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COMMUNITIES OF MOSQUITOES IN THREE TYPES OF FOREST LAND*

Investigation was made of the connection existing between the type of mosaic structure of the area and spatial distribution of mosquito fauna. It was found that communities of mosquitoes formed, in the microenvironments of the study areas, which differed as to numbers of mosquitoes, species composition, domination structure and relative activity. The character of the whole area imposed upon the communities the general proportions of the percentage of the dominanting species, the subdominant and accessory species: decrease of the participation of the dominant and the simultaneous increase of the participation of accessory species was observed in communities together with an increase in the degree of humidity and the mosaic structure of the whole area. Analysis was made of the seasonal variations in the structure of the mosquito communities, and it was found that penetration of the environment by mosquitoes in an area with a fine mosaic structure and considerable humidity depended on their numbers in such environments. In a dry area, unfavourable to mosquitoes, their penetration of the environments was the result of their numbers and activity. Depending on the type of area which determines the general activity of the mosquitoes, they are included primarily in the composition of the association of organisms of the forest herb layer or the undergrowth.

CONTENTS

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I. INTRODUCTION

The problem of the spatial distribution of an animal population, widely dealt with in biological literature, primarily in the form of descriptions of the fauna in different types of environment, is connected with many other ecological problems, one of which is the effect of the external environment on the spread of organisms, causing the formation of communities of these organisms differing as to structure and function. The idea of the formation of biocenotic communities against the background of micro-differences in the environment has been put forward by several authors (Diver and Good 1934, Diver 1936, 1938, Watt 1947, Elton 1949, Elton and Miller 1954, Beklemišev 1959). The most comprehensive treatment was given to this problem by Elton, who within the "major habitat" (habitats as the forest, meadow, river etc.) distinguished its small parts, the so-called "minor habitat" forming as a results of topographical or micro-climatic differences in the area, the patch-like occurrence of host plants etc. In this connection animal populations exhibit tendencies to characteristic aggregational occupation of the area. In the "minor habitat" "centres of action" are formed by the species distinguished by intensity of contacts between species or individuals and by intensity of biocenotic processes.

Similarly Beklemišev (1959) put forward the opinion that the areas were differentiated into microbiotopes which attracted round them communities of species with different degrees of constancy. He thus distinguished communities in micro-populations of species closely connected with the given type of environment, of species occuring there only during a certain period of their development or life and temporary aggregations of species.

Using Elton's concept of "centres of action" as a basis, MacLeod and Donnelly carried out research on a wide scale on the spatial distribution of an association of flies of the family *Calliphorinae* (MacLeod 1956, MacLeod and Donnelly 1957a, 1957b, 1958). This research was concerned with the character of the influence exerted by habitat factors (topography of the area and the type of vegetation and, in connection with this, the microclimate) on the distribution of the association. Their investigations enabled the authors to establish that different communities of flies formed, in connection with the mosaic structure of the habitat.

Mosquitoes, which are characterised by considerable sensitivity to habitat factors, should exhibit far-reaching differences in spatial distribution. As can be seen from the investigations made of the course taken by the 24-hour cycle of the mosquitoes activity, the microclimatic conditions, deteriorating during

the morning, oblige the mosquitoes to look for diurnal resting places in environments of different types, depending on the specific physiological requirement of the species. On this account a quantitative and qualitative system of mosquito fauna and a dynamic system of individuals active or inactive at a given time, should be formed characteristic of each environment (Dąbrowska-Prot 1961). Thus a structure of communities of mosquitoes constituting a real basis of biocenotic influences specific to each type of environment should be formed. Environments with considerable density of mosquitoes would form "centres of action", in which the mosquitoes would enter into particulary intensive relations with other organisms such as preys, hosts, external parasites, competitive species. The question therefore arises as to whether and to what degree the mosaic character of the area causes the spatial differentiation of mosquito fauna and the formation of a structure of communities specific to each type of microenvironment. Do these communities, if they exist, form a permanent structural element of mosquito fauna?

Investigations of the spatial distribution of mosquito fauna are concerned with the specificity of this fauna in relation to very large units of the environment such, as, for instance, forest, meadow, banana plantation etc. (Elton's major habitat) (e.g. Rejngard and Gucevič 1931, Haddow 1942, 1945a, 1945b, Bates 1944, Lumsden 1952, Lachmajer 1954, Ardö 1958, Dąbrowska 1959, Lachmajer and Skierska 1959, Łukasiak 9). A large number of studies, however, point to the fact that the character of the spatial distribution of mosquitoes during the day is primarily connected with the character of the mosaic structure of these extensive environment groups (Mitrofanova 1946, Nikiforova 1946, Mončadskij and Radzivilovska 1947, Rjabych and Bezukladnoj 1947, Smith 1961). These studies indicate the opportunities for research of the problem of the effect of the mosaic structure of the environment on the formation of the structure of mosquito communities. They register the possibility of the existence within biotopes of distinct differences in mosquito fauna, both as regards the quality and the quantity of their occurrence. They point to the possibility of verifying phenomena of the co-occurrence of species in one environment, by means of detailed and painstaking analysis of microenvironments.

II. METHODS

In each of three areas chosen for the investigations observations were made from mid-June to the end of October, that is, during the period of relative summer stabilisation of relations in mosquito fauna and during the period of the autumn decrease in its numbers. Captures were made by means of bait trapping (the bait being formed by a human standing motionless) on stations chosen for observations, captures being made for 30 minutes on each station. This bait trapping

gave a picture of the quantitative and qualitative composition of mosquito fauna active at a given time in the environment. Bait trapping was followed by sweeping consisting of 8 samples (each sample was formed by 25 sweeps with a sweep net, Tarwid 1952) which gave inactive mosquito fauna. Endeavour was made by the use of this method to explore a space approximately corresponding to the space in which mosquitoes were caught by bait trapping. A total of 3–4 samples by bait trapping and a series of sweep net samples were made during the week.

The total numbers of the mosquito fauna in the environments studied were obtained by adding up the results of trapping made by both the methods described above, adding together the results of the 30 min. bait trapping and series of 8 sweepnet samples. This was done when it was found that in an area unfavourable to mosquitoes their activity was very slight and about half the total number of mosquitoes were caught by means of the sweep-net, and therefore if conclusions were drawn from the results obtained by only one of the methods described above under conditions particularly unfavourable to mosquitoes, they might be subject to a considerable degree of error.

Bait trapping and sweeping were also used to enable an analysis of the activity of mosquitoes to be made. The percentage of active mosquitoes (bait trapping) calculated from the whole of the mosquitoes caught in a given environment (sum total of data from bait and sweep-net trapping) was taken as the index of relative activity. It had already been found that the index of relative activity provides a good description of the degree of spatial distribution of the mosquitoes in the given area, and in consequence the degree of suitability of each environment for these insects (Dąbrowska-Prot 1961). Also, in defining the intensity of penetration of the environment by the mosquitoes it may to a certain extent form an index of the intensity of biocenotic contacts between mosquitoes in the higher layers of the forest.

At the time as the trapping, observations were made of the microclimatic conditions of the habitats (temperature and humidity) at a height of approximately 2.0 m and at the level of the herb layer. The data given in Figs. 4, 5 and 6 refer to the period of maximum differences in the environments, as the observations were made on a hot day following a sequence of several days of good weather. Microclimatic observations supplement the description of environments made on the basis of the character of vegetation (discussed in the next section), and thus enabled a fuller assessment of their suitability for mosquitoes to be made.

The occurrence of the following species was established by means of the two trapping methods described above:

1. *Aedes* (*Ochlerotatus*) *punctor* Kirby, 1837 – Dz., W., L.[1]
2. *Aedes* (*Ochlerotatus*) *communis* De Geer, 1776 – Dz., W.

[1] The letters used as symbols indicate the areas in which the given species was found: Dz. – Dziekanów, W. – Wilkus, L. – Lemańsk.

3. *Aedes* (*Ochlerotatus*) *caspius* Pall., 1771	– Dz.
4. *Aedes* (*Ochlerotatus*) *maculatus* Meig., 1818	– Dz., W., L.
5. *Aedes* (*Ochlerotatus*) *annulipes* Meig., 1830	– Dz., W., L.
6. *Aedes* (*Ochlerotatus*) *excrucians* Walk., 1856	– Dz., W., L.
7. *Aedes* (*Ochlerotatus*) *flavescens* Müller, 1764	– Dz., W.
8. *Aedes* (*Ochlerotatus*) *riparius* Dyar et Knab 1907	– Dz.
9. *Aedes* (*Aedes*) *cinereus* Meig., 1818	– Dz., W., L.
10. *Aedes* (*Aedimorphus*) *vexans* Meig., 1830	– Dz., W., L.
11. *Theobaldia* (*Theobaldia*) *annulata* Schr., 1776	– Dz., W.
12. *Theobaldia* (*Culicella*) *morsitans* Theob., 1901	– L.
13. *Mansonia* (*Coquillettidia*) *richiardii* Fic., 1889	– Dz., W., L.
14. *Culex pipiens* Linn., 1758	– Dz., W., L.
15. *Anopheles* (*Anopheles*) *maculipennis* Meig., 1818	– Dz., W., L.
16. *Anopheles* (*Anopheles*) *claviger* Meig., 1804	– Dz., W., L.

The above list of species applies to the period from mid-June to the end of October.

III. DESCRIPTION OF THE STUDY AREA

The grounds for the choice of area were formed by the assumption that environment conditions determine the distribution of mosquitoes. Several stations were therefore selected, distributed in a gradient of density of trees, compactness of undergrowth and luxuriance of the herb layer. As is well known these features determine the microclimate of environments and hence the degree of attraction of the latter for mosquitoes.

The present study is the result of investigations made over a period of three years in three types of forest lands – the wet mixed forests of the Kampinos Forest (termed Dziekanów, 1954), dry pine woods near Częstochowa (termed Lemańsk 1955) and mixed forests near Giżycko (termed Wilkus, 1957). The first two of these formed exact opposites of each other as regards the degree of humidity and the mosaic structure of the area. Dziekanów formed a compact wooded area, of a fine mosaic character, with alternately distributed different types of environments from very wet to very dry, while Lemańsk represented outstandingly dry ground, generally unattractive to mosquitoes, with small patches of humid environments, surrounded by an extensive group of dry pine woods. Wilkus occupied an intermediate place between the above two as regards formation of the area.

A total of 9 stations were chosen at Dziekanów, arranged over a space of about 1 km, and 2 stations (stations *1* and *2*) situated deeper into the Forest (Fig. 1). Stations *3* and *11* received the greatest amount of light and were thus the most unsuitable for mosquitoes. In the first case it was sparse pine wood of old trees (*Pineto-Muscinietum* association, Kobendza 1930), and in the second a thick wood of pine trees of the same age (*Pineto-Callunetum*). The

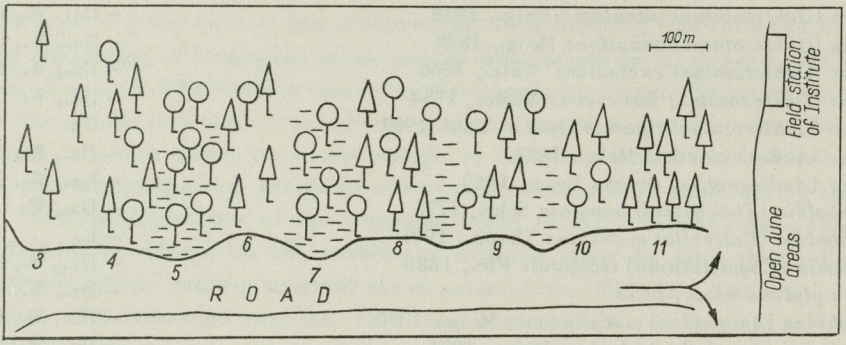

Fig. 1. Plan of the area – Dziekanów
3 – 11 – stations

undergrowth was formed by single bushes of juniper, oak and birch, and in the herb layer moss occurred on station *3*, and on station *11* large patches of heather and in places bilberries. In addition station *11* was a border area in relation to the open spaces adjacent to the Forest. Stations *1*, *2*, *4*, *8*, *9*, and *10* created mainly similar living conditions for mosquitoes, being shadier than the preceding ones, covered by an old pine wood with a considerable admixture of deciduous trees (oak, birch). The undergrowth was formed by self-sown species of trees occurring in the tree layer. Bilberry, fern and, in places, heather occurred in the herb layer (*Pineto-Vaccinietum myrtilli* association). The differences between them consisted in the generally small degree of difference in the density of the undergrowth and differences in distance from the boundary of the Forest. In addition station *1* was situated on the fringe of a large group of marshes. Stations 5 and 7 represented the shadiest type of environment, selected near canals which were filled with water in the spring, and which in the summer form marshy ground, and in dry summers muddy quaggy ground. In the tree layer the main mass was formed by alder, while pines occured singly. The dense undergrowth was formed by alder, grasses and mosses occurring in the herb layer (*Alneto-Muscinetum* association). The above two stations were separated from each other by station 6, which was closer in character to the second group of stations except that the older pine wood and undergrowth were sparser than in the preceding group.

The stations examined can be arranged according to the gradient of shade and distance from the boundary of the Forest. In the first case we obtain a sequence from the best lighted: stations *3*, *11* – *6* – *1*, *2*, *4*, *8*, *9*, *10*, – *5*,*7*: in the second sequence of stations from *1* to *11* (from the station situated deepest in the Forest to the one on the very edge).

