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INTRAPOPOPULATION RELATIONS AND REGULATION OF NUMBERS
IN SMALL FOREST RODENTS*

The relations between resident and migrating individuals were examined in respect of three species of small rodents. In the case of *Apodemus agrarius* (Pall.) these relations are tolerant, whereas in the case of *Apodemus flavicollis* (Melch.) the migrants are energetically repelled by the resident individuals. In the case of *Clethrionomys glareolus* (Schreb.) relations between the two categories of rodents become antagonistic with increasing occupation of the area by the resident individuals. The connections between resident and migrating rodents form the intrapopulation mechanism regulating numbers, the action of which depends on the intensity of antagonistic relations, the density of the resident part of the population and the degree of its residency. With *A. agrarius* the regulation of numbers is weakest, with *C. glareolus*, the strongest, while with *A. flavicollis* it is intermediate in degree between the first two species.

The aim of this study is to investigate the relations between resident and migrating rodents in a forest habitat and to analyze the effect of the intrapopulation connections observed on the regulation of numbers, in the light of the concept that population phenomena are structural in character.

AREA, MATERIAL, METHODS

The investigations were made in the Kampinos Forest near Warsaw, the Field Station of the Institute of Ecology, Polish Academy of Sciences, at Dzie-

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kanów Leśny, being used as a base. Data obtained from the sampling plot, covering approximately 3 hectares of forest with varied vegetation, were used for calculations. Captures were made once a week in this plot (two trappings over a 24-hour period) of the rodents, by means of permanent traps arranged in chequer-board fashion at intervals of 13 m. Captures were made by the method worked out by Andrzejewski and Pielowski (1956) by means of live traps, using oats as bait. Data on the three following species of rodents were used for an analysis of intrapopulation relations: *Clethrionomys glareolus* (Schreb.), *Apodemus agrarius* (Pall.) and *A. flavicollis* (Melch.). These data were obtained during the period 1955–1960, under the guidance of Dr. R. Andrzejewski and in 1961 under the author's guidance, by members of the staff of the population laboratory of the Institute of Ecology, Polish Academy of Science. Data from 6706 captures of 1582 rodents were used for the work. A detailed list of captures has been prepared separately for the different periods (Tab. I).

Comparison of material

Tab. I

Species	Period	Residents		Migrants		Total	
		indi- viduals	captu- res	indi- viduals	captu- res	indi- viduals	captu- res
<i>C. glareolus</i>	3 XI 1955–31 XII 1957	265	2177	179	329	444	2506
	1 I–19 VII 1961	144	653	45	57	189	710
	6 VII–22 VII 1961	43	359	33	41	76	400
<i>A. flavicollis</i>	3 XI 1955–30 V 1956	41	222	31	36	72	258
	13 VII 1960–31 VII 1961	84	224	53	74	157	298
<i>A. agrarius</i>	3 XI 1955–30 XII 1956	131	633	114	153	245	786
	6 V–26 XI 1959	198	1475	221	273	419	1748
	Total	906	5743	676	963	1582	6706

Data on the variations in numbers of the species examined were taken from material elaborated by Andrzejewski (1963).

Considerable difficulty is encountered in distinguishing migrating rodents from resident ones. Andrzejewski and Wierzbowska (1960, 1961), on the basis of data from captures made every week, established that migrants are found among individuals, the time of residence of which is less than one week. Trojan and Wojciechowska (1964), on the basis of data collected twice a day, demonstrated that there are migrants among the individuals remaining in the study area less than 12 hours, and therefore practically speaking among those individuals which were caught only once. Petruszewicz and Andrzejewski (1962) in analyzing this category of individuals, termed ephemeral rodents, found that it was not a uniform one, since in addition to really migrating individuals it contains rodents which, though apparently migrating, are resident

individuals. It is only possible to separate these two categories in the mass, as there is no way of defining individually which specimen is resident and which migrating. The category of apparently migrating individuals are rodents settling in, and they cannot be treated in the same way as fully resident animals, their connection with the area being as yet a very loose one (Trojan and Wojciechowska 1964), so that treatment of all ephemeral individuals as migrants is nearer the real biological value of these individuals. In the present study all individuals which remained less than one week in the sampling plot, or for which the interval between consecutive captures was so great (Petrusewicz and Andrzejewski 1962) that the individual was absent from the study area between these captures, were treated as migrants.

Individuals which remained in the sampling plot more than one week and exhibited a defined frequency of captures were counted as resident rodents (Petrusewicz and Andrzejewski 1962). In the case of individuals belonging to *C. glareolus* they were taken as present if the interval between consecutive trappings did not exceed four weeks. The threshold value of this interval is 7 weeks for *A. agrarius* and 4 weeks for *A. flavicollis*. These values were taken as a basis for estimating the presence of the rodents. If a rodent, after a series of captures indicating its presence in the area, ceased to be caught for a period exceeding the length of the interval accepted, and was then caught once, then it was taken that during the first period it had been a resident animal and then became a migrant. If a resident individual exhibited a series of captures indicating its presence in the plot, after a long interval in its presence, it was treated as a resident individual in both periods.

All the captures of rodents were entered on to a plan of the sampling plot, and the number of captures of resident rodents and that of migrants were set out separately on each point. Material arranged in this way formed a basis for further analysis. The quantitative methods used do not require discussion in detail. The distribution of captures of rodents in relation to the traps was examined by comparison with Poisson's distribution. In addition the character of the distribution was analyzed by means of the ratio σ^2/\bar{X} , where σ^2 — the variance, \bar{X} — arithmetical mean. The coefficients of encounter-probability of resident and migrant rodents were worked out on the basis of Kajak's (1957) proposals for the application of the product of probability:

Coefficient of encounter-probability (w) = $\frac{r \cdot n}{a \cdot b}$, where r — number of actual encounters of the two elements investigated, i.e. of a defined number of captures of resident and migrant rodents in the trap, n — number of samples in the series analyzed, a — number of samples with resident rodents, b — number of samples with migrating rodents.

The coefficient of variability with an analysis of variations in population numbers was calculated according to formula $V_c = \sigma/\bar{X} \cdot 100$.

SPATIAL DISTRIBUTION OF CAPTURES OF RESIDENT AND MIGRATING RODENTS

Determination of the distribution of resident rodents is of primary importance in analysis of connections between the two groups. Andrzejewski and Głogowska (1962) found that the distribution of captures of rodents is aggregational in character; the longer a resident individual lives in the study area the more strongly evidenced is its attachment to a certain section of the area. For the purposes of the present study investigation was made of the distribution of captures of resident rodents in relation to the whole area, without taking into consideration the participation which different resident individuals have in a given place. The distribution obtained therefore gives not a picture of the distribution of resident rodents in space, but a picture of the degree to which the area is penetrated by resident rodents. The differences in this distribution form grounds for further consideration of the relation of resident rodents to migrating individuals. Analysis of this distribution should provide a reply to the question as to whether the area is evenly penetrated by the rodents, or whether certain places in it are more frequently visited by the animals than others. These distributions were investigated for all the material mentioned in the introduction. Considerable similarity of distributions of captures occurs within the group of resident rodents, regardless of their species appurtenance, which justifies their being discussed jointly.

The distribution of resident rodents (Fig. 1) is a typical aggregational distribution, and in the case of all three species exhibits a surplus of points on which few resident rodents are caught. There are fewer traps with the mean number of captures than would appear to be case from the random distribution. Each of the distributions examined exhibited a considerable surplus of traps catching a non-fortuitously high number of rodents. In all six cases examined the difference between the distribution obtained and the random one, estimated by means of criterion χ^2 , is significant.

The distribution of captures of migrants of the three species examined in relation to the area (Fig. 2) differs, very little from the random one. In 5 out of 6 cases examined the number of traps catching 0 migrants is higher than that assumed by the random distribution. In all the distributions it is simultaneously the maximum of the curve agreeing with the maximum of the distribution. The frequency of multi-capture traps is slightly higher than in the random distribution. A distribution of penetration by migrants of this kind points to a certain similarity to the distribution of resident rodents. It consists in both the points on which no animals were caught (zero-points) and the points on which many animals were caught (multi-points) being represented more numerously in the material than is envisaged by the random distribution. The maxima and course taken by the curves, however, exhibit greater agreement with the random distribution in the case of migrants than in that of resident rodents. Criterion χ^2 gives differences between the distributions obtained and random distributions far smaller for migrants than for resident rodents.

