KOMITET EKOLOGICZNY - POLSKA AKADEMIA NAUK

EKOLOGIA POLSKA – SERIA A

Tom XV Warszawa 1967 Nr 14

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REMARKS ON FLUCTUATIONS IN DENSITY OF *CARABIDAE* POPULATIONS*

It has been found (Grüm 1962) that the areas of occurrence of imagines and larvae of the same species do not completely coincide. In this work it has been stated that fluctuations in density of imagines of *Carabidae* are considerable in that part of their living area in which larvae live, and are connected with the abundance of the new population of adult insects. These fluctuations are slight in that part of the imagines' living space in which larvae do not occur, probably as a result of the reduction in the new generation of imagines emigrating from the zone in which larvae occur.

Van der Drift (1959), who examined the annual fluctuations in density of populations of several species of *Carabidae*, observed that the course taken by variations in population density in different parts of its living area was similar. He also noticed that fluctuations in density in species belonging to a uniform development type took a similar course. On these grounds Van der Drift (1959) suggests that varying weather conditions exert an important influence on the creation of the fluctuations observed. Murdoch (1966) examined the mechanisms stabilizing fluctuations in the population density of *Carabidae*, and described a model of density stabilization based on the reverse proportionality between the number of eggs laid by females during their first reproduction season and survival of the females to the next reproduction season.

The present study contains a discussion aimed at showing that the amplitude of density fluctuations in different parts of a population's living area is not uniform. This phenomenon has been interpreted as the effect of stabil-

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ization of population density by means of reduction of the new generation of imagines.

1. STUDY AREA AND METHODS

1.1 General description

Quantitative data on the occurrence of *Carabidae* were obtained by means of trap captures. The traps consisted of 5–6 cm diameter cylinders, sunk level with the soil surface. Captures were made in two habitats in the Kampinos Forest, situated in its eastern part, near Dziekanów Leśny, outside Warsaw.

1. *Pineto-Vaccinietum*, about 40–45 years old, forming a small (approx: 0.25 ha) part of the mosaic of varied forest habitats, almost completely surrounded by *Alnetum* and *Caricetum*. A study area was arranged as follows: 80 live-traps were set chequerwise over a surface of about 400 m^2. *Carabidae* were caught on this area, which was given the symbol *A*, over a period of five years, from 1956 to 1960. Captures were begun each year on May 15th and ended on October 5th. The traps were examined every three days.

2. *Pino-Quercetum*, about 80 years old, distinguished by the very mosaic--like character of the forest herb layer and undergrowth – forming and elongated forest belt about 100 m wide, bounded on both its long sides by *Alnetum*. Study area *GG* was situated here, and four rows of traps were arranged on it, filled with a low percentage formalin solution – the distances from the fringe of *Alnetum* of these rows being as follows – about 1 m (row I), 16 m (row II), 31 m (row III), and 46 m (row IV). There were 15 points, each consisting of two traps arranged close together, in each row. The distance between the points in the row was 7.5 m. The traps on area *GG* were inspected every 2 to 7 days during the period from May 3rd to October 9th. The area was reserved for the capture of small mammals, and the representatives of *Carabidae* which were caught there I obtained throught the kindness of G. Bujalska, M. Sc.

Imagines of *Carabidae* were caught on both areas, the time and place of capture of each individual recorded, its species and sex identified and its approximate age. Two age classes of the imagines were distinguished: young, characterized by fragile elytra and old, with hard elytra. The time taken for the elytra to harden sufficiently to reach the stage in which the individual is classified as old is from 2 to 3 weeks after its pupation.

The representatives of *Carabidae* caught belong to eleven species, of which five (*Carabus arcensis* Hrbst., *C. clathratus* L., *C. granulatus* L., *C. nemoralis* Müll. and *Pterostichus vulgaris* L.) represent the spring type of development and the remainder (*Carabus coriaceus* L., *C. glabratus* Payk., *C. hortensis* L., *C. violaceus* L., *Pterostichus niger* Schall. and *Cychrus rostratus* F.) belong to the autumn type of development (Larsson 1939). The species with the spring type of development copulate in May and June, their larval development takes place in the summer and the young imagines begin to appear at the beginning of August. *Carabidae* with the autumn type of development copulate in July and August, their larval development takes place in the autumn and winter and the young imagines begin to appear at the beginning of summer. With both types of development the maximum number of captures[1] is made during the copulation period. Captures made on area *A* from May 15th to October 5th therefore cover the maxima of occurrence of all the species examined and give a good picture of the period of the active life of imagines of both the types of development. Similarly captures on area *GG* cover the period of active life of all the species examined.