The microclimatic characteristics of the station (Fig. 4) were correlated

with the properties discussed above. The shadier stations had a higher degree of humidity and lower temperature. It was also found in the case of all three study areas that environments unfavourable to mosquitoes, i.e. well-lit, were as a rule characterised by small differences in humidity and temperature between the herb and shrub layers. This is evidence of the unification of microclimatic conditions in vertical stratification in this type of environment. The differences in the humidity and temperature between the different layers examined in very shady environments permit of the mosquitoes finding suitable resting places.

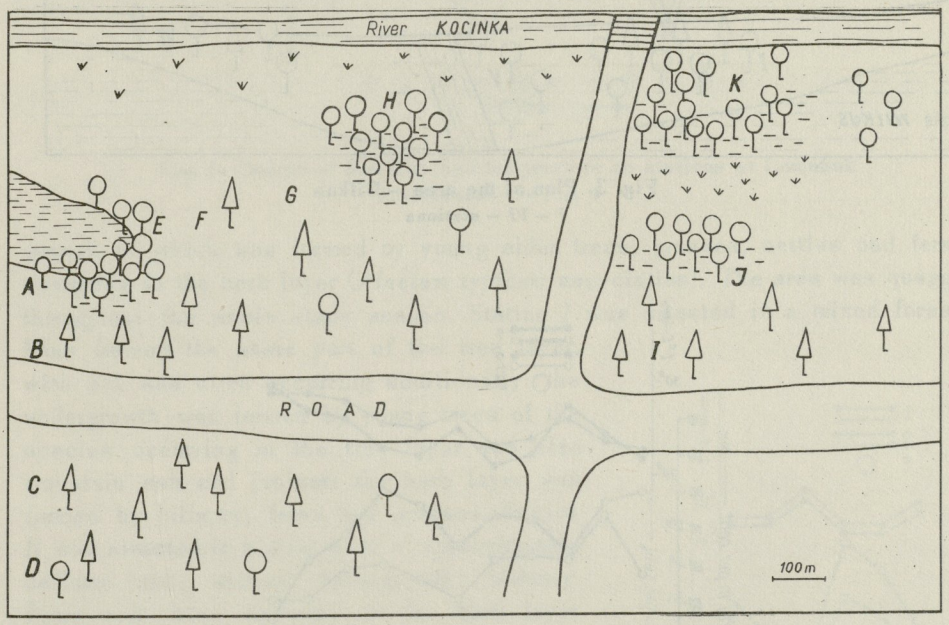

Fig. 2. Plan of the area — Lemańsk
A — *K* — stations

Lemańsk (Fig. 2) formed an area differing widely from that described above, and consisted in the great majority of dry stretches with small patches of wetter ground. The basic association was formed by pine woods without undergrowth, with patches of heather and bilberry occurring in the herb layer (similarity to the *Pineto-Callunetum* association distinguished in the Kampinos Forest by Kobendza), alternating with open areas (meadows, broad rides, clearings). Humid environments occurred in the form of small aggregations of alders growing on marshes (*Alnetum typicum* association). The undergrowth was formed by young alder trees, nettles and grasses occurring in the herb layer. A number of stations were chosen in this area in environments typical of it. Humid stations (*A*, *E*, *H*, *J*, *K*) differed from each other as to their extent: their gradient of size was as

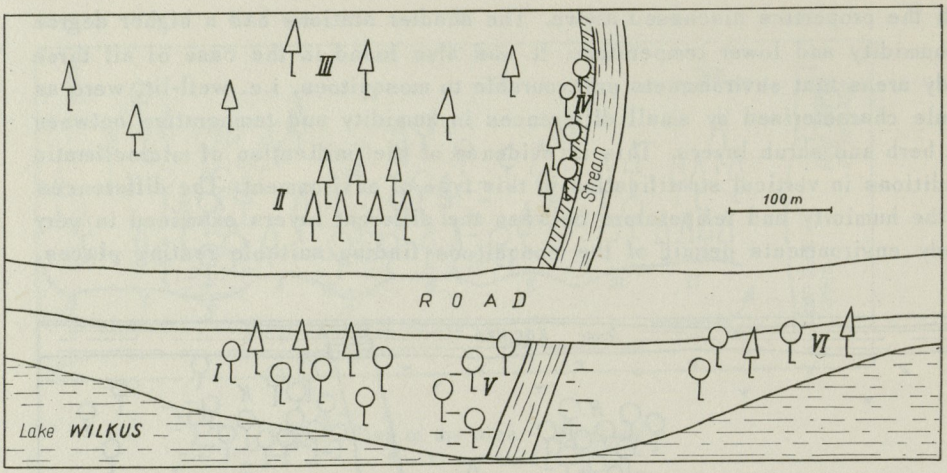

Fig. 3. Plan of the area – Wilkus
I – VI – stations

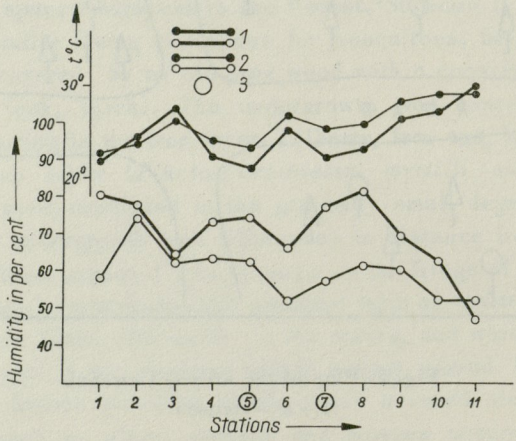

Fig. 4. Course of humidity and temperature on stations at Dziekanów
1 – on the surface of forest litter, *2* – at a height of 2 m, *3* – wet stations

follows, starting with the most extensive – *K-H, J-A, E*. The difference between dry stations consisted chiefly in their situation at different distances from the humid stations (Fig. 5).

Wilkus, taking the area as a whole, was drier than Dziekanów, and undoubtedly wetter than Lemańsk. A total of 6 stations were chosen in this area (Fig. 3). The stations were arranged in a gradient of humidity, beginning from the most humid and going to the driest, in the following order: *IV, V, I, II, VI, III*. Stations *IV* and *V* were formed by an alder wood growing in a marsh, the dense under-

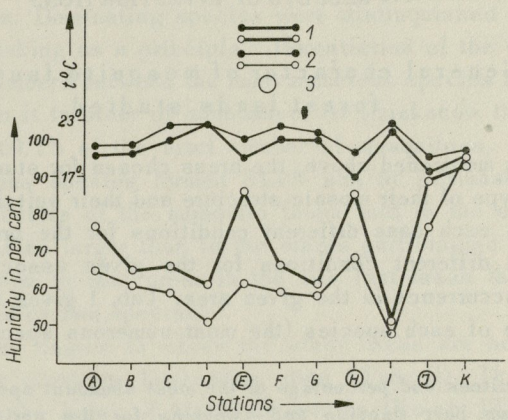

Fig. 5. Course of humidity and temperature on stations at Lemańsk
Explanations see Fig. 4

growth of which was formed by young alder trees, grasses, nettles and ferns occurring in the herb layer (*Alnetum typicum* association). The area was quaggy throughout the whole study season. Station *I* was situated in a mixed forest. Pine formed the basic part of the tree layer, with oak and birch occurring additionally: the undergrowth was formed by young trees of the species occurring in the tree layer and also mountain ash and juniper: the herb layer was formed by bilberry, ferns and grasses. Station *II* was situated in a pine wood of approximately uniform age, without undergrowth; bilberry ferns and moss occurred in the herb layer. Station *VI* – an alder wood growing on drained ground, and thus similar in structure to station *V*, although in fact far drier and with a far sparser undergrowth and less luxuriant herb layer.

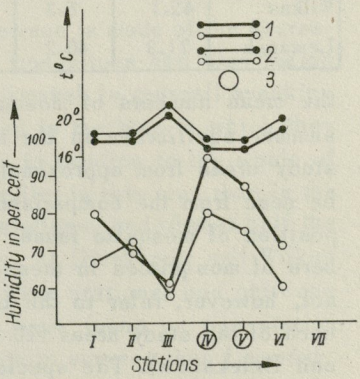

Fig. 6. Course of humidity and temperature on stations at Wilkus
Explanations see Fig. 4

The microclimatic characteristics of Lemańsk and Wilkus (Fig. 6) confirm the correctness of the classification made of the stations on the basis of the character of their vegetation. Dry environments, as at Dziekanów, were characterised by considerable dryness of the layer of air up to a height of 2 m, while differences in humidity of the layers of air examined on humid stations were considerable.

IV. RESULTS OF INVESTIGATIONS

A. General character of mosquito fauna in the forest lands studied

As has been mentioned above, the areas chosen for study differed fundamentally as to the type of their mosaic structure and their suitability for mosquitoes. This created in each case different conditions for the breeding of species of mosquitoes and different conditions for the given association of species to maintain their occurrence in the given area. Tab. I gives the species composition, percentage of each species (the most numerous species being given) and

Numbers of mosquitoes and percentage of the most abundant species in the given area (mean values from bait trapping and sweeping for the period of summer relative stabilisation)

Tab. I

Area	Mean number of mosquitoes	Percentage of species						
		A. cinereus	*A. maculatus*	*A. punctor*	*M. richiardii*	*A. vexans*	*A. annulipes*	Remaining species
Dziekanów	58.3	40.3	28.8	16.0	0.1	5.6	8.1	1.1
Wilkus	42.1	8.3	39.5	3.3	44.5	0.8	0.8	2.8
Lemańsk	21.3	40.2	2.0	7.1	0.3	45.0	0.6	4.8

the mean numbers of mosquito fauna in these areas for the period of relative summer equilibrium in the numbers of mosquitoes (the period covering, in the study areas from approximately the end of June, July and mid-August). It will be seen from the comparison made that the study areas differed as to the composition of mosquito fauna. The differences applied primarily to the total numbers of mosquitoes in these areas and the percentage of each species, but did not, however, refer to the total number of species found during the summer in each of the study areas (10 species at Lemańsk, and 11 species each at Wilkus and Dziekanów). The species structure of the mosquito fauna was different in each of the areas. If the list of species forming in each of the study areas a minimum of 90% of the total numbers of mosquito fauna is taken as index distinguishing the areas (using this index, species up to 10% participation in the mosquito fauna are taken into consideration) then it will be seen that, in the case of Lemańsk, the following species, in order of participation are: *A. vexans* Meig., *A. cinereus* Meig., *A. punctor* Kirby (92.3%). Correspondingly for Dziekanów: *A. cinereus*, *A. maculatus* Meig., *A. punctor*, *A. annulipes* Meig., (93.3%) and at Wilkus in turn: *M. richiardii* Fic., *A. maculatus*, *A. cinereus* (92.3%). Differences also applied to the percentage of the remaining accessory species

in the mosquito fauna. Dominating species were distinquished by the Renkonen (1938) method, taking as a principle differentiation of the dominant by the size of the jump in numbers between the most numerous species and the numbers of the species next to it in order of abundance. At Dziekanów the dominant and subdominant formed 69.1% of the total number of mosquitoes, while at Wilkus the two most numerous species formed 84.0% and at Lemańsk 85.2%. It can be seen from the structure of the mosquito fauna that in the case of the first area a number of species larger than in the others participated in the structure of mosquito association in this area. In the two last areas the main mass of mosquitoes was formed by two species.

An analysis of the degree to which the study areas are occupied by each species of mosquito provides interesting data (Tab. II). This degree was defined by means of the index of biotal dispersion (Koch 1957) according to the formula:

$$\frac{(T - S) : (n - 1)}{S} \cdot 100$$

when n – number of stations examined, S – number of species found in the whole study area, T – arithmetical sum of number of species found on stations within the study area.

Differences in the areas distinct both when comparison is made of the degree to which they are occupied by active and inactive mosquitoes and also taking into consideration the whole of the mosquito fauna. Lemańsk is generall speaking an unsuitable area for mosquitoes, which is reflected in the way in which they occupy the area. The index of dispersion of species in relation to the whole of the fauna (active and inactive) is about 1.5 times smaller in this area than in the others (Tab. II). Only one species occurred on all stations, and almost half the species (4 species) were found on one station only. At Dziekanów and Wilkus almost half the species (5 species) occurred on all the stations, and only one species at Dziekanów and two species at Wilkus were found on one station. These areas were far more uniform occupied by mosquito species than Lemańsk, which can be seen both by comparing the whole of the mosquito fauna caught and the active part of the mosquito fauna numerously represented in these areas.

Differences were also found to occur in the activity of mosquitoes in different areas. The index of relative activity during the period of relative summer equilibrium in the numbers of mosquitoes was, 95.2% for Dziekanów, 85.7% for Wilkus and only 45.5% for Lemańsk.

Thus during the period of summer stabilisation of relations in the mosquito fauna of the study areas, even where the species composition was similar differences were found in the numbers, structure of species domination, participation of accessory species and also in their dynamic properties, that

Degree to which areas are occupied by mosquitoes during the period of summer relative stabilisation, measured by the index of biotal dispersion (in per cent)

Tab. II

Area	Active and inactive mosquitoes	Active mosquitoes	Inactive mosquitoes
Dziekanów	56.4	59.0	38.8
Wilkus	65.5	69.0	55.6
Lemańsk	39.0	36.3	38.6

is, the level of activity and degree to which the study areas were occupied by mosquito species, these differences being particularly distinct when comparing Lemańsk with the other areas.