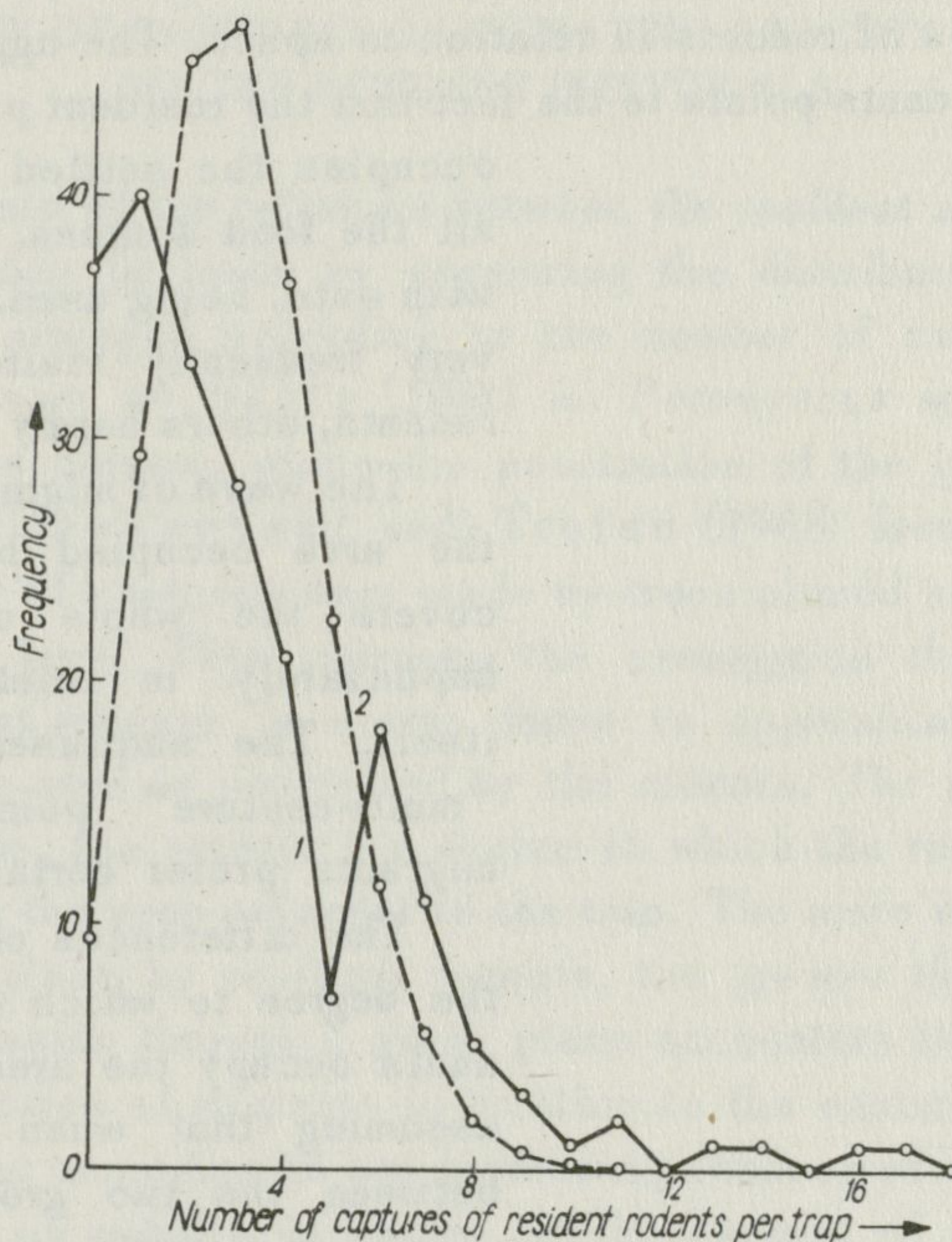


Fig. 1. *C. glareolus*, distribution of captures of resident rodents
1 — distribution of captures of resident rodents, 2 — random distribution

The estimate of the distribution, its tendencies to evenness or to an aggregational character were based on the ratio of variances to the arithmetical mean. Data on the three species were set out separately (Tab. II). For resident rodents this index exceeds 1.5 in all cases, which points to the aggregational character of penetration by this group of rodents. This index attains its maximum values in the case of *C. glareolus*, and its minimum in that of *A. flavicollis*. Penetration of the area is most aggregational with *C. glareolus*, less so with *A. agrarius*, and least with *A. flavicollis*. Similar differences in the index of spatial distribution is not, however, evident in the migrants of these three species, for which it varies within limits of 1 to 1.8. The migrants of the rodent species examined therefore penetrate the study area in a similar way. The value of the index in two cases differs only very slightly from 1.0. In such situations (1961) the migrants pass through the area in a wave spread completely fortuitously over the area. In other cases a slight tendency to aggregation occurs.

Value σ^2/\bar{X} has higher values for the distribution of resident rodents than for migrants, and it is only in the case of *A. flavicollis* that inconsiderable differences were observed. It is clear from this that resident mice belonging to this species exhibit a very low degree of aggregation.

The data referred to above make it possible to form a picture of the distribution of both groups of rodents in relation to space. The aggregational distribution of resident rodents points to the fact that the resident part of the population occupies the settled area unevenly, not all the food sources, including the traps with oats, being used. Certain places are very frequently visited by the resident rodents, others hardly at all.

The wave of migrants passing through the area occupied by resident rodents covers the whole area more or less haphazardly in relation to the space itself. The surpluses observed on the "multi-capture" points show that the migrants prefer certain paths to others.

The differences observed, especially the degree to which the resident individuals occupy the area, give grounds for assuming that when connections occur between the two groups of rodents we should observe deviations in the distribution of migrating rodents in relation to the resident specimens.

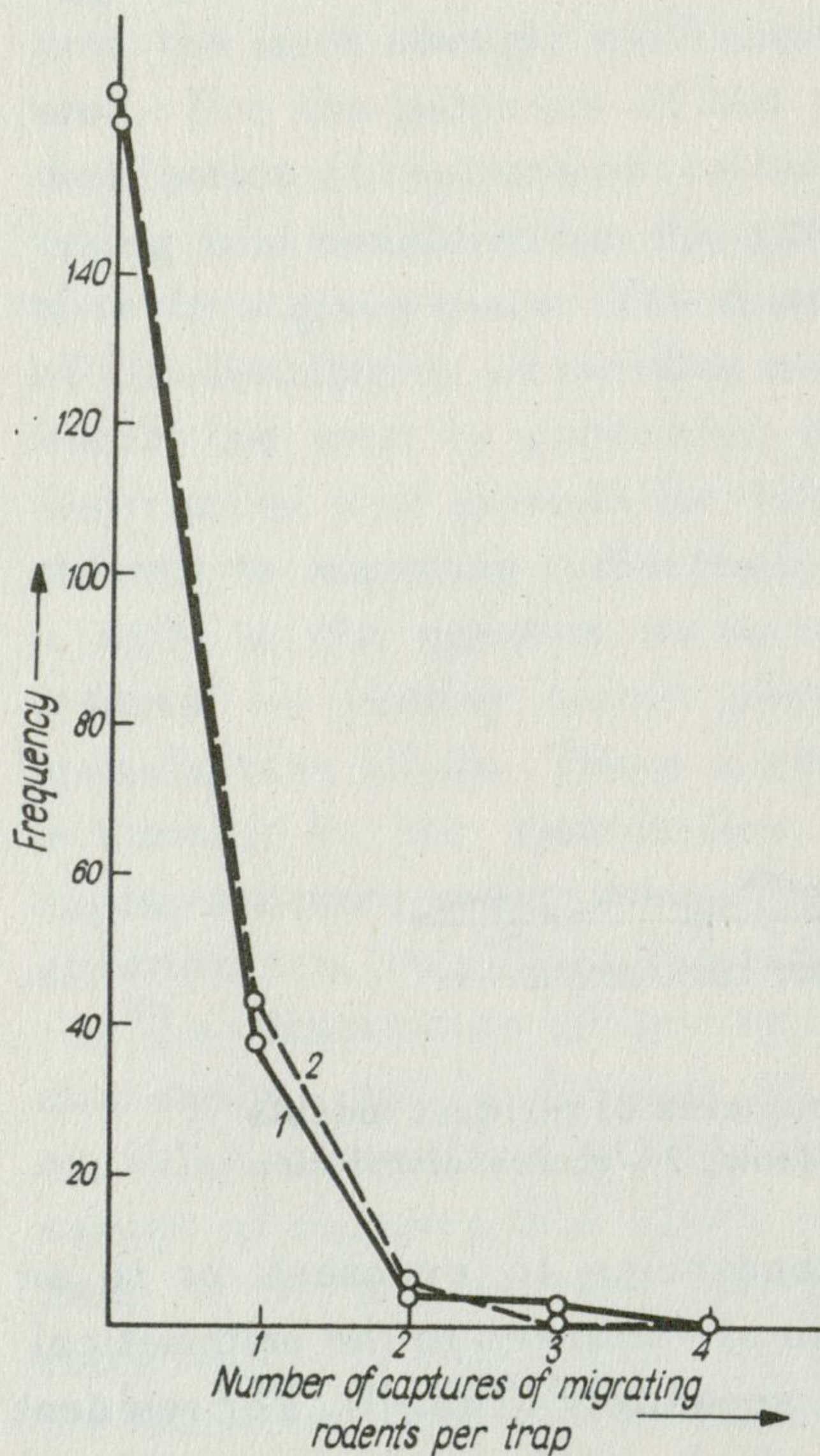


Fig. 2. *C. glareolus*, distribution of captures of migrants

1 - distribution of captures of migrants, 2 - random distribution

Distribution of captures of resident and migrating rodents in the Kampinos Forest

Tab. II

Species	Period	Resident rodents		Migrating rodents	
		\bar{X}	σ^2 / \bar{X}	\bar{X}	σ^2 / \bar{X}
<i>A. flavicollis</i>	1955-1956	1.50	1.5356	0.24	1.5378
	1961	1.07	1.5090	0.35	1.0057
<i>A. agrarius</i>	1955-1956	4.19	2.7834	1.02	1.5084
	1959	12.29	3.2152	2.28	1.5381
<i>C. glareolus</i>	1955-1957	14.51	6.2777	2.19	1.8185
	1961	3.11	2.9191	0.27	1.2262

\bar{X} - mean number of captures of rodents in traps,
 σ^2 / \bar{X} - ratio of variancy to arithmetical mean.