The question arises as to whether it is possible by means of trap captures, which depend on population density and individual activity (Heydemann 1956, M. Kaczmarek and W. Kaczmarek 1953), to ascertain population density and what errors are incurred when estimating density in this way. Kaczmarek's (1963) investigations prove that the activity of the soil macrofauna increases as its density decreases. It follows from the above that with low population density the number of captures in the traps is relatively high as a result of the considerable activity of individuals. When density is great the number of captures in the traps is low in relation to density, since the activity of individuals decreases as population density rises. The studies made by Grüm (1965), who showed that in years when the number of captures was small, the populations of *C. arcensis* and *P. niger* are composed entirely of individuals passing rapidly through the study area, i.e. they are very active, indicate a similar relation between the density, activity and number of captures. In years when the number of captures is large, these populations are divided into individuals passing rapidly through the study area (very active individuals) and those remaining for a certain time within or near the study area (i.e. less active individuals).

1.2 Localization of area *A* in the living area of populations of the species examined

Eleven species of *Carabidae* were caught on area *A* which differed from each other as to the mean number of captures per year (Tab. I) – calculated on the basis of five years of captures, which will henceforth be termed the mean annual number of captures and treated as an index of the mean annual population density in this area.

Area *A* formed only part of the living area of the populations of the species examined. This is indicated both by the constant passage of individuals through

[1] As some of the individuals were repeatedly caught in the live traps the term "number of captures" means the number of individuals caught and number of captures of an individual.

Mean number of captures per year of *Carabidae* occurring in area *A* and comparison of significance of differences in the annual variations in the population density of these species

Tab. I

No. of species	Species	Mean number of captures per year	log S_i^2	No. of species									
				2	3	4	5	6	7	8	9	10	11
1	*Pterostichus niger*	230.0	4.658	+*	+	+	+	+	+	+	+	+	+
2	*Carabus arcensis*	75.8	3.345		–**	+	+	+	+	+	+	+	+
3	*Carabus granulatus*	30.8	3.213			+	+	+	+	+	+	+	+
4	*Carabus hortensis*	56.2	1.485				–	–	–	+	+	+	+
5	*Cychrus rostratus*	11.0	0.875					–	–	–	–	–	–
6	*Carabus glabratus*	8.8	0.857						–	–	–	–	–
7	*Carabus coriaceus*	7.4	0.518							–	–	–	–
8	*Carabus nemoralis*	2.2	0.431								–	–	–
9	*Carabus clathratus*	4.4	0.361									–	–
10	*Pterostichus vulgaris*	2.0	0.301										–
11	*Carabus violaceus*	1.6	0.097										

* + Statistically significant difference.

** – Statistically non-significant difference.

the area (Grüm 1962, 1965) and the occurrence of species caught here in other biotopes of the Kampinos Forest. In order to define habitat preferences of the species referred to their distribution in the *Pino-Quercetum* biotope was investigated. It was found that the number of captures in each of four rows of traps in area *GG* (not at equal distances from *Alnetum*) points to a distinct increase in the population density of *C. arcensis*, *C. glabratus* and *C. hortensis* as the traps become more distant from *Alnetum* (Fig. 1). *C. coriaceus* and *C. violaceus* increase in the same direction, but apparently to a far lesser degree. The fringe of *Alnetum* is characterized by considerable density of *C. clathratus* and *C. granulatus*, which probably attain far greater densities within the *Alnetum* association itself. The density of *P. vulgaris*, and to a lesser degree of *P. niger*, *C. nemoralis*, and *Cychrus rostratus*, decreases as the traps become further from *Alnetum*. The species least numerously represented in these materials, presumably occur numerously in other biotopes of the Kampinos Forest which were not examined. According to Thiele and Kolbe (1962) *C. coriaceus* is characteristic of *Querceto-Carpinetum* and *Cychrus rostratus* for *Fageto-Quercetum*. *C. violaceus* attained considerable densities in oak woods in the studies made by Van der Drift (1959).