The level of abundance of mosquitoes and their relative activity and the degree to which they occupy the areas clearly define, in my opinion, the suitability of the areas for mosquitoes. Lemansk is therefore an example of an area extremely unfavourable to mosquitoes, with a low level of "mosquito occupation" and slight activity of mosquito fauna, which is concentrated in environments most suitable to them. Dziekanów, on the other hand, is an example of an area possessing directly opposite features to these of Lemańsk. The abundance of mosquitoes, their high relative activity and tendency of certain species to occupy the whole area form evidence of the considerable degree of suitability of typical environments in this area for mosquitoes. Wilkus taking into consideration the features mentioned above, exhibits a distinct tendency to similarity to the forest area of the type found in the Kampinos Forest.

The comparative analysis of communities of mosquitoes will therefore refer to types of areas with extreme differences in their suitability to mosquitoes. This makes it possible to grasp the degree to which their structure is dependent on the formation of the whole area.

B. Analysis of the structure of the communities against the background of the mosaic structure of the environment

1. Numbers of mosquitoes, number of species and the character of their occurrence, and the relative activity of mosquitoes as elements in the spatial distribution of mosquito fauna

Numbers of mosquitoes. It was found the abundance of mosquitoes differed in different environments (Tab. III; Figs. 7, 8, 9). It must be remembered that the observation stations were situated comparatively near each other, and the completely uniform distribution of mosquitoes over these areas was theoretically possible. Differences in the numbers of mosquitoes must therefore results from factual differences in the intensity of their occupation of different stations.

Distribution of mosquito fauna on stations during the period of summer relative stabilisation

Tab. III

Lemańsk

	Stations											Standard deviation in per cent		
	A	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*	active mosquitoes	inactive mosquitoes	whole of the fauna
Number of species	5	4	4	5	7	2	1	6	2	6	7			
Number of mosquitoes (mean)	24,1	8.2	5.2	21.1	27.9	8.3	0.4	33.4	1.6	41.1	68.1	116.7	74.5	98.7
Index of relative activity in per cent	46.9	12.2	9.6	13.3	38.9	27.6	–	52.1	–	66.9	48.6			58.1

Dziekanów

	Stations											Standard deviation in per cent		
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	active mosquitoes	inactive mosquitoes	whole of the fauna
Number of species	7	5	6	6	7	6	7	8	8	7	6			
Number of mosquitoes (mean)	161.4	64.8	16.2	24.1	62.9	32.6	84.4	117.9	32.2	32.2	9.0	82.5	97.1	82.8
Index of relative activity in per cent	95.5	97.5	86.5	97.8	96.8	95.4	98.8	93.0	99.0	95.0	46.6			19.9

Wilkus

	Stations						Standard deviation in per cent		
	I	*II*	*III*	*IV*	*V*	*VI*	active mosquitoes	inactive mosquitoes	whole of the fauna
Number of species	9	9	5	7	9	8			
Number of mosquitoes (mean)	54.3	48.7	5.2	72.3	53.8	48.2	64.8	118.0	59.9
Index of relative activity in per cent	89.6	94.0	93.7	95.0	62.5	81.7			14.5

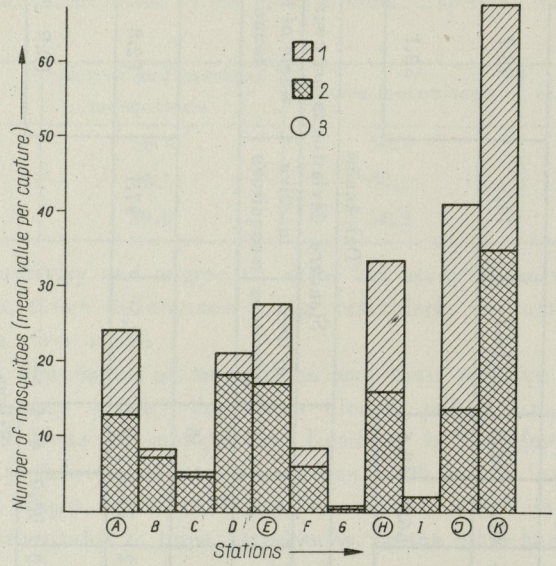

Fig. 7. Quantitative occurrence of mosquitoes on stations at Lemańsk
1 – active mosquitoes, *2* – inactive mosquitoes, *3* – wet stations

The study areas differed as to the degree of uniformity of the spatial distribution of the active, inactive and the whole of the mosquito fauna caught on the stations Tab. III – values of standard deviation. In the case of Wilkus and Dziekanów the most significant is the degree of spatial distribution of active mosquitoes, since they formed the main mass of mosquitoes caught in these areas, and hence comparison with Lemańsk serves a useful purpose primarily in relation to this part of the mosquito fauna. It was they which exhibited the most uneven spatial distribution at Lemańsk, where the mosquitoes concentrated chiefly in shady and humid environments, the abundance of the mosquitoes in these environments depending on the extensiveness of the latter (Tab. III).

Slighter differences between environments as regards the abundance of mosquitoes were observed at Dziekanów and Wilkus than at Lemańsk (Tab. III), neither was there any distinct preference for humid environments. On the other hand the phenomenon of avoidance of outstandingly dry, well-lit habitats was observed (Wilkus, station *III*, Dziekanów station *3*, *11*). The occupation of the remaining types of environment by mosquitoes did not reveal any close connection with the degree of shadiness. This would indicate that dense, fine-mosaic wooded areas create some criteria of selection by the mosquitoes of environments other than the criterion of humidity. It would seem, for instance, that the marginal part of the Kampinos Forest is subject to the influences of open areas and hence

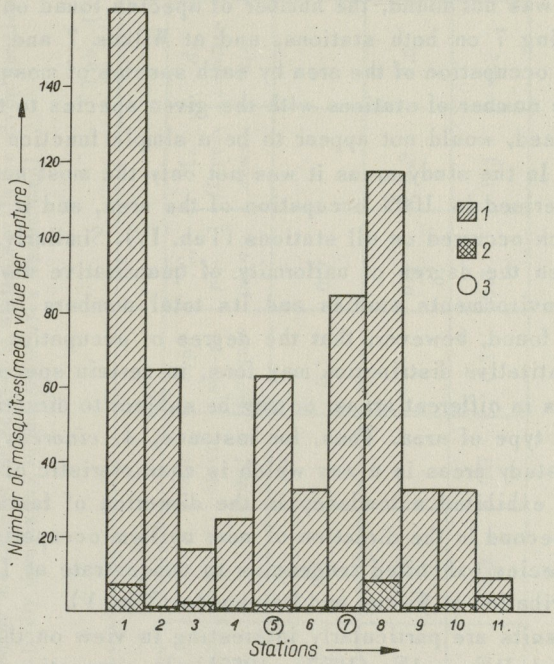

Fig. 8. Quantitative occurrence of mosquitoes on stations at Dziekanów
Explanations see Fig. 7

stations *8*, *9* and *10*, similar as regards vegetation, differ as to the numbers of mosquitoes in them (Tab. III).

Number of species and the character of their occurrence. Differences between environments as regards the abundance of mosquitoes were accompanied by differences in their species composition, differences consisting primarily in the number of species on each station (Tab. III). These differences were very great at Lemańsk (from 1 to 7 species per station) and the preference for humid stations was very marked. From 1 to 5 species were found on dry stations, and from 5 to 7 on humid stations.

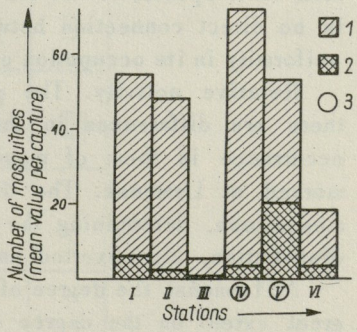

Fig. 9. Quantitative occurrence of mosquitoes on stations at Wilkus
Explanations see Fig. 7

These differences were far less distinct at Dziekanów and Wilkus, as can be seen from comparison of the number of species occurring on different stations – at Dziekanów from 5 to 8, and at Wilkus from 5 to 9, species. Preference for humid stations

over dry stations was not found, the number of species found on humid stations at Dziekanów being 7 on both stations, and at Wilkus 7 and 9 respectively.

The degree of occupation of the area by each species of mosquito, expressed in the ratio of the number of stations with the given species to the total number of stations examined, would not appear to be a simple function of the numbers of these species. In the study areas it was not only the most numerous species that were characterised by 100% occupation of the area, and it was not always the dominant which occurred on all stations (Tab. IV). Similarly, no connection was found between the degree of uniformity of quantitative distribution of the species in the environments studies and its total numbers in the given area (Tab. V). It was found, however, that the degree of occupation of an area and uniformity of quantitative distribution may form, in certain species, one of their permanent features in different areas, or may be subject to directional variations depending on the type of area. Thus, for instance, *A. cinereus* and *A. vexans* occupied all the study areas in a way which is characteristic of them. The first of these species exhibited a tendency in the direction of fastidious choice of habitat, and the second in the direction of more uniform occupation of the areas. The remaining species exhibited tendencies to concentrate at Lemańsk, and to more uniform distribution at Wilkus and Dziekanów (Tab. V).

The above results are particularly interesting in view on the data obtained by MacLeod and Donnelly (1957a, 1957b). In connection with analogical investigations made of species of fly of the family *Calliphorinae* they found that the structure of the environment was reflected primarily in the quantitative spatial distribution of accessory species. Species dominating in numbers in an association of flies were characterised by a far more uniform spatial distribution than other species. From the data obtained for mosquitoes it appears that there is no direct connection between the numbers of a species and the degree of uniformity in its occupation of a given area.

Relative activity. The phenomena discussed above indicate the fact that there are differences in the environments as regards the character of the occurrence in them of mosquito fauna, these differences being particularly marked at Lemańsk. The different degree of suitability of environments for mosquitoes, determining the quantitative and qualitative form of their spatial distribution, also exerted an influence on the degree of their biting activity.

At Lemańsk the degree of the mosquitoes activity proved to depend to a very great extent on the degree of humidity of the environment (Tab. III, Fig. 7), stations *G* and *I* forming exceptions to this rule. These two stations had no undergrowth or herb layer and therefore no mosquitoes were to be found there during the day, only single individuals being observed to fly there from neighbouring wet areas. Hence the index of activity for this type of environment has a completely different ecological sense than that of the index obtained for an environment with its own diurnal mosquito fauna, and on this account it

Degree to which the areas are occupied by different species, measured by the ratio of the number of stations with the given species to the total number of stations examined (species quantitatively dominating in the given area underlined)

Tab. IV

Area	Species										
	A. cinereus	*A. maculatus*	*A. punctor*	*A. annulipes*	*A. vexans*	*M. richiardii*	*An. claviger*	*An. maculipennis*	*C. pipiens*	*A. flavescens*	*A. communis*
Lemańsk	0.7	0.6	0.7	0.3	1.0	0.1	0.1	0.1	0.7		
Dziekanów	1.0	1.0	1.0	1.0	1.0	0.2			0.4	0.2	0.6
Wilkus	1.0	1.0	1.0	0.7	1.0	1.0	0.7	0.5	0.3	0.3	0.2

Degree of evennes of the quantitative distribution in space of each species (most numerous species) expressed in values of the standard deviation in per cent (species quantitatively dominating in the given area are underlined)

Tab. V

Area	Species						
	A. cinereus	*A. maculatus*	*A. punctor*	*M. richiardii*	*A. vexans*	*A. annulipes*	*C. pipiens*
Lemańsk	131.3	140.0	116.6	small numbers	71.9	small numbers	113.0
Dziekanów	121.7	76.1	64.4	small numbers	67.9	60.1	small numbers
Wilkus	149.6	57.4	72.4	77.4	small numbers	small numbers	90.0

should be excluded from analysis. If the value of the index of activity equal to 35% (arithmetical mean of values for each station) is taken as the discriminant of the stations, it then proves that four stations are characterised by an index with a value lower than, and five stations with a value higher than, the accepted borderline level. The first group is formed by dry stations, the second by humid ones.

At Dziekanów and Wilkus a far higher level of activity of mosquitoes was observed than at Lemańsk, and in addition it was in general equal on all stations (Tab. III, Figs. 8, 9). An exception to this rule is formed by the marginal station at Dziekanów (station *II*) and the place in which mass hatching of mosquitoes took place at Wilkus (station *V*), which were characterised by a lower index of activity than the remainder. Thus despite the welldefined mosaic structure of the area the activity of the mosquitoes in the environments studied was considerable and was not subject to the enfeebling effect of even the most unfavourable habitats.

Three of the most numerous species of mosquito analysed (*A. cinereus*, *A. maculatus* and *A. vexans*) were characterised by considerable variations in activity in different environments in one area, and also differed as to their mean activity for each of the areas (Tab. VI). They therefore exhibited the property of modifying, within wide limits, their activity depending on habitat conditions. On the other hand *A. punctor* and *C. pipiens* exhibited a constant level of activity in the three study areas. The first of these species is characterised by maximum activity in all the study areas, the second by minimum activity in all three areas. The minimum activity of *C. pipiens* during the day had previously been established by the authoress in her direct field observations made during the mass flight of this species to a moorland. The value of the index of activity obtained for this species may therefore be accepted as correct, despite the fact that it attacks rather birds than people and that the bait trapping method is therefore unsuitable for it.