DISTRIBUTION OF CAPTURES OF MIGRATING RODENTS IN RELATION
TO THE RESIDENT INDIVIDUALS

A correct estimate of the relations between the resident and migrating parts of the population can be made by comparing the distribution of captures of migrants in traps arranged according to the number of captures of resident individuals. As shown by Blair (1951) for *Peromyscus* sp. the number of captures in traps is greater, where the penetration of the given place by the rodents is greater. Opuszyński and Trojan (1963) found in addition that the greatest number of captures were made by traps placed near the burrows in which the rodents live. This warrants the assumption that the number of captures of resident rodents in a trap forms an approximate measure of the degree to which the area is penetrated by the rodents. The greater the number of captures in a trap, the greater the degree to which the resident part of the population occupies the area adjacent to the trap. The more intensive the penetration of a given place by resident rodents, the greater the probability that a migrant rodent passing through a given place encounters the resident rodent. Arrangement of captures of migrants in relation to the captures of residents is therefore arrangement according to the increasing chances of encounter between the two categories of rodents in nature. If the capture of migrating rodents, haphazard in relation to the area, did not also exhibit a connection with the degree of occupation by resident rodents of the habitat investigated, then the distribution of mean numbers of captured migrants should take a parallel course to the abscissa. In each of the distributions examined a decided deviation was obtained from the random distribution, which is evidence that the two groups of rodents are not indifferent to each other and that there are ecological connections between them which are reflected in the distribution of captures.

The distribution of captures of migrants in traps with a different number of captures of resident rodents differs in each of the three species examined from this aspect.

A. agrarius (Fig. 3) represents a simple kind of dependence from this aspect. The distribution of captures of migrating rodents in 1959 was in direct proportion to the distribution of captures of resident rodents. Two sections of the curve can be distinguished — the first covering the range of 0–18 captures of resident rodents exhibits a slight increase in the number of captures of migrants together with an increase in the degree to which the area is penetrated by resident rodents. The second section (20–36 captures of resident rodents) corresponds to areas intensively penetrated by resident rodents. It exhibits a considerable increase in the number of migrants caught together with an increase in the degree to which the area is penetrated by resident rodents. The course taken by the curve shows that places which have little attraction for resident rodents, do not attract migrating rodents, which in passing through

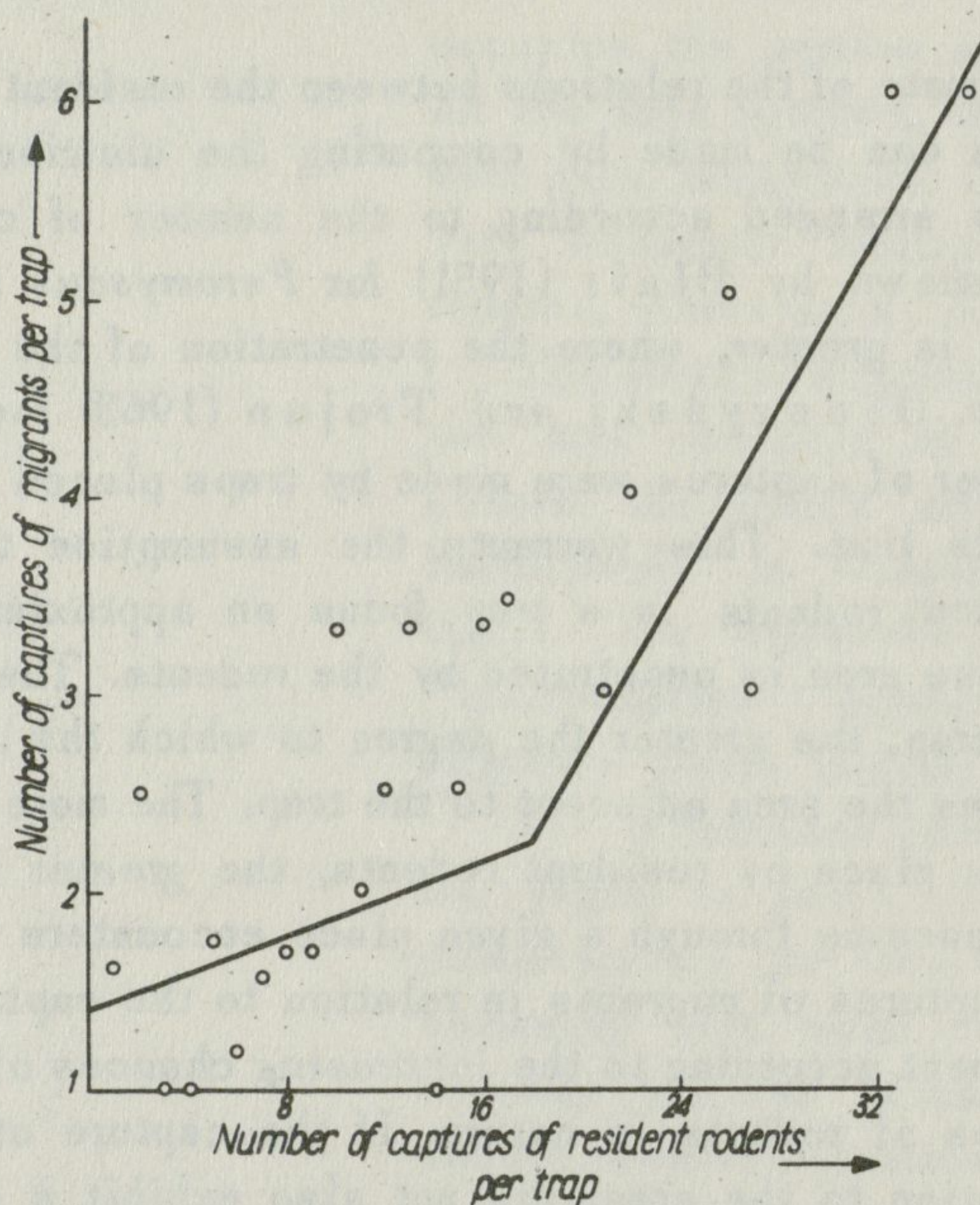


Fig. 3. *A. agrarius*, distribution of captures of migrants in relation to resident rodents in the Kampinos Forest

the sampling plot aim for the places in which the number of resident rodents is greatest, and in addition, that non-antagonistic connections occur between these two groups of rodents of this species. Resident individuals of *A. agrarius* in a forest habitat do not oppose the influx of migrants on to areas which they themselves have occupied. A similar distribution of migrants was also obtained in 1956.

A. flavicollis (Fig. 4) presents a different kind of connection. The curve begins on a higher level than in the case of the preceding species, if the differences caused by the smaller numbers of *A. flavicollis* in the study area than those of *A. agrarius* are ignored, and a considerable part of migrant individuals of *A. flavicollis* move about the areas occupied only to a small degree by the resident individuals of this species. In areas more intensively penetrated by resident individuals of *A. flavicollis*, the number of migrants of this species decreases evenly until a point when no captures of migrants are noted when the density of resident individuals reaches a peak. A similar picture to the above recurred in both the study periods (1955–1956, 1961). The first section of the curve for *A. flavicollis* (0–3) of captures of resident individuals in traps exhibits an increase in direct proportion to the degree of penetration

of the area by resident rodents. This part of the graph proves that migrants of *A. flavicollis* exhibit a similar tendency to that exhibited in the case of *A. agrarius*: they make for places settled by the resident individuals. The second part of the curve (4–7 captures of resident rodents in traps) points to the existence of a connection in reverse proportion that is, the greater the number of captures of resident rodents, the smaller the chances of catching a migrating rodent in the trap. A curve of this kind is evidence of the existence of strong antagonistic connections between the two groups of rodents.

In the case of *C. glareolus* (Fig. 5) the distribution of captures of migrating rodents in relation to the resident individuals is of an intermediate character, but is closer to that described for *A. flavicollis*. Over a considerable area the number of captures of migrants increases in direct proportion in relation the degree

to which the area is penetrated by resident individuals. As in the case of *A. agrarius*, areas only slightly penetrated by resident individuals are not very

