabidae* have often been described, and Larsson's (1939) investigations have defined the two types of development of *Carabidae* which determine the different course follwed, there are very few attempts so far at interpreting the differences in variations in the numbers of individuals belonging to one species found on different areas. These investigations were made in field habitats, and on this account their authors paid most attention to the effect of agro-technical operations on the migrations of *Carabidae*, which define the periods of occurrence of imagines in different crops (Heydemann 1955, Scherney 1955). Endeavour was made to compare

Percentage in recaptures of females in relation to males in the "over 1 year" class of captures, depending on the number of females in the population

Kształtowanie się stosunku procentu powtórnych złowień samic do samców w klasie złowień „ponad jeden rok", w zależności od udziału samic w populacji

Tab. III

Species Gatunek	Percentage of ♀♀ in the imagines population Procent ♀♀ w populacji imagines	Percentage of ♀♀ in "over 1 year" class of captures Procent ♀♀ w klasie złowień „ponad jeden rok"	Percentage of ♂♂ in "over 1 year" class of captures Procent ♂♂ w klasie złowień „ponad jeden rok"	Ratio of percentages of ♀♀ to percentage of ♂♂ in this class Stosunek procentu ♀♀ do procentu ♂♂ w tej klasie
Pterostichus niger Schall.	48.1	3.04	1.39	2.18
Carabus arcensis Hbst.	49.0	10.62	6.03	1.76
Carabus hortensis L.	55.7	9.28	2.50	3.71
Carabus clathratus L. *Carabus coriaceus* L. *Carabus glabratus* Payk. *Carabus granulatus* L.	average średnio 59.4	average średnio 4.29	average średnio 0.90	average średnio 4.76

the clearly non-uniform course of variations in numbers of imagines of *P. vulgaris* caught on four stations (Fig. 4) with the hypothetical model of distribution of imagines and larvae of this species.

P. vulgaris was included by Larsson (1939) with species reproducing in the autumn (Herbsttiere). Skuhravý (1959) conforms this in his latest investigations, according to which the young imagines of *P. vulgaris* appear in June and not long afterwards the females begin to lay eggs. Egg-laying takes place chiefly in August and September. The larvae develop in the autumn and winter. Part of the imagines hibernate. The females which survive the winter are probably capable of laying a certain number of eggs the following spring.

It was noticed that on the station with the smallest percentage of females (36.4%) *P. vulgaris* occurred only from April to June, while its presence was not noted during the egg-laying period (Fig. 4, station II). Where the sex ratio was more or less equal (46.1 and 53.0% of females), this species occurred in the first case from the beginning of May to the end of July, and in the second

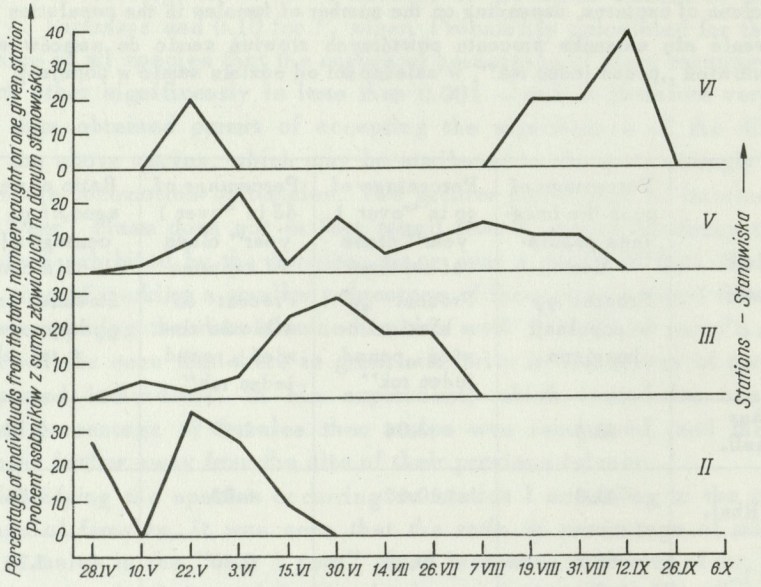

Fig. 4. Seasonal variations in numbers of imagines of *Pterostichus vulgaris* L.
Sezonowa dynamika imagines *Pterostichus vulgaris* L.

case continued until halfway through September (Fig. 4, stations III and V). On station VI, where the females formed 100% of the imagines caught, *P. vulgaris* occurred chiefly in September (Fig. 4, station VI), that is, during the egg-laying period.