2. Communities of mosquitoes

General assumptions. As has been stated above, the main aim of this study was to examine the character of the spatial distribution of mosquito fauna and to connect it with the type of mosaic structure of the area. The starting point was formed by the assumption that in view of the considerable sensitiveness of mosquitoes to microclimatic factors, each area must constitute for them a mosaic of environments creating different living conditions. These differences in the suitability of environments for mosquitoes result in differences in the spatial distribution of the population.

The assumption put forward by Tarwid (1952) lying at the basis of all distinction of an association of mosquitoes as an ecological unit – an associa-

Index of relative activity of each species (most abundant species)

Tab. VI

	Area	Species						
		A. cinereus	*A. maculatus*	*A. vexans*	*A. punctor*	*M. richiardii*	*A. annulipes*	*C. pipiens*
Lemańsk	value of the index for the whole area	60.7	69.5	28.9	82.6	small numbers	small numbers	1.6
	maximum and minimum values of the index for the sequence of stations	16.6–68.6	0–100	0–57.1	58.7–100	- " -	- " -	0–19.3
Dziekanów	value of the index for the whole area	96.6	98.4	86.7	97.3	- " -	92.2	0
	maximum and minimum values of the index for the sequence of stations	95.5–100	96.7–100	68.0–100	92.9–100	- " -	81.9–100	0
Wilkus	value of the index for the whole area	72.1	88.6	61.3	84.6	95.9	small numbers	0
	maximum and minimum values of the index for the sequence of stations	15.2–81.9	77.2–94.8	8.2–100	60.2–100	85.9–100	- " -	0

tion of organisms distinctly differing from the rest of the biocenosis on account of their specific way of life and ecological requirements, subject to internal quantitative regulation as the result of competition for food and avoidance of predators – apply to the whole of the mosquitoes occupying a given biotope. The domination structure is, in the author's opinion, proof of the existence of regulation of numbers in an association of mosquitoes and hence proof of the formation by them of a competitive association. The author, who did not analyse the variations in space of mosquito fauna, was not in a position to establish the fact of the superposition of two phenomena on each other: the formation of a domination structure, resulting from the regulation of numbers taking place in an association of mosquitoes, and resulting from effect of the environment determining the differences in spatial distribution of the association. Taking as a fact the formation by mosquitoes of a competitive association within the whole biotope, it is then necessary to define the part played in it by communities of mosquitoes. It would seem that the realisation of the phenomena of quantitative regulation resulting from the biocenotic contacts of mosquitoes takes place on the basis of their definite communities forming in each habitat as the result of the pressure exerted by the environment. The different structure of communities is the foundation of this regulation, the results of which are transmitted to the whole association during the evening increase in the activity of mosquitoes and their intensive mixing.

The communities of mosquitoes in each of the study areas were formed on a different structural basis of the whole of the mosquito fauna (see description of areas), exhibiting despite this certain general properties in the way in which they were formed in all the areas. Thus, for instance, it is a known fact that the communities distinguished differed as to the number of species and the abundance of each of them, yet always in fine mosaic environments (Dziekanów, Wilkus) differences in the number of species on each station were created as the result of the elimination of accessory species. At Lemańsk, on the other hand, elimination also applies to the subdominant of this area and only the dominating species occurred as a permanent component of all communities.

In addition, in the great majority of cases (in 24 out of the 38 communities examined) differences in the domination structure of the communities in regard to the two most numerous species consisted in their reciprocal replacement in the communities of the dominant and subdominant of the given area. It was only in one case that a species accessory to the whole of the study area occurred as a dominant in a community, and in three cases it was a subdominant in a community.

It will be seen from the above that the two most numerous species in a given area were the dominants and subdominants in the majority of the communities occurring in the given area. Taking into consideration also the fact that in

principle two species formed the main mass of the mosquitoes in the communities examined (at Dziekanów from 43.1% to 92.2% of the whole of the mosquitoes in communities, at Wilkus from 71.7% to 92.5%, and at Lemańsk from 80.3% to 100%), the structure of the mosquito communities may be analysed in our case the aspect of the following problems: the ratio of abundance of the dominant and subdominant; the ratio of abundance of the two basic species to the remaining accessory species which give the degree of participation of the latter in the communities: the ratios of relative activity of the basic components of the communities describing the dynamic side of interspecies relations among mosquitoes.

Characteristic of quantitative relations between the components of communities distinguished. As has already been stated, in all the study areas two species of mosquitoes usually formed the basis of the community. These were, in the majority of cases, the dominant and subdominant of the whole of the mosquito fauna of the given area. An exception to this was formed at Dziekanów by station *3*, where an accessory species, *A. vexans*, (Fig. 10) was the subdominant, at Wilkus by station *V*, where the subdominant was the accessory species *A. cinereus* (Fig. 11), and at Lemańsk by station *C*, where the accessory species *C. pipiens* was the subdominant, and station *I*, where *A. punctor* was the dominant in the community (Fig. 12). Apart from these exceptions domination in the remaing communities was formed variously from the two basic species. At Dziekanów these were *A. cinereus* and *A. maculatus*, at Wilkus *M. richiardii* and *A. maculatus*, and at Lemańsk *A. vexans* and *A. cinereus*.

Differences were observed in the participation of the dominating species, the subdominant and accessory species in associations of mosquitoes in the study areas and in different communities. Two directional regularities were found in relation to the whole of the areas: an increase in the participation of the dominant in an association with transition from fine-mosaic, humid areas to dry ones, and a decrease taking place in the same direction in the participation of accessory species (Tab. VII). From this it can be seen that in a dry area the structure of an association of mosquitoes is formed on the principle of favouring the species especially well adapted to the environment conditions prevailing there, whereas in the case fine-mosaic humid areas the variety of the environment makes it possible for other species also to play a prominent part.

A detailed description of the quantitative relations between the basic three components of the communities (Fig. 13) points to the considerable percentage of the dominant in the communities at Lemańsk, and that in principle at the expense of accessory species and the subdominant. It is only in humid environments that the percentage, of both these components, particularly of the subdominant, increased slightly. A decrease, in comparison with Lemańsk, was noticeable at Dziekanów in the participation in the communities of the dominating species with simultaneous increase in the participation of accessory species. The percentage of the dominant decreased distinctly in this area with increasing

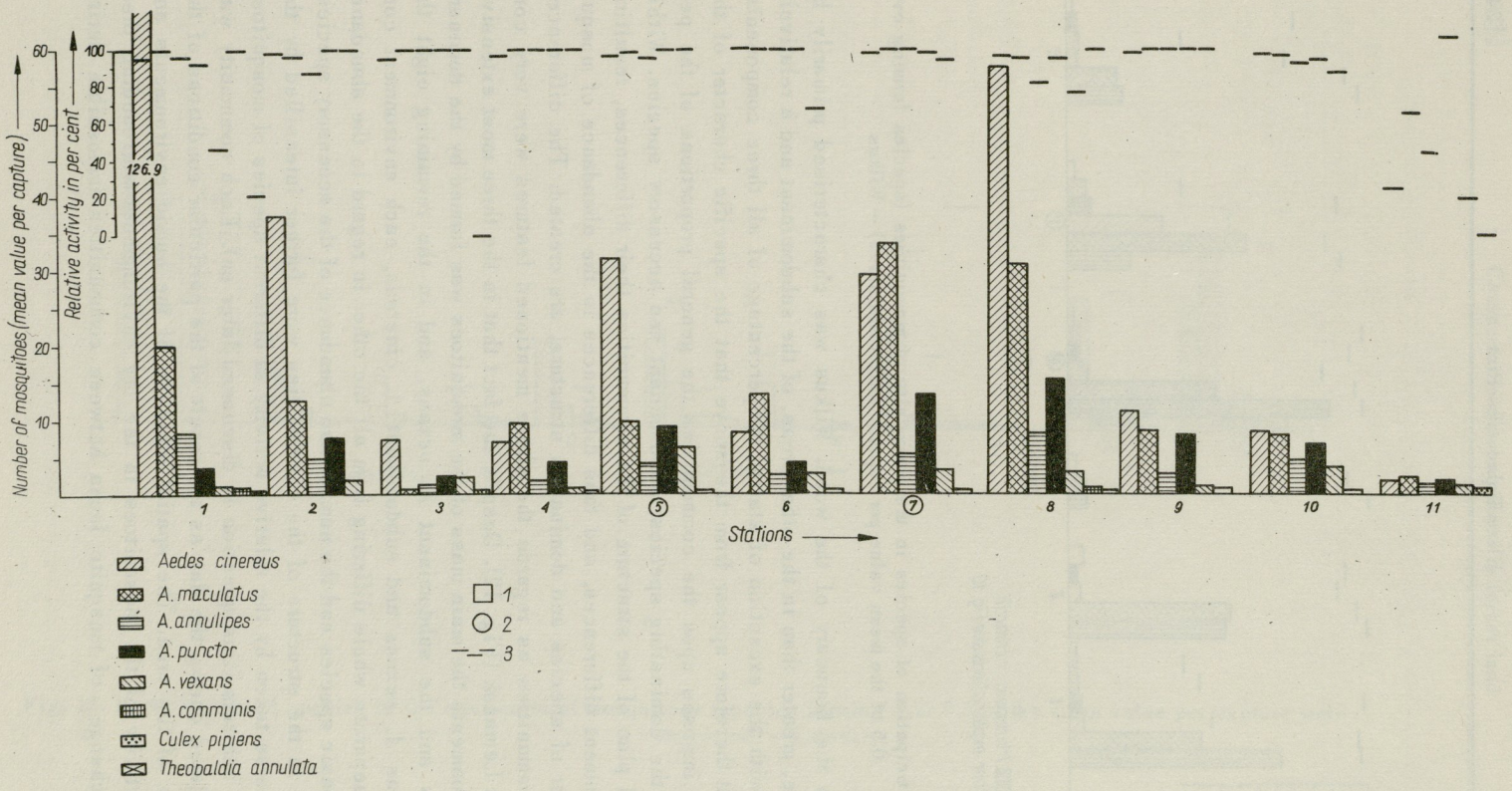

Fig. 10. Participation of species in the community of mosquitoes (species forming over 0.5 of the mean value per capture were considered) — Dziekanów

1 — the sum of species forming below 0.5 of the mean value per capture, *2* — wet stations, *3* — activity level of each species

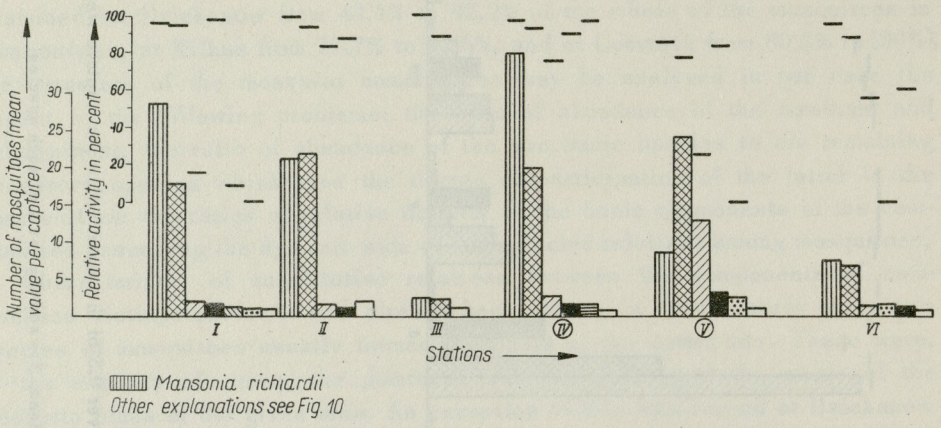

Fig. 11. Participation of species in the community of mosquitoes (species forming over 0.5 of the mean value per capture were considered) — Wilkus

nearness to the boundary of the wood. Wilkus was characterised primarily by a percentage, greater than in the other areas, of the subdominant and a relatively unvarying (with the exception of station V) percentage of all three components.

It would therefore appear from the above that the specific character of the whole area imposes upon the communities the general proportions of the percentage of the dominating species, subdominant and accessory species. Within this general plan of the structure of the communities their differences, resulting from environment differences, and thus differences in the abundance of mosquitoes, number of species and domination structure, are created. The differences between communities as regards the above mentioned features were very considerable at Lemańsk (Fig. 12). Despite the fact that in the three most extensive humid environments the main mass of the mosquitoes was formed by the dominant *A. cinereus* and the subdominant *A. vexans*, and in the remaining eight the dominant was *A. vexans* and subdominant *A. cinereus*, each environment constituted a separate whole differing from all the other in regard to the abundance of the two basic species and the number and abundance of the accessory species. Differences in the structure of the communities were further intensified by the different course taken by the relative activity of different species of mosquitoes in different habitats (this question is discussed later on). Each community was strictly isolated during the day as the result of the particular conditions of the organisation of the area. The spatial isolation of the humid environments and minimum activity of the mosquitoes in the dry environments surrounding them made interchange of mosquito fauna between communities impossible during the day.