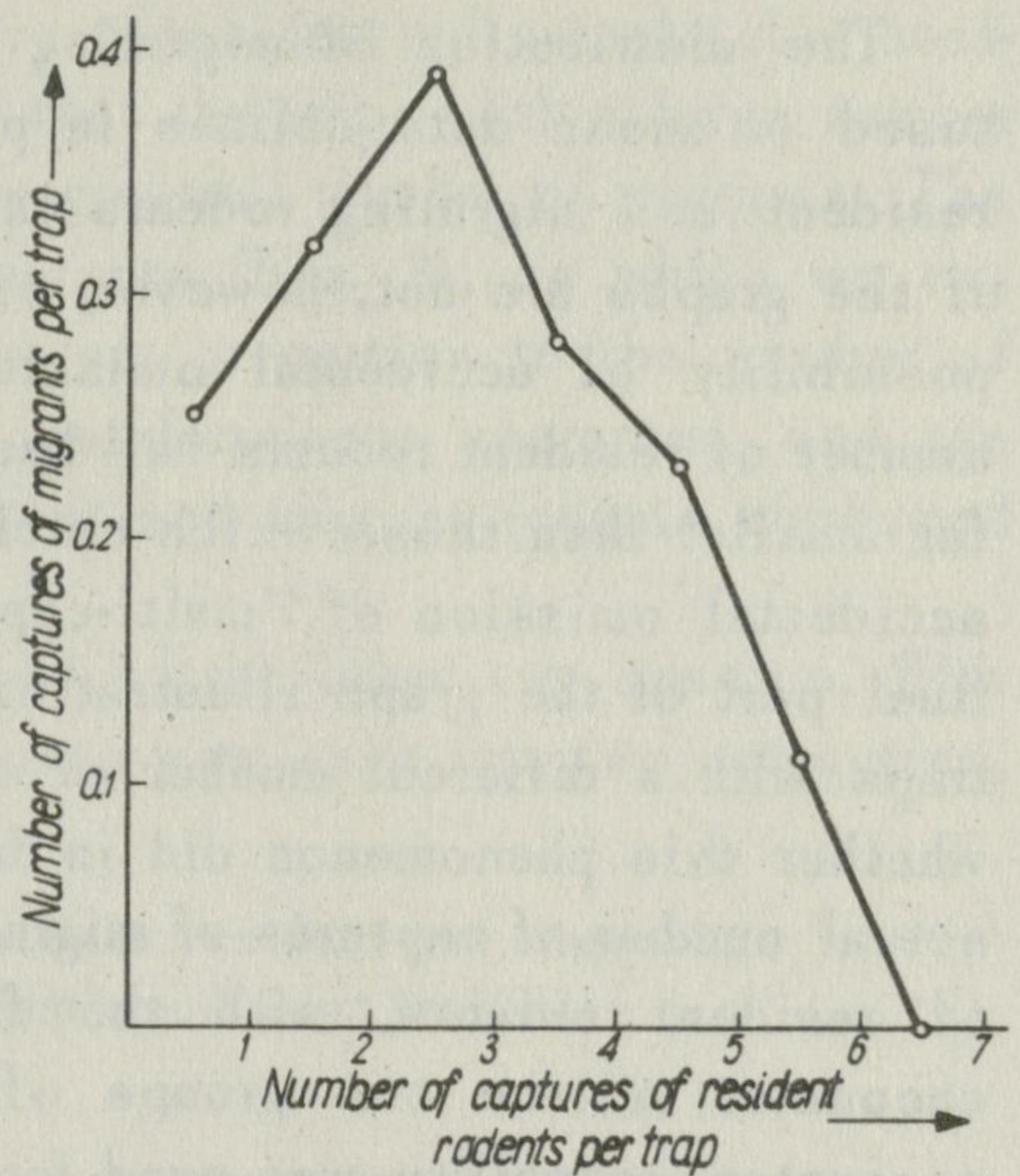


Fig. 4. *A. flavicollis*, distribution of captures of migrants in relation to resident rodents in the Kampinos Forest

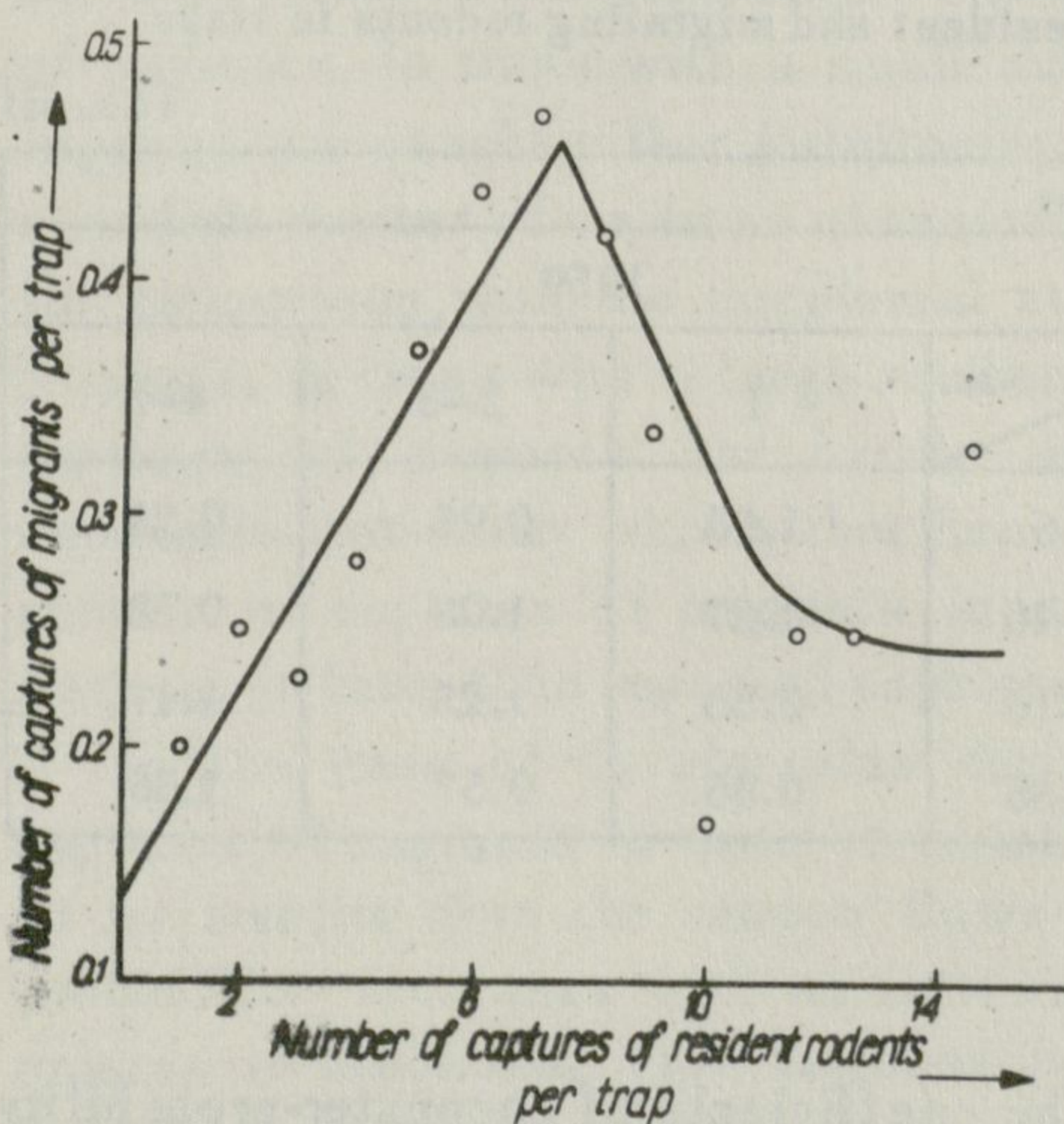


Fig. 5. *C. glareolus* distribution of captures of migrants in relation to resident rodents in the Kampinos Forest

attractive to migrants, the number of which increases together with an increase in the degree to which the habitat is penetrated by resident rodents. This relation is, however, inhibited in places which are most intensively penetrated by resident rodents. Here a reverse connection is observed: together with an increase in the number of resident rodents in the traps the number of captures of migrants decreases, although this decrease is not so sharp as in the case of *A. flavicollis*. Distributions were examined for material obtained from 1955–1957 and 1961, and in both cases a very similar picture was obtained.

PROBABILITY OF ENCOUNTER BETWEEN RESIDENT
AND MIGRATING RODENTS

The distribution of migrating rodents in relation to resident individuals based on mean data defines in principle the chances of encounter between resident and migrating rodents in a given places. The values of each point of the graphs are not, however, of equal value. In the first place there is the possibility of accidental omission by migrants of traps in which a large number of resident rodents had been caught, since the number of such traps is far smaller than those which catch average numbers of resident rodents. Such accidental omission of "multi-capture" traps might result in reduction of the final part of the graph illustrating the distribution of captures of migrants in traps with a different number of migrants (Fig. 4 and 5). In order to discover whether this phenomenon did in fact take place, comparison was made of the actual number of captures of migrants in traps with a large number of captures of resident rodents, with the figures which should occur with fortuitous encounter of the two groups of rodents in the traps. The coefficient of encounter-probability was used for this purpose. An analysis of its application to ecological investigations was made by Kajak (1957). The values of the coefficient of encounter-probability (w) with fortuitous encounters of the two elements examined are close to one. In cases of intense attraction of the two elements we are concerned with figures greater than one and in the case of repelling or non-accidental by-passing of the two elements, with values below one.

A. agrarius, encounters (w) between resident and migrating rodents in traps

Tab. III

Year						
1955-1956			1959			
$r \backslash m$	1-2	3-5	$r \backslash m$	1	2-3	4-8
1-2	0.84	0.18	2-6	1.65	0.95	0.23
3-6	1.08	0.73	7-10	1.27	1.08	0.78
7-10	1.10	1.97	11-16	0.55	1.25	1.17
11-15	0.69	3.94	17-36	0.86	0.57	1.66

r - captures of resident individuals in trap,
 m - captures of migrants in trap.

In the case of *A. agrarius* (Tab. III) the coefficients of encounter-probability are arranged similarly in both the study periods. The sequence of figures illustrating the encounter-probability of a large number of captures of migrants is of particular importance. With a small number of trappings of resident indi-

viduals the coefficient of encounter-probability is several times smaller than the unity, which indicates that the migrants omit not accidentally, but purposely, the places in which resident individuals stay only sporadically. On the other hand in traps with a high number of captures of resident individuals this coefficient is greater than one, which indicates that the traps with a large number of captures of resident individuals catch the greatest number of migrants. The graph of the distribution of captures of migrants (Fig. 3), on which we can see the number of migrants caught is in direct proportion to the number of captures of resident individuals, is of a non-fortuitous character, and the positive connection observed between resident and migrant rodents confirmed the analysis of their encounter-probability.