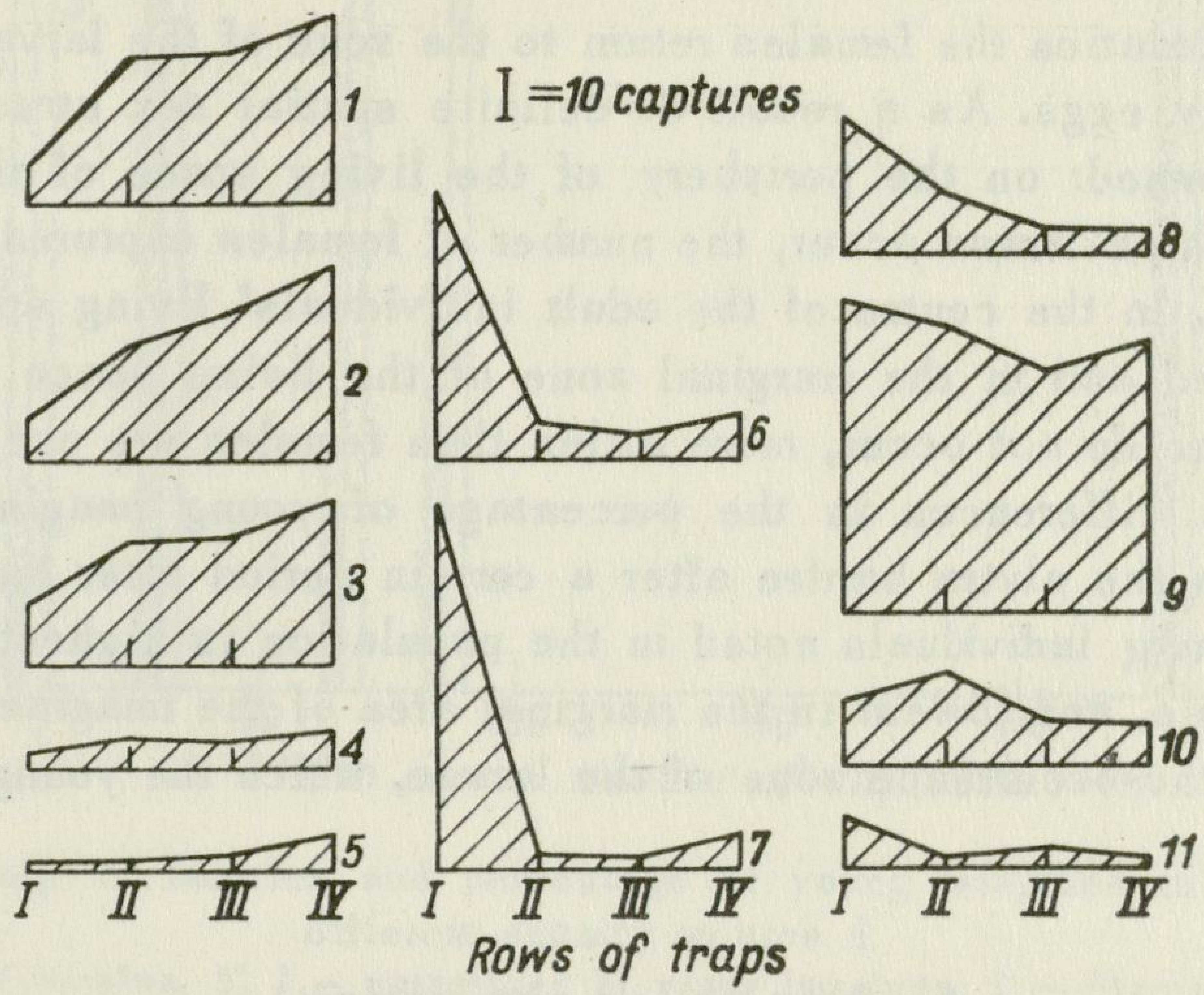


Fig. 1. Number of captures in rows of traps in area *GG*, situated at different distances from *Alnetum*

1 – Carabus arcensis, 2 – C. hortensis, 3 – C. glabratus, 4 – C. coriaceus, 5 – C. violaceus, 6 – C. clathratus, 7 – C. granulatus, 8 – Pterostichus vulgaris, 9 – P. niger, 10 – Carabus nemoralis, 11 – Cychrus rostratus

The differing habitat requirements of the species examined are evidence of the different value of area *A* as the living habitat of these species. A more detailed examination was made of what section of the population's living area is represented by area *A* for different species. Investigation of this section was based on a model of the spatial structure of a population given by Grüm (1962) for several species of the genus *Carabus* L. and *Pterostichus* Bon., living in the mosaic of the forest habitats in the Kampinos Forest. In this model the areas of occurrence of imagines and larvae belonging to the same species do not completely coincide, and therefore migrations of individuals occur in the population.

According to this model (Grüm 1962) the young imagines emigrate from the zone of the larvae's occurrence to the area in which the adult individuals live. After copulation the females return to the zone of the larvae's occurrence, where they lay eggs. As a result of definite spatial sex structure of the population is fomed: on the periphery of the living space of the imagines, in the zone in which larvae occur, the number of females captured is greater than that of males. In the centre of the adult individuals' living space the sex ratio is balanced and in the marginal zone of the living space of the imagines in which larvae do not occur, more males than females are caught. This model also includes differences in the percentage of young imagines with fragile elytra, i.e. as the elytra harden after a certain period after hatching, the percentage of young individuals noted in the population is highest in the larvae's occurrence zone, and lowest in the marginal area of the imagines' living space, furthest from the occurrence zone of the larvae, which the young imagines reach last.