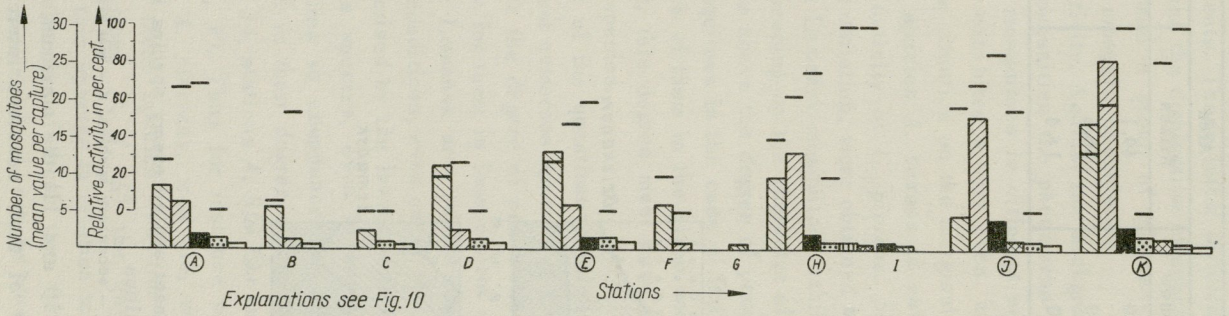

Fig. 12. Participation of species in the community of mosquitoes (species forming over 0.5 of the mean value per capture were considered) – Lemańsk

Percentage of the basic three groups of species in the mosquito fauna of the study areas

Tab. VII

Species	Area		
	Dziekanów	Wilkus	Lemańsk
Dominant	45.0	49.1	67.1
Subdominant	23.0	36.5	23.3
Accessory species	32.0	14.4	9.6

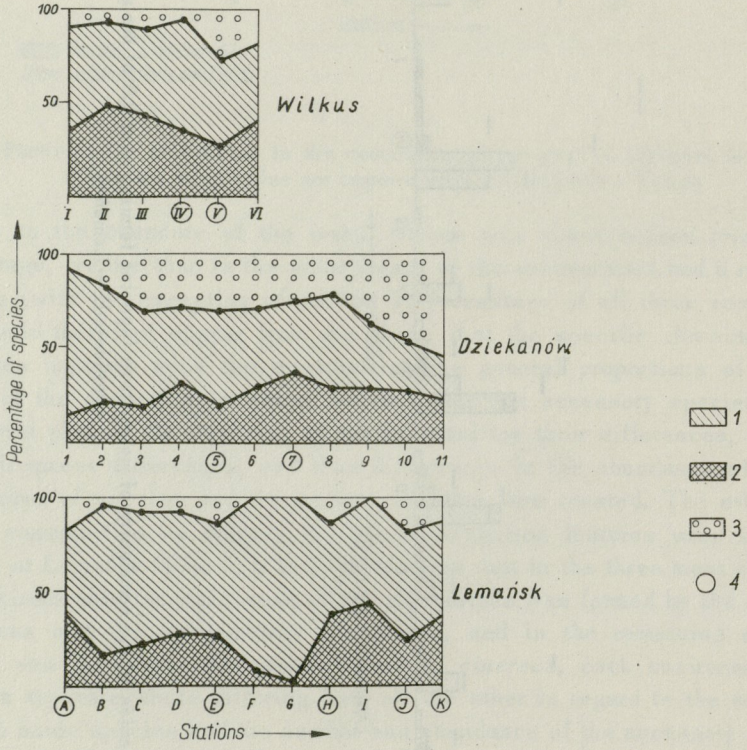

Fig. 13. Percentage of dominant, subdominant and accessory species in mosquito communities

1 – dominant, *2* – subdominant, *3* – accessory species, *4* – wet stations

At Dziekanów and Wilkus (Figs. 10 and 11) the maximum activity of the mosquitoes suggested the possibility of their constant interchange between different environments, but here also dry, well-lit environments and the environments in the marginal part of the forest formed a certain barrier. They

were characterised by the low level of occupation by mosquitoes and a tendency occurred in the domination structure of their communities to even up the percentage of each species, thus distinctly differing from the communities of the shady environments. These latter differed from each other as to the abundance of mosquitoes and the domination of species. It may therefore be said that these areas also formed a group of microenvironments causing differences in the structure of the mosquito association.

Relative activity. Against the background of the structure discussed above, of mosquito communities the phenomena connected with the specific nature of the activity of mosquitoes in different environments take place. At Dziekanów the mosquitoes exhibited a very even, high activity (Figs. 8, 10), with the exception of the situation on the marginal station and cases of reduction in the activity of the species *A. vexans* in environments unfavourable to it, and the generally low activity of *C. pipiens*. Similar pictures, characterised by only slightly greater variation, were obtained at Wilkus (Figs. 9, 11). Contrary to the above areas, at Lemańsk mosquitoes exhibited far greater variations in the level of activity, depending on the character of the environment (Figs. 7, 12). In connection with the above the degree of penetration of the environment by different species of mosquitoes in the case of Dziekanów and Wilkus was defined by the numbers of each of them in the given environment. In the case of Lemańsk, on the other hand, this degree must have been the resultant of the numbers and activity of the species.

Comparison of the quantitative relations of inactive and active individuals of the three most numerous species at Lemańsk (Fig. 14) gives a picture of the extent to which the degree of penetration of the environment by species in an area unsuitable for them is independent of their abundance. The most numerous species in the Lemańsk area reacted by a very distinct change in activity to environmental conditions, even under the conditions at Dziekanów. At Lemańsk it was characterised by the lowest activity of all the species (Tab. VI). In this connection this species, even in environments in which it was a dominant, greatly exceeding in abundance the numbers of the remaining species often failed to equal in their degree of penetration of the environment species less numerous (Fig. 14, stations *A*, *B*, *C*) or only very slightly exceeded them (Fig. 14, stations *D*, *E*, *F*). Thus for instance on station *A* the ratio of abundance of *A. vexans* to *A. cinereus*, was 1.3, while the ratio of numbers of active individuals of these species was 0.6. In environments in which *A. cinereus* dominated (stations *H*, *J*, *K*) the quantitative predominance of the active individuals of this species in relation to *A. vexans* was greater than the actual quantitative relations of these two species. Thus on station *J* the ratio of numbers of *A. cinereus* to *A. vexans* was 2.6 and the ratio of active individuals was 3.1. The figures for station *K* were respectively 1.4 and 2.5. Therefore the degree of penetration of the environment by *A. vexans* was in these environments

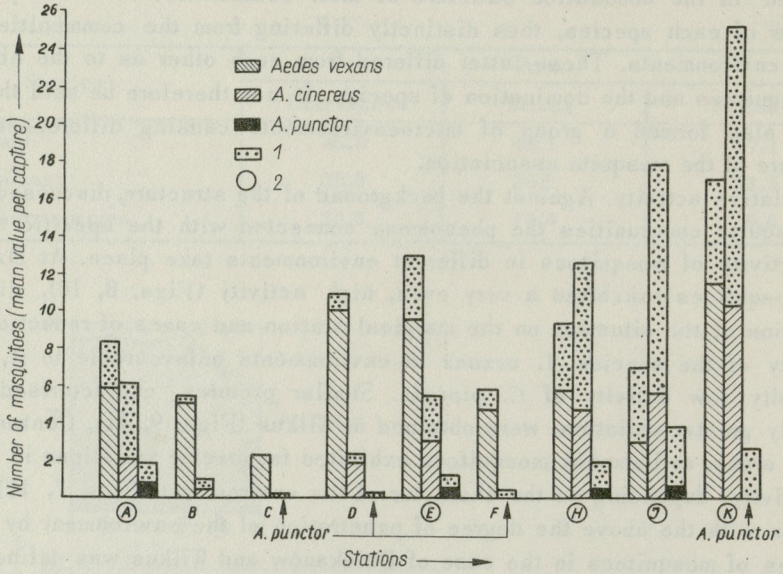

Fig. 14. Ratio of active and inactive individuals at Lemańsk
1 – inactive mosquitoes, *2* – wet stations

2.5–3 times less than in the case of *A. cinereus*, despite the fact that the quantitative relations of the two species did not exhibit such a difference. Under such circumstances *A. punctor*, exhibiting a high degree of activity in most unfavourable environments, despite the fact that it is less abundance than the two preceding species may play, in addition to them, a certain part in the phenomena determined by the degree of penetration of the environment by the species.

Thus at Lemańsk the effect of the environment causing differences in the behaviour of the mosquitoes permitted only part of the individuals of each species to become active during the day, depending on the degree of their sensitivity to environment factors. Hence the intensity of the biocenotic contacts of mosquitoes will be determined in this type of area not only by the abundance of species but chiefly by the level of their activity.

3. Seasonal variations in the structure of the mosquito communities

Variations in the character of the spatial distribution of mosquitoes in different periods of the season render the similarities and differences of the environments examined very distinct. They give a picture of the seasonal course of the phenomena observed there and degree of autonomy of the different parts of the area.

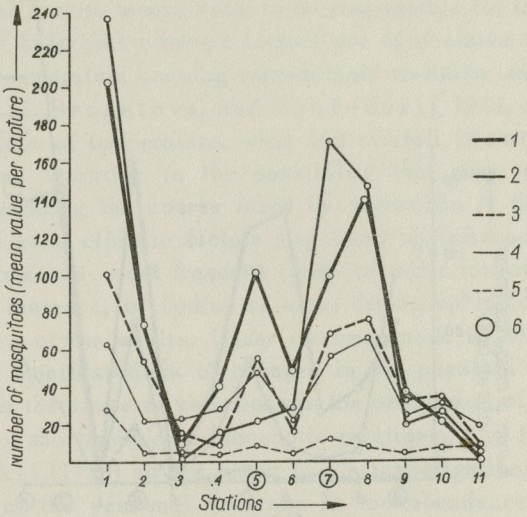

Fig. 15. Seasonal variations in the numbers of mosquitoes on stations at Dziekanów *1* – 1–15.VII, *2* – 16–31.VII, *3* – 1–15.VIII, *4* – 16–31.VIII, *5* – 1–15.IX, *6* – wet stations

Variations in numbers. First of all the fact that the differences in the quantitative level of mosquitoes on stations was maintained throughout almost the whole season in each of the study areas is worthy of attention, the plan of spatial distribution characteristic of the given area being maintained despite differences in the quantitative level of the mosquito fauna at different periods of the season (Figs. 15, 16, 17). At Dziekanów and Wilkus, with the passage of the season differences in the numbers of mosquitoes occurring on different stations decreased (Tab. VIII). An exception to this was formed by periods of mass occurrence of species which in occupying chosen environments by doing so increased the differences between stations. The smallest differences occurred in the first half of September. At Lemańsk, on the other hand, differences in the numbers of mosquitoes in communities during September correspondend to the differences in August and even increased in comparison with July. This resulted from the complete or almost complete non-occurrence of mosquitoes on dry stations

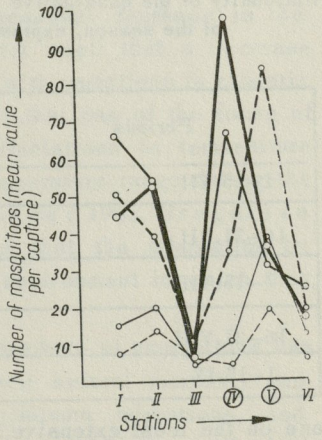

Fig. 16. Seasonal variations in the numbers of mosquitoes on stations at Wilkus
Explanations see Fig. 15

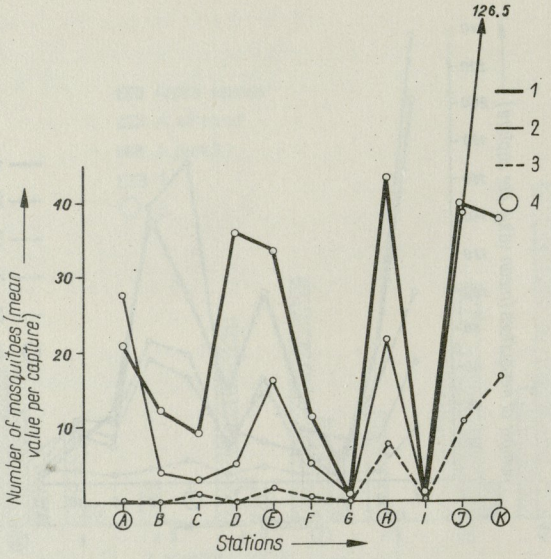

Fig. 17. Seasonal variations in the numbers of mosquitoes on stations at Lemańsk
1 – July, *2* – August, *3* – September, *4* – wet stations

Uniformity of the quantitative distribution in space of mosquitoes during different periods of the season, expressed by the values of standard deviation in per cent

Tab. VIII

Periods	Area		
	Dziekanów	Wilkus	Lemańsk
1–15.VII	77.6	80.1	92.1
16–31.VII	116.4	60.9	
1–15.VIII	69.1	80.8	160.2
16–31.VIII	48.9	68.0	
1–15.IX	33.0	53.5	157.8

and on the least extensive humid stations (mean number of mosquitoes on these stations was 0.4 per trapping) and the concentration of the remaining mosquito fauna on the most extensive, humid stations (mean number of mosquitoes 11.8). A similar tendency to concentration exhibited by mosquitoes in the autumn in the study area could also be observed at Dziekanów, where on station 1, situated deepest in the Forest, an average number of 28.7 individuals was captured at every trapping, and 7.0 for other stations.