We observe different relations in the case of the other two species. With *C. glareolus* (Tab. IV) the samples with migrants were split into two categories,

C. glareolus, encounters (w) between resident and migrating rodents in traps in the Kampinos Forest in 1961

Tab. IV

r \ m	1	2-3
1-2	0.70	1.08
3-5	0.69	1.41
6-17	1.29	0.61

r, m — see Tab. III.

the first of which included single captures of migrants, the second 2-3 captures of migrants. In traps with a small number of captures of resident rodents the migrants are caught either fortuitously, or they pass the traps by. In traps with a medium number of captures of resident rodents there is a considerable surplus (in comparison with the accidental number) of captures of a larger number of migrants. In traps with a large number of captures of resident rodents repeated captures of migrants are hardly encountered at all. The coefficient of encounter-probability shows that here there is a non-fortuitous decrease in the number of captures of migrants in such traps. Single captures are far more frequent in them than repeated captures.

In the case of *C. glareolus* during the period 1955-1957 the number of captures of migrants in traps in which resident rodents were caught only once is far smaller than the random figure (Tab. V). The coefficient of encounter-probability increases with an increase in the number of captures of resident rodents in the traps. This increase is not, however, constant in character as it is with *A. agrarius* and in the traps with the largest number of captures of resident rodents it falls to one, which points to the fortuitous capture of rodents in such traps. The repelling of migrating individuals from traps with

large numbers of captures of resident and migrating individuals in this material is not so clearly visible as in the previous table (Tab. IV).

C. glareolus, captures of migrants and residents in traps in the Kampinos Forest from 1955 to 1957

Tab. V

Captures of residents in trap	Numbers of traps with captures of rodents			Difference	Coefficient of encounter-probability
	residents only	residents and migrants			
		real	fortuitous		
1-5	25	11	19.2	-8	0.58
6-10	29	20	22.3	-2	0.89
11-17	42	34	31.9	+2	1.07
18-26	34	33	25.8	+7	1.28
27-55	16	12	12.1	0	0.99

The phenomenon of repelling migrant rodents is more clearly visible here when examining differences between the real and fortuitous number of traps in which resident and migrating rodents met each other (Tab. V). These differences are distributed almost exactly along a straight line. An exception to this is formed by the final figure, which shows that captures of rodents is of a fortuitous character in traps with the highest number of captures of resident rodents. If the direction pointed out by the series of preceding figures in this column of the table had been maintained, the difference should have been + 18 traps. The capture of migrants in traps with a non-fortuitously high number of captures of residents should be non-fortuitously high. The drop in the number of captures of migrants to a fortuitous level is the expression of the antagonistic relations between resident and migrating rodents in the area penetrated by the resident rodents.

No estimate was made of the strength of antagonistic relations, on the basis of the material examined, but it would seem that repelling of migrants in the case of *C. glareolus* was greater in 1961 than in 1955-1957. This question, however, requires further investigation.

A. flavicollis exhibits a similar distribution of coefficients of encounter-probability in both study periods to that of the previous species. Migrants avoid capture in traps not visited by resident individuals (Tab. VI). Their number, greater than fortuitous, is caught in traps which exhibit two captures of resident rodents during the six-months period. The migrants of this species only accidentally reach the traps most often visited by the resident rodents.

The non-fortuitous reduction in the number of captures of migrants of *C. glareolus* and *A. flavicollis* in traps with a large number of captures of resident

A. flavicollis, encounters between resident and migrating individuals in traps
in the Kampinos Forest

Tab. VI

Captures of residents in trap	Number of traps with captures of residents and migrants					
	1955-1956			1961		
	real	fortuitous	(<i>w</i>)	real	fortuitous	(<i>w</i>)
1	4	6.93	0.58	13	15.7	0.83
2	6	4.50	1.33	17	11.4	1.49
≥ 3	6	5.90	1.02	8	7.4	1.08

rodents may be due to the different degree to which the two groups of rodents are acquainted with the area. Resident individuals, which know where the traps are placed, can find them far more quickly than migrants, and as a result the traps in places often visited by resident rodents are closed chiefly by resident individuals, and the migrants cannot therefore be caught in these traps. As a result, although present in a given place, they cannot record the fact of their presence. The possibility of such a situation existing cannot be maintained when consideration is given to the differences in the distribution of migrants in relation to resident rodents, such as was found between the species. With *A. agrarius* the number of captures of migrants is in direct proportion to the number of captures of resident rodents, whereas it was in the case of this very species (Andrzejewski and Wrocławek 1961a) that a mass appearance took place. The density of resident individuals of *A. agrarius* in 1959 (Andrzejewski 1963) was about twice as high as with *C. glareolus* from 1955-1957. With a situation of this kind it must be expected that the traps would be occupied primarily by resident individuals, particularly in the places in which captures of resident rodents point to particularly dense concentration. This phenomenon did not, however, take place, and as in the other study period for this species, we observe that the greatest number of captures of migrants takes place in the traps in which resident rodents are most often caught.

In addition the occupation of traps by individuals belonging to other species may also contribute to the number of captures of migrants in traps for which a large number of captures of resident rodents were recorded. Andrzejewski (1963) compared data on the degree to which the traps were occupied on the same study area. Over a period of six years, for three species of rodents, the average degree of occupation of traps was 0.12, which means that one trap makes a capture only in 12 cases out of 100 trap settings. The traps thus stand empty for the greater part of the time and could therefore catch migrants. The decrease in the number of captures of migrants in certain traps cannot therefore be explained by the specific character of the method used for capturing rodents

or by the different degree to which migrating and resident rodents are acquainted with the area.

During the mass appearance of *A. agrarius* in 1959 the degree of occupation of the traps (0.17) was high, and it was not found during this period that the traps had previously been occupied by resident individuals. In 1961, when the degree of occupation of the traps was 0.09, that is, nearly twice smaller, in the case of *C. glareolus* it was found that the resident individuals distinctly repel the migrants.

The rejection of the above possible ways of explaining the distribution of migrants in relation to captures of resident rodents makes it possible to interpret the results obtained on the basis of the hypothesis assuming connections between the two groups analyzed. The distribution of captures of migrants may be explained as follows. The wave of migrants covers the whole study area more or less evenly. The migrants, however, make chiefly for the places in which the resident rodents live, and as a result the number of captures of migrants in traps in which resident rodents are caught only sporadically is as a rule lower than would appear from the distribution of fortuitous visits to traps by migrants. The inclination to make for places in which the settled part of the population lives is a property common to migrants of all three species. The number of captures of migrants and the coefficients of encounter-probability increase similarly, together with the number of captures of resident individuals. It is only in places in which the penetration of resident rodents is greatest that differences are observed between captures of migrants. In the case of *A. agrarius* the number of captures and coefficient of encounter-probability continue to increase evenly. This indicates that the migrants of this species are tolerated by the resident individuals and allowed free access to the places in which the latter have settled. With *A. agrarius* we are therefore concerned with tolerant non-antagonistic relations, and distinct tendency on the part of the migrants to make for the places in which the resident individuals are most frequently to be found.

Relations in the case of *C. glareolus* and *A. flavicollis* are different. As was the case with the previous species, the migrants make for the places in which the resident individuals live. There, however, when the density of the latter is very great, the number of captures and coefficients of encounter-probability of the two groups decrease. Resident individuals belonging to these two species oppose the influx of migrants into areas which they occupy. Where the number of captures of resident rodents is as yet small, and in consequence the area presents little attraction to them, the number of captures of migrants is also small. The values of the coefficient of encounter-probability in addition point to the fact that the migrants avoid these places. When the area is penetrated to a medium degree by resident rodents, the

occupation of the area by these rodents is not as yet complete, and owing to this the majority of migrants are caught there. Where the largest number of captures of resident rodents takes place, the occupation of the area by this group of rodents is so great that migrants entering into it meet with resistance from the settled part of the population and are driven out of the areas in which the numbers of the resident rodents are greatest. As a result we observe a drop in the coefficient of encounter-probability of migrants and resident rodents in the traps in which the greatest number of resident rodents are caught.

CONNECTIONS BETWEEN RESIDENT AND MIGRATING RODENTS AND THE CONCEPT OF THE ECOLOGICAL STRUCTURE OF A POPULATION

In research on the population structure of mammals and birds under natural conditions the population structure is described chiefly from the aspect of spatial relations between animals. Different types of territorial connections occur in nature. There is a complete absence of territorialism in the majority of hoofed animals, which lead a gregarious way of life. Permanent division of territories is encountered in the case of a large number of predators. Periodical territorialism was described by Errington (1943) in the case of *Ondatra zibethica* (L.) and by Klujiver (1951) in his studies of *Parus major* L. The phenomena of territorialism is not expressed so distinctly in small rodents. Naumov (1948) found territorialism only in the case of females of *C. glareolus* during the period they were nursing their young. With other species we encounter the phenomenon of the home-range or cruising-range. An interesting example of group territorialism was given by Carrick (after Andrewartha 1961). He found that in a population of *Gymnorhina dorsalis* there is a group of individuals with their own nests, which have their own jointly defended territory, while the remainder of the population, that is, individuals not exhibiting territorialism nor possessing a home range, stray over the whole area. Similar relations apply in the case of forest rodents, although here the areas on which resident and migrating individuals occur are not clearly separated. Probably, apart from the area of the burrow, control of the area occupied by resident individuals is not so strict as it is with birds, and hence fairly intensive penetration of migrants into areas occupied by resident rodents is possible. It is mainly the time spent by the migrant in the occupied area until it comes into contact with a resident individuals which is limited.