2. RESULTS AND DISCUSSION

A comparative table was drawn up on the basis of the above premises, in which, knowing the percentage of females and percentage of young individuals, the mean annual population densities of the different species observed on area *A* were transferred to the appropriate sections of the population's living area in the model referred to above (Grüm 1962). Of all the species examined the highest percentage of females and percentage of young individuals was noted in the population of *C. granulatus* (Fig. 2), the fourth in order of density. *P. niger* – a species with the highest mean annual density on area *A* – was characterized by balanced sex ratio and fairly high percentage of young individuals. *C. arcensis* is similarly characterized by balanced sex ratio, but slightly lower percentage of young individuals. In the *C. hortensis* population the percentage of females and also the percentage of young individuals were observed to be slightly smaller than in the two preceding species. In populations of the remaining species – with mean annual number of captures below 12 – the percentage of young imagines is in general very low, as is the percentage of females (sex was not distinguished in the case of *Cychrus rostratus*), as shown in Figure 2. There is thus in area *A* a peripheral zone of the living space of *C. granulatus* corresponding or close to the zone of occurrence of larvae (Fig. 3). In the case of *P. niger* and *C. arcensis* this area

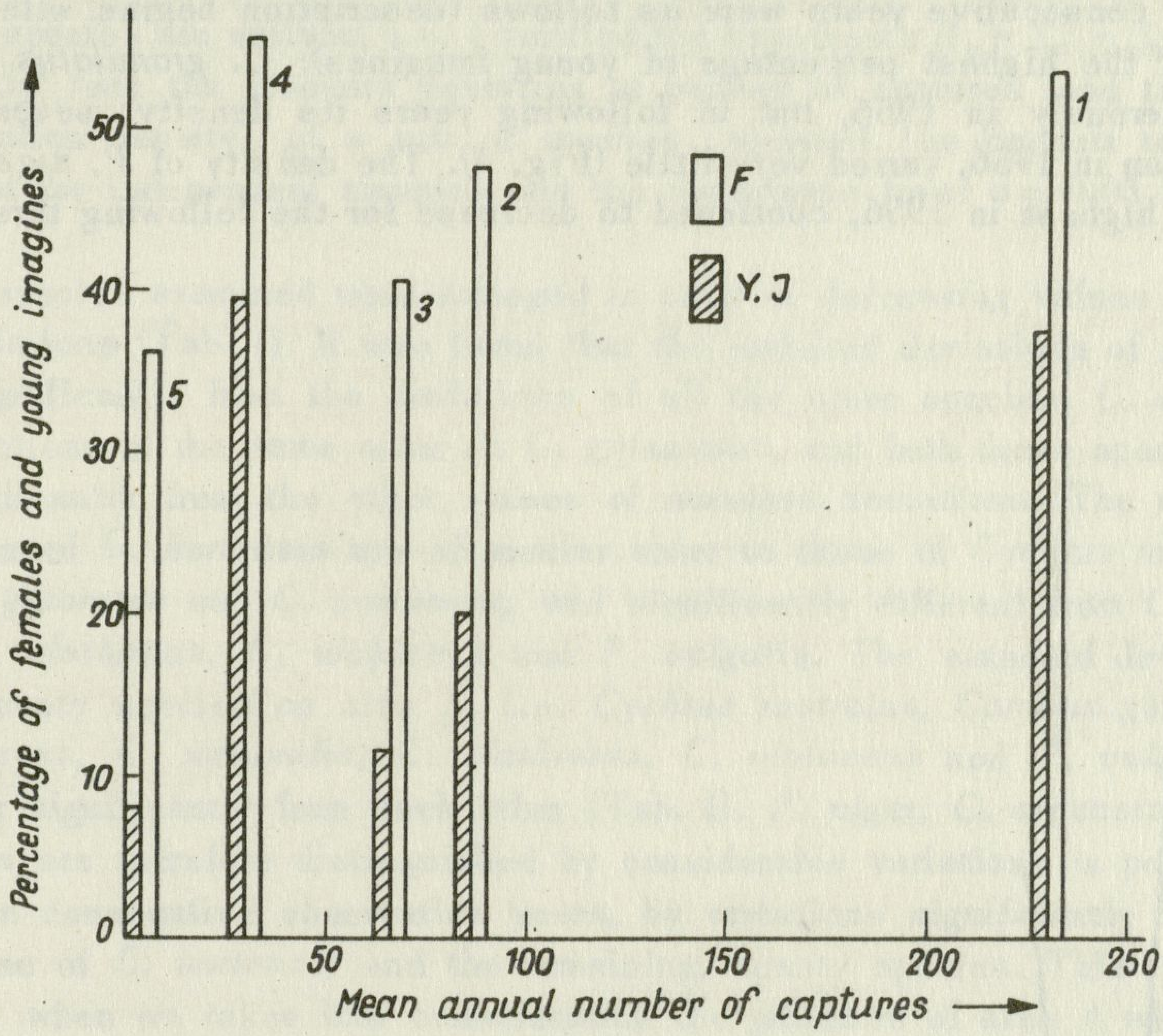
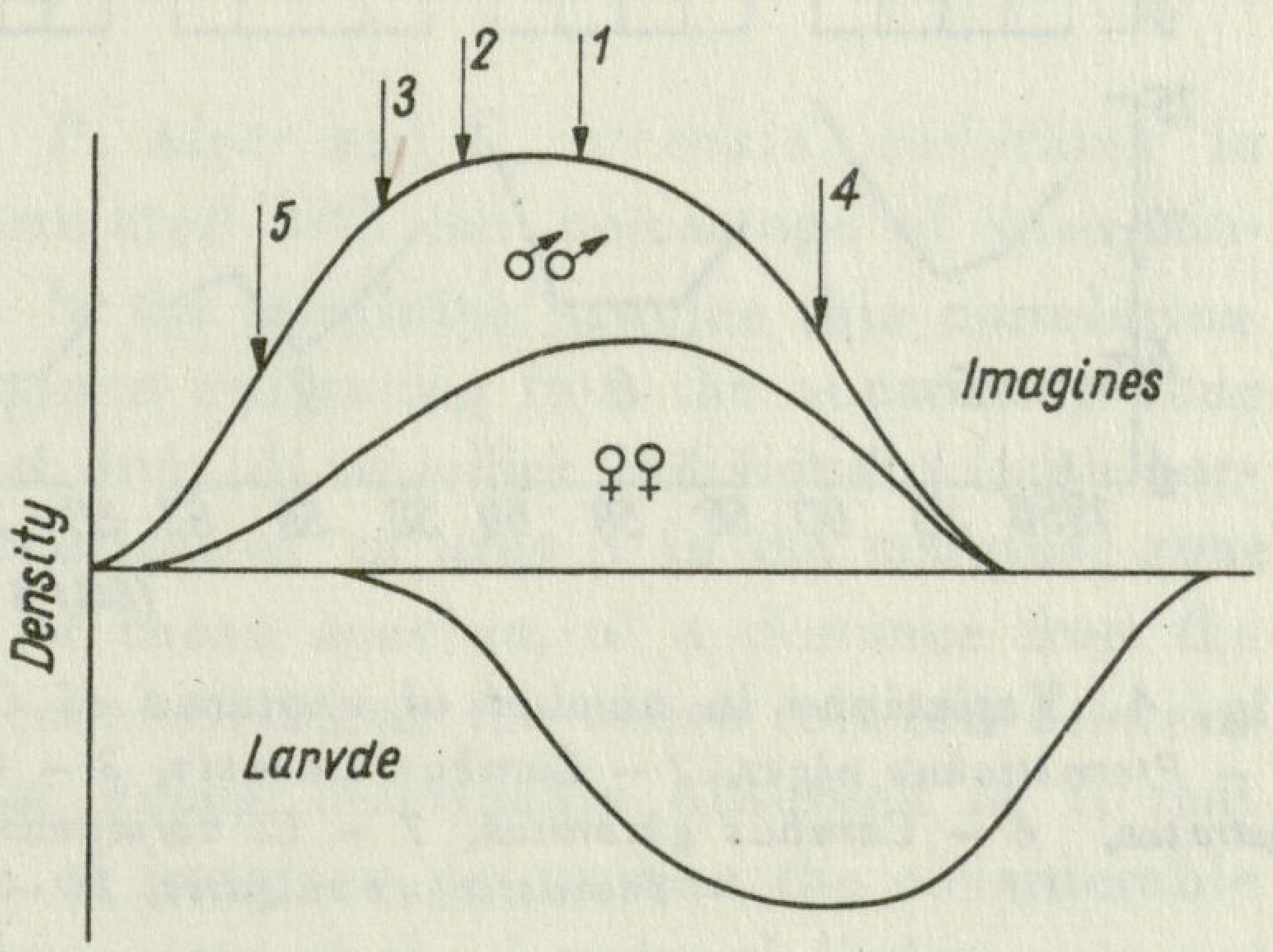


Fig. 2. Percentage of females and percentage of young imagines in populations of different density on area *A*

F – percentage of females, *Y. I* – percentage of young imagines, *1* – *Pterostichus niger*, *2* – *Carabus arcensis*, *3* – *C. hortensis*, *4* – *C. granulatus*, *5* – mean for remaining species caught on area *A*

Fig. 3. Diagram of localization of area *A* in the population's living space of species caught on this area *1* – *Pterostichus niger*, *2* – *Carabus arcensis*, *3* – *C. hortensis*, *4* – *C. granulatus*, *5* – remaining less numerous species



represents the centre of the imagines' living space, for *C. hortensis* the area situated between the centre and the zone without larvae in the imagines' living space, and for the remaining species, of which very few captures were made – the periphery of the imagines' living space most distant from the occurrence area of the larvae (Fig. 3).