The above observations are interesting from the point of viev of the possibili-

ty of interpreting the seasonal decrease in the abundance of mosquitoes. The influence of different factors would seem to be responsible for this phenomenon. The prevailing view held that climatic factors are of decisive importance, e.g. sudden changes in temperature causing considerable mortality among mosquitoes (Blagoveščevskij, Bregetova, and Mončadskij 1943, Šlenova 1955), or the combined effect of temperature, wind and rainfall (Mončadskij 1950). Bates (1945) draws attention to the possibility that more complicated mechanisms exist, regulating the course taken by variations in the abundance of mosquitoes. On one hand climatic factors may exert an influence, which in the author's opinion forms the most frequent cause of reduction of the developing larvae (caused, for instance, by bodies of water drying up), and thus indirectly affect the abundance of the adults. Under circumstances in which there is an absence of distinct manifestations of changes in the physical environment the author considers that the cause of variations in the abundance of mosquitoes lies in the disturbance of the balance of biocenotic relations, e.g. the predator-prey system. Mončadskij (1956) as the result of his investigations in the delta of the Volga found that the seasonal decrease in the abundance of mosquitoes, not correlated with climatic variations, was the resultant of the natural seasonal mortality of the first generation among the adults of each species and of the degree of reduction of larvae of the second generation (hence the entry into the association of adults of a limited number only of new individuals).

It is an undoubted fact that, excluding catastrophic situations, climatic factors cannot be considered responsible for the seasonal decrease in the abundance of mosquitoes. This is clear from the fact itself that a decrease was found in the numbers of mosquitoes not correlated with variations in climatic factors. In addition, it is a generally well-known fact that one of the forms of adaptation by species of mosquitoes to seasonal fluctations in temperature consists in their transition to the lower values in temperature range during the autumn in which mosquitoes maintain their activity (Činaev 1945, Bregetova 1946, Čagin 1945). This would point to the fact that the adaptation by mosquitoes to the type of seasonal variations in the environment in which they lived is genetically transmitted to progeny.

It would seem that the seasonal decrease in the numbers of mosquitoes has two aspects. On the one hand it is caused by their natural mortality and biocenotic reduction, and on the other by the autumn migrations, and their concentration in certain environments. Mončadskij (1956) draws attention to the fact that certain species of mosquitoes found during the summer season in the coastal belt of the Volga delta, migrated in the autumn into the hinterland in a search for more favourable environments. The data cited above on the concentration of mosquitoes at Dziekanów and Lemańsk on the stations chosen suggest the possibility of this phenomenon taking place there. In addition the authoress's own investigations on the seasonal variations in the abundance

of forest mosquitoes flying out of the Kampinos Forest into the open areas surrounding it, during the period of their evening maximum activity, revealed the phenomenon of the successive desertion by the mosquitoes, with the passage of the season, of environments unfavourable to them (Dąbrowska-Prot 1960). It was found that mosquitoes did not appear on the stations situated deepest in the dune area as from July 27th, on stations situated on the boundary of the Kampinos Forest and in open areas as from August 15th, whereas in the Forest itself single individuals were caught on the stations selected, during the period of minimum day activity, until as late as August 30th to September 4th.

The phenomena discussed above permit of assuming that phenomena of migration to environments more favourable to them during the autumn period play a certain part in the process of the seasonal decrease in the numbers of mosquitoes.

Variations in the structure of communities. Seasonal variations in the numbers of mosquitoes accompanied variations in the structure of their communities. It proved possible to distinguish two types of seasonal variations in the communities.

At Lemańsk (Fig. 18) three groups of the species of the communities (dominant, subdominant, accessory species) were maintained in all the environments only during the summer. The dominant and subdominant formed the basis of the communities during this period. The percentage of accessory species was small, increasing slightly in the second half of the summer, the same system of their participation in each station being maintained — the greatest on humid stations and minimum or zero on dry stations. Far-reaching changes in the mosquito fauna of each station took place in the autumn. Some of them were completely deprived of mosquito fauna during this period, on part of the stations only one species was found and it was only on the humid and most extensive stations that communities of several species of mosquitoes occurred (mean number of species on these stations for these months was, July — 3.6, August — 3.4 September — 1.6). Thus in this type of area it was only in certain chosen environments that a variety of species of mosquitoes, which probably found their most favourable living conditions there, continued to occur.

This same type of species structure of the communities, based on the domination of the two most quantitative species in that area, occurred at Lemańsk throughout the entire season (Fig. 21). In the three most humid environments (station *H*, *J*, *K*) the dominant was *A. cinereus*, and the subdominant *A. vexans*, while on the remaining, drier environments the reverse applied — *A. vexans* being the dominant and *A. cinereus* the subdominant. This system was maintained even during the period of the decrease in the numbers of *A. vexans* and the simultaneous considerable increase in the abundance of *A. cinereus* (Fig. 24), and also during the period of the general autumn decrease in the numbers of mosquitoes. It was therefore independent both of the numbers and of the age

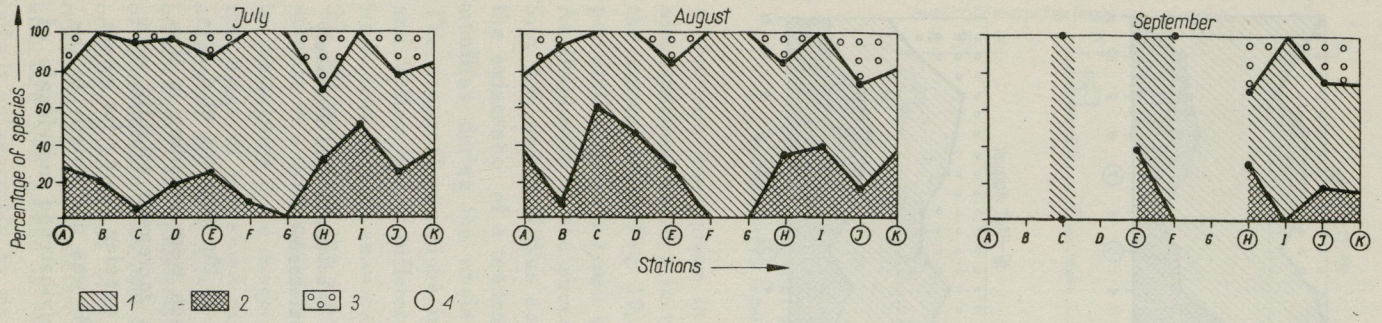

Fig. 18. Seasonal variations in the percentage of dominant, subdominant and accessory species in communities of mosquitoes at Lemańsk
1 — dominant, *2* — subdominant, *3* — accessory species, *4* — wet stations

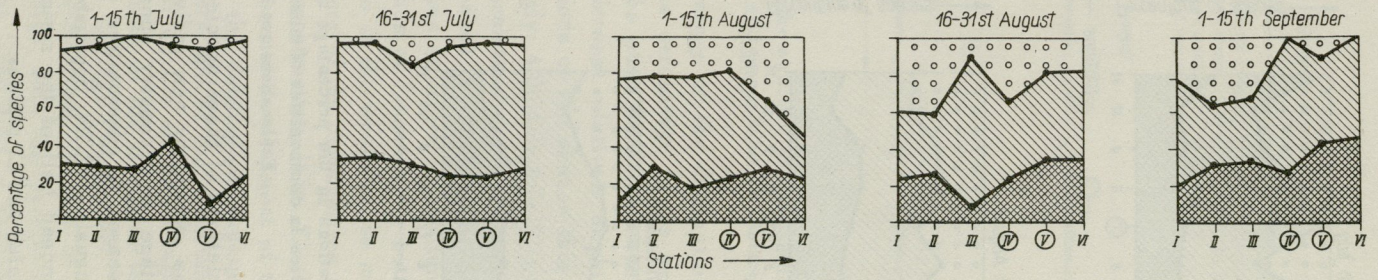

Fig. 19. Seasonal variations in the percentage of dominant, subdominant and accessory species in communities of mosquitoes at Wilkus
Explanations see Fig. 18

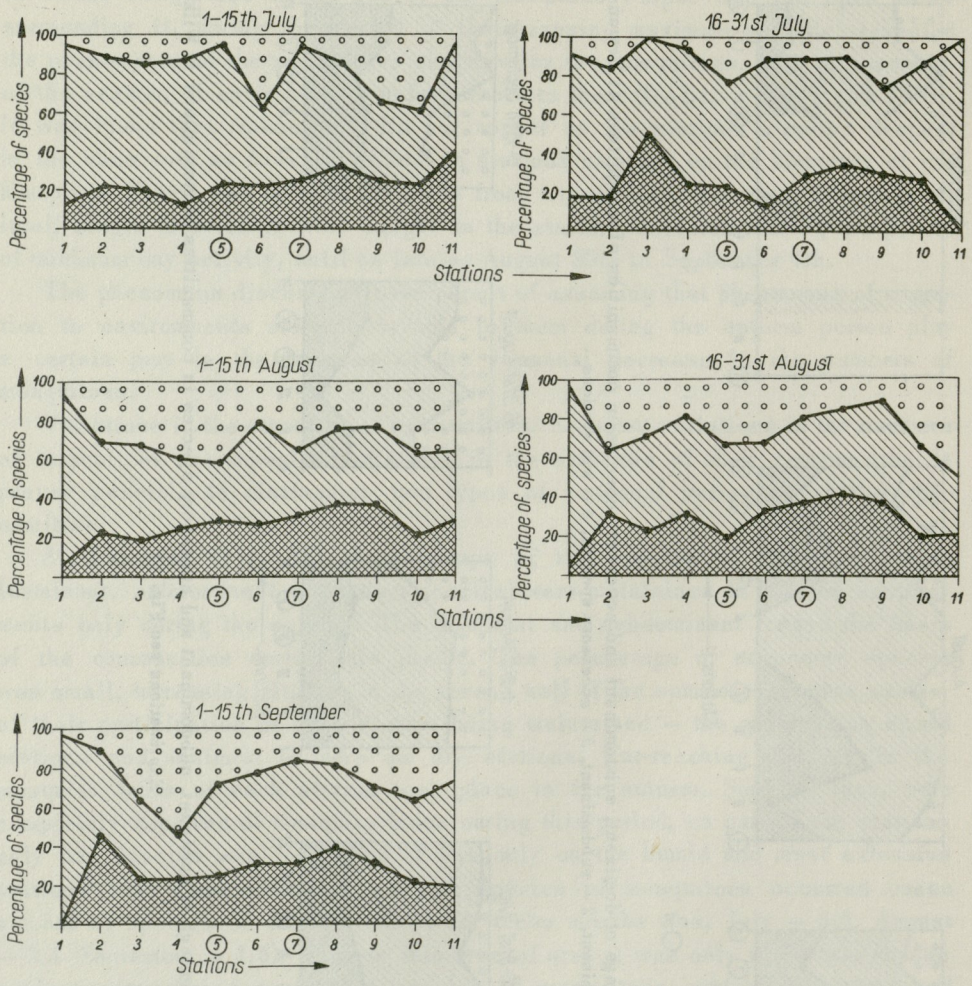

Fig. 20. Seasonal variations in the percentage of dominant, subdominant and accessory species in communities of mosquitoes at Dziekanów

Explanations see Fig. 18

structure of the populations of these species (the rise in the numbers of *A. cinereus* in August was caused by new individuals which were breeding in this period). The percentage of accessory species which increased slightly with the duration of the season in communities of several species (being for whole area: July 17.3%, August – 22.2%, September – 25.5%) was due chiefly to the appearance in the second half of the summer of newly-hatched individuals of the species *A. maculatus* and *C. pipiens*.