The two categories of rodents, migrants and resident individuals, form under natural conditions two separate ecological groups performing different functions. The group of resident rodents in many of the species occupies and controls the area in which it lives and does not allow migrating individuals entering the defended area to remain there. This phenomenon is particularly distinctly visible in the case of *C. glareolus* (Opuszyński and Trojan

1963) where groups of resident individuals live in burrows. Encounters with alien individuals, particularly male rodents, are usually antagonistic in character and lead under laboratory conditions to the establishment between them of hierarchic relations. Under such conditions an encounter of this sort usually takes the form of a fight, but in nature probably one of the individuals most often runs away without starting to fight. Important data on this are to be found in studies of the results of encounters (Petrušewicz 1959a, 1959b, Petrušewicz and Wilska 1959, Petrušewicz and Andrychowska 1960), from which it is clear that two factors determine which male is victorious: the home cage and the presence of its own population. The physical condition of the individuals, on the other hand, is not important. These data, applied to the relations discussed between resident and migrating rodents, point to the probable causes of the migrants being driven out. The resident rodent in its encounter with a migrant has two factors in its favour: its own home-range and its own population, that is, the group of individuals living with in the burrow.

Under normal conditions the group of resident rodents fulfils a protective function when antagonistic relations occur between resident and migrating individuals — it maintains the population numbers on a fairly low level in relation to the food resources of the habitat, since as Grodziński (1961) found, the number of rodents is far lower than the food capacity of the habitat. Reproduction is also connected with this group, among rodents a migrating female cannot rear her young. By driving out the migrants from the areas occupied by the resident individuals the wave of migrating animals is directed to empty areas in which there is no population of the given species.

Other biological functions are connected with the group of migrants. As Janion (1960) suggests, the degree of infestation by fleas of this category of rodents indicates that they did not have much contact with burrows. In the light of data on relations between migrating and resident rodents this conclusion would appear to be justified, as the burrows are occupied by resident rodents. Migrants form the expansive group of the population, it is they (Andrzejewski and Wrocławek 1961a, 1962) which settle in the areas from which the group of resident rodents has for one reason or other been eliminated. It is this group of individuals which owing to their different way of life are exposed to far more frequent contacts with predators than resident rodents. As stated by Pielowski (1961) the majority of the rodents which fall prey to snakes are migrants.

Under natural conditions the population of small rodents forms a differentiated unit, consisting of at least two ecological groups — resident and migrating individuals. Both these groups are connected with each other by ecological ties and each is situated differently in the same habitat, each of them performs a different ecological function. The appurtenance of individuals to one of these groups involves them in different biological results. The mortality among

migrants in traps is higher than the mortality of resident rodents (Andrzejewski and Wrocławek 1961b).

The concepts of an ecological population (Park 1950, Andrewartha and Birch 1954, Bodenheimer 1958) assume that the properties of an ecological population are derived from the characteristics of individuals. Petruszewicz (1962) adopted a different standpoint in this matter, putting forward the concept according to which the place of an individual in the ecological structure of a population determines its biological properties. This statement is fully borne out in the light of the data given, since it is known that the same individual may during its lifetime pass several times through periods of migration and residency.

An important question in analysing population structure is the definition of the function which it performs. Petruszewicz (1962) postulates the connection between population structure and variations in numbers. Ecological structures, even when treated descriptively and mechanically, are often referred to the variations in population numbers. Cole La Mont (1957) in equating a logistic curve, accepts as a governing factor the general state of population numbers in relation to the maximum capacity of the habitat. Concepts of the growth curve based on the so-called Malthusian parameter imply such elements as sex and age structure in the population examined (Severcov 1947), but these elements are derived from a knowledge of the numerical relations between categories of individuals. The population structure, if ecological, should point to such connections between the intrapopulation ecological groups as have an effect on the course taken by the variations in numbers in the population examined.

INTRAPOPOPULATION RELATIONS AND REGULATION OF NUMBERS

Interpretation of the course taken by the curve of variations in numbers presents several difficulties, due to the fact that abundance is the resultant of the action of many factors and mechanisms, which it is usually difficult to separate from each other. Two categories of phenomena play a basic role in the formation of the curve of population numerical variations: determination of the course taken by the curve and regulation of numbers. Both these phenomena are usually treated jointly, but they differ in character. The factors determining the course of the curve, apart from the well-known and described effects of periodical variation in habitat factors (Andrewartha and Birch 1954) may be biological in character. In the case of small rodents living under the conditions prevailing in Central Europe this factor is the periodical nature of reproduction by rodents. Increase in numbers may take place during the growing season of plants, and as a result the rodent populations exhibit an increase in numbers from the spring to autumn, with peak numbers during the autumn (Andrzejewski 1963).

The phenomena of regulation of numbers take place against the background of phenomena determining numbers, and may occur both during the period of increase in population numbers, or during a period of decrease in or stabilization of numbers. By regulating phenomena is meant not the direction taken by the course of population numbers, but only the character of this course.

A different definition of determination and regulation of numbers points to these two phenomena having been examined in different ways. Determination of numbers defines the general direction of the course taken by the curve estimated by the mean numbers – the level of population numbers in a given period or declination of the curve to the axis of time. Regulation of numbers in a given section of time defines the extent of fluctuations in the curve defined by the coefficient of variability (V_c) or the amplitude of fluctuation.

Investigation of changes of average numbers made it possible to analyze the factors determining the course of changes in numbers. The knowledge on fluctuations in the curve in a defined section of time made it possible to analyze the degree of regulation of populations numbers in this period. The population during a period of rapid one-direction changes in numbers and small fluctuations is better regulated than during a period of stabilised (average) numbers with simultaneous considerable fortuitous fluctuations. In the first case it is possible to speak of regulated growth, and in the second of unregulated stabilization of numbers.

The antagonistic and non-antagonistic relations observed between the migrating and resident part of the population may be reflected in the regulation of population numbers, similar to that which took place in the case of species exhibiting territorialism. The species in which the group of resident individuals does not allow migrants to settle into the area occupied by themselves should exhibit greater stability of numbers than those which do not exhibit this phenomenon. It may be presumed that the antagonistic relations between the two groups of rodents form the intrapopulation mechanism regulating numbers.

Data on the attitude of the resident part of the population to migrants are not sufficient to explain the strength of the effect of the resident part of the population on migrants, since this depends on a large number of factors. It is primarily the density of the resident part of population which decides the strength with which the migrants are driven out. The greater the number of resident individuals, the more effectively they can withstand the influx of migrants. The average density in the Kampinos Forest was exhibited by *C. glareolus* and *A. agrarius*. The numbers of the resident part of the population of *A. flavicollis* are far smaller than in the other two species.

The second factor defining the effect of the mechanism regulating numbers is the degree of residency of the rodent population. As shown by the investigations of Trojan and Wojciechowska (1964) the degree of residency in

a given place can be measured by the length of stay and the trappability of the rodents. The three species examined exhibit considerable differences in this respect. *C. glareolus* exhibits the greatest degree of attachment to given points. This is expressed in the far greater trappability of this species than in the other two, and the longer length of stay. *A. flavicollis* exhibits the least attachment to points in the area. The range of penetration by resident individuals of this species is far greater than in the other two species. As established by Opuszyński and Trojan (1963) in their initial investigations, the group of resident rodents exhibits much greater persistence and attachment to the area adjacent to their burrows in the case of *C. glareolus* than in the other two species.

The above data give grounds for assuming that the relations observed between the resident part of the population and migrants may act with different degrees of intensity as a regulating mechanism in each of the species. With *A. agrarius* the migrants were not found to be driven out by the resident individuals, and therefore this species does not exhibit a mechanism regulating numbers similar to the other species. Fluctuations in numbers in the case of *A. agrarius* should therefore be greater than in the other two species. With *C. glareolus* large numbers combined with a high degree of residency and attachment to a small area of penetration during the resident period makes it possible for them to exercise greater control of the area which they settle in, and regulation of numbers in this species should be most strongly expressed. *A. flavicollis* exhibits combined low resident populations number's the least tendency to concentration and a very slight degree of attachment to a given place. Although the species exhibits strong resistance to migrants, under natural conditions the action of intrapopulation relations as a mechanism regulating abundance has little chance of being effective particularly in situations in which the numbers of the resident part of the population are small. From the aspect of regulation of numbers this species should occupy a position intermediate between *A. agrarius* and *C. glareolus*.

Regulation of numbers should be perceptible primarily in the course taken by variations in the numbers of the species discussed. A detailed description of variations in the numbers of these species in the Kampinos Forest is given by Andrzejewski (1963), without however analyzing the phenomena of regulation of numbers. In the present study an estimate of the degree to which the populations were regulated was made by means of the coefficient of variability. Populations of rodents in the study area pass through periodical variations in numbers determined by the reproduction cycle. In the three species examined from this aspect we have to deal with two peaks in abundance over the course of the year (Andrzejewski 1963), the spring peak being more characteristic of the habitat examined than reflecting the real increase in population numbers. The greatest periodical variations occur from the spring to the autumn, when

an increase in population numbers takes place. The use in such a situation of the coefficient of variability is therefore attended with difficulty, and an estimate of fluctuations in numbers can be made only by equating coefficients in respect of each other, and not by discussing their absolute value.