Variations in the population density of different species caught on area *A* over five consecutive years were as follows (description begins with species exhibiting the highest percentage of young imagines): *C. granulatus* occurred most numerously in 1956, but in following years its density, several times smaller than in 1956, varied very little (Fig. 4). The density of *P. niger* and *C. arcensis*, highest in 1956, continued to decrease for the following three years,

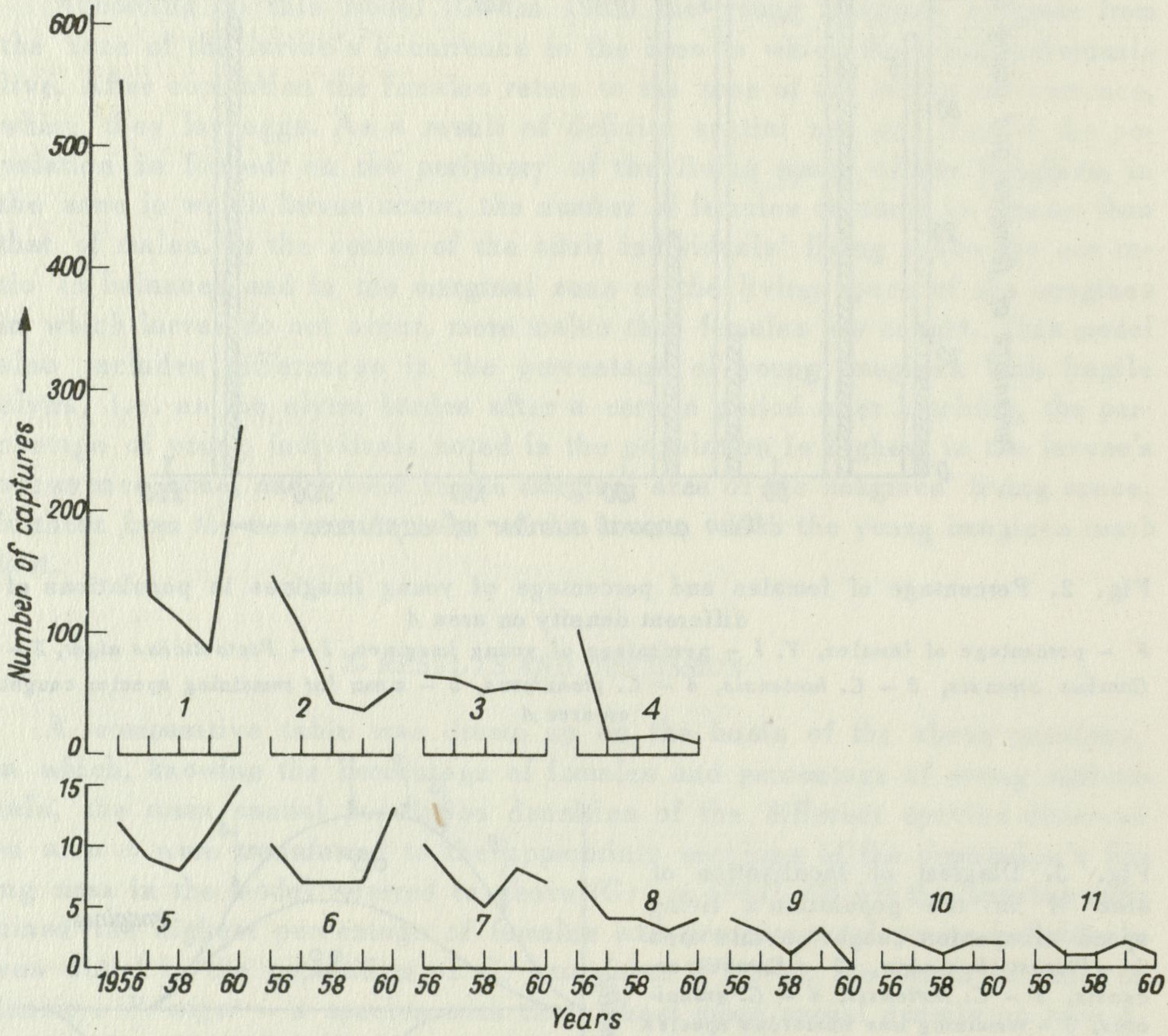


Fig. 4. Variations in number of captures of *Carabidae* in area *A* from 1956 to 1960
1 – *Pterostichus niger*, 2 – *Carabus arcensis*, 3 – *C. hortensis*, 4 – *C. granulatus*, 5 – *Cychrus rostratus*, 6 – *Carabus glabratus*, 7 – *C. coriaceus*, 8 – *C. clathratus*, 9 – *C. nemoralis*, 10 – *Pterostichus vulgaris*, 11 – *Carabus violaceus*

to increase slightly in 1960. The density of *C. hortensis* is almost identical over the whole five-year period, varying from 50 captures in 1958 to 63 in 1956. The remaining species are characterized by a generally larger number of captures in 1956 than in 1957–1959, which, however, increased in the case of some species in 1960 (Fig. 4).

In estimating the correctness of differences between the amplitudes of annual variations in the population density of species caught in area *A* a check was made to see whether the theoretical variances in the number of captures of these species are uniform, i.e. I verified the hypothesis $H_0 = S_1^2 = S_2^2$, where S_1^2 and S_2^2 form the standard deviation of number of captures (and therefore of population density) of a pair of species compared. The Bartlett test was also used for independent samples and the confidence level $a = 0.05$ was accepted.

The species examined were arranged in order of decreasing values of standard deviations (Tab. I). It was found that the standard deviations of *P. niger* differ significantly from the deviations of all the other species. *C. arcensis* has deviations of the same order as *C. granulatus*, and both these species differ significantly from the other values of standard deviations. The standard deviations of *C. hortensis* are of similar order to those of *Cychrus rostratus*, *Carabus glabratus* and *C. coriaceus*, and significantly different from *C. nemoralis*, *C. clathratus*, *C. violaceus* and *P. vulgaris*. The standard deviations of the