At Dziekanów and Wilkus, as at Lemańsk, with the lapse of the season

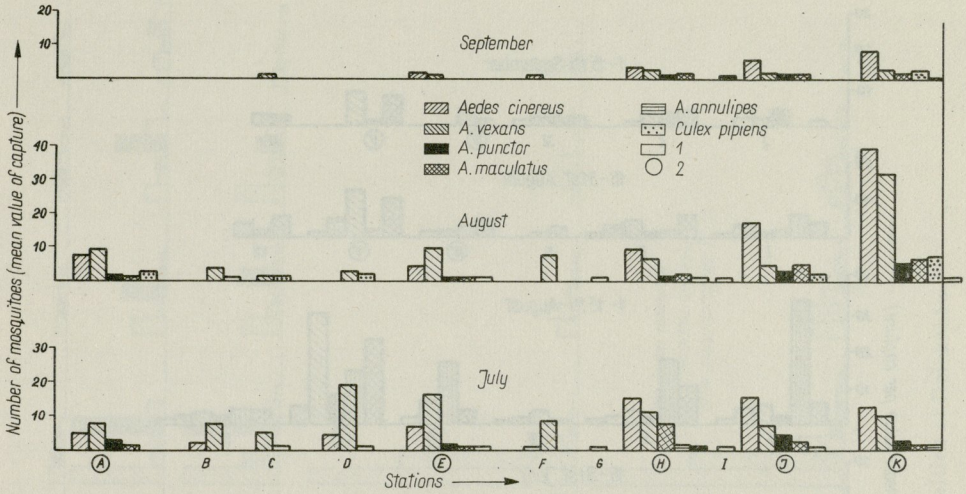

Fig. 21. Seasonal variations in the structure of communities at Lemańsk
1 – sum of species forming below 0.5 of the mean value per capture, *2* – wet stations

a decrease took place in the percentage of the dominating species and the simultaneous distinct increase in the percentage of the accessory species in the communities (Fig. 19, 20). On the other hand the mean number of species per station in both types of area underwent relatively slight seasonal changes. At Dziekanów in the successive periods of the season this was: 5.0: 4.0: 5.5: 5.0: 4.6, and at Wilkus correspondingly: 4.0: 4.3: 6.5: 5.7: 3.3. This points to the existence of a tendency to the maintenance of species variety in the communities during the whole of the season in the majority of the environments. The seasonal variations in the species structure of communities at Dziekanów and Wilkus took a different course than at Lemańsk. In both these areas there were considerable seasonal variations in the whole of the mosquito fauna (Fig. 25, 26) and hence the species structure of the communities in these areas was subject to a fundamental seasonal reconstruction, (Fig. 22, 23). It was possible to distinguish three stages in the seasonal development of the mosquito fauna: the stage of the sharp formation of the domination structure (July), then the stages of the interchange of dominants and of the simultaneously progressive balancing of the quantitative level of all the species (August), and the stage of considerable decrease in the numbers of the mosquito fauna combined with complete elimination of some of the species (September). These stages were reflected in the structure of the communities. In July a distinct domination structure was formed in the communities, with the exception of stations particularly unfavourable to mosquitoes (at Dziekanów – stations *3, 9, 10, 11;* at

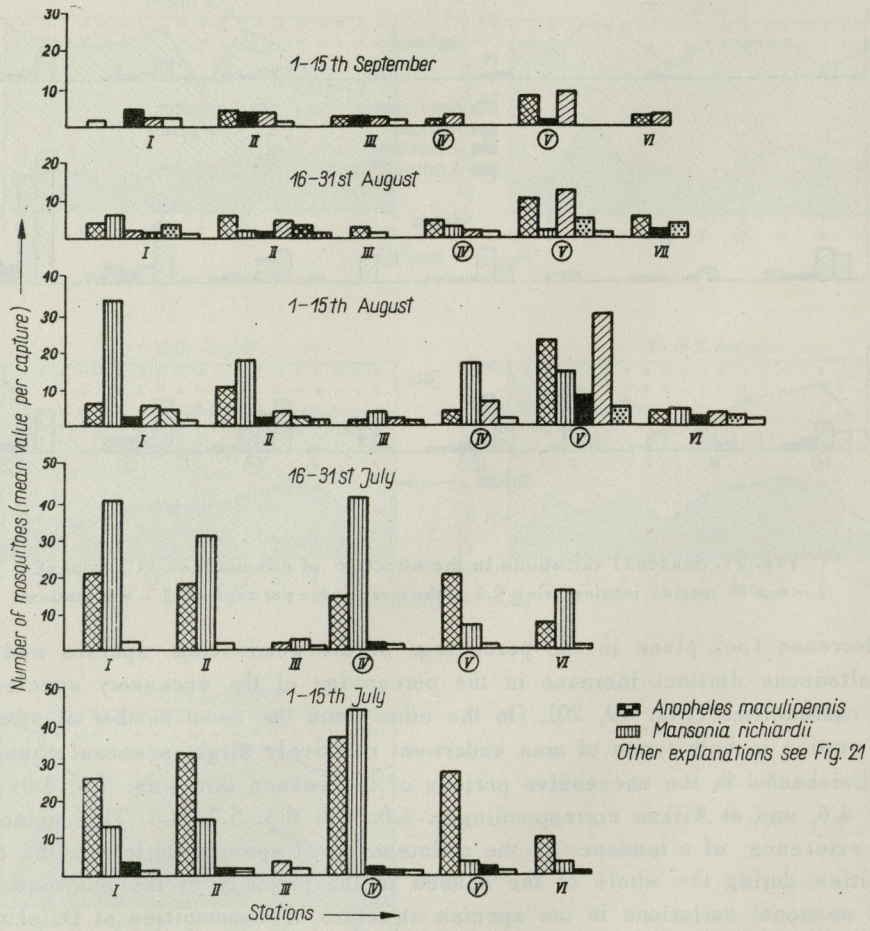

Fig. 22. Seasonal variations in the structure of communities at Wilkus

Wilkus station *III*). In the majority of cases the dominants and subdominants were, during this period, the two most numerous species in the given area: at Dziekanów *A. cinereus* and *A. maculatus*, at Wilkus – *M. richiaraii* and *M. maculatus*. Deviation from this regularity was observed at Dziekanów on dry, well-lit stations (stations *3*, *4*, *6*) and stations on the edge of the forest (stations *10*, *11*), where species which stood up well to environment conditions of this type occurred as subdominants, i.e. *A. punctor*, *A. vexans*, *A. annulipes*.

The next stage was characterised by a considerable decrease in the abundance of mosquitoes on different environments combined with a tendency to even up the percentages of species in the communities, this tendency being especially distinct in dry environments. Variations in the domination structure

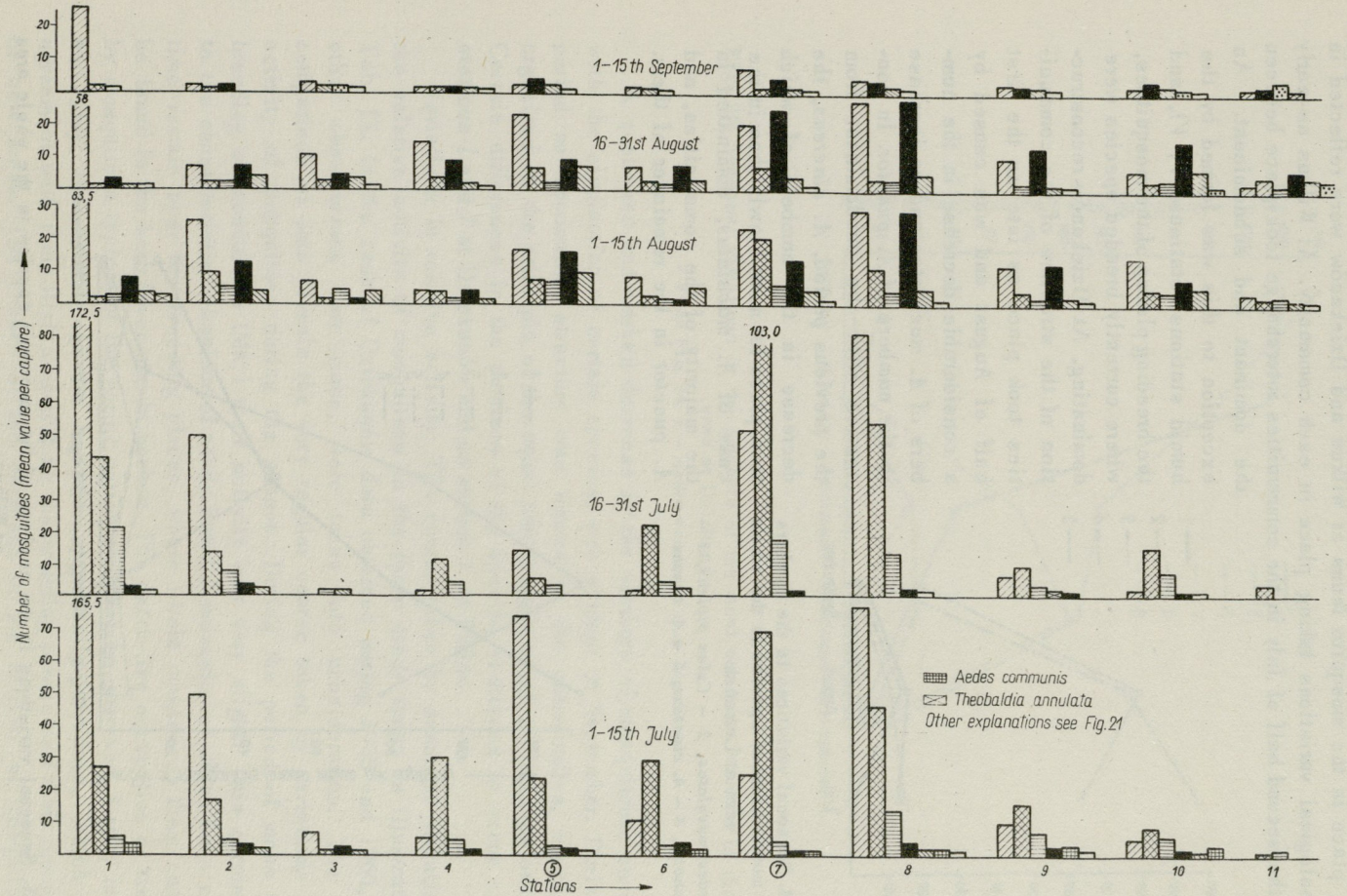

Fig. 23. Seasonal variations in the structure of communities at Dziekanów

taking place in the mosquito fauna at Wilkus and Dziekanów were reflected in the analogical variations taking place in each community. At Wilkus as early as in the second half of July in the communities interchange took place between the dominant and subdominant. An exception to this was formed by the humid stations (Stations *IV*, *V*), and the breeding places of the mosquitoes, where currently breaded species were dominating. At Dziekanów reconstruction of the structure of the communities took place as late as the first half of August and was caused by a considerable decrease in the numbers of *A. maculatus* and an increase in the numbers of *A. punctor*. In connection with the subdominant from the previous period, *A. cinereus*, the decrease in the numbers of which took place far more slowly than in the case of *A. maculatus*, dominated in the majority of the communities, and *A. punctor* in the remainder of them.

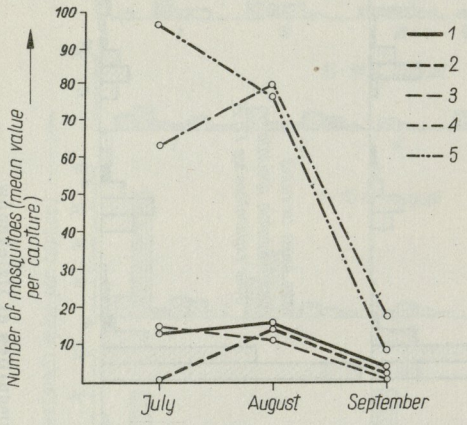

Fig. 24. Seasonal variations in the numbers of the most numerous species in the whole area at Lemańsk

1 – Aedes maculatus, 2 – Culex pipiens, 3 – A. punctor, 4 – A. cinereus, 5 – A. vexans

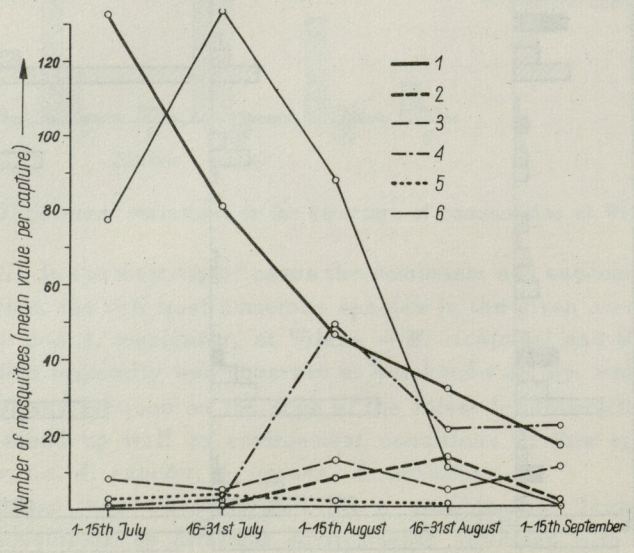

Fig. 25. Seasonal variations in the numbers of the numerous species in the whole area at Wilkus

1 – 4 see Fig. 24, *5 – Aedes annulipes, 6 – Mansonia richiardii*

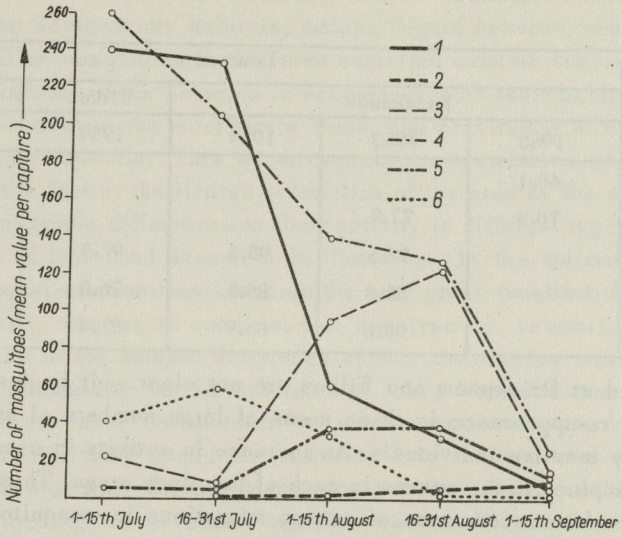

Fig. 26. Seasonal variations in the numbers of the most numerous species in the whole area at Dziekanów

1 – 4 see Fig. 24, *5 – Aedes vexans, 6 – A. annulipes*

A continued and marked decrease in the numbers of mosquitoes, connected with the elimination of certain species, was evident in September. During this period no domination structure was formed in the communities, which were organised on the principle of the equal percentages of all the species occurring. Certain differences in the numbers of the species continued to occur only on stations *1* and *7* at Dziekanów and on station *V* at Wilkus.