Comparison was made of the value of the coefficient of variability for the three species of small rodents examined (Tab. VII) for the period from Jan.

Variation (V_c) in numbers of three species of rodents in the Kampinos Forest

Tab. VII

Species	Residents	Migrants	Total
<i>A. agrarius</i>	129.28	146.44	126.21
<i>A. flavicollis</i>	106.22	147.66	100.19
<i>C. glareolus</i>	69.28	93.72	63.75

1st 1956 to Dec. 31st 1960. Comparison of the values of the index within the species shows that fluctuations in the numbers of resident individuals are far smaller than in the group of migrants. The wave of migrants passing through the study area is probably more unevenly spread out in time.

When comparing the coefficients of variability between the species, *C. glareolus* was found to exhibit the least variations in population numbers, *A. flavicollis* about one and a half times greater and *A. agrarius* almost twice greater. The same differences were found when considering the coefficients of variability calculated for fluctuations in the numbers of the resident part of the populations of these species. Andrzejewski (1963) gives a similar estimate of fluctuations in numbers, made by a different method. The regulative character of intrapopulation relations between resident and migrating rodents should be expressed not only in the character of the variations in numbers of the species examined, but also in the settling process of the rodents. Where antagonistic relations occur, when the numbers of the resident part of the population are high, the settlement of the rodents should become inhibited. Elaboration of the correlations between the number of resident and settling rodents in two species of forest rodents supply interesting data on this subject (Andrzejewski 1963). With *A. agrarius* the coefficient of correlation between the number of resident and settling rodents is fairly high ($r = 0.84$). With *C. glareolus* the correlation between the number of resident and settling rodents is also positive, but far smaller ($r = 0.64$), perhaps the low value of the coefficient of correlation in the case of this species is due to the fact that this correlation is curvilinear.

A more exact analysis of the connection between the number of settling and resident rodents makes it possible to examine the average number of rodents settling with different densities of resident individuals. With *A. agrarius* (Fig. 6), according to the results of Andrzejewski's investigations (1963), this correlation is rectilinear. The settling of migrating rodents is in direct proportion to the density of the resident rodents. Positive intrapopulation

relations in the case of this species do not restrict continued increase in population density even when the numbers of the resident population are very high.

The curve illustrating the connection between the number of settling and resident rodents for *C. glareolus* is of a different character (Fig. 7). The settling of migrants in areas in which the numbers of resident individuals are low is in direct proportion to the number of resident individuals. We can observe here a situation similar to that in the case of distribution of captures of migrants in relation to resident individuals (Fig. 5). The migrants not only most readily visit those sections of the environment which are occupied by resident individuals, but also most readily settle in places in which the local population of the given species occurs fairly numerous. The second section of the curve (Fig. 7), however, exhibits a course different from the first; the process of settlement of the migrants in populations in which the density of resident individuals exceeds 7 rodents per hectare, undergoes inhibition and even reduction.

The data given in addition confirm the hypothesis as to the regulative character of intrapopulation relations in the species of rodents examined.

Regulation of population numbers may have very different mechanisms at its base. In the first place mention must be made of the concept assuming that this mechanism is contained in the relation of the population to the habitat (Lack 1954, Andrewartha and Birch 1954). In the case of the species examined this phenomenon cannot, however, take place. Grodziński's investigations (1961) showed that in Central Europe food cannot be a factor limiting population numbers. Other habitat factors have a similar effect on all three species, and cannot therefore form a basis explaining the differences observed between them.

Biocenotic mechanisms and their effect on the regulations of numbers of the above species of rodents are difficult to estimate. We do not know of any investigations, apart from the fragmentary data given by Pielowski (1961) which would define the selectiveness of predators in relation to these three species. Andrzejewski and Wrocławek (1961a) found that certain changes in the habitat have a uniform effect on all three species and assume that they

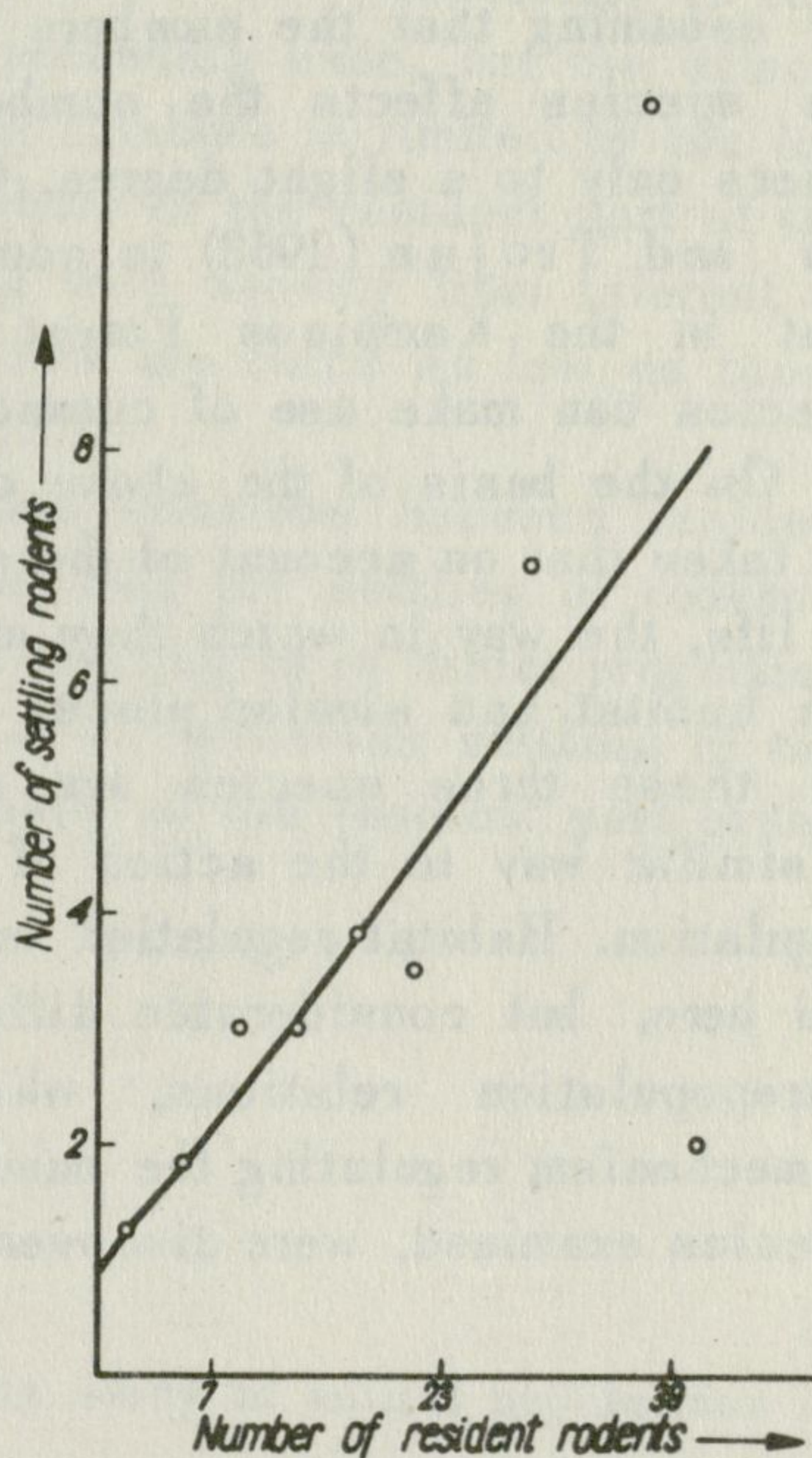


Fig. 6. *A. agrarius*, settling in of migrants with different degrees of density of resident rodents

have a common ecological niche. Andrzejewski (1963) emphasises the common rhythm of variations in numbers, the similarity of ecological reactions and of the biology of the three species examined. These data also give grounds for assuming that the numbers of each of the species affects the numbers of the others only to a slight degree. Opuszyński and Trojan (1963) in addition found that in the Kampinos Forest all three species can make use of common burrows.

On the basis of the above data it may be taken that on account of the similar way of life, the way in which they make use of the habitat and similar places of shelter, all these three species are exposed in a similar way to the action of biocenotic regulation. Habitat regulation is very limited here, but considerable differences, in intrapopulation relations, which create a mechanism regulating the numbers of the species examined, were discovered.