When comparing the different course followed by seasonal variations in the appearance of this species on the stations with the model of the mutual distribution of imagines and larvae of *P. vulgaris*, it must be assumed that the variations in appearance are explained by the imagines of the species transferring during the mating period to the area of occurrence of larvae (which would seem primarily to refer to females). With this model the previous migration of young beetles to the optimum zone for adult insects is essential.

SUMMING-UP OF RESULTS

1. Ratios between larvae and imagines vary with the population of one species. They are distinctly correlated with the percentage of females in the imagines population (coefficient of correlation is + 0.63). The variations in ratios between larvae and imagines lead to the assumption that these forms occupy different niches, which fail to overlap in the horizontal plane.

2. The hypothetical model of co-occurrence of imagines and larvae of *P. vulgaris* in the horizontal plane reveals that the living areas of larvae and adult insects do not overlap.

3. When examining the migrations of males and females of several species it was found that the females are characterised by a greater tendency to definite directions in their migrations than in the case of males, caused by the necessity for laying their eggs in territory suitable for the development of the larvae. On this account the females move about more than males in the living areas of larvae, and a greater percentage of them occurs in these areas.

4. The attempt made at comparing a model of the distribution of imagines and larvae of *P. vulgaris* with the non-uniform course followed by the seasonal variations of this species on different stations shows that during the egg-laying period the imagines of *P. vulgaris* occur chiefly in the living area of the larvae of this species.

LITERATURE

1. Arnoldi, L.W. 1954 – Poczwiennyje liczinki nasiekomych rajonow r. Urala i Wołżsko-Uralskogo mieżdurieczija – Trudy Zooł. Inst. AN SSSR 16.
2. Gilarow, M.S. 1949 – Osobiennosti poczwy kak sriedi obitanija i jejo znaczenije w ewolucji nasiekomych – Moskwa–Leningrad.
3. Grüm, L. 1959 – Sezonowe zmiany aktywności biegaczowatych (*Carabidae, Coleoptera*) – Ekol. Pol. A, 7.
4. Heydemann, B. 1955 – Carabiden der Kulturfelder als ökologische Indikatoren – Ber. 7. Wanderversammlung Dtsch. Entomol.
5. Kabacik, D. 1957 – Z badań nad biegaczowatymi lasu sosnowego – Ekol. Pol. B, 3.
6. Larsson, S.G. 1939 – Entwicklungstypen und Entwicklungszeiten der Danischen Carabiden – Ent. Medd. 20.
7. Scherney, F. 1955 – Untersuchungen über Vorkommen und wirtschaftliche Bedeutung rauberisch lebender Käfer in Feldkulturen – Z. Pflbau u. Pflschutz 6.
8. Skuhravý, V. 1956 – Studium pohybu některych střevlikovitych značkovanim jedinců – Acta Soc. Ent. Čsl. 53.
9. Skuhravý, V. 1959 – Příspevek k bionomii polnich střevlikovitých (*Col., Carabidae*) – Roč. Čsl. Spol. Ent. 53.

O HORYZONTALNYM ROZMIESZCZENIU LARW I IMAGINES KILKU GATUNKÓW *CARABIDAE*

Streszczenie

Przedstawione w tej pracy wyniki dotyczą horyzontalnego rozmieszczenia larw względem dorosłych owadów kilku gatunków *Carabidae*.

Badania były prowadzone we wschodniej części Puszczy Kampinoskiej. Biegaczowate łowiono na sześciu stanowiskach we wkopane w glebę słoiki lub plastykowe szklanki o średnicy otworu około 6 cm.

Z otrzymanych danych wynika, że rozpatrywane w płaszczyźnie horyzontalnej stosunki ilościowe pomiędzy larwami i owadami dorosłymi w obrębie populacji jednego gatunku są zmienne: korelują się one wyraźnie z procentem występowania samic w populacji imagines (współczynnik korelacji wynosi +0,63).

Zmienność stosunków ilościowych pomiędzy larwami i owadami dorosłymi pozwala przypuszczać, że zajmują one różne nisze, częściowo niepokrywające się w płaszczyźnie horyzontalnej. Mechanizm tworzenia się przewagi ilościowej samic nad samcami w obszarach występowania larw polega na kierunkowym przemieszczeniu się samic, wynikającym z konieczności złożenia jaj w miejscach dogodnych dla rozwoju larw.

Ponadto okazało się, że w obszarach występowania larw sezonowa dynamika imagines *Pterostichus vulgaris* L. jest inna niż w terenach na których larwy tego gatunku nie występują. Mianowicie, w obszarach bytowania larw imagines przebywają głównie w okresie składania jaj, natomiast tam, gdzie larwy nie występowały — nie notowano imagines w czasie składania jaj.