scanty species on area *A*, i.e. *Cychrus rostratus*, *Carabus glabratus*, *C. coriaceus*, *C. nemoralis*, *C. clathratus*, *C. violaceus* and *P. vulgaris* do not differ significantly from each other (Tab. I). *P. niger*, *C. arcensis* and *C. granulatus* are therefore distinguished by considerable variations in population density in consecutive observation years, by variations significantly different from those of *C. hortensis* and the remaining, scanty species. This is understandable when we taken into consideration the situation of area *A* within the living space of imagines of different species; considerable fluctuations in population density were observed in the centre of the imagines' living space and in the peripheral zone lying in the occurrence area of larvae. Conversely, very slight variations in population density occurred in the marginal zone of the population's living space at the greatest distance from the zone in which the larvae occurred.

In three species, *C. granulatus*, *P. niger* and *C. arcensis*, variations in population density are positively correlated with the percentage of young individuals with fragile elytra (Fig. 5). In the remaining species this correlation does not occur, since the young imagines emigrating from the occurrence zone of larvae were presumably caught on area *A* as older individuals (with hardened elytra), which is due to the localization of area *A* in the marginal zone of the living space of the imagines of these species, at a distance from the occurrence area of larvae. It may be concluded from the above relation between population density and percentage of young individuals observed in it that the abundance of the new generation of imagines determines the considerable variations in population density in the centre of the imagines' living area and in the zone of occurrence of larvae.

Greater stability of population density can be observed in the peripheral zone of the population's living space at a distance from the occurrence zone of larvae, probably due to intensive reduction of imagines with fragile elytra. It appears that individuals with soft elytra are more susceptible to the action of unfavourable weather conditions than old individuals, since in the live-traps there are individuals with soft elytra which predominates numerically among individuals died when the traps are flooded with rain water. The young imagines