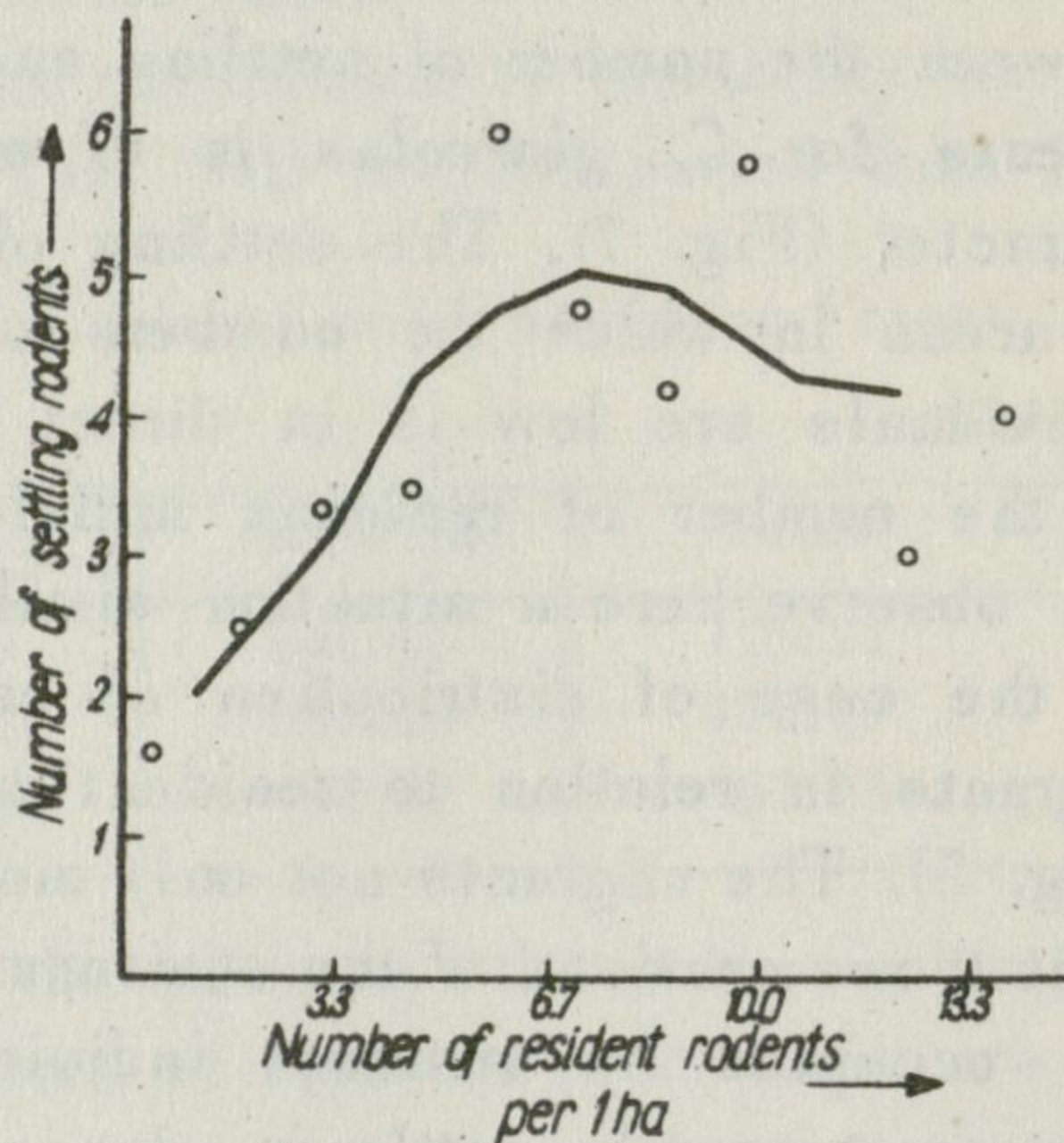


Fig. 7. *C. glareolus*, settling in of migrants with different degrees of density of resident rodents

CONCLUSIONS

1. On the basis of investigations of the distribution and encounter-probability of migrating rodents in relation to resident individuals it was found that with *A. agrarius* the relations between the two groups of rodents are tolerant. With *A. flavicollis*, in the areas occupied by resident individuals, the relations between the two groups of rodents are intensely antagonistic: resident individuals do not admit migrants into the areas which they themselves occupy. With *C. glareolus*, when the density of resident individuals is slight or medium, relations between the latter and migrants are tolerant: with considerable density of the resident rodents the tolerant relations change to antagonistic ones. The resident and migrating rodents form the two chief ecological groups in the population structure.

2. The intrapopulation mechanism regulating numbers in the three species examined is formed by:

- a. the strength of the antagonistic relations between resident and migrating rodents,
- b. the density of the resident part of the population,
- c. the degree of residency of the population.

Analysis of fluctuations in numbers showed that where connections between resident and migrating rodents are tolerant (*A. agrarius*) fluctuations in numbers

are greatest – the intrapopulation mechanism regulating numbers does not act in such cases. When the migrants are strongly repelled by the resident rodents, but the density of the resident part of the population (*A. flavicollis*) is low, fluctuations in numbers are lower than in the preceding case, but the effectiveness of the action of the mechanism regulating numbers is limited by the low density of the resident rodents. When large numbers of the resident part of the population and intrapopulation relations varying with density from tolerant to antagonistic (*C. glareolus*) fluctuations in numbers are twice as low as those in the case of tolerant relations were found.

3. The regulative character of intrapopulation relations between resident and migrating rodents is also evident when analyzing the settling of rodents. In the case of *A. agrarius* the number of rodents settling is in direct proportion to the number of resident rodents. In the case of *C. glareolus* settling of the migrants was found to be inhibited when the density of the resident part of the population exceeds 7 individuals per hectare.

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STOSUNKI WEWNĄTRZPOPULACYJNE I REGULACJA LICZEBNOŚCI U DROBNYCH GRYZONI LEŚNYCH

Streszczenie

Autor zbadał stosunki wewnątrzpopulacyjne u trzech gatunków drobnych gryzoni: *Clethrionomys glareolus* (Schreb.), *Apodemus agrarius* (Pall.) i *A. flavicollis* (Melch.). Materiał obejmuje dane z okresu 7 lat (tab. I) zebrane metodą znakowania na 3-hektarowej powierzchni w Puszczy Kampinoskiej pod Warszawą.

Rozkład złowień gryzoni osiadłych wykazał w przypadku trzech gatunków charakter skupiskowy (fig. 1) a zaobserwowane odchylenie od rozkładu przypadkowego jest istotne statystycznie. Największy stopień skupiskowości stwierdzono (tab. II) u *C. glareolus*, średni u *A. agrarius*, mały u *A. flavicollis*. Rozkład złowień migrantów (fig. 2) u tych trzech gatunków jest bliski przypadkowemu, migranty wskazują jednak preferencję do pewnych dróg lub miejsc.

Rozkład złowień migrantów do osobników osiadłych jest u wszystkich zbadanych gatunków nieprzypadkowy. U *A. agrarius* (fig. 3) stwierdzono wprost proporcjonalny wzrost liczby migrantów do stopnia opanowania terenu przez gryzonia osiadłe. Uzyskany obraz wskazuje na tolerancyjne stosunki między obiema grupami gryzoni. U *A. flavicollis* (fig. 4) liczba złowień migrantów, przy silniejszym spenetrowaniu terenu przez gryzonia osiadłe, jest odwrotnie proporcjonalna do liczby złowień osiadłych, co świadczy o silnie antagonistycznych stosunkach między obiema kategoriami gryzoni. U *C. glareolus* (fig. 5) rozkład złowień migrantów wskazuje na stosunki tolerancyjne przy małym zagęszczeniu złowień gryzoni osiadłych i antagonistyczne przy dużym zagęszczeniu gryzoni osiadłych.

Zbadanie współczynnika spotykalności w pułapkach (tab. III) osobników migrujących i osiadłych *A. agrarius* potwierdziło wniosek o tolerancyjnych związkach wewnątrzpopulacyjnych. U *A. flavicollis* i *C. glareolus* stwierdzono odpychanie migrantów w pułapkach o największej liczbie złowień gryzoni osiadłych.

Zaobserwowane stosunki między osobnikami osiadłymi i migrującymi w połączeniu z danymi na temat różnic między obiema kategoriami gryzoni potwierdzają koncepcję strukturalności zjawisk populacyjnych. Stwierdzono, że u badanych gatunków gryzoni występują dwie wewnątrzpopulacyjne grupy ekologiczne, które spełniają odrębne funkcje: gryzonia osiadłe – rozrodczą i czasem ochronną i gryzonia migrujące – ekspansywną.

Przy omawianiu zjawisk regulacji liczebności autor wyróżnił dwa odrębne procesy: determinacji liczebności, którą można mierzyć przeciętną liczebnością w danym odcinku czasu lub nachyleniem krzywej do osi czasu oraz regulacji liczebności, którą można mierzyć rozmiarami wahań krzywej w danym odcinku czasu.

Procesy regulacji liczebności zależą od trzech czynników wewnątrzpopulacyjnych:

1. siły związków antagonistycznych między migrantami i osiadłymi,
2. zagęszczenia osiadłej części populacji,
3. stopnia osiadłości populacji.

Najniższy stopień regulacji liczebności wykazał *A. agrarius*, u którego dzięki tolerancyjnym związkom między migrantami i osiadłymi stwierdzono brak wewnątrzpopulacyjnego mechanizmu regulacji liczebności. Większy o 25% stopień regulacji liczebności wykazał *A. flavicollis*, u którego stwierdzono silne odpychanie, ale niską liczebność populacji osiadłej. U *C. glareolus* stwierdzono dwukrotnie lepszą regulację liczebności niż u *A. agrarius*. Z trzech zbadanych w Puszczy Kampinoskiej gatunków, ten ma najwyższą liczebność oraz najwyższy stopień osiadłości, dzięki czemu mechanizm regulacji liczebności działa tu najsprawniej.

Zjawiska regulacyjne znalazły również swój wyraz w analizie procesów osiedlania się gryzoni. U *A. agrarius* (fig. 6) liczba gryzoni osiedlających się jest wprost proporcjonalna do liczebności gryzoni osiadłych. U *C. glareolus* (fig. 7) zaobserwowano zahamowanie osiedlania się migrantów w przypadkach, gdy liczba gryzoni osiadłych przekracza 7 osobników na hektar.

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