Variations in relative activity. The course taken by seasonal variations in the relative activity of mosquitoes in the three study areas is illustrated by Tab. IX. In the case of Dziekanów data obtained during 1953 and 1960, when other observations were made, were taken into consideration. The above comparison of data reveals the very regular course taken by variations in the activity of mosquitoes during the season. During the period of mass spring breeding of mosquitoes (May) their activity was very slight. This corresponds to the characteristic behaviour of newly-breeded mosquitoes, which for a certain time remain near the breeding places, where whole masses of them can then be found in the herb layer and in bushes. The patch-like occupation of the area by mosquitoes typical of the spring period can then be observed. Later, in June and July, the activity of the mosquitoes gradually increases, which is in agreement with their flights away from the breeding places and their occupation of new areas. The causes of the decrease in the activity of mosquitoes in

Seasonal variations in the relative activity index of mosquito fauna

Tab. IX

Months	Years				
	Dziekanów			Wilkus	Lemańsk
	1960	1953	1954	1957	1955
V	60.1				
VI	70.9	77.9			
VII		95.5	98.3	92.3	38.1
VIII		85.8	89.5	76.8	44.1
IX		90.0	86.9	81.4	60.3

August observed at Dziekanów and Wilkus are not clear – it is possible that it was due to the re-appearance in these areas of large numbers of newly-breeded and still largely inactive individuals. An increase in activity in comparison with the summer took place in the autumn in each of the study areas. This corresponds to the pictures of the occurrence of autumn migrations in mosquitoes, possibly correlated with the period of their increased activity.

V. SUMMARY OF RESULTS

The above investigations were made in three types of wooded areas differing as to environment conditions, that is, the degree of humidity and character of the mosaic structure in the area. Each area created different conditions for the development of mosquito fauna and hence differed from the others by the numbers of mosquitoes, number of species, domination structure, degree to which the area was occupied by different species of mosquito and their relative activity.

The investigations showed that the character of the mosaic structure of the area and the degree to which it dries up imposed a specific spatial structure on the mosquito fauna due to the differences in the way the different species of mosquito occupied different habitats. It was found that this structure is a constant phenomenon, maintained in each type of area examined throughout the whole of the growing season. It therefore constitutes a significant element, from the point of view of ecological consequences, in the differentiation of mosquito fauna in the given area.

It was also found that an area unfavourable to mosquitoes, the greater part of which being well-lit and dry, with only small, well-defined humid environments, created conditions which exerted a sharply determining influence on the character of the mosquito fauna and its spatial distribution. The distinct differences in this area in environment conditions caused the formation of communities of mosquitoes in microenvironments. They were characterised by a considerable degree of isolation resulting from the fact of separation in space of the places

in which mosquitoes occurred numerously and the minimum or zero activity of the insects in the adjacent dry habitats, making flights between humid environments impossible. The mosquitoes in this area exhibited extreme unevenness of quantitative distribution, which occurred in accordance with their habitat requirements, that is, preference for the most humid areas, and occurrence in small or minimum numbers in dry habitats. This occurrence in concentrations of the mosquitoes emphasised the fact of the limited occupation of the area by the different species and the considerable differences in their activity in different types of environment.

An area of this kind favoured the formation, in the majority of the microenvironments, of communities based on the very great quantitative preponderance of one species, adapted to conditions of this type (*A. vexans*). Increase in the abundance and in the number of species of the communities was connected with the degree of humidity of the environment. Single-species communities of the dry environments were transformed, in shadier environments, into two-species ones, and in the most humid environments into communities containing many species, with a sharply-defined domination structure. Even in these latter, however, the percentage of accessory species was small, and the dominant formed the basis of the community.

The strong pressure of the environment was manifested in the considerable modification of the activity of the mosquitoes. This led to differentiation of the community into an active part, moving about in the bush layer, and to part composed of inactive individuals which remained in the herb layer. The structure of both these parts of the fauna differed from the real quantitative relations of the species observed for the whole of the mosquito fauna in the given environment. It resulted from the fact that different species reacted to a different extent to environment conditions, by a change in their activity. Cases of extreme reaction were represented by *A. vexans* and *A. punctor*. The first of these exhibited a greatly developed capacity for modifying its activity and from this aspect may be treated as an index of the degree of unsuitability of the environment for mosquitoes. The second maintained a high degree of activity in each type of environment in which it occurred.

The observations made at Lemańsk revealed the many different directions taken by the reaction of species of mosquitoes to the abiotic environment. It was possible to distinguish species reacting very sharply to environment factors, and on this account limiting their occurrence only to these environments most favourable to them. Thus, for instance, *A. maculatus* occurred at Lemańsk in humid environments only. Another form of reaction by species was the limitation of their abundance in unfavourable environments, an example of which is provided by the behaviour of *A. cinereus*. The most complicated reaction to environments was that of *A. vexans*. On account of its extensive, and mainly uniform, spread over an area unfavourable to mosquitoes and of many phenomena forming evidence of its wide tolerance of microclimatic factors, it may be considered as an

eurytopic species. It was, however, simultaneously a species reacting most strongly by variations in activity to environment conditions. Under favourable conditions it was very active, and under unfavourable ones it occurred as an important component of the mosquito fauna, although its activity decrease sharply. This would point to the fact that the capacity of this species for maximum occupation of areas unfavourable to mosquitoes is closely bound up with its capacity for adaptation, consisting in the modification within wide limits of its activity.

Seasonal variations in the mosquito fauna in the type of area discussed led chiefly to a marked decrease in the abundance of the two quantitatively dominating species in this area. In connection with this the reconstruction of the communities took the direction of increasing the percentage of the accessory species and the elimination of communities in the driest environments. The agregational character of the occurrence of mosquitoes in this area was maintained throughout the whole season.

Humid areas with a fine mosaic structure provided opportunities for the development of several species, and by satisfying their habitat requirements made it possible for them to maintain their occurrence in an area of this type, and therefore the mosquito fauna here was richer both quantitatively and qualitatively. Differences in the spatial distribution of the mosquito fauna was observed in these areas also, but they were of a different character from those discussed previously. The microenvironments differed primarily as to the abundance of mosquitoes, although the degree of difference was smaller here than in the case of the first area and did not exhibit such marked dependence on environment conditions. It was determined to a certain extent by the shadiness of the environment, but limiting influence of the proximity of open areas was simultaneously observed. The different types of habitats did not exhibit fundamental differences in the number of species, which would point to the fact that the whole study area, including the driest environments, was penetrated by all the mosquito species occurring there. On the other hand different species reacted to different degree, by variations in their numbers, to the suitability of each environment.

The pictures discussed above suggest that in an area with a fine mosaic structure the merits of different environments become less pronounced. The humid environments did not act as foci concentrating the numbers of mosquitoes and hence the "mosquito occupation" of better-lit and dry environments was equal to that of the first type. The relative activity of the species, which was high throughout the whole study area, being limited only in the border environments, showed even more clearly the part played by the character of the whole area in the unification of the influences of the different environments.

The heterogeneity of the communities was manifested chiefly in the differences in the numbers of the mosquitoes and in the domination structure. In shady environments the domination of one or two species was sharply defined, while

in well-lot environments similar in type to the dry environments of Lemańsk (as was shown by, inter alia, the increase in the percentage of "dry-loving" species) a tendency occurred to balance in the percentages of different species. The communities of the border environments behaved similarly, a decrease in the percentage of the dominant and increase in the percentage of accessory species being observed in the communities the closer environments was to the boundary of the Forest. The great activity of all the species in the whole area, except in the border environments, breeding places and in cases of inhibition of the activity of *A. vexans* in dry environments, resulted in the degree of penetration of the environment by different species being defined in each case by the abundance the given species.

Seasonal variations in the mosquito communities in areas with a fine mosaic structure consisted primarily in the transformation of the domination structure of the communities, taking the form of an interchange of dominating species, which thus distinguished this area from the one previously discussed. On the other hand, as was the case in that area, an increase took place progressing with the passage of the season, in the percentage of accessory species in the communities. Despite the seasonal decrease in the abundance of mosquitoes the same type of differentiation of the communities as regards the abundance of mosquitoes was maintained throughout the whole study period.

To sum up it must be said that in each type of area communities of mosquitoes characterised by a specific structure constituting a real basis of biocenotic influences form in its microenvironments. Microenvironments with considerable density of mosquitoes constitute the Elton "centres of action" where the mosquitoes enter into particularly intense connections with other organisms as hosts, external parasites prey or competitive species. Since the phenomena of the activity of species are of particular importance in an estimate of the degree to which the mosquitoes are connected with different elements of the biocenosis, the communities of mosquitoes at Lemańsk, on account of their very small degree of activity, should primarily be included in the group of organisms of the herb layer. At Wilkus and Dziekanów the high degree of activity of the mosquitoes connects them with the biocenosis of the higher layers of the forest. In the classification used by Elton these will be organisms settling in and forming the group of organisms of the bush layer.

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ZGRUPOWANIA KOMARÓW W TRZECH TYPACH KOMPLEKSÓW LEŚNYCH

Streszczenie

Celem pracy było zbadanie zależności istniejącej między typem mozaikowatości terenu a zróżnicowaniem przestrzennym fauny komarów. Badania prowadzone były w trzech różnych kompleksach leśnych, z których każdy stwarzał inne warunki dla roz-

woju fauny komarów oraz inne możliwości utrzymania się określonego zespołu gatunków w danym terenie.

W każdym z terenów wytypowano kilka lub kilkanaście stanowisk badawczych o różnej atrakcyjności dla komarów, układających się w gradiencie stopnia zadrzewienia, zwartości podszytu i gęstości runa. Różnorodność tych stanowisk potwierdziły badania mikroklimatyczne (badano wilgotność i temperaturę na poziomie runa i na wysokości 2,0 m).

Połowów dokonywano dwiema metodami: czerpakiem entomologicznym, wychwytującym nieaktywną, siedzącą w runie w danym momencie część fauny komarów oraz na przynętę, wyławiającą część fauny latającą w warstwie podszytu. Wykorzystując fakt rozdzielenia, przy użyciu wyżej wymienionych metod połowu, występującej w danym środowisku fauny komarów na dwie frakcje, zastosowano wskaźnik aktywności względnej, charakteryzujący stopień uaktywniania się komarów w różnych typach środowisk. Wskaźnik ten jest to procentowo wyrażona ilość komarów złowiona na przynętę z całkowitej ilości komarów złowionej na przynętę i czerpakiem

W wyniku analizy materiału stwierdzono:

1. Mozaikowatość terenu determinuje charakter przestrzennego różnicowania się fauny komarów. W mikrośrodowiskach badanych terenów tworzyły się zgrupowania komarów różniące się liczebnością, składem gatunkowym, strukturą dominacyjną i aktywnością względną.

2. Charakter całego terenu narzucał zgrupowaniom ogólne proporcje udziału procentowego gatunku dominującego, subdominanta i gatunków akcesorycznych; obserwowano zmniejszanie się udziału dominanta i jednoczesny wzrost udziału gatunków akcesorycznych w zgrupowaniach, w miarę zwiększania się stopnia wilgotności i drobnomozaikowatości całego terenu. W ramach tego ogólnego schematu struktury zgrupowań badanych terenów, zgrupowania te wykazywały indywidualne zróżnicowania.

3. Struktura zgrupowań (liczba gatunków, liczebność komarów i aktywność) w terenie niedogodnym dla komarów była ściśle uzależniona od warunków mikroklimatycznych środowisk opanowanych przez zgrupowania. W terenie dogodnym dla komarów struktura zgrupowań nie wykazywała tak wyraźnej zależności od warunków środowiskowych, jak w przypadku pierwszego terenu. Dlatego środowiska wilgotne nie miały tu charakteru ognisk skupiających komary.

4. Zgrupowania komarów były trwałym i stąd ekologicznie ważnym elementem struktury przestrzennej komarów. Sezonowe zmiany w zgrupowaniach badanych terenów polegały na postępującym spadku liczebności komarów i tendencji do likwidacji struktury dominacyjnej. Ponadto, tylko w przypadku terenów wilgotnych, występował etap wymiany dominantów i subdominantów.

Mimo postępującego w ciągu sezonu spadku liczebności komarów, zachowywał się charakterystyczny dla danego terenu schemat zróżnicowania przestrzennego ich liczebności.

5. Stopień i równomierność opanowania terenu przez dany gatunek mogły być cechą stałą tego gatunku, niezależnie od typu terenu (np. *A. cinereus* i *A. vexans*) lub podlegać kierunkowym zmianom (np. *A. punctor* i *A. maculatus*).

6. Penetracja środowisk przez komary w terenie drobnomozaikowym, wilgotnym była uwarunkowana ich liczebnością w tych środowiskach.

W terenie suchym, niedogodnym dla komarów penetracja przez nie środowisk była wypadkową ich liczebności i aktywności.

7. Stwierdzono wielokierunkowość reakcji gatunków komarów na czynniki środowiskowe. Wyróżniono gatunki ograniczające swoje występowanie w niedogodnym dla nich terenie do wybranych środowisk (np. *A. maculatus*), gatunki reagujące tylko zmianą liczebności

(np. *A. cinereus*) oraz gatunek opanowujący cały teren, a na warunki środowiskowe reagujący zmianą aktywności (*A. vexans*).

8. W zależności od typu terenu, determinującego ogólną aktywność komarów, wchodzą one przede wszystkim w skład zespołu organizmów runa leśnego lub podszytu.

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