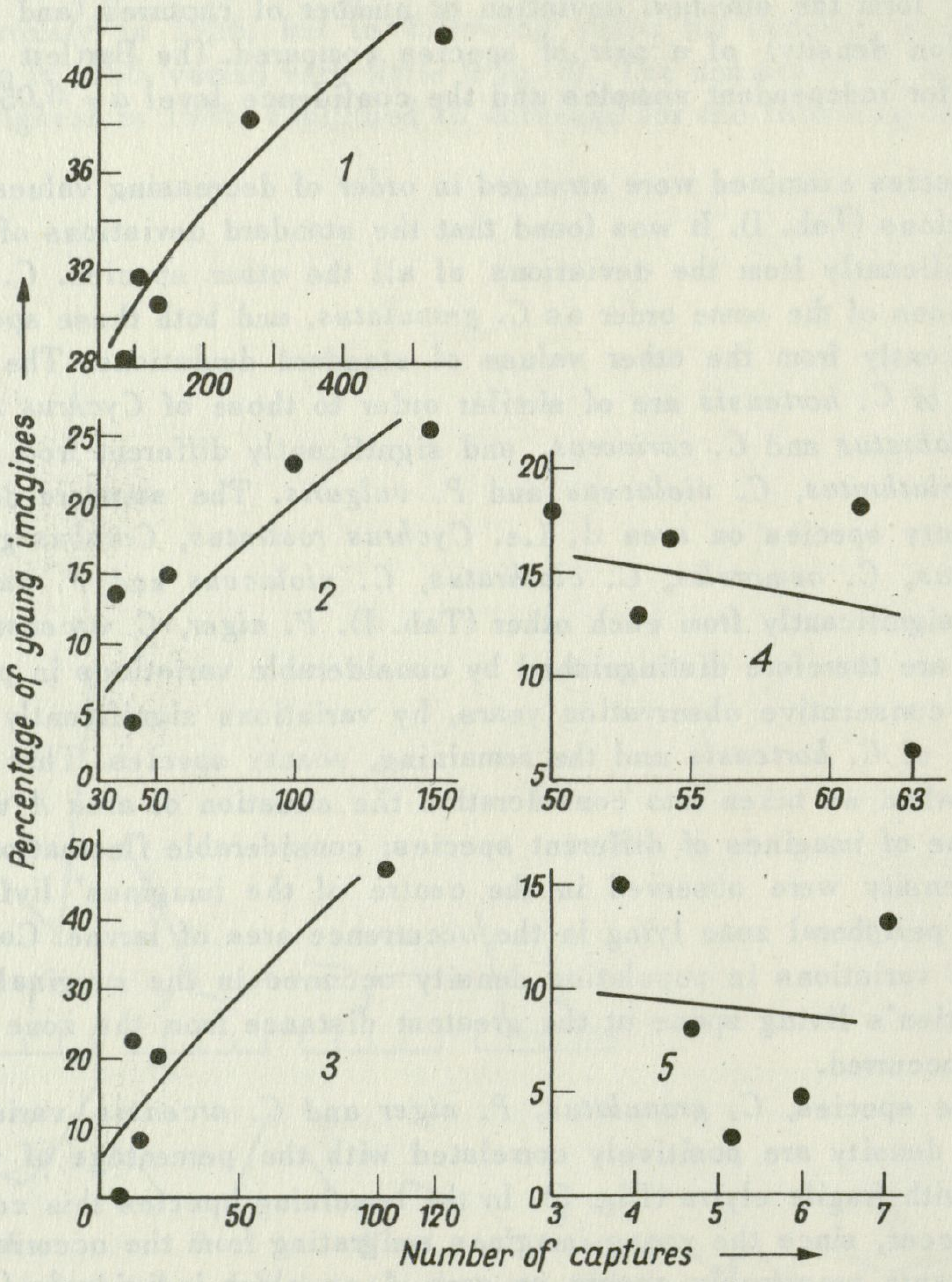


Fig. 5. Relation between number of captures and percentage of young imagines in a given year

1 – *Pterostichus niger*, 2 – *Carabus arcensis*, 3 – *C. granulatus*, 4 – *C. hortensis*, 5 – remaining species

are also more exposed to the attacks of predators than old individuals: cases of cannibalism were observed under natural conditions, the victims of which were always young individuals. Finally the young individuals are more affected by food shortage, as they are characterized by more intensive metabolism than older insects with hard elytra (Grüm 1966). The last two causes may lead to reduction of the new generation of imagines depending on density, contributing in this way to stabilization of population density fluctuations in the marginal zone of the population's living area at a distance from the occurrence area of larvae.

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UWAGI O FLUKTUACJACH GĘSTOŚCI POPULACJI *CARABIDAE*

Streszczenie

Badaniami (1956–1960) objęto imagines jedenastu gatunków z rodziny *Carabidae* występujących w Puszczy Kampinowskiej. Ilościowe informacje o ich występowaniu zdobywano przy pomocy odłowów pułapkowych. Stwierdzono, że fluktuacje gęstości populacji mają niejednakową amplitudę w różnych fragmentach areału. W tej części areału, w której żyją larwy (areały występowania imagines i larw tego samego gatunku niezupełnie się pokrywają), fluktuacje gęstości imagines są duże i wiążą się z liczebnością nowego pokolenia dorosłych owadów. W tej części areału, w której larwy nie występują, fluktuacje imagines są niewielkie, prawdopodobnie na skutek redukcji nowego pokolenia imagines emigrujących ze strefy występowania larw.

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